The Evolution of Scatterhoarding Behavior and Behavioral Adaptations of Eastern Gray Squirrels (*Sciurus carolinensis*)

by

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Abstract

We investigated the evolution of scatterhoarding behavior (storing food for future use) and behavioral adaptations of eastern gray squirrels (*Sciurus carolinensis*). First, we simulated the evolution of scatterhoarding compared to nonhoarding behavior at different levels of predation risk, food availability, and foraging efficiency. We found that scatterhoarding behavior was most likely to be adaptive when both predation and the amount of food were low. Further, predation risk could greatly impact the presence of scatterhoarding behavior in a population, regardless of food availability and how easily it could be found. Next, we conducted a range-wide citizen science based study (2019 – 2022) on geographic variation in scatterhoarding behavior of eastern gray squirrels (n = 4540 squirrels) We found that squirrels decreased their investment in hoarding behavior as winters get milder and as the need for scatterhoarded food to survive winter lessened. We also conducted small-scale studies on behavioral adaptations of eastern gray squirrels in a forest in Auburn, Alabama. We monitored 793 artificially scatterhoarded seeds over two scatterhoarding seasons and discovered that a multiyear supply of scatterhoarded food is possible, as 2.9% of all seeds (n = 23) were useful to hoarders at the end of the second scatterhoarding season. We also took a closer look at pilferage rates and selective pilfering of different seed types. We determined that scatterhoarders selectively pilfer seeds based on seed species and treatment (seeds with embryo artificially removed or whole seeds) and prefer to pilfer seeds commonly perceived as more valuable. Finally, by using tagged, germinating acorns, we found evidence that hoarders use seedlings as cues of food belowground and they may use other seed and seedling characteristics to determine how to handle the seed after digging it up.

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Chapter 1. Modeling the effects of predation risk, food availability, foraging efficiency, and reciprocal pilferage on the evolution of scatterhoarding behavior

Scatterhoarders are food-hoarding animals that hide food in many locations scattered throughout their home range to survive seasons with little food available, typically winter. For scatterhoarding to evolve within a population, the costs of the behavior must not exceed the benefits. Previous models have suggested that this strategy would be most beneficial during years with low food availability because being able to find stored food increases the fitness of hoarding individuals compared to nonhoarders in the population. However, predation risk may also increase for hoarders, as hoarding behavior often requires individuals to put themselves in riskier situations. We used a theoretical model to simulate the evolution of scatterhoarding behavior in three populations with different starting ratios of hoarders and nonhoarders: 19:1, 10:10, and 1:19. We ran our model through combinations of varying predation risk, food availability, and foraging efficiency. We also ran the same models with and without hoarders being able to pilfer from other hoarders (simulating the presence and absence of reciprocal pilferage). As expected, scatterhoarding behavior was favored when available food abundance and predation risk were low, though both the hoarding and nonhoarding strategies had difficulty invading a population of the opposite trait when the costs of these behaviors were similar. Interestingly, foraging efficiency did not influence appreciably which trait (hoarding or nonhoarding) evolved in the population. Thus, we demonstrated a potentially large impact of predators on the evolution of scatterhoarding behavior. Further research is needed to further explore the interactions between predation risk and food

availability and how these two components work together to help or hinder the evolution of scatterhoarding behavior in different habitats.

1.1 Introduction

Animals that face periods of food scarcity can cope by hoarding food when it is abundant. Larderhoarders hoard their food in one location (i.e., a larder) within their territory and actively defend that larder to avoid pilferage (theft) from other individuals (reviewed by Smith & Reichman, 1984). Scatterhoarders, on the other hand, hoard their food in many scattered locations around their home range (Morris 1962b) and use strategies during the hoarding process to reduce the risk of pilferage of their stored food such as burying seeds at an optimal density (Gálvez et al. 2009a), placing caches in riskier locations (Steele et al. 2014), or creating false caches when a potential pilferer is watching (Steele et al. 2008). In general, hoarding should occur when the benefits of doing so outweigh the costs (Andersson and Krebs 1978). Thus, understanding the benefits and costs of hoarding is critical to understanding the evolution of such behavior.

The costs and benefits of a behavior shape the overall contribution of that behavior to an animal's fitness and these costs and benefits can take many different forms. Animals are able to benefit from hoarding behavior when they or a relative eat their hoarded food. These benefits are typically in the form of increased reproduction or survival. For example, Eurasian red squirrels (*Sciurus vulgaris*) who ate more hoarded food during winter had higher lifetime reproductive success due to entering the spring breeding season in better body condition than individuals who ate less hoarded food (Wauters et al. 1995). Similarly, gray jays (*Perisoreus canadensis*) used cached food to gain weight prior to laying eggs in late winter when no other food was available (Sechley et al. 2014). Alternatively, some animals experience increased over-winter survival when they have a supply of hoarded food to eat, especially when little other food is available (e.g., eastern chipmunk, *Tamias striatus*, Wrazen and Wrazen 1982; Eurasian red squirrel, Wauters et al. 1995; yellow pine chipmunk, *Tamias amoenus*, Kuhn and Vander Wall 2008; collared pika, *Ochotona collaris*, Morrison et al. 2009). Other species, such as Canada jays (*Perisoreus canadensis*) even feed their young from stored food supplies before spring foods become available (Derbyshire et al. 2018). However, many costs associated with hoarding behavior exist, including increased predation risk (Leaver 2004, Steele et al. 2014, 2015, Lichti et al. 2020) and increased energy investment by the hoarder (Jansen et al. 2002, Muñoz and Bonal 2011). Additionally, the benefits of hoarding behavior may decrease if the hoarded food is lost due to germination (Fox 1982a, Xiao et al. 2009), rot (Sechley et al. 2015), insect infestation (Fukumoto and Kajimura 2000, Smallwood et al. 2001, Weckerly and Nicholson 2017), or pilferage by other animals (Vander Wall and Jenkins 2003). Given that hoarding behavior should only evolve and persist in a population when the benefits exceed the costs, understanding the factors that influence those benefits and costs is important.

The costs and benefits of scatterhoarding behavior should be a function of the different conditions experienced by a hoarding population, such as how much food is available, how difficult it is for hoarders to find food, risk of pilferage from other animals, and predation risk to hoarders. When more food is available during a typical food-scarce season (either storable food or perishable, unstorable food), then animals should need to rely on hoarded food less during that period, which should decrease the benefit of hoarding food. Differences in winter food availability between populations could occur due to how harsh winter conditions are, which could then impact how much time and energy animals need to invest in hoarding behavior (See Chapter 2: Geographic Variation). Similarly, the foraging efficiency of an animal should influence the relative benefits of hoarding food; if food is hard to find, then the benefits of storing food should be greater. Foraging efficiency could be related to the innate ability to find available food (i.e., both stored and unstored food), but should also be a function of the anti-pilferage strategies used by other animals to hide their cached food (i.e., less investment in pilferage reduction strategies results in food being easier to steal). In terms of the costs of hoarding, hoarding individuals within a population should face higher predation risk than nonhoarding individuals due to the simple fact that hoarding often requires the animal to be in an exposed location while hiding food (Steele et al. 2015). Furthermore, pilferage reduction strategies such as storing food in risky places can also disproportionately increase predation risk (Steele et al. 2014, Bogdziewicz et al. 2020). Thus, studies are needed to evaluate the relative importance of food availability, foraging efficiency, risk of pilferage, and predation risk on the benefits and costs of food hoarding, and, more importantly, the evolution of the behavior.

However, demonstrating that food availability, foraging efficiency, and predation risk influence the benefits, costs, and evolution of food hoarding in field studies or lab experiments can be particularly difficult (but see (Stapanian and Smith 1978, Lucas and Walter 1991, Jokinen and Suhonen 1995, Steele et al. 2015). Yet one way in which the effect of these factors can be explored in an evolutionary context is with models. Indeed, previous models have suggested that food availability and foraging efficiency should be important in the evolution of scatterhoarding behavior. For example, using a series of mathematical models, Andersson and Krebs (1978) concluded that in a population of hoarding and nonhoarding individuals, the net benefits of hoarding, and hence the propensity for the behavior to evolve, should decrease with increases in both the implicit costs of hoarding (such as reduced survival due to higher risks assumed while foraging) and the likelihood of finding food (i.e., foraging efficiency). As foraging efficiency increased and food became easier to find, hoarding behavior would be less likely to be adaptive within the population. However, Smulders (1998) used a game theoretical model to suggest that scatterhoarding could easily establish within a population when there is a high ratio of stored food to other available food, regardless of the costs of hoarding behavior (Smulders 1998), which suggests that with lower food availability, hoarding would be adaptive regardless of any increase in predation risk caused by hoarding behavior. Vander Wall and Jenkins (2003) used a simulation to show that high pilferage rates (which impact an individual's ability to find their own food) favor scatterhoarding behavior (rather than larderhoarding) in a population, due to the ability of scatterhoarders to increase their own pilferage behavior when they experience theft of their stored food (i.e., reciprocal pilferage). Thus, previous models have generated variable predictions about the relative importance of food availability, foraging efficiency, and reciprocal pilferage on the evolution of the behavior. Furthermore, differential predation risk has not yet been explicitly included in previous theoretical models of the evolution of hoarding behavior, though predation risk is known to have an impact on foraging behavior of many species (Lima et al. 1985, Brown et al. 1988, Lima and Dill 1990). Thus, further consideration is needed to fully discern the impact of food availability, foraging efficiency, reciprocal pilferage, and prediction risk on the evolution of hoarding behavior within a population.

In this study, we modeled the adaptiveness of scatterhoarding in relation to variation in food availability, foraging efficiency, and prediction risk. We varied storable food production, foraging efficiency, and predation risk to determine how these variables could impact the evolution of hoarding or nonhoarding behavior in a population of nonsocial, scatterhoarding animals with overlapping home ranges. The adaptive value of hoarding in our model was based on survival through winter, rather than reproductive output (Smulders, 1998; Vander Wall & Jenkins, 2003). We expected scatterhoarding behavior to be adaptive when food production was low, available food was hard to find, and the cost of hoarding behavior (i.e., predation risk) was low. Additionally, we examined the importance of reciprocal pilferage on the adaptiveness of hoarding behavior by comparing populations where both hoarding and nonhoarding individuals were able to pilfer from hoarders (representing reciprocal pilferage) and populations where only nonhoarding individuals were able to pilfer (no reciprocal pilferage is present so hoarders cannot compensate for pilferage by nonhoarding cheaters). The combined effects of varied food availability, foraging efficiency, and predation risk have not yet been thoroughly investigated in terms of impacts on the evolution of scatterhoarding behavior in a population. Investigating this set of conditions could help explain why food-hoarding species are able to persist in a wide variety of environmental conditions and habitats.

1.2 Methods

We loosely based our model on the scatterhoarding habits of eastern gray squirrels. Eastern gray squirrels bury single seeds, about 2-3 cm deep (Wilson et al.

2023), in hundreds of locations around their home range during fall through early spring (See Chapter 2: Geographic Variation). They engage in many behaviors to avoid pilferage of their buried seeds, such as deceptive caching (Steele et al. 2008) or burying seeds in riskier locations (Steele et al. 2014). Squirrels are able to use memory to locate their own cached seeds (Macdonald 1997) and use scent of nearby cached seeds to pilfer from other individuals (Thompson and Thompson 1980). If squirrels pilfer a seed, they either eat the seed or recache it elsewhere (Bartlow et al. 2018). This species is not territorial and can be found in dense populations, though they are not particularly social during the nonbreeding season (Koprowski 1994). The native range of the eastern gray squirrel encompasses the eastern half of the United States across a wide range of environmental conditions (Koprowski 1994).

Our model was built and modified from the model described by Vander Wall and Jenkins (2003). A specified amount of storable food items (e.g., hard mast such as acorns that can be stored for a long period of time) was available from the start of the model. We assumed there was no difference in the nutritional benefits of different storable food items and food did not spoil or degrade over time. Hoarders and nonhoarders were both equally as efficient at finding public food and pilfering food stored by other animals (except in the case where hoarders couldn’t pilfer), so higher values of foraging efficiencies resulted in higher probabilities of detecting a food item of any kind. Each population started with 20 individuals at the beginning of each model run. We tested the ability of hoarders or nonhoarders to invade different populations by using 3 different starting ratios of hoarders to nonhoarders: 1:19, 10:10, and 19:1. Hoarders were defined as being able to pilfer (reciprocal pilferage) or not being able to pilfer (no reciprocal pilferage). Nonhoarders could always pilfer. Hoarders faced a cost of storing food in the form of higher predation risk; specifically, the predation risk for hoarders was always double the predation risk for nonhoarders.

At the beginning of each day, each animal automatically ate a food item from its stored food supply, if available, and would not die of starvation that day (Figure 1). Thus, hoarders always had food to eat if they had at least one seed in their stored food supply. Individuals without any stored food started the day hungry and needed to eat one food item that day to survive to the next day. During each of 20 foraging bouts per day, and one at a time in a random order, each living animal foraged for food, with a different random foraging order for all animals during each of the 20 foraging bouts. While foraging, the animal detected food based on the probability of finding food, which was dependent on how easy food was to find (foraging efficiency) and the total amount of public food (storable seeds on the ground, available for all animals to find) and already stored food available for pilfering. Thus, the probability of an animal detecting a food item (either pilfered, stored food or public food) while foraging was calculated using the equation,

$$D = 1 - (1 - E_f)^{(F_p + F_s)}$$

Where E_f was the foraging efficiency of the population (the probability of finding a single food item), F_p was the amount of public storable food available, and F_s was the amount of stored food owned by other individuals. We note that the probability of finding food was the same for stored food and public food and that the probability of finding any given item was independent of the probability of finding other items. If there was food to find ($D > 0$) and a randomly generated number ($0 < X < 1$) was less than D, the animal randomly harvested a public food item or pilfered a food item from another animal based on the proportions of available public and stored food. If public food was harvested, the animal either ate the food item if they were hungry, stored the food item if they were a hoarder, or ignored the food item if they were a nonhoarder; the ignored food remained in the available food supply. Animals that pilfered stored food pilfered from a randomly selected individual based on the proportion of food each individual owns. Hoarders that pilfered stored food and had already eaten during that day added the food item to their own supply of stored food. Nonhoarders or hoarders that could not store pilfered food would eat pilfered food if they had not already eaten during the day, but otherwise, they ignored the pilfered food and the food item remained buried and in the supply of its owner. Eating, storing, or ignoring food marked the end of that foraging bout. If there was no food available to find ($D = 0$) or X was not less than D, the animal did not find any food during that foraging bout. At the end of each foraging bout, each animal potentially encountered a predator with probability defined by the 'predation risk'. If a randomly generated number was less than that individual's predation risk, the animal was killed by the predator and any stored food owned by this individual remained available for the rest of the population to pilfer. At the end of each day (after 20 foraging bouts), all hungry individuals died of starvation after not eating any food all day. The population continued to cycle through foraging bouts and days until the season ended after 100 days.

At the end of each 100-day season, if there was at least one surviving individual, the next generation of 20 individuals was created by randomly choosing one parent from among the survivors, with replacement, for each animal in the next generation. The offspring inherited its parent's hoarding trait completely: if the parent was a hoarder, the offspring was a hoarder and there was no intraspecific variation in hoarding ability between hoarding individuals. There was no overlap of individuals between generations; each surviving individual was assumed to have only stayed in the population for one generation. Each run of the model ended when either the hoarding or nonhoarding trait fixated within the population (i.e., all individuals of one trait had died) and the next generation containing only that trait was able to survive through one season or when all individuals died before the end of a season (i.e., population extinction).

We defined our parameter space based on varying total storable food item production (1000, 1600, 2000, 2200 items), foraging efficiency (used to calculate probability of finding any given food item in a foraging bout: 0.0005, 0.001, 0.0025, 0.005, 0.0075, 0.01), and animal predation risk (probability of predation in a foraging bout = 0.0001, 0.00025, 0.0005, 0.00075, 0.001, 0.00125, 0.0015, 0.00175, 0.002, 0.00225, 0.0025). Storable food was added to the public food supply (i.e., acorns falling to the ground) at the beginning of the first day of the model. We determined our range of storable food production based on the amount of food needed for each of 20 animals to eat one food item each day and survive the 100-day season (2000 food items). We also included values of storable food production to represent poor mast crop years (50% deficit in food production: 1000 food items; 20% deficit: 1600) and one value to represent a good mast year (10% surplus: 2200). For each combination of parameter values in the parameter space, the model was run 100 times, with each run cycling through generations until the population went extinct or either the hoarding or nonhoarding trait fixated. We executed our model using Python 3.11.0 on the High Performance Computing system at the Alabama Supercomputer Center. See Appendix A for definitions of all variables used in our model code, presented in Appendix C. We created our results graphs using the levelplot function in the package latticeExtra (Sarkar and Andrews 2022) in Program R (R Core Team 2022), as well as other packages for improved interpretation of our results: cowplot (Wilke 2020), rasterVis (Lamigueiro and Hijmans 2023), ggplot2 (Wickham 2016), and gridExtra (Auguie 2017).

1.3 Results

1 hoarder and 19 nonhoarders

For populations with 1 hoarder, 19 nonhoarders, and without reciprocal pilferage, hoarding behavior fixated up to 100% of the time when predation was low and there was not enough food for all animals to survive the season (1000 or 1600 storable mast items; Figure 2). Foraging efficiency appeared to have very little impact on the population, as changes in foraging efficiency seemed to have relatively little effect on either population extinction rates or the evolution of hoarding or nonhoarding. Conversely, predation risk had a sizeable impact on both probability of population extinction and probability of hoarding evolving in the population. At higher levels of mast crop production (2000 and 2200), when there was enough food for all animals to eat if they could find it, increasing predation risk simply increased the probability that the population went extinct. If the population did not go extinct, however, nonhoarding behavior always fixated in the population. Conversely, when mast crop production was slightly insufficient for the population (1600), increases in predation risk also increased the probability of population extinction, except at very low predation risk in which increases in predation risk decreased the probability of extinction up to a predation risk of about 0.00075, after which increases in predation risk increased probability of extinction. We attribute this result to the fact that moderate levels of predation killed off just enough individuals to prevent them from all starving. In this scenario, if the population did not go extinct, then decreases in predation risk always resulted in an increased probability that hoarding evolved in the population. At very low levels of mast crop production (1000 items), the population went extinct a majority of the time. However, when it didn't go extinct decreases in predation risk always resulted in an increased probability that hoarding evolved in the population. When reciprocal pilferage was present in the population, our results did not change from those described above (Figure S1).

10 hoarders and 10 nonhoarders

Results were nearly identical for populations with 10 hoarders, 10 nonhoarders, and either reciprocal pilferage (Figure S2) or no reciprocal pilferage (Figure 3) as those population with 1 hoarder and 19 nonhoarders. The main difference was seen at 1000 mast, when at least 50% of populations survived when predation was low (up to 0.0005% for nonhoarders, 0.001% hoarders) and hoarding fixated a majority of the time up to a slightly higher level of predation (0.0005% for 10:10 population compared to 0.0001 for 1:19 population).

19 hoarders and 1 nonhoarder

In populations starting with 19 hoarders, 1 nonhoarder, and no reciprocal pilferage, predation was still the main factor influencing the fixation of hoarding in the population (Figure 4). Nonhoarding could only invade a hoarding population when predation levels were high regardless of the amount of food available or foraging efficiency. However, we note that the population was also more likely to go extinct as predation levels increased. Adding reciprocal pilferage to the model did not result in any changes in extinction rates or the fixation of hoarding within extant populations (Figure S3).

1.4 Discussion

As we had expected, hoarding behavior fixated within all populations with reciprocal pilferage at low levels of mast crop production and low predation risks, when the benefits of having a hoarded food supply were high and the costs hoarding behavior were low. Overall, we found strong effects of predation risk on the extinction of populations and the persistence of hoarding individuals within the population. For extant populations, nonhoarding became more adaptive as predation increased. Thus, predation could be a strong factor in the evolution of scatterhoarding behavior within a population. Surprisingly, foraging efficiency, however, did not have the strong effect that we had expected, though some small impacts of foraging efficiency on extinction rates could be seen at low food availability (both 1000 and 1600 mast) within populations with hoarder to nonhoarder ratios of 10:10 and 1:19. Generally, increased foraging efficiency could result in many animals finding food and thereby increase the chances of extinction if all food was eaten before the end of the season.

In our model, nonhoarders could use hoarded food without experiencing the costs of hoarding, while hoarders mainly benefited from a lower risk of starvation during periods of low food availability. Hoarders had a recovery advantage for food they buried, meaning there was a much greater chance of a hoarder finding stored food items than a nonhoarder. Similar to previous models, this recovery advantage resulted in hoarding behavior being most advantageous during seasons with low food availability when predation was also low (Andersson and Krebs 1978, Smulders 1998). However, because there was no difference in the ability of hoarders and nonhoarders to pilfer stored food, this recovery advantage was not as beneficial when there were large amounts of available food (resulting in > 90% probabilities of finding some food). Indeed, in mixed populations of 10 scatterhoarders and 10 nonhoarders, we found that scatterhoarding behavior rarely fixated when there was enough food for all animals to eat. This finding raises questions about the maintenance of scatterhoarding in areas with short food scarce seasons and supplemental food available during mild winters.

Smulders (1998) asserted that if the cost of hoarding is low, nonhoarders should not be able to invade a population of hoarders. Indeed, when little food was available in our model, hoarding behavior was adaptive when predation risk was low to intermediate. However, contrary to Smulders' prediction that both hoarding and nonhoarding could invade a population of the other strategy when the costs of both strategies were similar, our model predicted the opposite: hoarders and nonhoarders had difficulty invading a population of the other trait. Specifically, we observed a small chance that nonhoarding behavior could invade a population of hoarders at similar costs (low predation and low starvation risk) and a hoarder was rarely able to invade a nonhoarding population when there was little starvation risk, regardless of predation risk. However, Smulders included predation as a fixed variable for all individuals, so animals primarily differed in their starvation risk, while in our model, varying predation impacted which strategy could persist. Low predation levels increased the likelihood of hoarding being adaptive while higher predation levels were important in allowing nonhoarding to become adaptive within a population of hoarders. For a scatterhoarder to invade a nonhoarding population, nonhoarders would have to experience increased starvation risk to put the odds in favor of the hoarder, and such predictions are supported by our model.

Our model predicted that predators could play a key role in the evolution of scatterhoarding behavior in a population. Predation risk was previously included as a fixed risk for all individuals (Vander Wall and Jenkins 2003) or an assumed part of mortality risk (Andersson and Krebs, 1978; Smulders 1998) rather than having a direct tradeoff between hoarding and predation risk for scatterhoarders. Andersson and Krebs (1978) even posited that in group-living species, survival rates should have little impact on the adaptiveness of hoarding because lower survival results in less competition for food. However, we found this to be more applicable to the adaptiveness of nonhoarding behavior, rather than scatterhoarding behavior. Unexpectedly, nonhoarding behavior was able to fixate during a mast deficiency with intermediate levels of predation because predation reduced the starvation risk for surviving animals. We speculate that year-to-year fluctuations in predation risk could also have important implications for the maintenance of scatterhoarding behavior within a population as in our model hoarders were fairly sensitive to increases in predation risk.

Mcnamara et al. (1990) proposed that a variable food supply throughout winter should favor scatterhoarding behavior, and this idea could potentially be applied to variable food supplies across different years, which is common for species relying on masting species. Previous studies have provided evidence of hoarding behavior in mild climates where scatterhoarding would seemingly not provide much benefit when other food is available over winter (See Chapter 2: Geographic Variation, Wilson et al. 2023). Our model suggests that hoarding behavior can be maintained in populations that experience years of increased food availability over winter because even small proportions of hoarding individuals would have an advantage over nonhoarders during subsequent years of mast failures. However, we have also provided evidence that the adaptiveness of scatterhoarding behavior across different environmental conditions could be dependent on predation risk. A poor mast year combined with low predation risk could increase the proportion of hoarders in a population while high predation risk should always favor nonhoarders in the population. Additionally, a higher proportion of years with good mast crops could result in populations fluctuating around an even proportion of hoarding and nonhoarding individuals within the population. During good mast years, the population may start shifting towards favoring nonhoarding individuals, whereas a single poor mast crop year could quickly shift the population back towards favoring the hoarding trait. More research is needed to further delve into the interactions between fluctuations in both mast crop production and predation and how these fluctuations affect the adaptiveness of scatterhoarding behavior within a population.

We did not find any effect of reciprocal pilferage on the evolution of scatterhoarding in any combination of parameters in our model, though pilferage is thought to be important in the maintenance of scatterhoarding behavior in a population (Vander Wall and Jenkins 2003). Pilferage behavior increases the amount of food each individual has access to, while reciprocal pilferage results in high pilferage rates within the population, where all individuals are constantly engaging in pilferage behavior, but the relative amount of food owned by each hoarder stays fairly constant (Vander Wall and Jenkins 2003). Field studies provide examples of hoarders tolerating pilferage, rather than completely avoiding it, such as an individual increasing scatterhoarding effort when pilfered from (Huang et al. 2011). However, animals in our model were able to quickly build up their stored food supplies and predation lowered competition enough that pilfered seeds might not have been as integral to the survival of the population as we had expected. Reciprocal pilferage behavior may be more important to populations that experience very low quantities of available food when hoarders must add pilfered food to their stores to have enough food to survive winter.

In conclusion, we propose four reasons why hoarding has evolved in such a variety of environmental conditions. First, conditions of many environments support the evolution of hoarding, such as when there is little food over winter and predation risk is low; under such conditions the benefits of having a consistent food source greatly outweigh the costs. Second, environmental conditions may not support the evolution of hoarding, such as during years of high food availability or higher predation risk, but by chance, hoarding evolves. Third, hoarding has not evolved to fixation in a population, but the proportions of hoarding and nonhoarding individuals in a population may fluctuate in response to changing conditions (e.g., mast crop sizes, predation risks, population size) within their habitat. Finally, the conditions may not support hoarding in a population causing the population to go extinct, perhaps due to a large increase in predator populations. However, nearby meta-populations of the species are able to immigrate to the area and bring the hoarding trait in a form of source-sink dynamics (Hanski 1991). We have demonstrated that both predation risk and food availability are important to the evolution of scatterhoarding behavior, though it is difficult for either the scatterhoarding or nonhoarding trait to invade a population of the opposite strategy without a particular set of conditions conducive to the invading behavior.

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1.6 Literature Cited

Andersson, M., and J. Krebs. 1978. On the evolution of hoarding behaviour. Animal Behaviour 26:707–711.

Auguie, B. 2017. _gridExtra: Miscellaneous functions for "grid" graphics_. R package version 2.3. https://CRAN.R-project.org/package=gridExtra.

Bartlow, A. W., N. I. Lichti, R. Curtis, R. K. Swihart, and M. A. Steele. 2018. Re-caching of acorns by rodents: Cache management in eastern deciduous forests of North America. Acta Oecologica 92:117–122.

Bogdziewicz, M., E. E. Crone, and R. Zwolak. 2020. Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. Journal of Ecology 108:1009–1018.

Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408–415.

Derbyshire, R., D. R. Norris, K. A. Hobson, and D. Strickland. 2018. Isotopic spiking and food dye experiments provide evidence that nestling Canada Jays (*Perisoreus canadensis*) receive cached food from their parents. Canadian Journal of Zoology 97:368–375.

Fox, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. Evolution 36:800–809.

Fukumoto, H., and H. Kajimura. 2000. Effects of insect predation on hypocotyl survival and germination success of mature *Quercus variabilis* acorns. Journal of Forest Research 5:31–34.

Gálvez, D., B. Kranstauber, R. W. Kays, and P. A. Jansen. 2009. Scatter hoarding by the Central American agouti: A test of optimal cache spacing theory. Animal Behaviour 78:1327–1333.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal ofthe Linncan Sociep 42:17–38.

Huang, Z., Y. Wang, H. Zhang, F. Wu, and Z. Zhang. 2011. Behavioral responses of sympatric rodents to complete pilferage. Animal Behaviour 81:831–836.

Jansen, P. A., M. Bartholomeus, F. Bongers, J. A. Elzinga, J. den Ouden, and S. E. Van Wieren. 2002. The role of seed size in dispersal by a scatter-hoarding rodent. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation:209–225.

Jokinen, S., and J. Suhonen. 1995. Food caching by willow and crested tits: A test of scatterhoarding models. Ecology 76:892–898.

Koprowski, J. L. 1994. *Sciurus carolinensis*. Mammalian Species 480:1–9.

Kuhn, K. M., and S. B. Vander Wall. 2008. Linking summer foraging to winter survival in yellow pine chipmunks (*Tamias amoenus*). Oecologia 157:349–360.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. Behavioral Ecology 15:729–734.

Lichti, N. I., H. J. Dalgleish, and M. A. Steele. 2020. Interactions among shade, caching behavior, and predation risk may drive seed trait evolution in scatterhoarded plants. Diversity 12:1–19.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

Lima, S. L., T. J. Valone, and T. Caraco. 1985. Foraging-efficiency predation-risk trade-off in the grey squirrel. Animal Behavior 33:155–165.

Lucas, J. R., and L. R. Walter. 1991. When should chickadees hoard food? Theory and experimental results. Animal Behaviour 41:579–601.

Macdonald, I. M. V. 1997. Field experiments on duration and precision of gray and red squirrel spatial memory. Animal Behaviour 54:879–891.

Mcnamara, J. M., A. I. Houston, and J. R. Krebs. 1990. Why hoard? The economics of food storing in tits, *Parus* spp. Behavioral Ecology 1:12–23.

Morris, D. 1962. The behavior of the green acouchi (Myoproctapratti) with special reference to scatter hoarding. Proceedings of the Zoological Society of London 139:701–732.

Morrison, S. F., G. Pelchat, A. Donahue, and D. S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159:107–116.

Muñoz, A., and R. Bonal. 2011. Linking seed dispersal to cache protection strategies. Journal of Ecology 99:1016–1025.

Lamigueiro, O. P. and Hijmans, R. 2023, rasterVis. R package version 0.51.5.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Sarkar D. and F. Andrews. 2022. _latticeExtra: Extra graphical utilities based on lattice_. R package version 0.6 – 30. https://CRAN.R-project.org/package=latticeExtra.

Sechley, T. H., D. Strickland, and D. R. Norris. 2014. Causes and consequences of pre-laying weight gain in a food-caching bird that breeds in late winter. Journal of Avian Biology 45:85–93.

Sechley, T. H., D. Strickland, and D. R. Norris. 2015. Linking the availability of cached food to climate change: An experimental test of the hoard-rot hypothesis. Canadian Journal of Zoology 93:411–419.

Smallwood, P. D., M. A. Steele, and S. H. Faeth. 2001. The ultimate basis of caching preferences of rodents, and the oak-dispersal syndrome: Tannins, insects, and seed germination. American Zoologist 41:840–851.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329–351.

Smulders, T. V. 1998. A game theoretical model of the evolution of food hoarding: Applications to the *Paridae*. The American naturalist 151:356–66.

Stapanian, M. A., and C. C. Smith. 1978. A model for seed scatterhoarding: Coevolution of fox squirrels and black walnuts. Ecology 59:884–896.

Steele, M. A., T. A. Contreras, L. Z. Hadj-Chikh, S. J. Agosta, P. D. Smallwood, and C. N. Tomlinson. 2014. Do scatterhoarders trade off increased predation risks for lower rates of cache pilferage? Behavioral Ecology 25:206–215.

Steele, M. A., S. L. Halkin, P. D. Smallwood, T. J. McKenna, K. Mitsopoulos, and M. Beam. 2008. Cache protection strategies of a scatterhoarding rodent: Do tree squirrels engage in behavioral deception? Animal Behaviour 75:705–714.

Steele, M. A., G. Rompré, J. A. Stratford, H. Zhang, M. Suchocki, and S. Marino. 2015. Scatterhoarding rodents favor higher predation risks for cache sites: The potential for predators to influence the seed dispersal process. Integrative Zoology 10:257–266.

Thompson, D. C., and P. S. Thompson. 1980. Food habits and caching behavior of urban gray squirrels. Canadian Journal of Zoology 58:701–710.

Vander Wall, S. B., and S. H. Jenkins. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology 14:656–667.

Wauters, L. A., J. Suhonen, and A. A. Dhondt. 1995. Fitness consequences of hoarding behaviour in the Eurasian red squirrel. Proceedings of the Royal Society B: Biological Sciences 262:277–281.

Weckerly, F. W., and K. E. Nicholson. 2017. Experimental test of discrimination by squirrels for insect-infested and noninfested acorns. The American Midland Naturalist 12:412–415.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wilke, C. 2020. _cowplot: Streamlined plot theme and plot annotations for 'ggplot2'_. R package version 1.1.1. https://CRAN.R-project.org/package=cowplot.

Wilson, S.B., R. A. Gitzen, S. S. Ditchkoff, and T. D. Steury. 2023. Behavioral adaptations of scatterhoarders to seasonal flooding. Canadian Journal of Zoology. Just-IN https://doi.org/10.1139/cjz-2023-0024

Wrazen, J. A., and L. A. Wrazen. 1982. Hoarding, body mass dynamics, and torpor as components of the survival strategy of the eastern chipmunk. Journal of Mammalogy 63:63–72.

Xiao, Z., X. Gao, M. Jiang, and Z. Zhang. 2009. Behavioral adaptation of Pallas's squirrels to germination schedule and tannins in acorns. Behavioral Ecology 20:1050–1055.

Software Citations:

Python: Python Software Foundation. Python Language Reference, version 3.11.0. Available at http://www.python.org

Packages used in model:

Decimal: decimal — Decimal fixed point and floating point arithmetic — Python 3.11.2 documentation

Copy: copy — Shallow and deep copy operations — Python 3.11.2 documentation

Statistics: statistics — Mathematical statistics functions — Python 3.11.2 documentation

Random: Van Rossum, G. (2020). The Python Library Reference, release 3.8.2. Python Software Foundation.

Math: Van Rossum, G. (2020). The Python Library Reference, release 3.8.2. Python Software Foundation.

Numpy: Harris, C. R., Millman, K. J., van der Walt, S. J., Gommers, R., Virtanen, P., Cournapeau, D., … Oliphant, T. E. (2020). Array programming with NumPy. Nature, 585, 357–362. https://doi.org/10.1038/s41586-020-2649-2

Csv: Van Rossum, G. (2020). The Python Library Reference, release 3.8.2. Python Software Foundation.

Figures

Figure 1.01. Flow chart of model simulation of the effects of food availability, foraging efficiency, risk of pilferage, and predation risk on the evolution of hoarding behavior. The model was run through 100-day seasons until fixation of hoarding behavior, nonhoarding behavior, or extinction of the population.

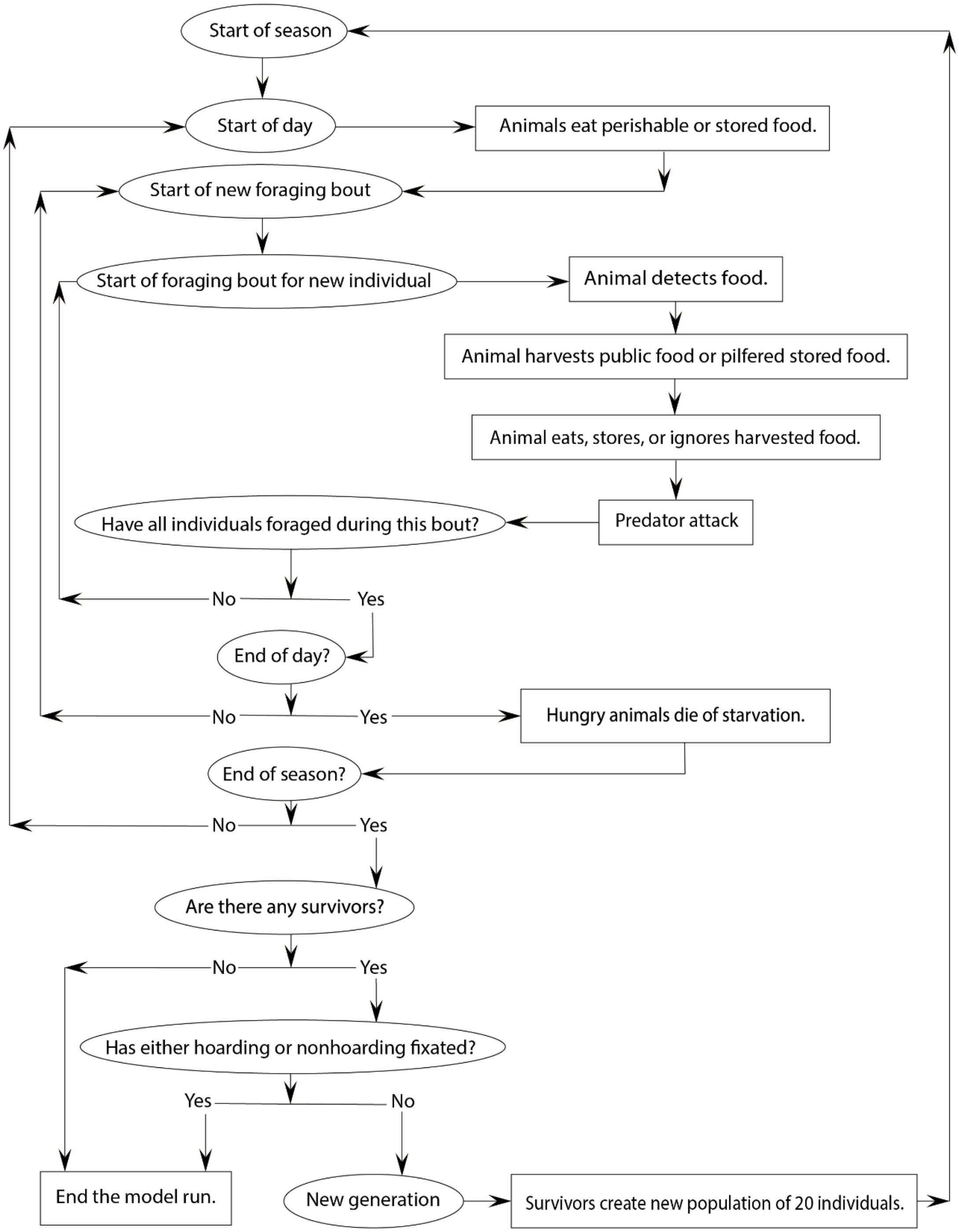


Figure 1.02. Proportion of times populations went extinct, and proportion of times hoarding behavior fixated within extant populations that began with **1 scatterhoarders and 19 nonhoarder**. Nonhoarding individuals could pilfer (steal) buried food items from hoarders, but hoarders were unable to pilfer. Mast represents the number of storable food items available at the beginning of the 100-day scatterhoarding season. Predation risk shown represents risk assumed by nonhoarders, while hoarding individuals experienced twice the risk, and foraging efficiency represents how easy all food items were to detect while foraging.

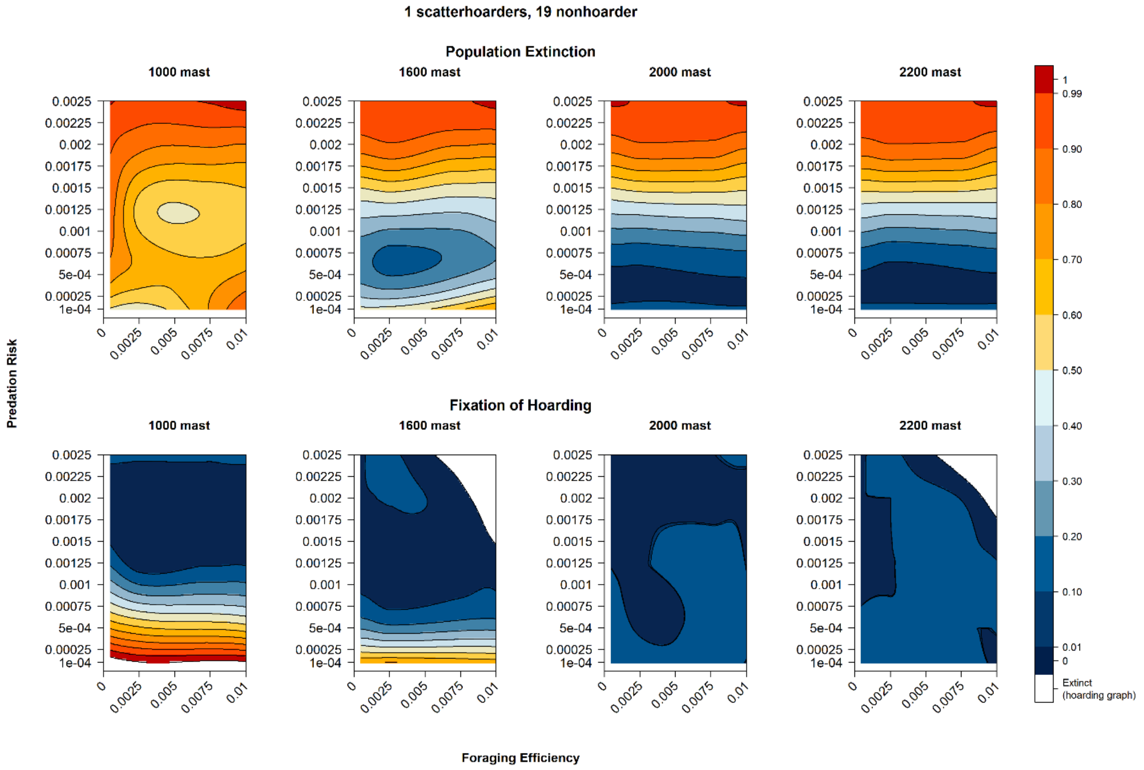


Figure 1.03. Proportion of times populations went extinct, and proportion of times hoarding behavior fixated within extant populations that began with **10 scatterhoarders and 10 nonhoarders**. Nonhoarding individuals could pilfer (steal) buried food items from hoarders, but hoarders were unable to pilfer. Mast represents the number of storable food items available at the beginning of the 100-day scatterhoarding season. Predation risk shown represents risk assumed by nonhoarders, while hoarding individuals experienced twice the risk, and foraging efficiency represents how easy all food items were to detect while foraging.

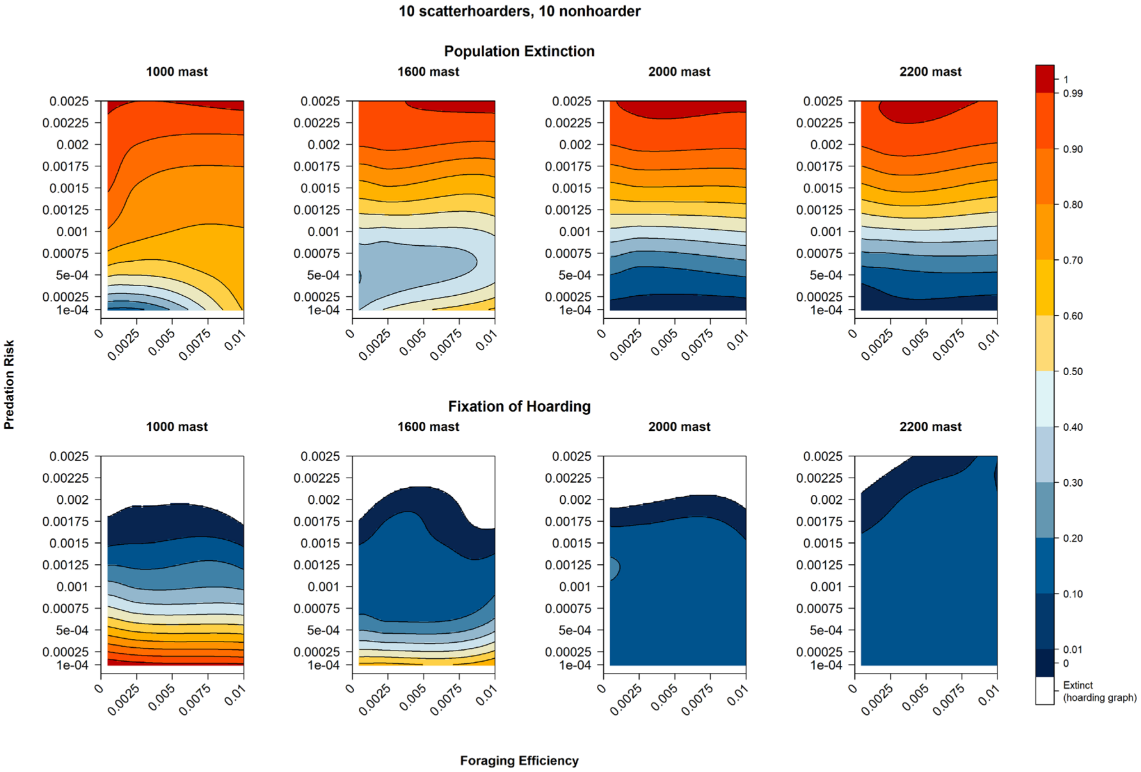
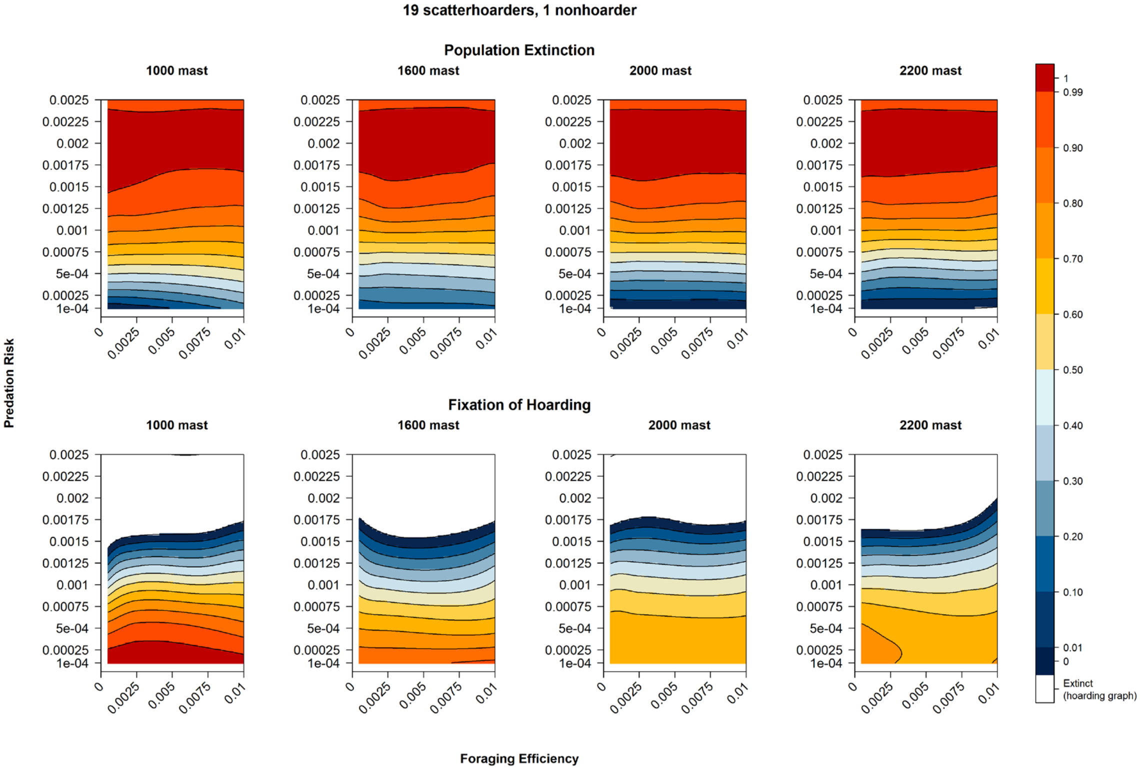


Figure 1.04. Proportion of times populations went extinct, and proportion of times hoarding behavior fixated within extant populations that began with **19 scatterhoarders and 1 nonhoarders**. Nonhoarding individuals could pilfer (steal) buried food items from hoarders, but hoarders were unable to pilfer. Mast represents the number of storable food items available at the beginning of the 100-day scatterhoarding season. Predation risk shown represents risk assumed by nonhoarders, while hoarding individuals experienced twice the risk, and foraging efficiency represents how easy all food items were to detect while foraging.



Appendix A: Definitions of Model Parameters

Number of hoarders, *hoarders_num*- number of hoarding individuals within the population (i.e. animals that can store food); other individuals in the population will automatically be nonhoarders (i.e. animals that can use stored food but cannot store food themselves)

Perishable days, *days_perish*- starting from the beginning of the season, number of days with perishable food is available (i.e., no starvation risk)

Number of storable food items, *mast_crop*- number of storable food items available starting at the beginning of the first day of the season

Population predation risk, *pred_risk_pop*- predation risk used to calculate individual predation risk of hoarding and nonhoarding individuals; equal to nonhoarder predation risk

Foraging efficiency, *for_eff*- ease of finding food; used to calculate probability that food will be detected during foraging bouts

Population size, *pop_size*- number of animals in the population at the beginning of the model and the beginning of each subsequent generation

Days total, *days_tot*- total number of days in the scatterhoarding season

Runs, *runs_*- number of times the model is run to fixation for each combination of *hoarders_num*, *days_perish*, *days_mast*, *for_eff*, and *pred_risk_pop*

Scatterhoarder pilferage ability, *SH_pilfer_ability*- 1 or 0, denotes whether hoarders can pilfer from other hoarders (1), or hoarders can bury their own seeds but cannot pilfer (0)

Animal survival state, *state*- value denoting if an individual is alive (0), if they are hungry (-1), if they died from starvation (998), or if they died from predation (999)

Animal storage effort, *storage_effort*- 1 or 0, denotes if an animal can store food; 1 for hoarders, 0 for nonhoarders

Individual predation risk, *pred_risk* = *pred_risk_pop* + (*pred_risk_pop* * *storage_effort*); denotes predation risk for each individual, differing for hoarders and nonhoarders

Animal characteristics, *hoarder_values*- a dictionary containing the state (*state2*), id number (*hoarder_id*), number of owned stored food items (*hoarder_stored*), predation risk, and storage effect of each individual animal (including both hoarders and nonhoarders).

Season tracker, *season*- a dictionary containing the current day, foraging bout, generation, and run number

Seasonal mast crop production, *dailyfood_production*- dictionary containing the number of food items (*day_0*) added to the available storable food supply at the beginning of each day (*day_no2*)

Foragers, *foragers*- dictionary containing random order of *hoarder_id*s which denotes foraging order of individuals for that foraging bout and whether each animal has foraged yet that bout (*forage_status*, 0 = has not foraged, 1 = has foraged)

Forager id, *forager_id*- identifies which animal in a random order of *hoarder_id*s in *foragers* is foraging currently; begins at 0 and continues sequentially to 1 – *pop_size*; when *forager_id* is greater than *pop_size*, the current foraging bout is over; when *forager_id* = -1, a new random order of *forager_id*s will be generated

Food stored by other hoarders, *other_SH* = total stored food items – stored food items owned by the foraging animal

Available storable food, *public_food*- total storable food items available to forage that have not yet been eaten or stored by other animals

All available food, *food_avail* = *public_food* – *other_SH*; represents number of food items available for the foraging animal to find (*public_food*) or steal (*other_SH*)

Detection probability, *detection_prob*- probability of finding a particular food item, calculated using the following equation:

$$detection\_prob = 1 - (1 - for\_eff)^{(food\_avail)}$$

Harv_rand- randomly generated number between 0.0000 and 1.0000; if this number is larger than *detection_prob*, the animal will find a food item, otherwise, the animal does not find any food that foraging bout

Proportions of available food types, *Food_prop*- list of the proportion of all food that is available storable food (*public_prop*) and the proportion of all food that is stored by animals other than the current foraging animal (*other_SH_prop*)

Harvested food type, *harv_foodtype*- 0 or 1, indicates the type of food that was harvested, available storable food (0) or scatterhoarded food pilfered from another individual (1)

food_rand- a randomly generated number between 0.0000 and 1.0000; if this number is greater than or equal to the foraging individual's *storage_effort* then the food item they found is ignored

Hoarder pilfered from, *pilf1*- the hoarder that an animal pilfers from is randomly chosen from a list of hoarders with stored food (*pilf*), weighted by how many stored food items each hoarder owns

pred_rand- a randomly generated number between 0.0000 and 1.0000; if this number is less the animal's *pred_risk*, then they die from a predator attack

Surviving animals, *survivors*- list of animals that survived the previous scatterhoarding season which is then used to choose one parent for each of the 20 individuals of the next generation of the population

Hoarding traits of next generation, *phenotype*- list of *storage_effort*s of each individual in the next generation

Appendix B: Reciprocal Pilferage Figures

Figure S1.01. Proportion of times populations went extinct, and proportion of times hoarding behavior fixated within extant populations that began with **1 scatterhoarders and 19 nonhoarder**. Both hoarding and nonhoarding individuals could pilfer (steal) buried food items from hoarders. Mast represents the number of storable food items available at the beginning of the 100-day scatterhoarding season. Predation risk shown represents risk assumed by nonhoarders, while hoarding individuals experienced twice the risk, and foraging efficiency represents how easy all food items were to detect while foraging.

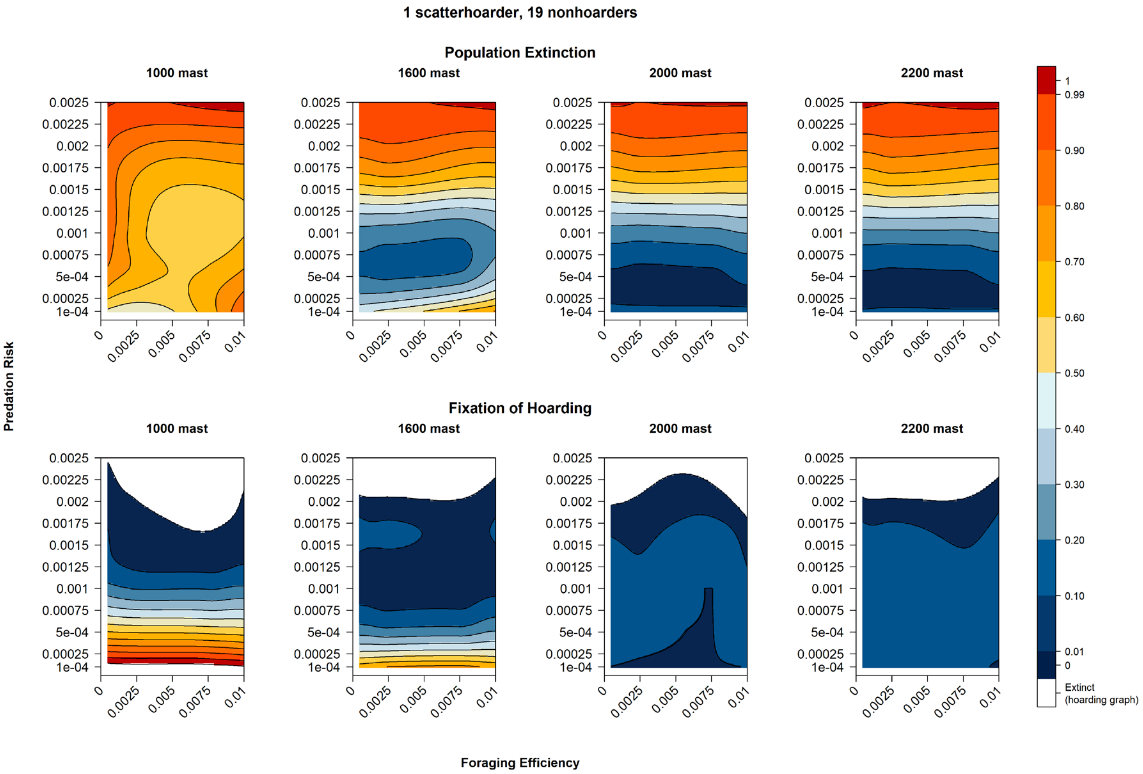


Figure S1.02. Proportion of times populations went extinct, and proportion of times hoarding behavior fixated within extant populations that began with **10 scatterhoarders and 10 nonhoarders**. Both hoarding and nonhoarding individuals could pilfer (steal) buried food items from hoarders. Mast represents the number of storable food items available at the beginning of the 100-day scatterhoarding season. Predation risk shown represents risk assumed by nonhoarders, while hoarding individuals experienced twice the risk, and foraging efficiency represents how easy all food items were to detect while foraging.

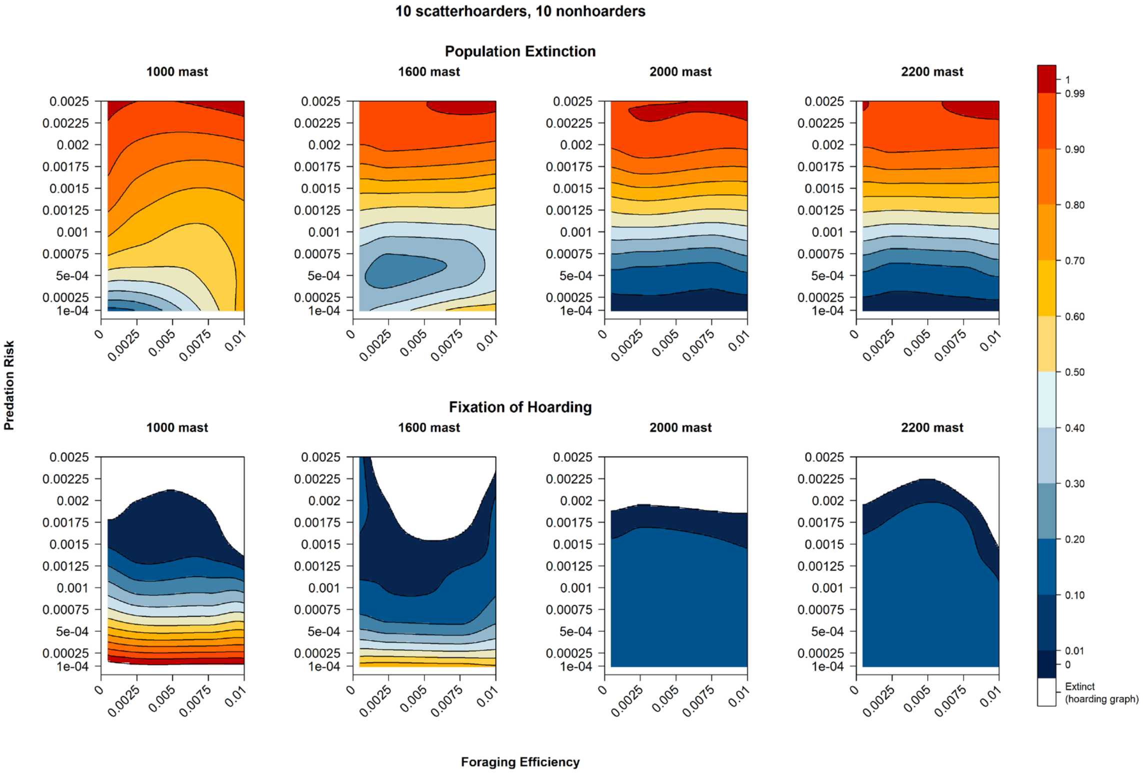
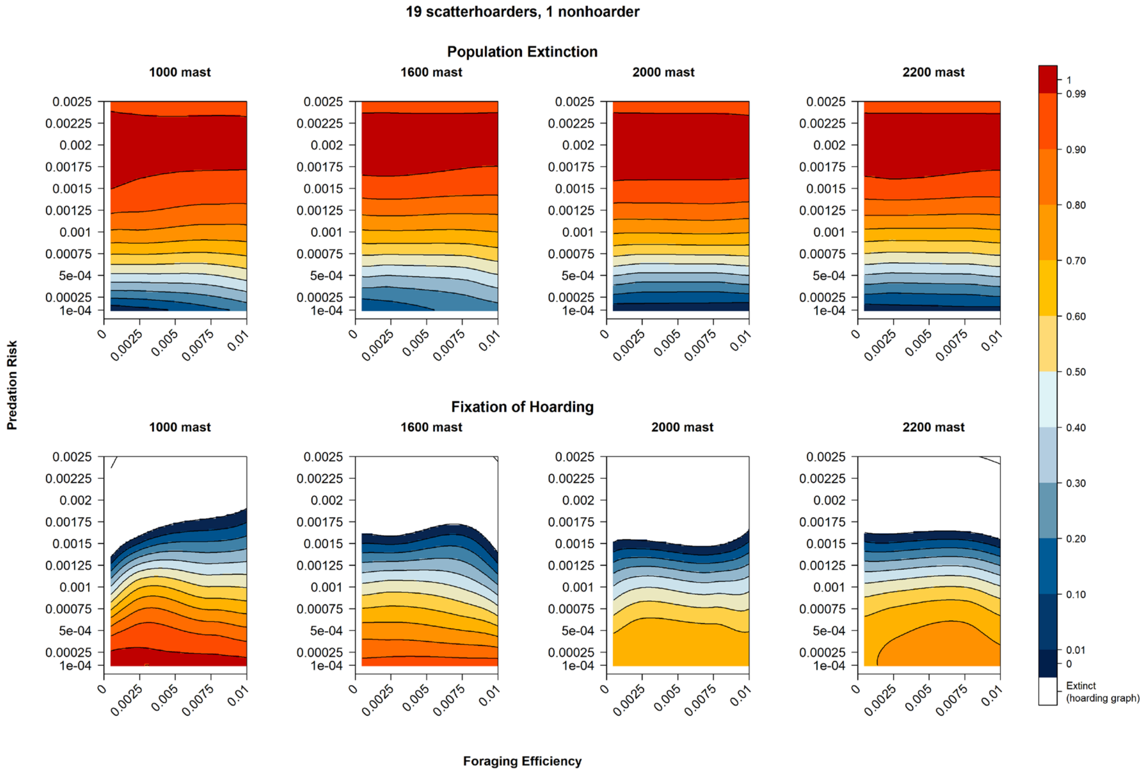


Figure S1.03. Proportion of times populations went extinct, and proportion of times hoarding behavior fixated within extant populations that began with **19 scatterhoarders and 10 nonhoarders**. Both hoarding and nonhoarding individuals could pilfer (steal) buried food items from hoarders. Mast represents the number of storable food items available at the beginning of the 100-day scatterhoarding season. Predation risk shown represents risk assumed by nonhoarders, while hoarding individuals experienced twice the risk, and foraging efficiency represents how easy all food items were to detect while foraging.



Appendix C: Model code

```
#!/usr/bin/env python3

''' Model Summary.

This model simulates the evolution of scatterhoarding in a
population of 20 squirrels with a specified number of
hoarders and nonhoarders. There is a trade-off being being
able to hoard food and predation risk. Predation, foraging
efficiency, and mast crop production can be manipulated.
Population of 20 squirrels each go on 20 foraging bouts
each day for 100 days. Each squirrel has a chance of
predation at the end of each foraging bout. If a squirrel
does not eat 1 food item by the end of the day, they starve
and die. Storable food is produced and added to the public
food supply at the beginning of the first day (i.e. acorns
falling to the ground). If a hoarder has stored food, the
squirrel automatically eats that and is satiated before
foraging. If the squirrel was not able to eat anything
before foraging, they eat the first food they find through
foraging. After eating one food item each day, all other
foods found are stored, if the animal can store food. Each
day, squirrels are all chosen to forage in a random order.
When a squirrel forages, a detection probability is
calculated and if a random number is less than that prob,
the squirrel finds food to harvest. If detection prob <
random number, the squirrel is marked as foraged and the
next squirrel forages. If the squirrel detected food to
harvest, it's either public food or food stored by other
hoarders, based on amount of each available. If public
food, squirrel eats or stores the food. If the squirrel
detected stored food, they steal from another hoarder,
depending on proportions of food stored by each other
hoarder. After foraging is completed with eating or storing
food, they may be eaten by a predator. At the end of each
days 20 foraging bouts, if the squirrel hasn't eaten any
food, it starves and dies.
'''

#Load packages needed for code.
#
#    if 'import' doesn't work;
#    use: 'pip install #package#'

import copy #to copy dict under new name to act separately
import statistics #calculate mean for inheritance
```

```
import csv #exporting to csv
import gc #garbage collecting
import sys
import random #to generate random numbers
import decimal #to specify decimal places? (might not be
needed if code is changed)
import math #exponents and natural logs
import numpy as np #math with lists; making arrays
# if numpy won't import; from command prompt, run: python3
-m pip install numpy


#prevents issues with the foraging function calling itself
many, many times.
sys.setrecursionlimit(500000000)


def reset(): #restarting entire simluation; first
generation of first run only
    """
    Resets variables to initial values at the beginning of
a run.

    Restarts the entire run of the model.
    Only used before the first generation of the first run
of the model

    """
    global season
    global state2
    global hoarder_id
    global hoarder_stored
    global hoarder_values
    global public_food_harv
    global foragers
    global forager_id
    global _id
    global phenotype
    global phenotype2
    global pred_risk
    global fixation
    global results
    global storage_effort
    season = {'Day' : 1, 'Bout' : 0, 'Generation':1,
'Run':1}
    state2 = (pop_size)*[0] # repeated pop_size times
    hoarder_id = [*range(0,pop_size)]
```

```
    hoarder_stored = (pop_size)*[0] #0 repeated pop_size
times
    nonhoarder_num = pop_size - hoarders_num #storage
effort is 0
    storage_effort_h = [1]*hoarders_num #repeats 1, for the
number of hoarders
    storage_effort_nh = [0]*nonhoarder_num #repeats 0 for
the number of nonhoarders
    storage_effort = []
    for i in storage_effort_h: #choose list to add to end
of other list
        storage_effort.append(i) #add chosen list to end of
this list
        #storage_effort is now list of hoarders
    for i in storage_effort_nh: #choose list to add to end
of other list
        storage_effort.append(i) #add chosen list to end of
this list
        #storage_effort is now entire list of hoarders and
non hoarders
    pred_risk = pred_risk_pop +
np.multiply(pred_risk_pop,storage_effort)
    hoarder_values = {'state':state2, 'id':hoarder_id,
'stored food':hoarder_stored,
    'predation risk': pred_risk, 'storage
effort':storage_effort}
    public_food_harv = 0
    foragers = 0 #define global variable
    forager_id = -1
    _id = pop_size #for making list of survivors
    phenotype = [] #for calculating new phenotype
    phenotype2 = [] #calculating new phenotype
    fixation = -1
    results = {'hoarder': 0, 'nonhoarder':0, 'dead':0}


def reset4(): #any first generation after first run
    """
    Resets variables to initial values for the first
generation of
    any run after the first run.

    """
    global season
    global state2
    global hoarder_id
    global hoarder_stored
```

```
    global hoarder_values
    global public_food_harv
    global foragers
    global forager_id
    global _id
    global phenotype
    global phenotype2
    global pred_risk
    global public_food
    global public_food_tot
    global hoarders_num
    global fixation
    global results
    global storage_effort
    season['Day'] = 1
    season['Bout'] = 0
    season['Generation'] = 1
    state2 = (pop_size)*[0]
    hoarder_id = [*range(0,pop_size)]
    hoarder_stored = (pop_size)*[0]
    nonhoarder_num = pop_size - hoarders_num
    storage_effort_h = [1]*hoarders_num
    storage_effort_nh = [0]*nonhoarder_num
    storage_effort = []
    for i in storage_effort_h:
        storage_effort.append(i)
    for i in storage_effort_nh:
        storage_effort.append(i)
    pred_risk = pred_risk_pop +
np.multiply(pred_risk_pop,storage_effort)
    hoarder_values = {'state':state2, 'id':hoarder_id,
'stored food':hoarder_stored,
    'predation risk': pred_risk, 'storage
effort':storage_effort}
    public_food_harv = 0
    foragers = 0
    forager_id = -1
    _id = pop_size #for making list of survivors
    phenotype = [] #for calculating new phenotype
    phenotype2 = [] #calculating new phenotype
    fixation = -1
    results = {'hoarder': 0, 'nonhoarder':0, 'dead':0}


### Define variables for starting the model
```

```
pop_size = 5 # number of animals in the population, always
20
days_tot = 5 # number of days in the season, always 100
runs_ = 5 #100 total for each combination of parameters

#Below variables are manipulated prior to running a
specific variation of the model
pred_risk_pop = 0.0001 #population background risk, varies
SH_pilfer_ability = 1 #1 = hoarders can pilfer, 0 =
hoarders cannot pilfer
hoarders_num = 1 #number of animals with storage effort of
1 (i.e., hoarders); 1, 10, or 19

#Below variables defined in function to run all code at end
days_perish = [] #days without starvation risk, defined in
function to run all code
for_eff = [] #used to calculate detection probability,
defined in function to run all code
mast_crop = [] #amount of storable food available starting
the food day of the model

### Define starting values that are not manipulated
manually
season = {'Day' : 1, 'Bout' : 0, 'Generation': 1, 'Run':1}
#dictionary to keep track of time
public_food_harv = 0
foragers = 0
forager_id = -1
_id = pop_size
survivors = 0
fixation = -1 #-1 = not present, 0 = nonhoarding trait, 1 =
hoarding trait
results = {'hoarder': 0, 'nonhoarder':0, 'dead':0}
detection_prob = 0
harv_foodtype = 0
public_total = -1
surv = 0
phenotype = []
phenotype2 = []

#Creating list of different probabilities for storing vs.
ignoring pilfered food.
nonhoarder_num = pop_size - hoarders_num #number of
nonhoarders in the population

#Define number of animals with each type of storage effort
```

```
#Storage effort = 0 for nonhoarders and nonpilfering
hoarders, 1 for pilfering hoarders
storage_effort_h = [1]*hoarders_num #repeats 1 for the
number of hoarders
storage_effort_nh = [0]*nonhoarder_num #repeats 0 for the
number of nonhoarders
storage_effort = [] #create empty list to add values to

for i in storage_effort_h: #choose list to add to end of
other list
    storage_effort.append(i) #add chosen list to end of
this list
#storage_effort is now a list of hoarders

for i in storage_effort_nh:
    storage_effort.append(i)
#storage_effort is now the full list of hoarders and non
hoarders

# predation risk for each individual is a function of their
storage effort
# hoarders = pred_risk_pop + pred_risk_pop; nonhoarders =
pred_risk_pop
pred_risk = pred_risk_pop +
np.multiply(pred_risk_pop,storage_effort)

#hoarder_values is a dictionary used to reference values
#associated with specific animals, that consists of:
#state; 0 = satiated, -1 = hungry, 999/998 = dead
state2 = (pop_size)*[0]
#hoarder_id = individual id of each animal (hoarders and
nonhoarders)
hoarder_id = list(range(0,pop_size))
#hoarder_stored = number of food items currently stored by
each animal
hoarder_stored = (pop_size)*[0]

hoarder_values = {'state':state2, 'id':hoarder_id, 'stored
food':hoarder_stored,
    'predation risk': pred_risk, 'storage
effort':storage_effort}


def choose_forager():
    '''
    This function chooses a new random foraging order for
all animals.
```

```
    Run after each animal forages to see if all animals
have foraged yet.
    If all animals have foraged, a new random order is
created for all
    animals in the population to forage. The next foraging
bout begins.
    All animals are reset to not having foraged yet that
bout.

    Returns:
    foragers: dictionary with new randomly ordered list of
all animals
    in the population and 0s for foraging status
(indicating they have
    not foraged yet)
    '''
    global forager_id
    global foragers
    if forager_id == -1: #nobody has foraged, it's the
start of a new bout
        rand_forage = random.sample(hoarder_id,pop_size)
#create random list of foragers without replacement
        forage_status = [0]*pop_size #will indicate animal
has not yet foraged this bout
        foragers = {'hoarder':rand_forage,
        'foraged':forage_status} #dictionary for ease of
calling variables
        forager_id = 0 #start with first forager in order
        season['Bout'] += 1 # move to the next bout


def fun(hoarders_num, days_perish, mast_crop, for_eff):
    '''
    This function allows animals to forage.

    Determines if animals have foraged yet and passes them
to the next appropriate
    function to determine if they are hungry, detect food,
or to finish the generation
    at the end of a season. Moves to the next day after all
individuals
    have foraged during a day. This function calls on
itself many times in order
    to cycle through 100 days of 20 foraging bouts per 20
individuals.
```

```
    Attributes:
    hoarders_num ############################ DON'T THINK
THIS IS NEEDED ANYMORE
    days_perish: number of days at the beginning of each
season when perishable food is available
    mast_crop: total number of storable food items
available at the beginning of each season
    for_eff: foraging efficiency of all individuals in the
population
    '''
    global forager_id
    global foragers
    global season
    choose_forager()
    if forager_id < pop_size: #if the forager is in the
population
        if
hoarder_values['state'][foragers['hoarder'][forager_id]] <
1: #if state of forager identified by forager_id is alive
            if foragers['foraged'][forager_id] == 0: #and
if they HAVEN'T foraged yet
                foragers['foraged'][forager_id] += 1 #then
define them as foraged,
                if season['Bout'] == 1: #if it's the first
bout of the day
                    state() #determine state based on
perishable and stored food
                detect() #and let them continue foraging
            elif foragers['foraged'][forager_id] == 1: #or
if they HAVE already foraged
                forager_id = forager_id + 1 #set forager to
next hoarder in the order
                fun(hoarders_num, days_perish, mast_crop,
for_eff)
        elif
hoarder_values['state'][foragers['hoarder'][forager_id]] >
1: #or if they are dead
            forager_id = forager_id + 1 #set forager to
next animal in the order
            fun(hoarders_num, days_perish, mast_crop,
for_eff)
    #End of the day or bout:
    elif forager_id == pop_size: #if the forager is not in
the population (all have foraged that bout)
        if season['Bout'] == 20: #and it's the last bout of
the day
```

```
            if season['Day'] == days_tot: #and it's the
last day of the season
                next_gen() #find survivors, check for
fixation, check runs
            elif season['Day'] < days_tot:
                season['Day'] += 1
                season['Bout'] = 0
                forage_status = [0]*pop_size
                foragers['foraged'] = forage_status #reset
all foragers to not foraged yet
                forager_id = -1 #reset to to able to choose
new order
                fun(hoarders_num, days_perish, mast_crop,
for_eff)
        elif season['Bout'] < 20: #but if it's not the last
bout of the day
            forage_status = [0]*pop_size
            foragers['foraged'] = forage_status #reset all
foragers to not foraged yet
            forager_id = -1 #reset to be able to choose new
order
            fun(hoarders_num, days_perish, mast_crop,
for_eff)


def state(): #define forager's state based on available
food
    '''
    Defines state of each individual as satiated, hungry,
or dead.

    Other functions can define state as 998 for starvation
mortality
    and 999 for predation mortality. If the animal is
alive, this
    function checks for available food and determines if
they are
    satiated or hungry. If there is perishable food
available,
    the animal will be satiated (state = 0). If there is no
perishable food,
    but the animal has stored food available, the animal
will be
    satiated (state = 0). If neither food type is
available, the
    animal will be defined as hungry (state  = -1).
    '''
```

```
    global forager_id
    global hoarder_values
    #if perishable food or stored food is available to eat,
    if season['Day'] <= days_perish or 
hoarder_values['stored 
food'][foragers['hoarder'][forager_id]] > 0:
    #if the forager is alive,
        if 
hoarder_values['state'][foragers['hoarder'][forager_id]] < 
995:
    #forager is satiated

hoarder_values['state'][foragers['hoarder'][forager_id]] = 
0
    #if no perishable food and no stored food is avilable 
to eat
    elif season['Day'] > days_perish and 
hoarder_values['stored 
food'][foragers['hoarder'][forager_id]] == 0:
    #if the forager is alive,
        if 
hoarder_values['state'][foragers['hoarder'][forager_id]] < 
995:
    #forager is hungry

hoarder_values['state'][foragers['hoarder'][forager_id]] = 
-1


def detect():
    '''
    Determines amount of food available and calculates 
detection probability.

    This function calculates how much food (both stored and 
not yet stored) is available
    to harvest and then calculates the detection 
probability using the animal's foraging effiency
    and the total number of available food items. When 
calculating available food, items
    stored by the current forager are not included in the 
total value. If there is available
    food, the detection probability is calculated and the 
harvest_event function is
    called for the animal to continue foraging. If there is 
no food available, the predation
```

```
    function is called to determine mortality due to
starvation or predation.
    '''
    global forager_id
    global detection_prob
    global mast_crop
    global food_avail
    global public_food
    global other_SH
    total_stored = sum(hoarder_values['stored food']) #find
total number of seeds stored by all animals
    other_SH = total_stored - hoarder_values['stored
food'][foragers['hoarder'][forager_id]] #find food hoarded
by others animals
    public_food = mast_crop - public_food_harv # total mast
not yet eaten or stored
    food_avail = public_food + other_SH #total storable
food items available to locate or pilfer
    if food_avail == 0:  #if there IS NOT food left to
harvest or pilfer
        predation()
    elif food_avail > 0: #if there IS storable food left to
harvest or pilfer
        #detection_prob = 1 - ((1 -
pub_for_eff)**(public_food))*((1 -
pilf_for_eff)**(other_SH))
        # ^^^ different probabilities of finding public
food vs scatterhoarded food
        detection_prob = 1 - (1 - for_eff)**food_avail
#probability of finding a particular food item
        # ^^^ all food is equally as easy to find (public
and hoarded)
        harvest_event()


def harvest_event(): #determine if detected food is
harvested
    '''
    This function determines if food is detected and then
calls either
    the harvest_item function to continue foraging, or the
predation
    function to end the foraging bout and determine
mortality.

    '''
```

```
    harv_rand = random.random() #generates 0.#### number
between 0 and 1
    if detection_prob > harv_rand: #item IS harvested
        harvest_item() #determine what type of food is
harvested
    else: #item is NOT harvested
        #foraging bout is over for this individual; need to
check for predator motality
        predation()


def harvest_item(): #determine which item is harvested
    '''
    This function determines if unstored food (e.g., public
food) is harvested
    or stored food is pilfered.

    '''
    global public_food_harv
    global forager_id
    global harv_foodtype
    global public_total
    total_stored = sum(hoarder_values['stored food']) #find
total stored seeds
    other_SH = total_stored - hoarder_values['stored
food'][foragers['hoarder'][forager_id]] #find food hoarded
by others
    public_total = mast_crop - public_food_harv #total
public food currently available
    if other_SH > 0: #if any seeds are stored
        other_SH_prop = other_SH / (other_SH +
public_total)
        public_prop = public_total / (other_SH +
public_total)
        food_prop = [public_prop, other_SH_prop]
        food_types = [0,1] # 0 = public; 1 = hoarded
        #choose food type to harvest based on proportions
of public and hoarded
        harv_foodtype = random.choices(food_types,
weights=food_prop,k=1)
    elif other_SH == 0: #if there are no seeds stored
        harv_foodtype = [0] #public food is automatically
harvested
    food_fate()


def food_fate():
```

```
    '''
    This function determines if harvested food is eaten,
stored, or ignored.

    If the animal is hungry, they always eat the food item
and become satiated for the day.
    If already satiated, a hoarder can store public food,
while a nonhoarders will always ignore it.
    If stored food is pilfered, actions depend on whether
the animal can pilfer food or not.
    Those that can pilfer can either eat or store pilfered
food. Those that cannot pilfer will ignore
    pilfered food.

    '''
    global public_food_harv
    global harv_foodtype
    global public_total
    global mast_crop #total amount of storable food
available at beginning of season
    if harv_foodtype == [0]: #if harvested food is public
        public_total = mast_crop - public_food_harv #public
food currently available
        if public_total > 0: #if there is public food
available
            if
hoarder_values['state'][foragers['hoarder'][forager_id]] ==
-1: #if forager is hungry
                public_food_harv = public_food_harv + 1

hoarder_values['state'][foragers['hoarder'][forager_id]] =
0 #forager is satiated
            elif
hoarder_values['state'][foragers['hoarder'][forager_id]] ==
0: #if forager is satiated
                if hoarder_values['storage
effort'][foragers['hoarder'][forager_id]] == 1: #if animal
can store food
                    hoarder_values['stored
food'][foragers['hoarder'][forager_id]] += 1 #food item is
stored
                    public_food_harv = public_food_harv + 1
                elif hoarder_values['storage
effort'][foragers['hoarder'][forager_id]] == 0: #if animal
CANNOT store food
                    pass #seed is ignored
        else:
```

```
            pass #there is no public food available
    if harv_foodtype == [1]: #if harvested food is stored
        #copy hoarder values dictionary to new variable to
manipulate
        hoarders =
copy.deepcopy({'id':hoarder_values['id'],'stored food':
hoarder_values['stored food']})
        del hoarders['id'][foragers['hoarder'][forager_id]]
#remove current forager id from dictionary
        del hoarders['stored
food'][foragers['hoarder'][forager_id]] #remove current
forager's stored items from dictionary
        pilf = random.choices(hoarders['id'],
weights=hoarders['stored food'],k=1) #select from other
hoarders weighted by seeds stored
        pilf1 = pilf[0] #pull hoarder value from list
        if hoarder_values['storage
effort'][foragers['hoarder'][forager_id]] == 0 or
(hoarder_values['storage
effort'][foragers['hoarder'][forager_id]] == 1 and
SH_pilfer_ability == 1):
        # ^ if forager is a cheater or pilfering hoarder
        # they eat pilfered food if they are hungry
            if
hoarder_values['state'][foragers['hoarder'][forager_id]] ==
-1: #if forager is hungry
                hoarder_values['stored food'][pilf1] -= 1
#take 1 food item from hoarder's food supply for pilferage

hoarder_values['state'][foragers['hoarder'][forager_id]] =
0 #forager is satiated
        # they recache pilfered food if they are satiated
            elif
hoarder_values['state'][foragers['hoarder'][forager_id]] ==
0: #if forager is satiated
                if hoarder_values['storage
effort'][foragers['hoarder'][forager_id]] == 1: #if animal
can store food
                    hoarder_values['stored food'][pilf1] -=
1 #take 1 food item from owners's food supply for pilferage
                    hoarder_values['stored
food'][foragers['hoarder'][forager_id]] += 1 #food item is
stored by pilfering forager
                elif hoarder_values['storage
effort'][foragers['hoarder'][forager_id]] == 0: #if animal
CANNOT store food
                    pass #seed is ignored, nothing happens
```

```
        elif hoarder_values['storage
effort'][foragers['hoarder'][forager_id]] == 1 and
SH_pilfer_ability == 0: #if forager is a hoarder and NOT
able to pilfer
            pass #do nothing, forager cannot pilfer
    predation()


def predation():
    '''
    This function determines mortality due to starvation or
predation.

    Animals face the risk of predation each foraging bout.
If they die,
    their state is set to 999. At the end of each day,
animals are checked
    for starvation. If they had not eaten a food item that
day, they
    starve and their state is set to 998.

    Commented out blocks of code can be used to record
survival data.
    '''
    global forager_id
    global hoarders_num
    global days_perish
    global mast_crop
    global for_eff
    global public_total
    global hoarder_values
    global foragers
    if season['Bout'] == 20: # if its the last bout of the
day
    # on the last bout of the day, any starving animals
will die after their attempt to forage
        if
hoarder_values['state'][foragers['hoarder'][forager_id]] ==
-1: #and if forager is starving on the last bout of the day

hoarder_values['state'][foragers['hoarder'][forager_id]] =
998 #forager dies from starvation
            #   input_variable = [season['Run'], # run
number
            #   [foragers['hoarder'][forager_id]], #hoarder
id
```

```
            #   hoarder_values['storage
effort'][foragers['hoarder'][forager_id]], #hoarder or
nonhoarder
            #   season['Day'],
hoarder_values['state'][foragers['hoarder'][forager_id]],
#day of event, event type
            #   1, 0, 1, #censor_starve, censor_pred,
censor_dead
            #   hoarders_num, pred_risk_pop,
detection_prob, food_avail, for_eff,
            #   days_perish, mast_crop, SH_pilfer_ability]
            #   print(input_variable) #mort data for those
that starve
        elif -1 <
hoarder_values['state'][foragers['hoarder'][forager_id]] <
995: # if the forager is alive
            pred_rand = random.random() #generate random
number between 0 and 1
            if pred_rand < hoarder_values['predation
risk'][foragers['hoarder'][forager_id]]: #if random number
is less than forager's predation risk

hoarder_values['state'][foragers['hoarder'][forager_id]] =
999 #forager is now dead from predation
             #   input_variable2 = [season['Run'], # run
number
             #   [foragers['hoarder'][forager_id]],
#hoarder id
             #   hoarder_values['storage
effort'][foragers['hoarder'][forager_id]], #hoarder or
nonhoarder
             #   season['Day'],
hoarder_values['state'][foragers['hoarder'][forager_id]],
#day of event, event type
             #   0, 1, 1, #censor_starve, censor_pred,
censor_dead
             #   hoarders_num, pred_risk_pop,
detection_prob, food_avail, for_eff,
             #   days_perish, mast_crop, SH_pilfer_ability]
             #   print(input_variable2) #mort data for
those that are eaten by predators
    else: #if it is not the last bout of the day
        if
hoarder_values['state'][foragers['hoarder'][forager_id]] <
995: # if the forager is alive (starving doesn't matter)
            pred_rand = random.random() #generate random
number between 0 and 1
```

```
            if pred_rand < hoarder_values['predation
risk'][foragers['hoarder'][forager_id]]: #if random number
is less than forager's predation risk

hoarder_values['state'][foragers['hoarder'][forager_id]] =
999 #forager is now dead from predation
            #    input_variable3 = [season['Run'], # run
number
            #    [foragers['hoarder'][forager_id]],
#hoarder id
            #    hoarder_values['storage
effort'][foragers['hoarder'][forager_id]], #hoarder or
nonhoarder
            #    season['Day'],
hoarder_values['state'][foragers['hoarder'][forager_id]],
#day of event, event type
            #    0, 1, 1, hoarders_num, pred_risk_pop,
detection_prob, food_avail, for_eff, #censor_starve,
censor_pred, censor_dead
            #    days_perish, mast_crop, SH_pilfer_ability]
            #    print(input_variable3) #mort data for
those that are eaten
        else: # random number is larger; they survive the
predator attack
            pass
           # if season['Day'] == days_tot: #if its the last
day of the season
           #     ## write to Mortality data file for
animals still alive at the end of the season
           #     input_variable4 = [season['Run'], # run
number
           #     [foragers['hoarder'][forager_id]],
#hoarder id
           #     hoarder_values['storage
effort'][foragers['hoarder'][forager_id]], #hoarder or
nonhoarder
           #     season['Day'],
hoarder_values['state'][foragers['hoarder'][forager_id]],
#day of event, event type
           #     0, 0, 0, #censor_starve, censor_pred,
censor_dead
           #     hoarders_num, pred_risk_pop,
detection_prob, food_avail, for_eff,
           #     days_perish, mast_crop, SH_pilfer_ability]
           #     print(input_variable4) #animals that
survive the last day of the season
           # else: #it's not the last day of the season
```

```
           #     pass #forager escapes predation and
survives to the next bout
    forager_id = forager_id +1 ###### added 3-26-23, move
to the next forager
    fun(hoarders_num, days_perish, mast_crop, for_eff)
#restart foraging function


# end the model if an entire generation dies
def checkIfDuplicates_1(): #check for duplicates
    '''
    This funciton checks all animals at the end of a season
to
    see if all animals died.

    Returns:
    surv: variable is set to -1 if population went extinct
or 0 if there were survivors.
    '''
    global surv
    if set(hoarder_values['state']) == {999,998} or
set(hoarder_values['state']) == {999} or
set(hoarder_values['state']) == {998}: #if the entire
population died
        surv = -1
    else:
        surv = 0 #there are survivors


def checkIfDuplicates_trait():
    '''
    This function checks to see if either nonhoarding or
hoarding had fixated at the end of the season.

    Returns:
    fixation: -1 (no fixation), 0 = nonhoarding, 1 =
hoarding
    '''
    global fixation
    if set(survivors['storage effort']) == {0}: #if the
entire population are nonhoarders
        fixation = 0 #nonhoarding trait has evolved
    elif set(survivors['storage effort']) == {1}:
        fixation = 1 #hoarding trait has evolved


def next_gen():
```

```
    '''
    This function creates a list of survivors from the
season that just ended.

    If there are no survivors, this population is recorded
as extinct and either the
    model ends or moves to the next run. If there are
survivors, a list is created
    of the surviors and if they were hoarders or
nonhoarders. The offspring
    function is then called to create a new generation and
continue the run
    with a new season. If the previous population fixated
with either
    hoarding or nonhoarding behavior, that is recorded and
the model run is ended.
    '''
    global hoarder_values
    global _id
    global survivors
    global surv
    global fixation
    global results
    global hoarders_num
    global days_perish
    global mast_crop
    global for_eff
    global runs_
    checkIfDuplicates_1() #check to see if everyone is dead
    if surv == -1: #no survivors from previous generation
        results['dead'] += 1
        if season['Run'] == runs_: #end model at end of
last run
            write()
        elif season['Run'] != runs_:
            reset3() #check runs and continue if needed
    elif surv == 0: #there are some survivors
        if _id == pop_size: #start of function
            survivors = copy.deepcopy(hoarder_values) #copy
population survival data
            _id = _id - 1 #if some survived, move to first
forager
            next_gen()
        elif _id > -1 and _id < pop_size: #0 is included as
an id; if forager is in the population
            if survivors['state'][_id] > 997: #if forager
is dead
```

```
                del survivors['id'][_id]
                del survivors['stored food'][_id]
                _id = _id -1 # move to next animal
                next_gen()
            elif survivors['state'][_id] < 998: #if forager
is alive
                _id = _id -1 #move to next forager in list
                next_gen()
        elif _id == -1: #if all survivors have been checked
for death
            checkIfDuplicates_trait() #check to see if one
trait died out
            if fixation == -1:
                offspring() #determine phenotypes of
offspring
                reset2() #add a generation, reset other
values
                fun(hoarders_num, days_perish, mast_crop,
for_eff) #start a new foraging season
            if fixation > -1: #if a trait HAS fixated
                if fixation == 1: #hoarding fixated
                    results['hoarder'] += 1
                elif fixation == 0: #nonhoarding fixated
                    results['nonhoarder'] += 1
                if season['Run'] == runs_: #end model at
end of last run
                    write()
                elif season['Run'] != runs_:
                    reset3() #check runs, stop model if
needed; continues foraging if needed


def offspring():
    '''
    Reproduction by suvivors of a season to create a new
generation of foragers.

    A new population of animals is created by randomly
choosing parents from
    the list of survivors. Each offspring's hoarding
phenotype is determined
    by the phenotype of a single parent. e.g., If the
parent is a hoarder,
    the offspring is a hoarder.

    '''
    global phenotype
```

```
    global phenotype2
    global survivors
    if len(phenotype2) < pop_size: #if all animals have not
yet been checked
        parents = random.choices(survivors['id'],k=1)
#choose 1 parent, NOT WEIGHTED
        young = survivors['storage effort'][parents[0]]
#offspring has same storage effort as parent
        phenotype2.append(young) #add offspring to new
generation
        phenotype2 = phenotype2
        offspring() #repeat until entire new population is
created
    elif len(phenotype2) == pop_size: #if new population is
correct size
        phenotype = copy.deepcopy(phenotype2)


def reset2(): #all generations after the first, within a
run
    '''
    Reset variables to initial values after the first
generation,
    but within a run.
    '''
    global season
    global state2
    global hoarder_id
    global hoarder_stored
    global hoarder_values
    global public_food_harv
    global foragers
    global forager_id
    global phenotype
    global phenotype2
    global _id
    global fixation
    season['Day'] = 1
    season['Bout'] = 0
    season['Generation'] += 1
    state2 = (pop_size)*[0]
    hoarder_id = [*range(0,pop_size)]
    hoarder_stored = (pop_size)*[0]
    pheno = copy.deepcopy(phenotype)
    pred_risk = pred_risk_pop +
np.multiply(pred_risk_pop,pheno)
    pred_risk = pred_risk.tolist()
```

```
    pred_risk = pred_risk
    hoarder_values = {'state':state2, 'id':hoarder_id,
'stored food':hoarder_stored,
    'predation risk': pred_risk, 'storage effort':pheno}
    public_food_harv = 0
    foragers = 0
    forager_id = -1
    _id = pop_size
    phenotype = []
    phenotype2 = []
    fixation = -1


def write():
    '''
    This function checks to see if the appropriate number
of runs have been completed
    for this combination of parameters within the model.

    Each time this function is called, data is exported to
a cvs file.

    '''
    input_variable = [season['Run'],season['Generation'],
results['hoarder'], results['nonhoarder'],
        results['dead'],hoarders_num, pred_risk_pop,
for_eff,
        days_perish, mast_crop, SH_pilfer_ability]
    with open('Evolution_model1.csv', 'a', newline = '') as
csvfile:
        my_writer = csv.writer(csvfile, delimiter = ',')
        my_writer.writerow(input_variable)
    gc.collect() #garbage collecting- might free up some
memory?
    if season['Run'] == runs_:
        reset() #reset back to first generation of first
run
        season['Run'] = 1
    else:
        pass


def reset3(): #after end of each run
    '''
    This function moves the model to the next run.

    '''
```

```
    global season
    global surv
    global hoarders_num
    global days_perish
    global mast_crop
    global for_eff
    surv = 5
    write()
    season['Run'] += 1 #directly add a run to the season
dict
    reset4() #reset values back to first generation
    fun(hoarders_num, days_perish, mast_crop, for_eff)
#start foraging and running the season


def run_fun():
    ''' Run the simulation. '''
    global days_perish
    global mast_crop
    global for_eff
    for days_perish in [0]: #always 0, in the current
version of the model
        for mast_crop in [1000,1600,2000,2200]:
            for for_eff in
[0.0005,0.001,0.0025,0.005,0.0075,0.01]:
                fun(hoarders_num, days_perish, mast_crop,
for_eff)

# Run the model!
run_fun()
```

Chapter 2. Geographic patterns in scatterhoarding behavior of eastern gray squirrels (*Sciurus carolinensis*)

Scatterhoarding is a time- and energy-intensive behavior for animals in which they store food in many places around their home range, and later recover and consume that food during a season of scarcity (typically winter). Due to the costs of this behavior, scatterhoarders should only collect and hoard the amount of food that they need to survive during the period of food-scarcity or otherwise that they can benefit from at a later date. The purpose of this study was to examine geographic patterns of scatterhoarding behavior of eastern gray squirrels (*Sciurus carolinensis*). We hypothesized that squirrels would exhibit variation in scatterhoarding behavior due to the differing severity of winter experienced at different latitudes, which should impact the availability of food over winter and hence the necessity and benefit of hoarded food. We recruited over 750 volunteers around the eastern United States to collect observational data on scatterhoarding activity of eastern gray squirrels for 4 years (2019 – 2022). We used the United States Department of Agriculture Plant Hardiness Zones as an index of winter conditions experienced by eastern gray squirrel populations in different areas of the species' range. The plant hardiness zones GIS data were provided by the PRISM Climate Group at Oregon State University. Volunteers conducted 4,540 10-minute observations of squirrel behavior throughout 12 plant zones. We used hurdle models to determine the effect of period of the year and plant zone on scatterhoarding behavior. We found that scatterhoarding behaviors (all hoarding behaviors, caching, recaching, and eating recovered food) during the fall increased significantly as plant zone decreased, indicating that squirrels in areas with harsher winter conditions invested more time and energy in building a scatterhoard. However, we found that even in areas with virtually no winter (e.g., south Florida), squirrels still engaged in some scatterhoarding behavior. These findings suggest that scatterhoarding appears to become a more important behavior as one moves north and encounters harsher winter conditions.

2.1 Introduction

Some animals mitigate seasonal scarcity in food availability by scatterhoarding: storing food in hundreds of locations around their home range to recover and eat when needed (Morris 1962). The ultimate benefit of food hoarding behavior commonly is assumed to be increased likelihood of survival through the food-scarce season. Additionally, animals may benefit from storing food via improved body condition at the start of the late winter or spring breeding season (Wauters et al. 1995, Sechley et al. 2015) or increased food for young born in early spring (Vander Wall, 1990). Notably, the fitness benefits of scatterhoarding are only gained when the animal consumes the stored food. However, scatterhoarding can incur many costs, most notably time and energy required for foraging, burying food (caching), recovery, or reburying food (recaching) in another location after recovery (Lichti et al. 2017). Stored food may also be stolen (pilfered) by another animal prior to recovery (Vander Wall et al., 2005), and predation risk increases for animals while hoarding food on the ground (Steele et al. 2014). Thus, researchers have put considerable effort into understanding the net benefits of scatterhoarding behavior and ultimately the conditions under which the benefits of this behavior would outweigh the costs, resulting in scatterhoarding behavior evolving (e.g., Andersson and Krebs 1978, Smulders 1998, Vander Wall and Jenkins 2003). Yet, different populations of the same scatterhoarding species may experience conditions that cause the benefits from or costs of their hoarding behavior to vary, and this topic has not yet been studied in depth with several populations of the same species.

Importantly, differences in local environmental conditions experienced by scatterhoarders could affect the costs and benefits of scatterhoarding in a variety of ways. For example, the length and intensity of the food-scarce season (i.e., winter) could have an impact on the benefits of scatterhoarding behavior due to the length of time animals must rely on scatterhoarded food and the possibility of finding alternate food sources. Specifically, longer, colder winters should generate greater benefit from stored food as animals simply may not be able to find sufficient non-stored food to survive over winter. Alternatively, shorter, warmer winters allow plants to begin growth earlier in the year (e.g., early February in Alabama; personal observation, SBR) which releases scatterhoarders from their reliance on hoarded food earlier in the year compared to areas with longer, colder winters (e.g., late March, Toronto, ON; Thompson and Thompson 1980). One way to examine the effect of differences in season length is to study geographic variation in the characteristics of scatterhoarding. Many scatterhoarding species have large geographic ranges with varying local conditions throughout their range that could result in variation in scatterhoarding behavior. Such geographic variation in scatterhoarding behavior (i.e., start and end of scatterhoarding season, energy invested in scatterhoarding, etc.) would allow animals to respond to differences in local environmental conditions in a way that optimizes the differences between the benefits and costs of scatterhoarding. However, while many studies have been conducted on the costs and benefits of scatterhoarding behavior in single locations (e.g., Vander Wall

1993, Vander Wall et al. 2006, Wang et al. 2013, Yang et al. 2016), a broader examination of scatterhoarding behavior as a function of geographic location and the associated climate is needed.

The eastern gray squirrel (*Sciurus carolinensis*) is an ideal food-hoarding species for investigating scatterhoarding behavior over a broad geographic range. These animals are easy to observe, and therefore behavioral data can easily be collected during the scatterhoarding season. Furthermore, as the species inhabits the entire eastern half of the United States and bordering portions of Canada (Koprowski 1994), the large range of the eastern gray squirrel encompasses considerable climatic variation over which scatterhoarding behavior may similarly vary. In this study, we tested the hypothesis that in areas where the ability to recover scatterhoarded food during winter provides benefits over a longer period of time (e.g., areas with longer food-scare seasons), scatterhoarders should invest more time and energy in scatterhoarding. To investigate this idea, we created the Auburn Squirrel Project, a citizen science effort where eastern gray squirrels were observed throughout their range in the United States to determine if more time was spent scatterhoarding and if more seeds were scatterhoarded in areas with colder, longer winters compared to those with milder, shorter winters. Thus, this study allowed us to investigate whether scatterhoarding behavior is influenced by the local environment, or if it is purely a fixed instinctual behavior that is exhibited by all gray squirrels, regardless of environmental changes.

2.2 Methods

Volunteer Recruitment

We recruited volunteers throughout the range of the eastern gray squirrel in the United States to record observational data of scatterhoarding from September 2019 – July 2022. Volunteers were recruited via social media, word of mouth, and via a website that contained more details about this project (www.auburnsquirrelproject.weebly.com). Additionally, undergraduates from universities within the range of the eastern gray squirrel were recruited by sending e-mails to biology-related departments about the project. The website contained in-depth details about the project, video and text descriptions of common behaviors, and instructions for recording and submitting data for the observation period. Recruitment of volunteers began March 2019 to allow ample time to contact undergraduates before summer break began, since the observation period began around the same time as classes for most schools in August 2019. New volunteers were recruited each January and August through 2022.

Data collection

Volunteers observed squirrels for 10 minutes at a time and recorded the squirrel's behavior every 20 seconds. We asked each volunteer for a minimum of five, 10-minute observation periods per week (~18 hours over 5-month survey period) in 2019. In 2020-2022, we put more effort into recruiting volunteers from the same areas to lessen the data collection burden of each individual volunteer. Common potential behaviors were predefined, but many behaviors were grouped together when recording observations (Table 1). If the squirrel moved out of sight of the observer or was far enough away that the behavior could not be accurately assessed, "out of sight" was recorded. Observers also reported the location (coordinates or address) of their observation. For each 10-minute observation period, observers submitted their data through an online survey.

Analysis

We used the United States Department of Agriculture (USDA) Plant Hardiness Zones, which use several aspects of climate to categorize locations in the United States into discrete zones, as an indicator of the severity of winter experienced by observed squirrels (USDA 2012). We assumed that conditions impacting scatterhoarding behavior were linked to the climatic factors used in the classification of the plant zones, such as precipitation, humidity, and temperature. For each location where squirrel behavior was observed, we determined the USDA plant hardiness zone of that location using the intersect tool in ArcGIS Pro 3.0.2 (ESRI). We then included plant hardiness zones as an independent variable in our models (see below).

We also included the calendar months as an independent variable in our models, as scatterhoarding behavior is typically more common in fall – spring, and the types of scatterhoarding behavior may change throughout the scatterhoarding season. However, because we had underrepresented plant zones in certain months of each year, we combined months to ensure that we had at least five observation periods with scatterhoarding within each plant zone and within each pooled group of months. We pooled months based on similar weather conditions that could impact scatterhoarding and available food and with the goal of meeting the above conditions for adequate representation of the plant zones and pooled months: January and February (n = 370 observation periods), March and April (n = 971), August and September (n = 847), November and December (n = 615). October was kept separate due to having a large sample size of observation periods throughout all plant zones (n = 1309). We removed observation periods recorded during May – July of each year from our analyses due to low sample sizes; 84% of these observation periods were in zones 8a and 8b (n = 409 observation periods removed). We also removed potential bias due to outliers by removing any observation periods without at least one other observation period at a different location within 100 km (n = 19). Finally, we included an interaction between pooled calendar months and plant zones in each of our models to see if differences in squirrel behavior among plant zones changed through the different seasons. If these interactions were significant, we analyzed the effect of the plant zones separately for each of our pooled calendar months to see how squirrels behaved differently throughout the scatterhoarding season.

The different behavioral response variables analyzed included the number of time points during each observation period that squirrels were observed scatterhoarding (sum of all scatterhoarding behaviors), caching, recaching, or recovering and eating seeds during the observation period (Table 2). The scatterhoarding response variables also included instances where squirrels were observed recovering food but went out of sight of the observer before they could determine if the squirrel ate or recached the recovered food item. The total number of times each squirrel was observed during the observation period was included as an offset in the model due to many squirrels moving out of sight of the observer before the observation period was finished. We used the software platform R (R Core Team 2021) to run hurdle models (package “pscl”; Zeileis et al. 2008) which included a logistic regression for the presence or absence of the scatterhoarding behavior during each observation period (to account for an over-abundance of observation periods with zero scatterhoarding) and a truncated Poisson regression that described the number of times squirrels were seen scatterhoarding for those observation periods where scatterhoarding was observed. All models had the same dependent and independent variables for both the binomial and truncated Poisson portions of the model. We created our graphs using the packages “emmeans” (Lenth 2023), “ggplot2” (Wickham 2016), and “cowplot” (Wilke 2020) in R.

2.3 Results

Our volunteers (n = 757) recorded 4,540 10-minute observation periods of squirrel behavior at 20-second intervals for a total of 118,810 instances of behavior over 4 different years (2019: n = 421 10-minute observation periods; 2020: n = 2145; 2021: n = 1520; 2022: n = 335). Most observation periods were recorded October – December of each year. Squirrels were observed throughout 12 different USDA plant hardiness zones (Figure 1). The most observed behaviors were traveling, foraging, and watching for predators (i.e., alert; Figure 2). Our volunteers observed scatterhoarding behavior in 42.9% (n = 1949) of all observation periods and in those observation periods where squirrels engaged in some scatterhoarding behavior, they typically spent an average of 15.7% (standard deviation = 12.2%) of the observation period scatterhoarding. After removing summer data and observation periods in isolated locals (see methods), our final dataset contained 4,112 eastern gray squirrel observation periods.

We first compared models where USDA plant zones were treated as a continuous variable (‘b’ plant zones were coded 0.5 – e.g., 6b = 6.5) to those where plant zones were treated as a categorical variable in order to explore potential non-linearities in the relationship between plant zone and scatterhoarding behavior. Due to having underrepresented plant zones in various months of each year, we combined plant zones (and months; see methods) to have at least 5 observation periods with scatterhoarding within each pooled plant zone and within each pooled group of months. Thus, we pooled plant zones 4a, 4b, 5a, and 5b together as well as 8a, 8b, 9b, and 10a together, while all other plant zones were kept separate. No squirrel observations were recorded in zone 9a. In our analysis, we determined that the continuous version of the plant zone variable generated a far better model for each of our response variables (all ΔAIC > 575 from models with categorical compared to continuous plant zone, Table 3). Thus, we used the continuous version of the plant zone variable in all of our analyses.

In our examination of total scatterhoarding behavior, we found a significant interaction between the USDA plant zone and the pooled months (P = 0.008, Table 4). Specifically, our model indicated that at the beginning of the hoarding season (August – September), squirrels in the coldest sampled plant zone spent a much greater total proportion of their time scatterhoarding (zone 4a, 29%) compared to squirrels in the warmest plant zone (10a, 0%; Figure 3). By October, squirrels in moderate plant zones (6 – 8) had increased their scatterhoarding behavior from that in August and September, while scatterhoarding behavior by squirrels in zones 4 and 5 had declined slightly (Figure 3). Consequently, the decrease in scatterhoarding behavior with increasing plant zone was not quite as strong in October as in August and September, but the relationship was still quite prominent. Scatterhoarding behavior in all zones decreased in November – December relative to October, but the relationship between plant zone and scatterhoarding behavior persisted. However, by January, squirrels in all plant zones spent relatively little time engaging in scatterhoarding behavior regardless of plant zone, although scatterhoarding behavior still appeared to decrease slightly with increasing plant zone, a pattern which persisted through March. Notably, squirrels in plants zones 9 and 10 always spent relatively little time engaging in scatterhoarding behavior (Figure 3).

In order to better understand the interaction between plant zone and pooled category month, we investigated the relationship between scatterhoarding behavior and plant zones separately for each of the five pooled monthly categories. Specifically, we sought to understand if the relationships between plant zone and scatterhoarding behavior was primarily driven by decreases in the likelihood of scatterhoarding with increasing plant zone (i.e., warmer, less severe winters), decreases in the proportion of time spent scatterhoarding when squirrels engaged in the behavior, or both. We found that in August/September, October, and November/December, the odds that squirrels engaged in any scatterhoarding behavior increased by 4.78 (3.89 – 5.86; 95% confidence limits [C.L.]), 1.95 (1.63 – 2.34), and 2.41 (1.87 – 3.11) times for each 1 unit decrease in plant zone (all $P < 0.0001$). Conversely, we found that the proportion of time squirrels engaged in scatterhoarding behavior (conditional upon them engaging in the behavior at all) changed by a factor of 1.01 (0.92 – 1.10), 0.97 (0.93 – 1.01), and 1.10 (1.02 – 1.18), respectively, for each 1 unit decrease in plant zone during those calendar periods; we note that the observed changes were only statistically significant for November/December ($P = 0.014$), but not August/September ($P = 0.91$) nor October ($P = 0.117$). Thus, the observed decrease in scatterhoarding behavior with increases in plant zone in the fall months were primarily driven by changes in the likelihood that squirrels scatterhoarded, rather than changes in the amount of time spent scatterhoarding, during any given 10-minute period. In the spring months (January/February, and March/April), we observed no statistically significant changes in either the likelihood of engaging in scatterhoarding behavior (January/February: odds ratio [OR] = 1.18, C.L = 0.90 – 1.54, P = 0.22; March/April: OR = 1.20, C.L. = 0.96 – 1.51, P = 0.107) or the amount of time spent scatterhoarding (January/February: rate ratio [RR] = 0.98, C.L. = 0.89 – 1.08, P = 0.688) with decreasing plant zone, with the exception of time spent scatterhoarding in the March/April period (RR = 1.12, C.L. = 1.02 – 1.24, p = 0.021).

We also found significant interactions between USDA plant zone and the pooled calendar months for both caching and recovery behavior (both $P < 0.05$, Table 4), so we analyzed these behaviors separately for each of the pooled months. Though the interaction for recaching behavior was not significant (P = 0.30), we analyzed this behavior separately for the pooled months to compare patterns in recaching with the other behaviors. Caching, recaching, and recovery behaviors showed similar patterns to those described above for all scatterhoarding behaviors combined (Figure 3, Table 5). Though not statistically significant, the proportion of time hoarding squirrels spent caching, recaching, or recovering food in August/September decreased for each 1 unit decrease in plant zone (all $P > 0.12$, Table 5). The odds of observing a squirrel caching, recaching, or recovering food in October and November/December all increased for each 1 unit decrease in plant zone, but these relationships were not statistically significant for recaching behavior in both months (October, P = 0.75; November/December, P = 0.11) or recovery behavior in October (P = 0.54, Table 5). During the spring months, squirrels were significantly more likely to be seen recaching food in January/February (OR = 1.40, C.L. = 1.02 – 1.94) and March/April (OR = 1.50, C.L. = 1.01 – 2.22) as plant zone decreased, while the odds of observing squirrels recovering at least one food item in

March/April were significantly more likely as plant zone decreased (OR = 1.35, C.L. = 1.02 – 1.79). In March/April, hoarding squirrels spent more time recovering food (OR = 1.21, C.L. = 1.02 – 1.45) with each 1 unit decrease in plant zone (P = 0.03). The odds of observing caching behavior and rates of caching food during the spring months followed many of the same patterns as described above for all scatterhoarding behaviors combined (Table 5).

2.4 Discussion

Our hypothesis that eastern gray squirrels experiencing more severe winters would spend more time and effort scatterhoarding was supported. Indeed, squirrels living in environments with regular harsh winter conditions in the northern portion of the species range spent considerable time caching new seeds than squirrels living in the warmer southern portion of the range. Interestingly, when squirrels decided to engage in scatterhoarding behavior during a 10-minute observation period, the proportion of that period they spent scatterhoarding did not change with increasing plant zone. Rather, as plant zone increased, squirrels were less likely to engage in scatterhoarding behavior during any 10-minute observation period. These results suggest that squirrels may not engage in long-periods of scatterhoarding, potentially due to high costs of hoarding, but scatterhoarding is a behavior squirrels engage in throughout the day in increasing amounts with greater winter severity.

Interestingly, squirrels in the warmer latitudes presumably did not need to rely on hoarded food over winter, yet they still assumed the costs of hoarding and spent time scatterhoarding food during October when the mast crop became available. There are several possible explanations for these populations spending time hoarding food that they may not need to eat that winter. First, if squirrels experience high costs due to their hoarding behaviors, there may not have been enough time yet for these behaviors to disappear from the population. However, we found squirrels in areas with colder, harsher winters were eating hoarded food at the same rate as squirrels in areas with warmer, milder winters, which could indicate that scatterhoarding is a lower-cost behavior than previously assumed. Finally, though hoarders may not need their stored food every year in areas with warm winters, there is a potential long-term value of scatterhoarding and an increased value of having hoarded food in years of hard mast failure. Indeed, we found squirrels in warmer areas were spending more time recaching food when the mast crop became available to them in October than in other months. Ultimately, we have demonstrated that investment in scatterhoarding behavior is likely dependent on local climatic conditions during winter, though squirrels that may not rely on hoarded food over winter still scatterhoard to some extent.

Previous studies provide conflicting evidence of food hoarders adapting to winter conditions that could impact recovery of their stored food. Populations of coal tits (*Parus ater*) at different latitudes showed adaptations to winter conditions by varying their effort at scatterhoarding food depending on winter conditions typical for the latitude of each population (Brotons and Haftorn 1999). Likewise, crested tits (*Parus cristatus*) hoarded more food in higher latitude populations (Brodin et al. 1994). However, populations of willow tits (*Poecile montanus*) did not differ in their hoarding intensity at different latitudes (Brodin et al. 1996). These previous studies were limited in the number of populations studied (n = 2 for each of the three studies) and the length of time hoarders were observed for (focused on intensive hoarding periods during winter). Our study is novel, as it is the first to describe hoarding behavior over a species' entire native range and throughout the entire scatterhoarding season.

As expected, caching behavior primarily occurred during the fall months, when the mast crop dictated the start of the scatterhoarding season. Contrary to our expectation, however, the squirrels living in colder areas ate the most recovered food at the beginning of the scatterhoarding season (August – September), rather than later in winter. Low rates of recovery behaviors in January and February in colder areas may have resulted from squirrels trying to conserve energy (Reichman and Van De Graaff 1973). We were not able to distinguish between food recovery by owners or pilferers. Scatterhoarders are able to locate and pilfer food based on scent (Vander Wall 2000), so more time devoted to cache maintenance in August – September could have resulted in more pilfered seeds but was recorded as recovery behavior. During the winter months, squirrels in all plant zones spent little of their time eating hoarded food and benefiting from the time and energy invested in caching food earlier in the scatterhoarding season. Storing large amounts of food without spending similar amounts of time on recovery suggests hoarders may store more food than is needed to survive the winter. Due to the difficulties of keeping track of an individual's entire stored food supply, we have little information on how many seeds are cached compared to how many cached seeds are recovered and eaten by the individual. Storing large amounts of food could be a strategy to counteract losses due to pilferage (Vander Wall and Jenkins 2003), germination (Soné et al. 2002), rot (Forget 1997), or memory loss. High amounts of initial caching and recaching behavior could also be evidence for the rapid sequestration hypothesis where hoarders cache many seeds in a short period of time, then later recache those seeds in better locations to reduce pilferage risk (Jenkins and Peters 1992). Alternatively, the costs of scatterhoarding behavior may be lower than previously assumed. If hoarders are not assuming much higher risks than nonhoarders would (i.e., increased predation risk, energy expenditure, opportunity costs), scatterhoarding would persist in populations that did not experience many benefits from the behaviors.

We found evidence that eastern gray squirrels may focus on recaching food more during the beginning and end of the scatterhoarding season. Recaching behavior can be used to check the condition of cached seeds, manipulate recovered seeds if needed to prolong storage time, and rebury (Vander Wall et al. 2005b). We found that squirrels spent the most time recaching and eating recovered food in colder zones in August and September, which could indicate checking caches from the previous year, recaching food that was still storable, while eating food that was close to spoiling. Scatterhoarders that experience colder winters may have more use for multi-year supplies of scatterhoarded food. If seeds are not useful the following year, then eating food recovered at the end of the scatterhoarding season would be a more beneficial behavior than recaching those seeds. Using hoarded food over multiple scatterhoarding seasons could have important implications for the benefits of scatterhoarding behavior and adaptiveness of this behavior in different climates (see Chapter 3: Multiyear Supply).

Ultimately, we have found evidence of variation in scatterhoarding behavior among local climatic conditions, which has important potential implications on the prevalence and intensity of scatterhoarding behavior in response to global climate change. Many masting plant species have complex evolutionary relationships with scatterhoarders (reviewed by Steele 2008) and depend on scatterhoarders to disperse their seeds away from the parent tree into areas more favorable for seedling growth (Briggs et al., 2009; Hirsch et al., 2012; Lichti et al., 2020; Pesendorfer et al., 2016, but also see Bogdziewicz et al., 2020). For example, northern red oak (*Quercus rubra*) is believed to have evolved to have a dormancy period to discourage pre-dispersal predation and encourage hoarding behavior, as dormant seeds pose less risk of germination during long-term storage (Smallwood and Peters 1986, Steele et al. 2001). Scatterhoarders often take more risks for seeds with greater future-value (e.g., larger, more nutritious seeds), by traveling further before storing the seed (Wang & Yang, 2014; Xiao et al., 2005) and assuming greater predation risk on themselves to benefit from lower pilferage risk for those valuable seeds (Steele et al. 2014). However, scatterhoarders invest less time and energy in dispersing seeds away from the parent tree in years of high food availability (Moore et al. 2007); hoarding behavior in warm climates is likely to be similar that that when food is abundant due to the decreased need for creating and maintaining a hoard. Additionally, some plants increase their above-ground growth following freeze-thaw events, which are predicted to increase with climate change (Kreyling et al. 2010) and could provide additional food for scatterhoarders to supplement their diets overwinter, further reducing the reliance on stored food (Wilson et al. 2020). Consequently, as the global climate change progresses and winter climate patterns trend towards warmer conditions, tree species that depend on dispersal through scatterhoarding may experience lower recruitment rates due to a decrease in scatterhoarding behavior.

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2.6 Literature Cited

Allen, D. S., and W. P. Aspey. 1986. Determinants of social dominance in eastern gray squirrels (*Sciurus carolinensis*): A quantitative assessment. Animal Behaviour 34:81–89.

Andersson, M., and J. Krebs. 1978. On the evolution of hoarding behaviour. Animal Behaviour 26:707–711.

Bogdziewicz, M., E. E. Crone, and R. Zwolak. 2020. Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. Journal of Ecology 108:1009–1018.

Briggs, J. S., S. B. Vander Wall, and S. H. Jenkins. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. Ecology 90:675–687.

Brodin, A., K. Lahti, L. Lens, and J. Suhonen. 1996. A northern population of willow tits *Parus montanus* did not store make food than southern ones. Ornis Fennica 73:114–118.

Brodin, A., L. Lens, and J. Suhonen. 1994. Do crested tits, *Parus cristatus*, store more food at northern latitudes? Animal Behaviour 48:990–993.

Brotons, L., and S. Haftorn. 1999. Geographic variation of the storing behaviour in the Coal tit *Parus aterr* role of winter residency and environmental conditions. Ibis 141:587–595.

Forget, P. M. 1997. Effect of microhabitat on seed fate and seedling performance in two rodent- dispersed tree species in rain forest in French Guiana. Journal of Ecology 85:693–703.

Hirsch, B. T., R. Kays, V. E. Pereira, and P. A. Jansen. 2012. Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. Ecology Letters 15:1423–1429.

Jenkins, S. H., and R. A. Peters. 1992. Spatial patterns of food storage by Merriam's kangaroo rats. Behavioural Ecology 3:60–65.

Koprowski, J. L. 1994. *Sciurus carolinensis*. Mammalian Species 480:1–9.

Koprowski, J. L. 1996. Natal philopatry, communal nesting and kinship in fox squirrels and gray squirrels. Journal of Mammalogy. 77:1006–1016.

Kreyling, J., C. Beierkuhnlein, and A. Jentsch. 2010. Effects of soil freeze–thaw cycles differ between experimental plant communities. Basic and Applied Ecology 11:65–75.

Lenth, R. V. 2023. emmeans: Estimated marginal means, aka least-squares means. R package version 1.8.6. https://CRAN.R-project.org/package=emmeans

Lichti, N. I., H. J. Dalgleish, and M. A. Steele. 2020. Interactions among shade, caching behavior, and predation risk may drive seed trait evolution in scatterhoarded plants. Diversity 12:1–19.

Lichti, N. I., M. A. Steele, and R. K. Swihart. 2017. Seed fate and decision-making processes in scatter-hoarding rodents. Biological Reviews 92:474–504.

Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. Ecology 88:2529–2540.

Morris, D. 1962. The behavior of the green acouchi (*Myoproctapratti*) with special reference to scatterhoarding. Proceedings of the Zoological Society of London 139:701–732.

Pesendorfer, M. B., T. S. Sillett, W. D. Koenig, and S. A. Morrison. 2016. Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. Ornithological Applications 118:215–237.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reichman, O. J., and K. M. Van De Graaff. 1973. Seasonal activity and reproductive patterns of five species of Sonoran Desert rodents. The American Midland Naturalist 90:118–126.

Sechley, T. H., D. Strickland, and D. R. Norris. 2015. Linking the availability of cached food to climate change: an experimental test of the hoard-rot hypothesis. Canadian Journal of Zoology 93:411–419.

Smallwood, P. D., and Wm. D. Peters. 1986. Grey squirrel food preferences: The effects of tannin and fat Concentration. Ecology 67:168–174.

Smulders, T. V. 1998. A game theoretical model of the evolution of food hoarding: Applications to the *Paridae*. The American naturalist 151:356–66.

Soné, K., S. Hiroi, D. Nagahama, C. Ohkubo, E. Nakano, S. I. Murao, and K. Hata. 2002. Hoarding of acorns by granivorous mice and its role in the population processes of *Pasania edulis* (Makino) Makino. Ecological Research 17:553–564.

Steele, M. A. 2008. Evolutionary interactions between tree squirrels and trees: A review and synthesis. Current Science 95:871–876.

Steele, M. A., T. A. Contreras, L. Z. Hadj-Chikh, S. J. Agosta, P. D. Smallwood, and C. N. Tomlinson. 2014. Do scatterhoarders trade off increased predation risks for lower rates of cache pilferage? Behavioral Ecology 25:206–215.

Steele, M. A., P. D. Smallwood, A. Spunar, and E. Nelsen. 2001. The proximate basis of the oak dispersal syndrome: Detection of seed dormancy by rodents. American Zoologist 41:852–864.

Thompson, D. C. 1978. The social system of the gray squirrel. Behaviour 64:305–328.

Thompson, D. C., and P. S. Thompson. 1980. Food habits and caching behavior of urban gray squirrels. Canadian Journal of Zoology 58:701–710.

United States Department of Agriculture Plant Hardiness Zone Map [USDA]. 2012. Agricultural Research Service, U.S. Department of Agriculture. Accessed from https://planthardiness.ars.usda.gov.

Vander Wall, S. B. 1990. Diet of Offspring. Pages 31–35 *in*. Food Hoarding in Animals. The University of Chicago Press, Chicago.

Vander Wall, S. B. 1993. A model of caching depth: Implications for scatterhoarders and plant dispersal. The American Naturalist 141:217–232.

Vander Wall, S. B. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behavioral Ecology 11:544–549.

Vander Wall, S. B., J. S. Briggs, S. H. Jenkins, K. M. Kuhn, T. C. Thayer, and M. J. Beck. 2006. Do food-hoarding animals have a cache recovery advantage? Determining recovery of stored food. Animal Behaviour 72:189–197.

Vander Wall, S. B., E. C. H. Hager, and K. M. Kuhn. 2005*a*. Pilfering of stored seeds and the relative costs of scatterhoarding versus larderhoarding in yellow pine chipmunks. Western North American Naturalist 65:248–257.

Vander Wall, S. B., and S. H. Jenkins. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology 14:656–667.

Vander Wall, S. B., K. M. Kuhn, and M. J. Beck. 2005*b*. Seed removal, seed predation, and secondary dispersal. Ecology 86:801–806.

Wang, B., and X. Yang. 2014. Teasing apart the effects of seed size and energy content on rodent scatter-hoarding behavior. PLoS ONE 9:1–8.

Wang, B., C. X. Ye, C. H. Cannon, and J. Chen. 2013. Dissecting the decision making process of scatterhoarding rodents. Oikos 122:1027–1034.

Wauters, L. A., J. Suhonen, and A. A. Dhondt. 1995. Fitness consequences of hoarding behaviour in the Eurasian red squirrel. Proceedings of the Royal Society B: Biological Sciences 262:277–281.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wilke, C. O. 2020. cowplot: Streamlined plot theme and plot annotations for 'ggplot2'. R package version 1.1.1. https://CRAN.R-project.org/package=cowplot.

Wilson, S. B. 2018. Ecology of scatterhoarding in a flooded ecosystem. Auburn University.

Wilson, S. B., T. D. Steury, R. A. Gitzen, and S. S. Ditchkoff. 2020. Fall and winter diets of eastern gray squirrels in a seasonally flooded ecosystem in Alabama. Southeastern Naturalist 19:771–780.

Xiao, Z., Z. Zhang, and Y. Wang. 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. Acta Oecologica 28:221–229.

Yang, Y., M. Zhang, and X. Yi. 2016. Small rodents trading off forest gaps for scatter-hoarding differs between seed species. Forest Ecology and Management 379:226–231.

Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression models for count data in R. Journal of Statistical Software 27(8). http://www.jstatsoft.org/v27/i08/.

Tables

Table 2.01. Common behaviors presented by the eastern gray squirrel (*Sciurus carolinensis*). Adapted from previous studies with descriptions of some behavior added for this study (new descriptions indicated by *). Scatterhoarding recovery behavior was broken up into three subcategories for the purposes of this study: recache, eaten, and unknown. Bolded terms indicate behaviors included in the observation survey of eastern gray squirrels for this study.

Behavior	Subcategories	Description		
Scatterhoarding	**Caching**[1]	locates a food item, puts in mouth, turns nut in mouth 1-2 times; carries nut in mouth to a spot where squirrel digs hole with forepaws; arches body over hole, thrusts body to push nut into ground; covers nut with dirt and packs with light tapping of forepaws; must result in burial or hiding of a food item		
	Recovery[1]	locates nut in ground using foraging behavior, pulls nut out of ground using mouth, may dig	**Recache***	squirrel moves to a new location and reburies/hide the food

	with forepaws to get nut out; tail held out straight or slightly arched	**Eaten***	may transport food to another location; must end by eating food
		Unknown*	carries food out of sight, cannot determine if eaten or reburied
Foraging[1]	walking forward with nose to ground, moving head side to side; generally straight tail, may stop to sniff a particular spot on ground; eating food that was not dug up first; can also occur in tree		
Resting*	still but not tense/alert, sitting or lying down, usually in a drey (stick nest) or on a tree branch; may have tail draped over head		
Grooming*	scratching body with hind or forefoot; using mouth to lick or bite at own body		
Vocalizing[2,3]	incisor teeth rapidly chattering, may not be sound; accompanied by rapid tail jerking movements; repeated squeaking; gnawing like noises		

Travel*		movement on the ground or in the trees seemingly not related to interaction with another squirrel or foraging; head up, not in leaf litter
Alert[3]		standing, attentive posture with both paws held against chest or vertical posture with one paw held against chest
Interaction	Nonaggressive interaction[3]	within 5 m of another squirrel and not interacting aggressively
	Allogrooming[4]	licking, mouthing, and grooming with forepaw of another squirrel's fur
	Greeting[4]	oral-nasal contact between two squirrels
	Playing[4]	amicable wresting and forelimb boxing between individuals
	Nest sharing[4]	two or more animals simultaneously inhabiting a single nest
	Running at[2,3]	squirrel runs toward another squirrel; on ground
	Jumping-at[2,3]	first squirrel approaches and orients towards second squirrel, crouches and leaps towards second squirrel with one or both paws forward
	Chasing[2,3]	one squirrel runs after another; can result in wrestling match

Aggressive contact[2,3,4]	behavior involving contact between two squirrels, varies from swatting with the forepaws to wrestling and biting

Sources: [1]Thompson & Thompson, 1980, [2]Allen & Aspey, 1986, [3]Thompson, 1978, [4]Koprowski, 1996, *This study

Table 2.02. Descriptions of response variables used in analyses of eastern gray squirrel (*Sciurus carolinensis*) observations collected September 2019 – July 2022 throughout the species' native range in the United States of America.

Response Variable	**Definition**	**Interpretation**
Time spent scatterhoarding	Total number of time points during the observation period that a squirrel was seen foraging for and burying seeds, digging up seeds, reburying seeds, or eating dug up seeds	Total time invested in scatterhoarding behavior relative to other behaviors
Time spent caching	Total number of time points during the observation period that a squirrel was seen foraging for and then burying seeds	Time invested on initial burial of seeds
Time spent recaching	Total number of time points during the observation period that a squirrel was seen digging up and reburying seeds	Time invested on cache maintenance behaviors
Time spent recovering and eating food	Total number of time points during the observation period that a squirrel was seen digging up and eating seeds	Time invested on benefitting from scatterhoarding behavior

Table 2.03. Akaike Information Criterion (AIC) values comparing different forms (continuous or categorical) of the United States Department of Agriculture Plant Zones to determine the effect of plant zone on the proportion of time eastern gray squirrels (*Sciurus carolinensis*) were observed scatterhoarding, caching, recaching, or recovering and eating food during behavioral observations across the species' native range in 2019 – 2022.

Model		**AIC**	**ΔAIC**
Scatterhoarding			
	Continuous plant zone	38728	0
	Categorical plant zone	39728	1000
Caching			
	Continuous plant zone	22622	0
	Categorical plant zone	23374	752
Recaching			
	Continuous plant zone	8689	0
	Categorical plant zone	9264	575
Recover and eating			
	Continuous plant zone	11851	0
	Categorical plant zone	12617	766

Table 2.04. Analysis of variance (ANOVA; two-way sum of squares) for main effects and interactions between the United States Department of Agriculture plant hardiness zones and pooled months of the year to determine effect on proportion of time eastern gray squirrels (*Sciurus carolinensis*) were observed engaging in hoarding behavior during 10-minute observation periods throughout their native range in the eastern United States, 2019 – 2022. Behaviors are reported as all scatterhoarding behaviors combined and only caching, recaching, or recovery behaviors. * indicates significance

Variable	P-value	
All Scatterhoarding		
Plant Zone	0.70	
Month	< 0.0001	*
Plant Zone:Month	0.008	*
Caching		
Plant Zone	0.01	*
Month	< 0.0001	*
Plant Zone:Month	0.001	*
Recaching		
Plant Zone	0.18	
Month	0.046	*
Plant Zone:Month	0.30	
Eating Recovered Food		
Plant Zone	0.15	
Month	< 0.0001	*
Plant Zone:Month	0.033	*

Table 2.05. Effect of United States Department of Agriculture plant hardiness zones on the likelihood of observing eastern gray squirrels (*Sciurus carolinensis*) scatterhoarding during 10-minute observation periods (logistic, odds ratio [OR]) and of the squirrels that did scatterhoard, the effect of plant zone on the proportion of time those squirrels were observed scatterhoarding during observation periods (Truncated-Poisson, rate ratio [RR]), with *decreasing* plant zones (i.e., lower-valued plant zones have colder, wetter winters). LCL = lower confidence limit, UCL = upper confidence limit. Squirrels were observed throughout the eastern United States, 2019 – 2022. Scatterhoarding behaviors included caching, recaching, and eating recovered food (recovery).

	Logistic Regression					Poisson Regression				
Months	OR	LCL	UCL	P-value		OR	LCL	UCL	P-value	
All Scatterhoarding Behaviors										
Jan/Feb	1.18	0.90	1.54	0.217		0.98	0.89	1.08	0.688	
Mar/Apr	1.20	0.96	1.51	0.107		1.12	1.02	1.24	0.021	*
Aug/Sept	4.78	3.88	5.89	< 0.0001	*	1.01	0.92	1.10	0.905	
Oct	1.95	1.63	2.34	< 0.0001	*	0.97	0.93	1.01	0.117	
Nov/Dec	2.41	1.87	3.11	< 0.0001	*	1.10	1.02	1.18	0.014	*
Caching										
Jan/Feb	0.92	0.71	1.19	0.521		0.91	0.79	1.06	0.224	
Mar/Apr	1.19	0.87	1.61	0.263		1.06	0.90	1.24	0.489	
Aug/Sept	3.83	3.08	4.78	< 0.0001	*	0.92	0.80	1.06	0.235	
Oct	1.52	1.28	1.80	< 0.0001	*	1.04	0.99	1.10	0.103	
Nov/Dec	1.62	1.27	2.06	< 0.0001	*	1.25	1.13	1.38	< 0.0001	*

Recaching										
Jan/Feb	1.40	1.02	1.94	0.036	*	1.32	0.83	2.08	0.227	
Mar/Apr	1.50	1.01	2.22	0.041	*	1.02	0.73	1.42	0.922	
Aug/Sept	2.14	1.62	2.81	< 0.0001	*	0.88	0.70	1.09	0.235	
Oct	1.03	0.87	1.21	0.748		1.11	1.00	1.23	0.051	*
Nov/Dec	1.24	0.95	1.62	0.108		1.00	0.78	1.27	0.969	
Recovery										
Jan/Feb	1.13	0.84	1.52	0.417		0.96	0.77	1.19	0.687	
Mar/Apr	1.35	1.02	1.79	0.030	*	1.21	1.02	1.45	0.030	*
Aug/Sept	2.35	1.82	3.03	< 0.0001	*	0.87	0.73	1.04	0.120	
Oct	1.05	0.89	1.24	0.536		0.92	0.82	1.03	0.129	
Nov/Dec	1.67	1.29	2.17	< 0.0001	*	0.82	0.65	1.03	0.087	

Figures

Figure 2.01. Locations of eastern gray squirrel (*Sciurus carolinensis*) observations (n = 4540) recorded by Auburn Squirrel Project volunteers from September 2019 – July 2022 with the 2012 United States Department of Agriculture [USDA] Plant Hardiness Zones shown to represent differences in winter conditions experienced by the squirrels. Plant zone polygon data was provided by the PRISM Climate Group at Oregon State University.

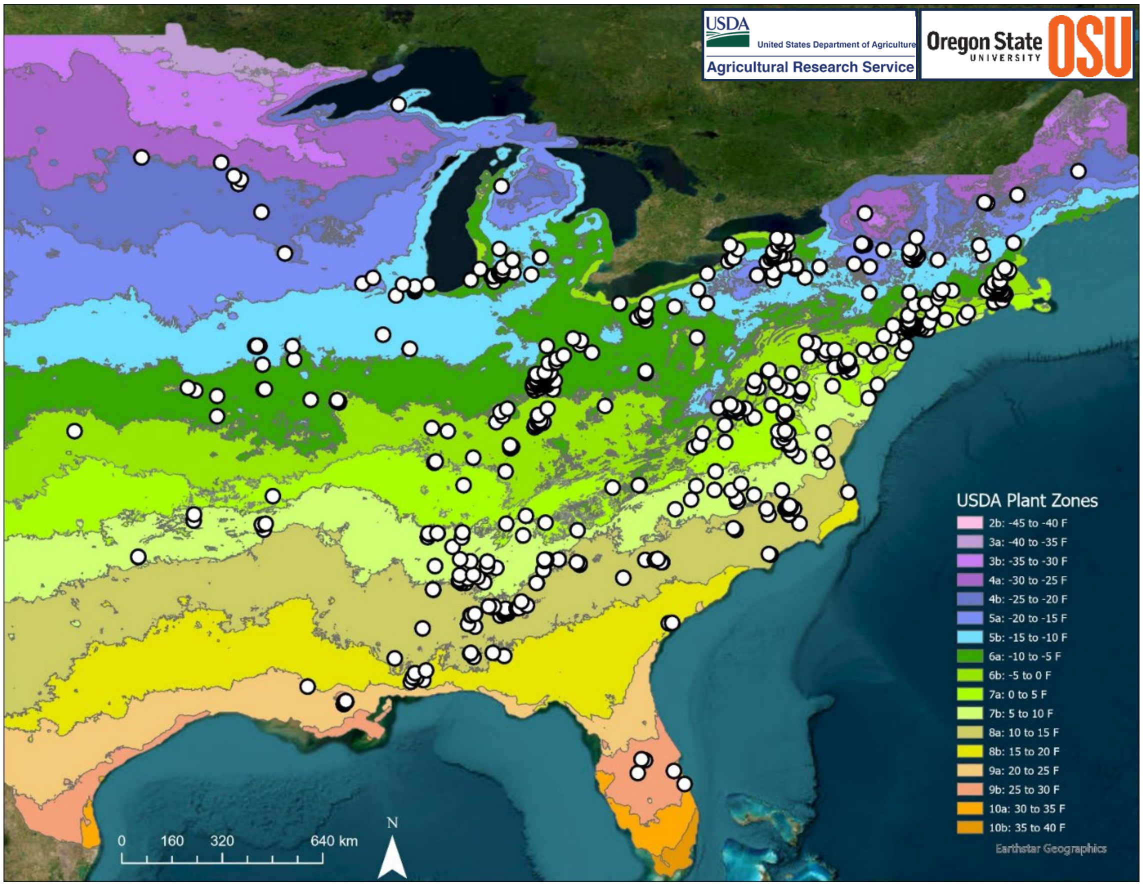


Figure 2.02. Proportion of time eastern gray squirrels (*Sciurus carolinensis*) exhibited different behaviors during 10-minute observation periods throughout the United States, September 2019 – July 2022. Bars within boxes indicate median and “X” represents mean proportion of time observed per observation period. Distribution of raw data points are shown in gray behind boxes.

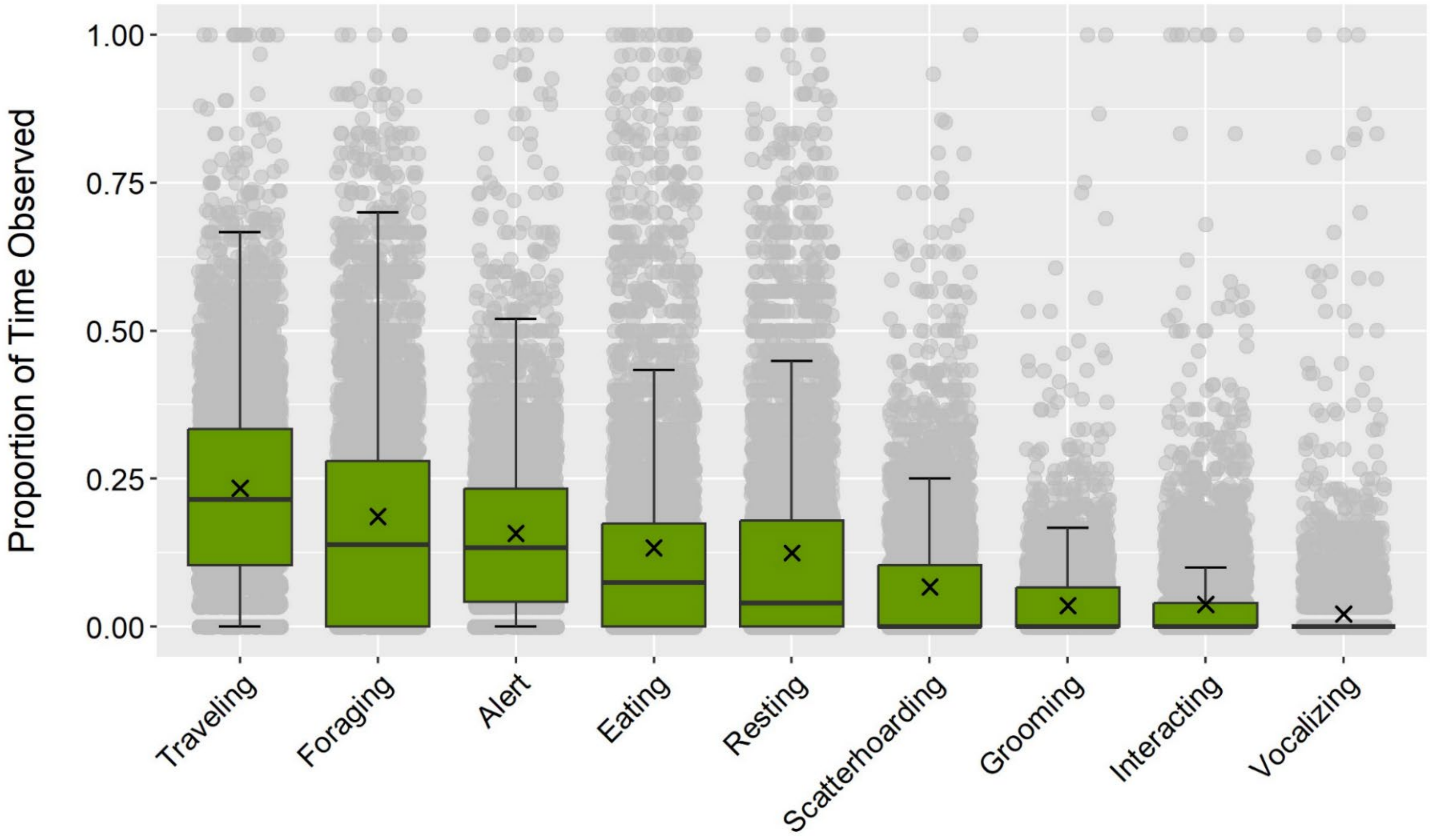
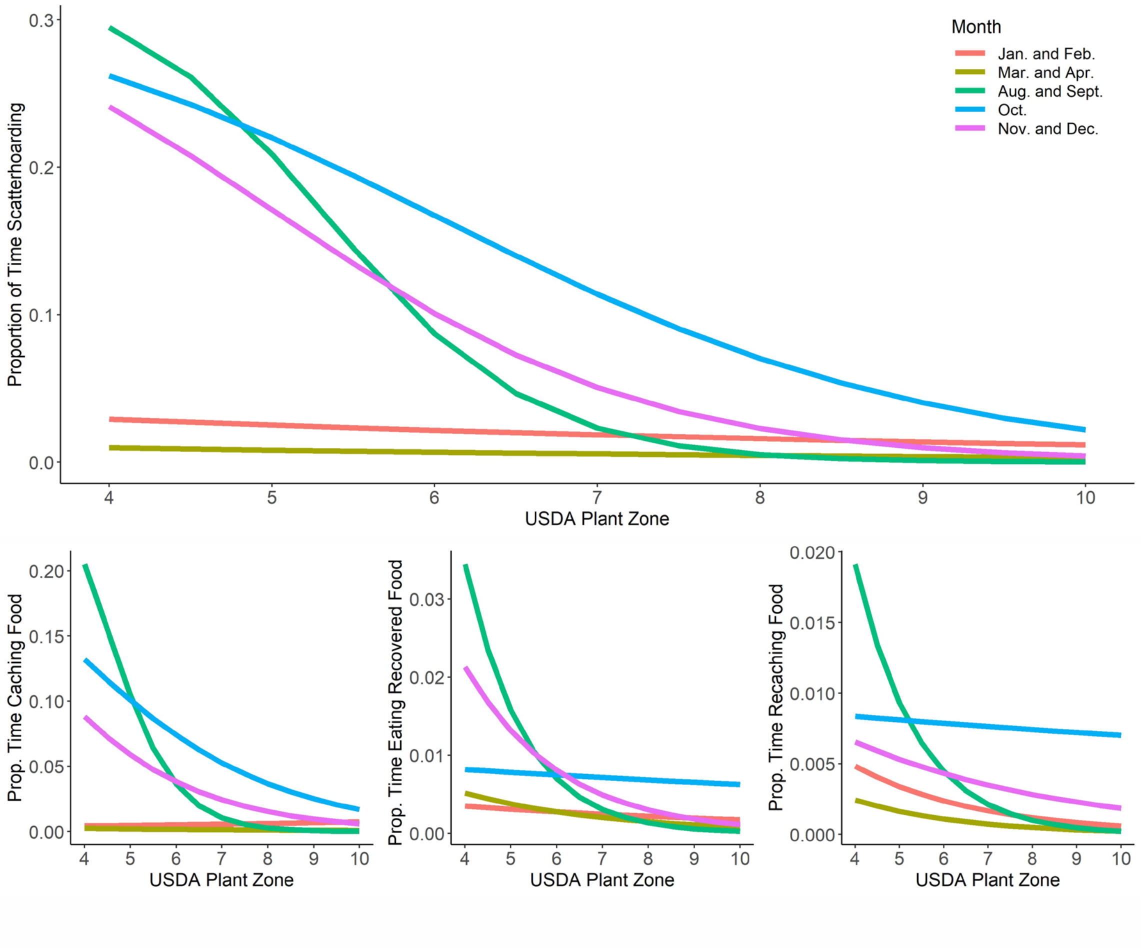


Figure 2.03. Model-estimated average proportion of time eastern grays squirrels (Sciurus *carolinensis*) were observed engaging in any scatterhoarding behavior (A), caching (B), eating recovered food (C), and recaching (D) during 10-minute observations throughout 12 different United States Department of Agriculture (USDA) Plant Hardiness Zones in the United States, estimated using a hurdle model. Observations were split into groups of months to pool sample sizes within zones and to compare behavior during different times of the year. Note: The y-axis of each graph has a different maximum value.



Chapter 3. Scatterhoarded seeds remain useful to hoarders over multiple hoarding seasons in central Alabama

To mitigate the danger from annual periods of food scarcity, scatterhoarders store hundreds of food items in many locations around their home range. To maximize the potential benefit, hoarders use several techniques putatively to prolong the longevity of their stored food, such as killing the embryo within the seed (i.e., embryo excision) and preferentially storing dormant seeds over nondormant seeds. Researchers have previously assumed that scatterhoarders rebuild their hoarded food supply every year and then only benefit from that hoard shortly thereafter, during the following period of food scarcity. We tested the idea that food types selected by hoarders have greater longevity than less-selected food types. We also tested the assumption that scatterhoarded food could only be used in the year after it was initially buried. Over an 18-month period, we monitored survival of 793 total cached seeds of 6 seed types (whole mockernut hickory, *Carya tomentosa*; whole American beech, *Fagus grandifolia*; excised and whole white oak, *Quercus alba*; excised and whole water oak, *Q. nigra*) in 15 plots in a small forest in Auburn, Alabama. Ultimately, we found that 5.2% (n = 41) of our buried seeds survived to the end of the first scatterhoarding season after burial and 56.1% (n = 23, all hickory or water oak seeds) of these surviving seeds were later pilfered, eaten, or stored by scatterhoarders. The estimated survival rate for all of our seeds through the end of the first scatterhoarding season (October 2020 – March 2021, 182 days) was 0.40. The cumulative mortality risk from rotting through the first scatterhoarding season (182 days) was 0.56 and 4% of all seeds germinated, though germination was not considered a final fate. We have provided evidence that a multi-year supply of scatterhoarded food is

possible, which could extend the time in which hoarders benefit from their hoarded food supply, potentially increasing the benefits of scatterhoarding behavior.

3.1 Introduction

Food hoarding is a behavior that creates a stored food supply that can be accessed when other food sources are scarce, such as during winter. Generally, food caches are classified into one of two types: larderhoards and scatterhoards. Species that larderhoard store concentrations of food at one or a few locations within their home range, and consequently are able to defend the hoarded food supply (e.g., red squirrels, *Tamiasciurus hudsonicus*; reviewed by Smith and Reichman 1984). In fact, larderhoards may be built up over time to be used in food-scarce years and even passed on to the owner's offspring (Price and Boutin 1993). Scatterhoarders, on the other hand, bury single or small numbers of food items in many locations around their home range and typically do not directly defend stored food from pilferage (theft) by other animals (Morris 1962, Brodbeck 1994). Scatterhoarding is of particular interest to evolutionary biologists due to the possible tradeoffs of allocating the time and energy necessary to hoard over a large area, versus the potential loss of food items to various causes.

Any given item that a scatterhoarder has buried can be lost for a variety of reasons, including germination (Shaw 1968, Forget 1997, Soné et al. 2002, Suselbeek et al. 2013), fungal infections or rot (Forget 1997, Suselbeek et al. 2013), insect predation (Ueda 2000), pilferage (reviewed by Vander Wall and Jenkins 2003), and simply being unable to relocate the buried item. Consequently, scatterhoarders have acquired ways to decrease the risk of many of these threats to their stored food. For example, to avoid germination of buried seeds, eastern gray squirrels (*Sciurus carolinensis*) selectively bury seeds with a dormancy period (such as water oak, *Quercus nigra*; Hadj-Chikh et al. 1996, Smallwood et al. 2001, Steele et al. 2006) or chew out the embryo before burial to kill seeds that are not dormant (such as white oak, *Quercus alba*; Fox 1982, Smallwood et al. 2001, Steele et al. 2001) and occasionally seeds with a dormancy period (Steele et al. 2006). Similarly, scatterhoarders often avoid burying seeds with evidence of fungal infections, rot, or insect predation (Steele et al. 1996). Additionally, many behaviors exist that combat pilferage, such as burying seeds in areas with greater predation risk (Leaver 2004, Steele et al. 2014), increasing hoarding activity after experiencing pilferage (Huang et al. 2011), and avoiding caching in areas where pilferage was previously experienced (black-capped chickadee, *Poecile atricapillus*; Hampton and Sherry 1994). Remembering landmarks near stored food is a recognized mechanism for relocating scatterhoarded food (black-capped chickadee, Herz et al. 1994; Xiao and Zhang 2006; Eurasian magpie, *Pica pica*, Feenders and Smulders 2011; Siberian chipmunk, *Tamias sibiricus*, Zhang et al. 2016), though food loss due to limited memory is poorly studied. Scatterhoarders are also thought to monitor their stored food after burial to refresh their memory of cache locations, as well as check on the condition of the seeds (Central American agouti, *Dasyprocta punctata*, Hirsch et al. 2013) and then eat, or modify and rebury, seeds that have begun to spoil (eastern gray squirrel, Steele et al. 2001; red acouchy, *Myoprocta excilis*, Jansen et al. 2006; Pallas's squirrel, *Callosciurus erythraeus*, Xiao et al. 2009a). Each of these behavioral adaptations may help mitigate the threats to the survival of stored food and thus increase the duration of time that stored items may be available to the hoarder.

Given that the main benefit of food hoarding is thought to be increased winter survival (Vander Wall 1990, Kuhn and Vander Wall 2008), researchers typically assume that an individual's scatterhoarded food supply is not maintained through the spring and summer and instead is completely rebuilt each fall. Due to this assumption, previous studies have focused primarily on how long scatterhoarding species rely on their stored food supply within a given scatterhoarding season, typically consisting of a food storing period in fall followed by a food recovery and usage period in winter and early spring. Few studies have examined the total length of time scatterhoarded food remains available for use (reviewed in Smith and Reichman 1984), primarily due to the difficulties of monitoring the hundreds of food items buried and maintained by a single hoarder in the wild. To overcome this limitation, researchers often imitate scatterhoarding behavior by burying and monitoring seeds, which can then be used to examine the fate of hoarded food after burial (reviewed by Vander Wall and Jenkins 2003). For example, using a combination of artificially scatterhoarded (buried 5 cm) and larderhoarded seeds (buried 10-15 cm), Soné et al. (2002) estimated that only a combined 0.8% of larderhoarded and scatterhoarded Japanese stone oak (*Pasania edulis)* seeds survived one year without loss to germination, rot, pilferage by mice (*Apodemus speciosus* and *A. argenteus*), or predation by insects. However, the authors' estimate is potentially inaccurate for scatterhoarded food as large amounts of larderhoarded food can potentially be lost all at once; scatterhoarding can reduce this risk by spreading out food caches. Another study found less than 30% of acorns buried 2 cm deep and protected from seed predators survived through the scatterhoarding season without germinating (Haas and Heske 2005). However, the potential for scatterhoarded food to be used for more than a single season has not been tested, and such information is important for understanding the costs, benefits, and thus evolution of scatterhoarding behavior.

In this study, we tested the expectation that scatterhoarded food may be available for more than a year after it is buried. If supported, the finding would suggest that the benefits of scatterhoarding food may persist into subsequent years and potentially even passed on to offspring. We also examined whether various maintenance behaviors that scatterhoarders perform while hoarding food, including embryo excision of acorns and selectively burying viable, dormant seeds, may increase the longevity of hoarded seeds. Due to the difficulties of monitoring a wild scatterhoarder's entire supply of stored food over a long period of time, we used artificial caches to estimate the proportion of stored seeds that may remain viable until and through the following food-scarce season (winter). We mimicked cache management strategies used by scatterhoarders by burying viable seeds and artificially excising the embryos of a portion of the acorns. Because pilferage can be the principal source of seed loss to individual scatterhoarders (Vander Wall and Jenkins 2003), but pilfered seeds aren't always removed from the food supply (i.e., if the pilferer buries the seed rather than eat it), we attempted to lower the risk of pilferage. If scatterhoarders are able to benefit from scatterhoarded food beyond the immediate winter, this information could greatly enhance our understanding about the costs and benefits of scatterhoarding behavior.

3.2 Methods

Study area

We conducted this study in a 4.5 ha forest on the outskirts of Auburn University's main campus in southeast Alabama (32.594°W, -85.489°N; ~220m a.s.l.). The study area consisted of 2.5 ha with a closed canopy of oak (*Quercus* spp.), hickory (mockernut hickory, *Carya tomentosa*; pignut hickory, *C. glabra*), American beech (*Fagus grandifolia*), and pine (longleaf pine, *Pinus palustris*; loblolly pine, *P. taeda*) with a moderate to dense understory of greenbriar (*Smilax* spp.), American beech saplings and hickory saplings. There was also 1 ha of forest with more dispersed mature oak, pine, and hickory, providing a moderately closed canopy, and 1 ha with mature oak, hickory, and pine trees with open canopy between trees. These 2 ha had little to no understory cover due to university maintenance of the area (i.e., mowing and control of weeds). Common scatterhoarders present in the area were eastern gray squirrels, while eastern chipmunks (*Tamias striatus*) employed both larderhoarding and scatterhoarding to store food. Mean temperatures were 7.6 degrees Celsius in January and 26.7 degrees Celsius in July; mean annual precipitation was 129.8 cm (NCEI 2019).

Seed collection and preparation

As the masting season began in September 2020, we collected seeds available at the study site that were likely to be scatterhoarded, including acorns from water oak and white oak (with caps removed), mockernut hickory nuts (with outer husks removed), and American beech nuts. Seeds were stored in a refrigerator at 3 degrees C until placed in the field (see below). To ensure that all seeds used in this study were viable, we placed collected seeds in a bucket of water and those that floated were discarded due to indications of decay (Allen et al. 2001). Seeds with holes in the seed coat were discarded due to the indication of insect presence, commonly weevils (Coleoptera: Curculionidae, Hou et al. 2010). Seeds observed to have holes in the seed coat at any point during this study were removed from our dataset because squirrels tend to avoid burying weevil-infested seeds (Steele et al. 1996). To account for the possibility of a small percentage of seeds surviving until the second scatterhoarding season, we used a total of 842 viable seeds in this study (165 mockernut hickory seeds, 110 American beech seeds, 255 white oak acorns, and 312 water oak acorns; Table 1). Using 842 seeds would allow us to observe at least one surviving seed even if only 1% of each seed species persisted after being scatterhoarded. We drilled into the radicle end of 176 water oak acorns and 120 white oak acorns to mimic embryo excision by a scatterhoarder (Xiao et al. 2009). We were unable to find evidence of embryo excision used on beech or hickory seeds in the literature and only buried whole seeds of those species.

Seed Deployment

We could not deploy all 842 seeds at one time due to the logistics of placing and monitoring such a large number of seeds. Therefore, we used a fully-factorial, randomized block design that also included start date as a factor. Beginning October 2020, we attempted to bury 2 of each of the six seed types in each of 15 plots every 4 weeks until February 2021 (180 seeds deployed during each of 5 deployment periods). Originally, we had started with 900 seeds, but some seeds (n = 58) had rotted in storage before the last of the seeds were deployed in February 2021, so only 122 seeds were deployed in February 2021. To mimic scatterhoarding behaviors of eastern gray squirrels, we buried each seed approximately 1-2 cm below the soil surface, tamped down the soil on top of the seed, and re-covered the seed with any leaf litter that was present before burial (Steele et al. 2008). No seeds were buried after February 2021, as scatterhoarders in our study area had typically switched from caching to recovering food by this time (personal observation, SBR). Individual seeds were randomly assigned to one of 80 cells (8 X 10 cell grid) within one of the 15 (24cm x 30cm) plots. Each seed was buried at least 3 cm away from another seed. The 15 plots were placed at various locations throughout the study area to capture the different microhabitat characteristics that might influence the longevity of scatterhoarded food (i.e., canopy cover, Steele et al. 2014; soil moisture, Vander Wall 1995; Figure 1). Due to the uncertainty of seed fate after pilferage (seeds could be ignored, eaten, or recached elsewhere; we were unable to relocate untagged seeds), access to artificial caches by food hoarders was restricted by covering each plot with plastic garden netting (Barnett 1977). However, some seeds were pilfered despite our efforts, as indicated by holes chewed in the mesh over locations of missing seeds.

Seed Monitoring

To estimate how seed type impacts the longevity of scatterhoarded seeds, at least 15 seeds from each seed type were selected to be monitored each month from the point of burial until the end of the scatterhoarding season (March 2021). Every ~4 weeks after burial, we dug up the seeds selected to be evaluated that month. We then determined whether or not the seeds were available for consumption by hoarders and removed them from the plot if either weevil presence (holes in the seed coat, Hou et al. 2010) or rot (seed was squishy or wet inside) was observed. Weevil-infested seeds were removed from the study because scatterhoarders are known to avoid burying seeds with weevils in them (Steele et al. 1996) and though we attempted to avoid using seeds with weevils, some seeds with early weevil infestation passed our float test during seed prep and were initially buried in our plots. We recorded the presence of fungus on a few seeds (seen on the outside of the seed coat), but these remained in the study because we could not determine how much of the seed was impacted within the shell. We also recorded when seeds began to germinate and reburied them to monitor the progress of seedling growth throughout the scatterhoarding season and to record potential pilferage or other loss of germinated seeds.

After March 2021, all cached seeds remaining in the plots were rechecked for viability in December 2021, before the start of the following recovery season. We did not monitor seeds between the scatterhoarding season because scatterhoarders in our study area did not scatterhoard during the late spring and summer months when other foods were available (personal observation, SBR). To determine how many seeds were still available at the end of the 2021 – 2022 scatterhoarding season, we performed a final recheck on all seeds in March 2022. Seeds recovered from the plots at that time, and that appeared to be viable, were tin-tagged; a ~30 cm fishing leader wire with a numbered aluminum tag and flagging were attached to the seed (Li and Zhang, 2007). These tagged seeds were then deployed on a log within our study area to determine if the resident hoarders (eastern gray squirrels and eastern chipmunks) would store, eat, or ignore our longest-lasting seeds. Seeds were recorded as stored if they were moved from the site of deployment and found intact (or excised) under soil or leaf litter while seeds were recorded as eaten when they were found in pieces with some or all of the seed meat missing.

Analyses

After removing seeds with indication of weevil presence throughout our study (2 hickory nuts, 25 water oak acorns and 22 white oak acorns), we had a final dataset of 793 seeds to use in analyses. We did not include seeds with weevils in our analyses because scatterhoarders can detect weevil presence before physical cues appear (i.e., holes in the seed coat) and avoid burying these seeds (Steele et al. 1996), whereas predation by other insects (e.g., ants, termites) occurs after the seed is buried.

Seed Survival

We used the "survival" package in Program R version 4.1.1 (Therneau 2022, Therneau and Grambsch 2000, R Core Team 2021) to estimate Kaplan-Meier survival rates (at 182 days) to the end of the first scatterhoarding season (March 31, 2021) and the total survival rate to the end of the second scatterhoarding season (March 31, 2022), for each seed type. We used the staggered-entry method because all seeds did not enter the dataset on the same day. We assumed all seeds survived at least one day following initial burial and defined a seed's time of becoming unavailable as the last date the seed was known to be available to hoarders or one day after burial if the seed was determined missing or unavailable at its first recheck. Scatterhoarders typically overlap home ranges so pilfered seeds could be recached nearby and still be available to hoarders, so we right-censored seeds that were pilfered, had unknown fates (due to construction in the study area in March 2021), or survived to the end of one of the study periods (first or second scatterhoarding season). For an analysis of seed pilferage rates, see Chapter 4: Pilferage.

We used mixed-effects Cox Proportional Hazards regression (hereafter, Cox PH) in the "coxme" package in Program R to compare between seed types the length of time that past until items were removed from the stored food supply between seed types (Therneau 2022). We ran two analyses; one in which seeds that survived to March 2021 were right-censored, and another in which only seeds that survived to March 2022 were right-censored. We included a random effect of plot in our models because our 15 plots varied in unquantified habitat characteristics (soil moisture, soil type, canopy cover, etc.) that could have had impacts on seed survival time. Again, seeds were also right-censored in these analyses if they were pilfered or if their fates were unknown.

Seed Usefulness

Seeds were considered useful to hoarders after the first scatterhoarding season if they were pilfered after March 31, 2021, or survived to the end of the study and were then used by scatterhoarders after being tagged and released. We assumed that seeds pilfered after March 31, 2021, were useful under the assumption that if they were not useful, an animal would not have removed them. We ran a mixed-effects logistic regression model using the package “lme4” in Program R to determine the effect of seed type on the likelihood of seeds being deemed useful after that first scatterhoarding season, conditional upon the fact that they had survived to that point (Bates et al. 2015). We excluded seeds from this analysis if they had unknown fates (due to construction in the study area) because we were unable to determine if they were ultimately useful to scatterhoarders or not. We also included a random effect of plot number in this analysis, for the same reasons as previously described in our methods above.

Causes of Cache Loss

We ran separate, cause-specific mortality analyses to determine the effects of seed type on the likelihood of a cached seed becoming unavailable to scatterhoarders due to the different causes of loss. For example, we used mixed-effects Cox PH with the response being whether the seeds succumbed to environmental causes of loss (rot, fungus, or insect infestation; all other losses were right-censored) to compare loss rates from environmental causes between seed types. Alternatively, we also used mixed-effects logistic regression to test for the effect of seed type on the likelihood of seeds germinating. We used logistic regression for germination because germination was often not the final fate of our buried seeds; germinated seeds were occasionally pilfered or found rotten at a later date. However, in this analysis, we included any seed that germinated, even if that seed later was pilfered, rotted, or had an unknown final fate. We reported and discussed cumulative mortality risk due to pilferage for all seeds and seed types elsewhere (See Chapter 4: Pilferage). As we had done previously, we included a random effect of plot in each of these models. We calculated cumulative mortality rates as one minus the cumulative survival rates from the cause-specific loss for all seeds and for each seed type (Jager et al. 2008). Due to the low number of seeds that were available after the first scatterhoarding season, we only analyzed causes-specific losses to the end of the first scatterhoarding season.

3.3 Results

Seed Survival

Forty-one of our 793 buried seeds were still present in the plots after March 31, 2021 (5.2% of all seeds; 2 beech, 25 hickory, 3 excised water oak, 10 whole water oak, and 1 white oak). Twenty-nine of the 793 (3.7%) buried seeds survived until the end of the study (March 15, 2022; Table 2). The one remaining white oak seed germinated and then was pilfered before the end of the study and only one of the nine surviving water oak acorns was an excised seed.

The Kaplan-Meyer estimated survival rate of seeds to the end of the first scatterhoarding season (March 31, 2021, 182 days) was 0.40 (0.34 – 0.48, 95% confidence limits [C.L.], Figure 2). Estimated survival rates to the end of the first scatterhoarding season for excised white oak (0.07, 0.02 – 0.21, 95% C.L.) and whole white oak (0.23, 0.12 – 0.47, 95% C.L.) were the lowest of all seed types, while those for hickory (0.71, 0.59 – 0.85, 95% C.L.) and whole water oak (0.70, 0.49 – 0.98, 95% C.L.) were the highest (Table 3, Figure 2). Whole water oak acorns were less likely to become lost than excised white oak ($P = 0.001$), whole white oak ($P < 0.001$), and excised water oak seeds ($P < 0.001$) but were more likely to be lost than beech ($P = 0.04$; Table 4). Within each oak species, excised seeds were more likely to become lost than whole seeds (white oak OR = 1.75, water oak OR = 3.81, both $P < 0.02$; Table 4).

Total estimated survival of all seeds to the end of the second scatterhoarding season (518 days) was 0.39 (0.33 – 0.47, 95% C.L.; Table 3). We found similar results for differences in survival to the end of the second scatterhoarding season between seed types as those for differences in survival to the end of the first scatterhoarding season (Table 4).

Seed Usefulness

Of the 41 seeds that were still present in the plots after March 2021, 6 were pilfered between March 2021 and March 2022; 1 whole white oak, 1 excised water oak, 2 whole water oak, and 2 hickory seeds. Furthermore, we determined that 13 of the 793 buried seeds (1.6% of all seeds) were still useful to scatterhoarders in the area at the end of March 2022 as 5 of those seeds were hoarded and 8 were eaten when presented with tin-tags to scatterhoarders (Table 5). Animals removed the tin-tags from 4 additional seeds (3 hickory and 1 water oak), and we were unable to relocate those seeds to determine the final fate, but we assumed the seeds were useful because they were transported away from the release spot. Four hickory seeds were chewed on by rodents, but the animals were unable to open the thick shell and eat the seed inside, so these seeds may still have been viable, but we concluded they were not useful to the rodents. The two beech seeds that survived were ignored by rodents when tin-tagged and released. Thus, we determined that 23 seeds (2.9 % of the original 793 buried) were available and useful to scatterhoarders after the end of the first scatterhoarding season (March 2021). Seeds that were useful in March 2022 had survived for 426 ± 106 days (mean ± standard deviation).

Given the limited number of beech, white oak, and excised water oak that were deemed to be useful after March 2021 (0 beech, 1 white oak, 1 excised water oak), we only compared usefulness of hickory and all water oak. In this analysis, we found that, of seeds that had survived the first scatterhoarding season, water oak seeds were 18.00 (1.92 – 168.41; 95% C.L) times as likely to be useful as hickory seeds ($P < 0.01$).

Causes of cache loss

Through March 2021, seeds were lost to recovery for a variety of reasons (Table 2). Though we attempted to prevent pilferage from our plots by covering them with garden mesh, animals chewed through the mesh and pilfered 67% of our buried seeds through March 2022 (Table 2; See Chapter 4: Pilferage). We re-emphasize, however, that pilfered seeds were right-censored in our analysis of survival rates above. For more detailed results and analysis regarding pilferage rates of our cached seeds, see Chapter 4: Pilferage.

Environmental causes (insect infestation not including weevils, rot, evidence of fungus) were the culprit of 16.1% of all seeds being removed from the experimental food supply through March 2022. Specifically, five seeds succumbed to insect predation, 7 had extreme fungal infections, and 116 seeds rotted; thus, hereafter all environmental causes of cache mortality will simply be referred to as “rot”. Our cached seeds had a Kaplan-Meyer estimated mortality rate due to rot of 0.56 (0.48 – 0.62, 95% C.L.) to the end of the first scatterhoarding season (i.e., at 182 days; Table 6; Figure 3). Hickory seeds were significantly less likely to rot (0.18 mortality rate, 0.06 – 0.29, 95% C.L) than all other species (all $P < 0.001$, Table 7), except whole water oak (0.29 mortality rate, 0 – 0.50, 95% C.L., $P = 0.40$). Excised seeds were more likely to rot than their whole counterparts of the same species (white oak $P = 0.03$, water oak $P = 0.001$; Table 7). There was no significant difference in the likelihood of rotting between whole white oak and beech seeds ($P = 0.14$), however, both excised and white oak acorns were more likely to rot than all other seed types (all $P < 0.01$).

Through March 2022, 4.0% of all seeds germinated, produced a large seedling, and were considered no longer available to scatterhoarders (Table 2). However, eighty-six seeds (10.8%; 28 hickory, 6 excised water oak, 2 whole water oak, and 12 excised white oak, and 38 whole white oak) germinated at some point, but germination was not recorded as the final fate of these seeds as the seedling did not persist to the end of the study. For example, twenty-five seeds were observed to have germinated and were later pilfered. Whole white oak acorns were the only seeds more likely to germinate than hickory seeds (OR = 3.03, 1.61 – 5.70, 95% C.L., $P < 0.001$), although there was no significant difference in likelihood of germination between excised white oak acorns and hickory (OR = 0.64, 0.72 – 3.39, 95% C.L., $P = 0.25$, Table 8). Notably, embryo excision did not significantly affect the likelihood of water oak acorns germinating ($P = 0.32$), while excised white oak acorns were 0.21 (0.10 – 0.46, 95% C.L.) times as likely to germinate as whole white oak acorns ($P < 0.001$). However, both excised and whole water oak acorns were less likely to germinate than excised white oak acorns (excised water oak OR = 0.22, 0.07 – 0.63, 95% C.L; and whole water oak OR = 0.09, 0.02 – 0.46, 95% C.L.; Table 8).

3.4 Discussion

We found support for our expectation that multi-year use of scatterhoarded food is possible, as at least 2.1 – 2.9% of our buried seeds were still useful to hoarders at the end of the second scatterhoarding season after initial burial. Of the 4 species and 6 seed types we studied, whole water oak acorns appear to be the best for long-term storage; a result that is similar to prior studies, which showed that hoarders prefer to store acorns with a dormancy period (Smallwood et al. 2001, Steele et al. 2006). Only one white oak acorn survived past the first scatterhoarding season and was pilfered after germinating, so seeds without a dormancy period may typically only be suitable for short-term storage due to the higher risk of germination (reviewed by Lichti et al. 2017) or rot. As expected, embryo excision of acorns decreased the risk of germination in white oak seeds, however embryo excision also increased the risk of rot or fungus establishment in the seed. Contrary to our findings, previous studies have found that excised seeds are not more likely to rot than whole seeds (Smallwood et al. 2001). Our results suggest that squirrels face a trade-off between reducing germination risk and increasing the risk of the seed succumbing to other causes of cache mortality. Thus, embryo excision may only be used on low value seeds or those that that will not be left buried for very long.

The total length of time scatterhoarded food is available and usable by hoarders has not been studied in depth before, to our knowledge. Indeed, only a few studies tracked a large supply of artificially stored food with the purpose of determining condition and longevity of that stored food (e.g., Brewer and Webb 2001, Soné et al.

2002, Delgado and Jacobs 2019). However, previous studies did not assess the useability of the seeds or focused on survival of seeds to germination, though we found that seeds in early stages of germination were still eaten by hoarders (also see Chapter 5: Cues of Belowground Food). For example, Soné et al. (2002) tracked seeds and reported 10% (48 of 477) of buried Makino (*Pasania edulis*) seeds survived to germination, though no seedlings survived past 2 years. Brewer and Webb (2001) reported palm seeds (*Astrocaryum mexicanum*) lasted up to 9 months before being consumed by spiny pocket mice (*Heteromys desmarestianus*), suggesting long-term storage of seeds from one hoarding season to the next was possible, though they did not state how many seeds survived 9 months. Additionally, Delgado and Jacobs (2019) reported 30 of 292 hazelnuts (*Corylus* sp.) buried by fox squirrels (*Sciurus nigra*) were still cached after 482 days, but they did not check the condition of these seeds and assumed the squirrels had forgotten about them. If these seeds were indeed still in usable condition for hoarders, that would indicate about 10% of hoarded hazelnuts could survive to be used the following scatterhoarding season. Our results show that seeds can survive a long time underground, and some of those seeds will still be considered useful to hoarders.

We have little information about maintenance behaviors and preferences of hoarders towards beech and hickory seeds, other than studies showing these seed species are handled by hoarding species (beech: blue jays, *Cyanocitta cristata*, Johnson and Adkisson 1985; Eurasian red squirrels, *Sciurus vulgaris*, Wauters and Casale 1996; hickory: western fox squirrel, *Sciurus niger rufiventer*, Cahalane 1942; southern flying squirrel, *Glaucomys volans*, Thomas and Weigl 1998). Hickory nuts are considered a preferred food source for scatterhoarding squirrels (Ivan and Swihart 2000), though researchers have noted the increased time to open the hard shells (Cilles et al. 2016). By burying a hickory nut, hoarders store a high energy food but transfer the seed's high handling costs to the future (Jacobs 1992, Cilles et al. 2016), which could explain why hickory nuts were the most likely seeds to survive to the end of our study. Ultimately, we found whole water oak acorns and hickory nuts were suitable for long term storage past the scatterhoarding season when they were buried, though whole water oak acorns were more likely to be usable by hoarders at the end of the second scatterhoarding season after burial.

Previously, researchers have relied on the assumption that scatterhoarders built up a new supply of stored food each year. However, we have shown that it is possible for hoarders to use a small amount of the scatterhoarded food that was buried the previous year, which provides a longer period of time to benefit from scatterhoarding behavior. For hoarding behavior to remain in a population, hoarders should experience greater net fitness benefit from hoarding compared to cheaters (animals that do not hoard but eat hoarded food) or non-hoarders (animals that do not hoard or eat hoarded food; Andersson and Krebs 1978, Smulders 1998). Other research suggests that eastern gray squirrels spend a much larger proportion of their time scatterhoarding during fall than they spend eating recovered food during winter (See Chapter 2: Geographic Variation). Investing more time and energy in hoarding than is needed for the current year could convey an additional benefit if some of the stored food was available to be recovered and eaten in later years. The potential for extra long-term storage of food also has important implications for populations during years of mast failures (Nixon et al. 1975) when hoarders do not appear to be able to bury enough food to last the winter. Having stored food available from previous years would be especially important to lessen the effects of nutritional stress during those times of scarcity. The fact that scatterhoarders may benefit from their behavior for many years after the fact may help explain why the trait evolved in the first place and persists in populations around the globe.

3.5 Acknowledgments

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3.6 Literature Cited

Allen, J. A., B. D. Keeland, J. A. Stanturf, A. F. Clewell, and H. E. Jr. Kennedy. 2001. A guide to bottomland and hardwood restoration.

Andersson, M., and J. Krebs. 1978. On the evolution of hoarding behaviour. Animal Behaviour 26:707–711.

Barnett, R. J. 1977. The effect of burial by squirrels on germination and survival of oak and hickory Nuts. The American Midland Naturalist 98:319–330.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Brewer, S. W., and M. A. H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. Oikos 93:32–41.

Brodbeck, D. R. 1994. Memory for spatial and local cues: A comparison of a storing and a nonstoring species. Animal Learning & Behavior 22:119–133.

Cahalane, V. H. 1942. Caching and recovery of food by the western fox squirrel. Journal of Wildlife Management 6:338–352.

Cilles, S. E., G. Coy, C. R. Stieha, J. J. Cox, P. H. Crowley, and D. S. Maehr. 2016. A comparison of seed predation, seed dispersal, and seedling herbivory in oak and hickory: Species with contrasting regenerating abilities in a bluegrass savanna—woodland habitat. Northeastern Naturalist 23:466–481.

Delgado, M. M., and L. F. Jacobs. 2019. How squirrels protect their caches: Location, conspicuousness during caching, and proximity to kin influence cache lifespan. bioRxiv 738237.

Dixon, M. D., W. C. Johnson, and C. S. Adkisson. 1997. Effects of caching on acorn tannin levels and blue jay dietary performance. The Condor 99:756–764.

Feenders, G., and T. V. Smulders. 2011. Magpies can use local cues to retrieve their food caches. Animal Cognition 14:235–243.

Forget, P. M. 1997. Effect of microhabitat on seed fate and seedling performance in two rodent- dispersed tree species in rain forest in French Guiana. Journal of Ecology 85:693–703.

Fox, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. Evolution 36:800–809.

Haas, J. P., and E. J. Heske. 2005. Experimental study of the effects of mammalian acorn predators on red oak acorn survival and germination. Journal of Mammalogy 86:1015–1021.

Hadj-Chikh, L. Z., M. A. Steele, and P. D. Smallwood. 1996. Caching decisions by grey squirrels: A test of the handling time and perishability hypotheses. Animal Behaviour 52:941–948.

Hampton, R. R., and D. F. Sherry. 1994. The effects of cache loss on choice of cache sites in black-capped chickadees. Behavioral Ecology 5:44–50.

Herz, R. S., L. Zanette, and D. F. Sherry. 1994. Spatial cues for cache retrieval by black-capped chickadees. Animal Behaviour 48:343–351.

Hirsch, B. T., R. W. Kays, and P. A. Jansen. 2013. Evidence for cache surveillance by a scatterhoarding rodent. Animal Behaviour 85:1511–1516.

Hou, X., X. Yi, Y. Yang, and W. Liu. 2010. Acorn germination and seedling survival of *Q. variabilis*: Effects of cotyledon excision. Annals of Forest Science 67:1–7.

Huang, Z., Y. Wang, H. Zhang, F. Wu, and Z. Zhang. 2011. Behavioral responses of sympatric rodents to complete pilferage. Animal Behaviour 81:831–836.

Ivan, J. S., and R. K. Swihart. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. Journal of Mammalogy 81:549–562.

Jacobs, L. F. 1992. The effect of handling time on the decision to cache by grey squirrels. Animal Behavior 43:522–524.

Jager, K. J., P. C. Van Dijk, C. Zoccali, and F. W. Dekker. 2008. The analysis of survival data: The Kaplan-Meier method. Kidney International 74:560–565.

Jansen, P. A., F. Bongers, and H. H. T. Prins. 2006. Tropical rodents change rapidly germinating seeds into long term food supplies. Oikos 113:449–458.

Kuhn, K. M., and S. B. Vander Wall. 2008. Linking summer foraging to winter survival in yellow pine chipmunks (*Tamias amoenus*). Oecologia 157:349–360.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. Behavioral Ecology 15:729–734.

Li, H., and Z. Zhang. 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). Forest Ecology and Management 242:511–517.

Lichti, N. I., M. A. Steele, and R. K. Swihart. 2017. Seed fate and decision-making processes in scatter-hoarding rodents. Biological Reviews 92:474–504.

Morris, D. 1962. The behavior of the green acouchi (*Myoproctapratti*) with special reference to scatterhoarding. Proceedings of the Zoological Society of London 139:701–732.

National Centers for Environmental Information [NCEI]. 2019. Global summary of the month for Auburn, Alabama. https://www.ncei.noaa.gov/.

Nixon, C. M., M. W. McClain, and R. W. Donohoe. 1975. Effects of hunting and mast crops on a squirrel population. The Journal of Wildlife Management 39:1–25.

Price, K., and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. Behavioral Ecology 4:144–150.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Shaw, M. W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales: II. Acorn losses and germination under field conditions. Journal of Ecology 56:647–660.

Smallwood, P. D., M. A. Steele, and S. H. Faeth. 2001. The ultimate basis of caching preferences of rodents, and the oak-dispersal syndrome: Tannins, insects, and seed germination. American Zoologist 41:840–851.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329–351.

Smulders, T. V. 1998. A game theoretical model of the evolution of food hoarding: Applications to the *Paridae*. The American naturalist 151:356–66.

Soné, K., S. Hiroi, D. Nagahama, C. Ohkubo, E. Nakano, S. I. Murao, and K. Hata. 2002. Hoarding of acorns by granivorous mice and its role in the population processes of *Pasania edulis* (Makino) Makino. Ecological Research 17:553–564.

Steele, M. A., T. A. Contreras, L. Z. Hadj-Chikh, S. J. Agosta, P. D. Smallwood, and C. N. Tomlinson. 2014. Do scatterhoarders trade off increased predation risks for lower rates of cache pilferage? Behavioral Ecology 25:206–215.

Steele, M. A., L. Z. Hadj-Chikh, and J. Hazeltine. 1996. Caching and feeding decisions By *Sciurus carolinensis*: Responses to weevil-infested acorns. Journal of Mammalogy 77:305–314.

Steele, M. A., S. L. Halkin, P. D. Smallwood, T. J. McKenna, K. Mitsopoulos, and M. Beam. 2008. Cache protection strategies of a scatterhoarding rodent: Do tree squirrels engage in behavioral deception? Animal Behaviour 75:705–714.

Steele, M. A., T. Knowles, K. Bridle, and E. L. Simms. 1993. Tannins and partial consumption of acorns: Implications for dispersal of oaks by seed predators. The American Midland Naturalist 130:229–238.

Steele, M. A., S. Manierre, T. Genna, T. A. Contreras, P. D. Smallwood, and M. E. Pereira. 2006. The innate basis of food hoarding decisions in gray squirrels: Evidence for behavioral adaptations to the oaks. Animal Behaviour 71:155–160.

Steele, M. A., G. Turner, P. D. Smallwood, J. O. Wolff, and J. Radillo. 2001. Cache management by small mammals: Experimental evidence for the significance of acorn-embryo excision. Journal of Mammalogy 82:35–4235.

Suselbeek, L., P. A. Jansen, H. H. T. Prins, and M. A. Steele. 2013. Tracking rodent-dispersed large seeds with Passive Integrated Transponder (PIT) tags. 513–519.

Therneau, T. 2022a. A package for survival analysis in R. R package version 3.4-0. https://CRAN.R-project.org/package=survival.

Therneau, T. M.2022b. coxme: Mixed Effects Cox Models. R package version 2.2-18.1. https://CRAN.R-project.org/package=coxme.

Terry M. Therneau, Patricia M. Grambsch. 2000. Modeling Survival Data: Extending the Cox Model. Springer, New York. ISBN 0-387-98784-3.

Thomas, R. B., and P. D. Weigl. 1998. Dynamic foraging behavior in the southern flying squirrel (*Glaucomys volans*): Test of a Model. The American Midland Naturalist 140:264–270.

Ueda, A. 2000. Pre- and Post-dispersal damage to the acorns of two oak species (*Quercus serrata* Thunb. and *Q. mongolica* Fischer) in a species-rich deciduous forest. 4.

Vander Wall, S. B. 1990. 2.3 Long-term food storage. Page 445 *in*. Food Hoarding in Animals. The University of Chicago Press, Chicago.

Vander Wall, S. B. 1995. Influence of substrate water on the ability of rodents to find buried seeds. Journal of Mammalogy 76:851–856.

Vander Wall, S. B., and S. H. Jenkins. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology 14:656–667.

Wauters, L. A., and P. Casale. 1996. Long-term scatterhoarding by Eurasian red squirrels (*Sciurus vulgaris*). Journal of Zoology 238:195–207.

Xiao, Z., X. Gao, M. Jiang, and Z. Zhang. 2009. Behavioral adaptation of Pallas's squirrels to germination schedule and tannins in acorns. Behavioral Ecology 20:1050–1055.

Xiao, Z., and Z. Zhang. 2006. Nut predation and dispersal of Harland Tanoak *Lithocarpus harlandii* by scatter-hoarding rodents. Acta Oecologica 29:205–213.

Zhang, D., J. Li, Z. Wang, and X. Yi. 2016. Visual landmark-directed scatter-hoarding of Siberian chipmunks *Tamias sibiricus*. 175–181.

Zhang, Y., Y. Shi, A. M. Sichilima, M. Zhu, J. Lu, J.-C. Ruel, and E. J. Jokela. 2016. Evidence on the adaptive recruitment of Chinese cork oak (*Quercus variabilis* Bl.): Influence on repeated germination and constraint germination by food-hoarding animals.

Tables

Table 3.01. Seeds (white oak, Quercus alba; water oak, Q. nigra; mockernut hickory, Carya *tomentosa*; American beech, *Fagus grandifolia*) buried October 2020 – February 2021 in Auburn, Alabama to determine survival of scatterhoarded seeds. All hickory seeds were husked (thick outer shell removed). Excised seeds were drilled into to mimic embryo excision by scatterhoarders while whole seeds were buried without manipulation. We buried 842 seeds but 49 were removed from the study due to weevil-infestation, leaving a final dataset of 793 seeds used for analyses. Seeds buried per month is reported as mean ± standard deviation.

Seed species	Total no. buried	Seeds buried per month	No. removed due to weevils
Excised white oak	120	20 ± 12	10
Excised water oak	176	29 ± 16	7
Whole white oak	135	23 ± 12	12
Whole water oak	136	23 ± 9	18
Hickory	165	28 ± 16	2
American Beech	110	18 ± 22	0
Total Seeds	842	140 ± 75	49

Table 3.02. Fates of four species of seeds (mockernut hickory, Carya tomentosa; American beech, Fagus grandifolia; white oak, Quercus *alba*; water oak, *Q. nigra*) recorded October 2020 through March 2022. Seeds were originally buried in 15 plots of up to 80 seeds in Auburn, Alabama, October 2020 – February 2021. White oak (WO) and water oak (RO) acorns were buried either whole or artificially excised to mimic strategies used by scatterhoarding eastern gray squirrels (*Sciurus carolinensis*). Fate of all remaining seeds was determined in March 2022. Environmental fates included seed mortality due to insect infestation, rot, or visible fungus. Percentages represent how much each fate contributed to total mortality for each species.

	Hickory		Beech		Excised WO		Whole WO		Excised RO		Whole RO		Total	
Pilfered	99	61%	75	68%	67	61%	74	60%	120	71%	95	81%	530	67%
Germinated	21	13%	0	0%	0	0%	8	7%	2	1%	1	1%	32	4%
Environmental	8	5%	20	18%	37	34%	27	22%	30	18%	6	5%	128	16%
Survived	18	11%	2	2%	0	0%	0	0%	1	1%	8	7%	29	4%
Unknown	17	10%	13	12%	6	5%	14	11%	16	9%	8	7%	74	9%
Total	163		110		110		123		169		118		793	

Table 3.03. Kaplan-Meier estimated survival rates for seed types (mockernut hickory, *Carya tomentosa*; American beech, *Fagus grandifolia*; excised and whole white oak, *Quercus alba*; excised and whole water oak, *Q. nigra*) buried in Auburn, Alabama, October 2020 – February 2021. Seeds were monitored for monthly survival through March 2021 (end of first scatterhoarding season) and through March 2022 (end of second scatterhoarding season). C.L. = confidence limits

Time Period	Seed Type	Survival Rate	95% C.L.
Beginning of study to end of **first** scatterhoarding season (182 days)	All	0.40	0.34 – 0.48
	Beech	0.44	0.30 – 0.67
	Hickory	0.71	0.59 – 0.85
	Excised Water Oak	0.34	0.20 – 0.60
	Whole Water Oak	0.70	0.49 – 0.98
	Excised White Oak	0.07	0.02 – 0.21
	Whole White Oak	0.23	0.12 – 0.47
Beginning of study to end of **second** scatterhoarding season (518 days)	All	0.39	0.33 – 0.47
	Beech	0.44	0.30 – 0.69
	Hickory	0.68	0.56 – 0.83
	Excised Water Oak	0.34	0.20 – 0.60
	Whole Water Oak	0.70	0.49 – 0.98
	Excised White Oak	0.07	0.02 – 0.20
	Whole White Oak	0.23	0.12 – 0.47

Table 3.04. Results from Cox Proportional Hazards regression analyzing impacts of seed type (mockernut hickory, *Carya tomentosa*; American beech, *Fagus grandifolia*; excised and whole white oak, *Quercus alba*; excised and whole water oak, *Q. nigra*) on availability of seeds buried in Auburn, Alabama, October 2020 – February 2021. A random subset of seeds was monitored for availability to scatterhoarders every month after burial until March 2021 (end of the first scatterhoarding season). Final fates for all seeds were recorded in March 2022 (end of the second scatterhoarding season). OR = odds ratio, CL = confidence limits, * indicates statistical significance

Time Period	Predictor		OR	95% C.L.	P-value	
Beginning of study to end of **first** scatterhoarding season	Hickory	(vs. beech)	0.41	0.20 - 0.84	0.01	*
	Whole water oak	(vs. beech)	0.39	0.16 - 0.95	0.04	*
	Excised water oak	(vs. beech)	1.48	0.84 - 2.62	0.17	
	Whole white oak	(vs. beech)	1.65	0.92 - 2.97	0.09	
	Excised white oak	(vs. beech)	2.89	1.66 - 5.04	< 0.001	*
	Whole water oak	(vs. hickory)	0.94	0.37 - 13.20	0.90	
	Excised water oak	(vs. hickory)	3.58	1.89 - 6.78	< 0.001	*
	Whole white oak	(vs. hickory)	3.99	2.05 - 7.74	< 0.001	*
	Excised white oak	(vs. hickory)	6.99	3.70 - 13.20	< 0.001	*
	Excised water oak	(vs. whole water oak)	3.81	1.65 - 8.78	0.001	*
	Whole white oak	(vs. whole water oak)	4.22	1.80 - 9.94	< 0.001	*
	Excised white oak	(vs. whole water oak)	7.44	3.21 - 17.17	< 0.001	*
	Whole white oak	(vs. excised water oak)	1.11	0.67 - 1.85	0.68	
	Excised white oak	(vs. excised water oak)	1.95	1.21 - 2.14	0.01	*
	Excised white oak	(vs. whole white oak)	1.75	1.07 - 2.88	0.02	*
Beginning of study to end of **second**	Hickory	(vs. beech)	0.42	0.21 - 1.85	0.01	*
	Whole water oak	(vs. beech)	0.38	0.15 - 0.93	0.03	*

scatterhoarding season	Excised water oak	(vs. beech)	1.47	0.83 - 2.61	0.17	
	Whole white oak	(vs. beech)	1.65	0.92 - 2.97	0.09	
	Excised white oak	(vs. beech)	2.97	1.71 - 5.15	< 0.001	*
	Whole water oak	(vs. hickory)	0.90	0.36 - 2.25	0.81	
	Excised water oak	(vs. hickory)	3.49	1.87 - 6.54	< 0.001	*
	Whole white oak	(vs. hickory)	3.91	2.04 - 7.52	< 0.001	*
	Excised white oak	(vs. hickory)	7.04	3.77 - 13.12	< 0.001	*
	Excised water oak	(vs. whole water oak)	3.89	1.69 - 8.98	0.001	*
	Whole white oak	(vs. whole water oak)	4.23	1.80 - 9.94	< 0.001	*
	Excised white oak	(vs. whole water oak)	7.42	3.21 - 17.17	< 0.001	*
	Whole white oak	(vs. excised water oak)	1.12	0.67 - 1.87	0.66	
	Excised white oak	(vs. excised water oak)	2.03	1.25 - 3.24	0.17	
	Excised white oak	(vs. whole white oak)	1.78	1.10 - 2.95	0.02	*

Table 3.05. Seeds (mockernut hickory, *Carya tomentosa*; American beech, *Fagus grandifolia*; white oak, *Quercus alba*; and water oak, *Q. nigra*) originally buried October 2020 – February 2021 that survived until March 31, 2021 were monitored in December 2021 and March 2022. Seeds that were not pilfered or germinated (with empty seed shell present) by March 2022 were tin-tagged and released to determine if they were useful to scatterhoarding eastern gray squirrels (*Sciurus carolinensis*) and eastern chipmunks (*Tamias striatus*). Seeds with unknown fates were taken away from the release site by scatterhoarders and relocation was not successful.

Fate	Hickory	Beech	White oak	Water oak	Total	Percentage
Pilfered	2	0	1	3	6	15%
Germinated	5	0	0	1	6	15%
Hoarded	1	0	0	4	5	12%
Eaten	4	0	0	4	8	20%
Chewed/Ignored	8	1	0	0	9	22%
Ignored	1	1	0	0	2	5%
Unknown	3	0	0	1	4	10%
Total	25*	2	1	13	41*	

*One hickory seed was rotten and fell apart during the tagging process, so was not able to be tagged and released.

Table 3.06. Cause-specific mortality rates (due to environmental causes of loss) for seeds buried October 2020 – February 2021 in Auburn, Alabama. Seeds (mockernut hickory, *Carya tomentosa*; American beech, *Fagus grandifolia*; excised and whole white oak, *Quercus alba*; excised and whole water oak, *Q. nigra*) were monitored for survival monthly until March 2021. Environmental causes of death included rot, fungus, or insect infestation. Mortality rates are reported at 182 days, the length of the scatterhoarding season in our study: October – March. C.L. = confidence limits

Seed Type	Mortality Rate	95% C.L.
All	0.56	0.48 – 0.62
Beech	0.53	0.60 – 0.68
Hickory	0.18	0.06 – 0.29
Excised Water Oak	0.63	0.36 – 0.79
Whole Water Oak	0.29	0.00 – 0.50
Excised White Oak	0.89	0.70 – 0.96
Whole White Oak	0.75	0.50 – 0.87

Table 3.07. Effect of seed type on cache loss due to environmental causes (including rot, fungus, or insect infestation) for seeds originally buried October 2020 – February 2021 in Auburn, Alabama. Seeds (mockernut hickory, *Carya tomentosa*; American beech, *Fagus grandifolia*; excised and whole white oak, *Quercus alba*; excised and whole water oak, Q. *nigra*) were monitored for survival monthly from burial until March 2021. OR = odds ratio, CL = confidence limits, * indicates statistical significance

Predictor		OR	95% CL	P-value	
Hickory	(vs. beech)	0.18	0.07 – 0.43	< 0.001	*
Whole water oak	(vs. beech)	0.28	0.16 – 0.50	0.01	*
Excised water oak	(vs. beech)	1.25	0.68 – 2.28	0.46	
Whole white oak	(vs. beech)	1.57	0.85 – 2.88	0.14	
Excised white oak	(vs. beech)	2.78	1.56 – 4.97	< 0.001	*
Whole water oak	(vs. hickory)	1.58	0.53 – 4.71	0.40	
Excised water oak	(vs. hickory)	6.98	3.07 – 15.86	< 0.001	*
Whole white oak	(vs. hickory)	8.77	3.80 – 20.25	< 0.001	*
Excised white oak	(vs. hickory)	6.98	6.89 – 35.17	< 0.001	*
Excised water oak	(vs. whole water oak)	4.42	1.79 – 10.92	0.001	*
Whole white oak	(vs. whole water oak)	5.54	3.97 – 24.38	< 0.001	*
Excised white oak	(vs. whole water oak)	9.84	2.21 – 13.88	< 0.001	*
Whole white oak	(vs. excised water oak)	1.26	0.73 – 2.16	0.40	
Excised white oak	(vs. excised water oak)	2.23	1.33 – 3.72	< 0.01	*
Excised white oak	(vs. whole white oak)	1.78	1.05 – 3.00	0.03	*

Table 3.08. Likelihood of seeds germinating after being buried October 2020 – February 2021 in Auburn, Alabama. Seeds (mockernut hickory, *Carya tomentosa*; excised and whole white oak, *Quercus alba*; excised and whole water oak, *Q. nigra*) were monitored monthly until March 2022. OR = odds ratio, CL = confidence limits, * indicates statistical significance

Predictor		OR	95% CL	P-value	
Whole water oak	(vs. hickory)	0.06	0.01 – 0.27	< 0.001	*
Excised water oak	(vs. hickory)	0.14	0.05 – 0.36	< 0.001	*
Whole white oak	(vs. hickory)	3.03	1.61 – 5.70	< 0.001	*
Excised white oak	(vs. hickory)	0.64	0.72 – 3.39	0.25	
Excised water oak	(vs. whole water oak)	2.28	0.44 – 11.86	0.32	
Whole white oak	(vs. whole water oak)	49.91	10.86 – 229.43	< 0.001	*
Excised white oak	(vs. whole water oak)	10.54	2.18 – 51.02	0.003	*
Whole white oak	(vs. excised water oak)	21.87	8.15 – 58.72	< 0.001	*
Excised white oak	(vs. excised water oak)	4.62	1.59 – 13.44	< 0.01	*
Excised white oak	(vs. whole white oak)	0.21	0.10 – 0.46	< 0.001	*

Figures

Figure 3.01. Locations of 15 plots where we buried white oak acorns (*Quercus alba*), water oak acorns (*Q. nigra*), mockernut hickory seeds (*Carya tomentosa*), and American beech seeds (*Fagus grandifolia*) October 2020 – February 2021 to investigate survival of scatterhoarded seeds in Auburn, Alabama.

Figure 3.02. Staggered-entry Kaplan-Meyer survival curves for (A) 6 seed types (American beech *Fagus grandifolia*, mockernut hickory, *Carya tomentosa*, white oak *Quercus alba*, water oak *Quercus nigra*) of artificially scatterhoarded seeds through **one scatterhoarding season** (October 2020 – March 2021) and (B) all seed combined. Seeds were buried in Auburn, Alabama, and monitored monthly for survival. Shaded areas represent 95% confidence limits.

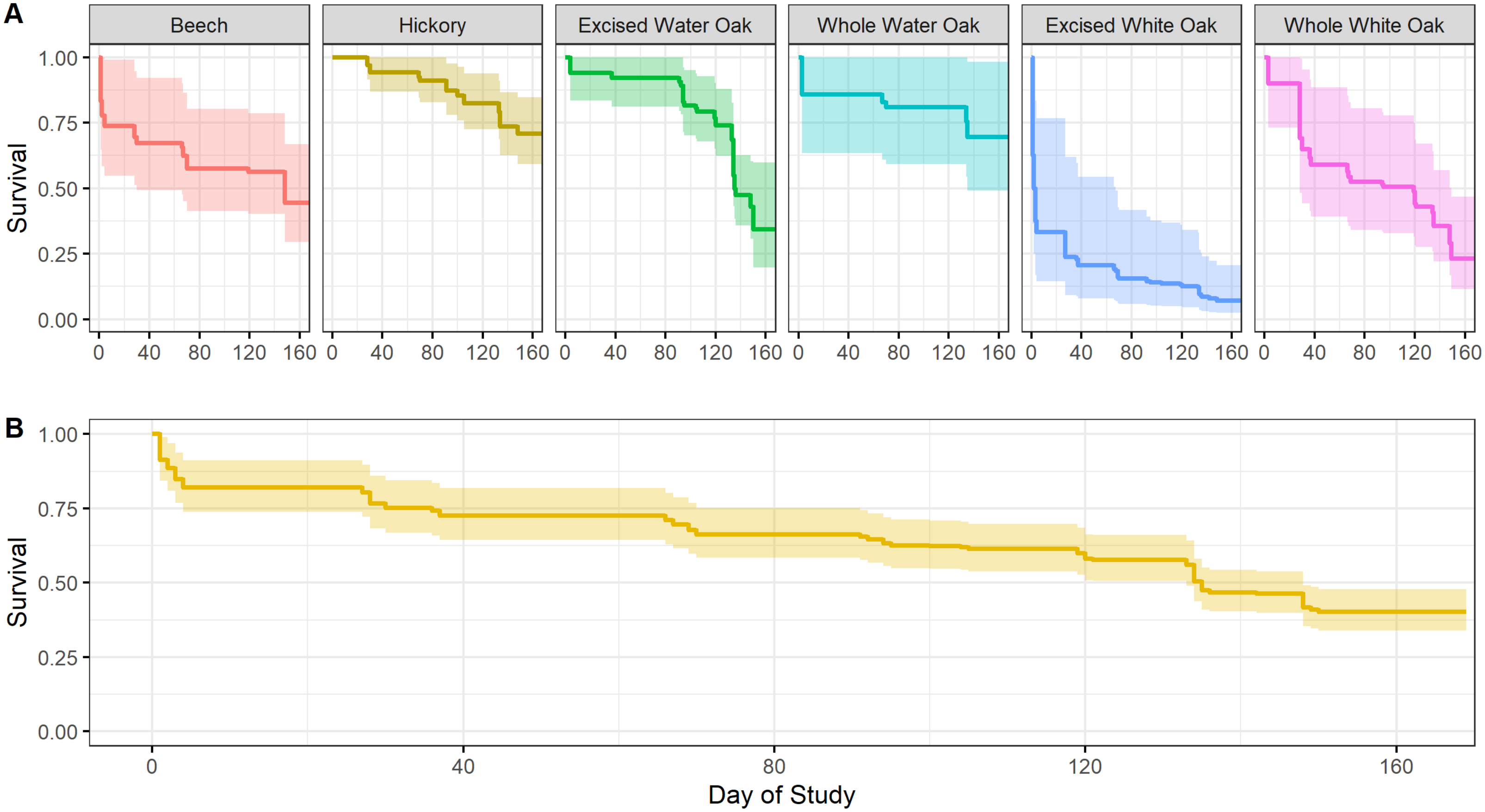
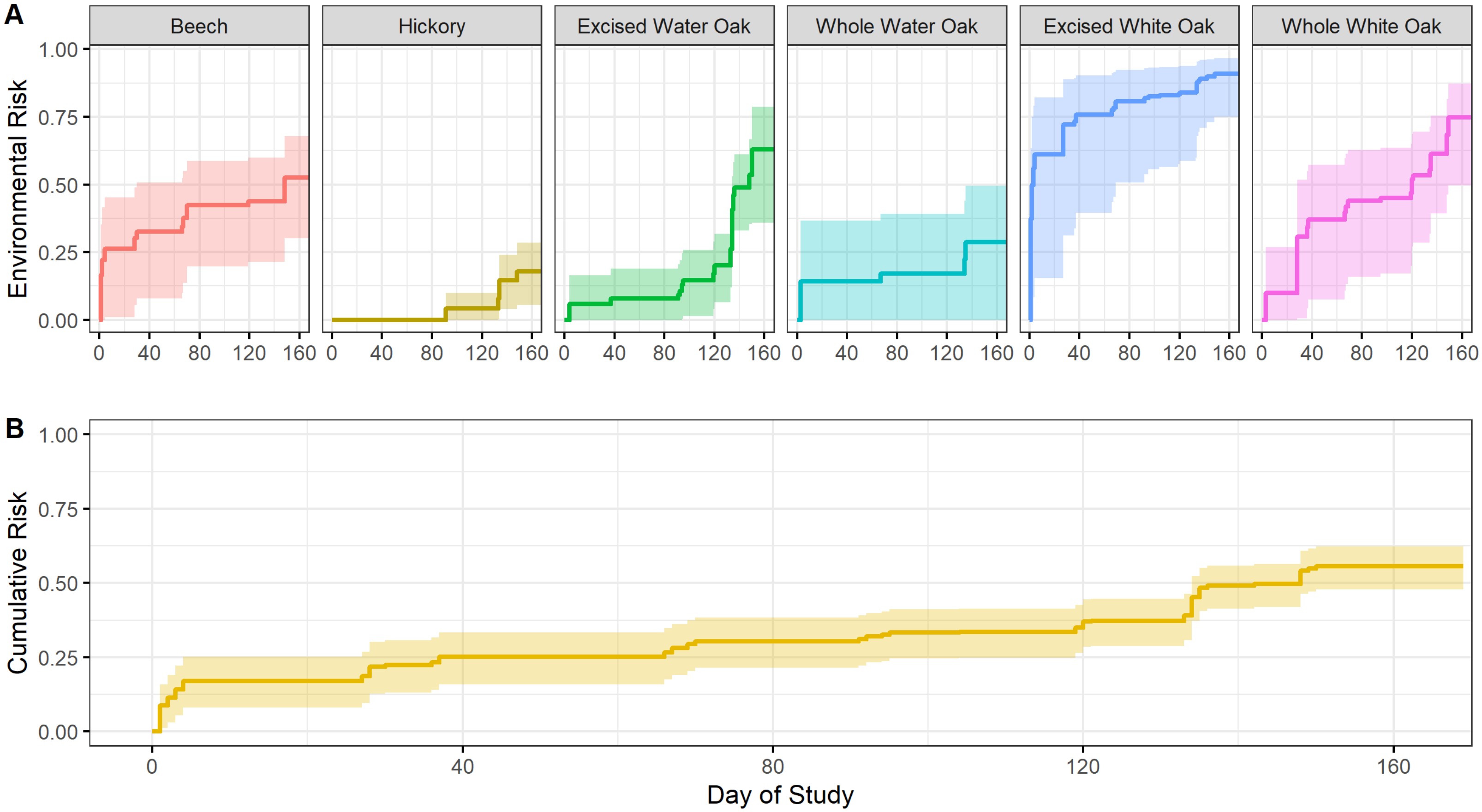


Figure 3.03. **Cumulative risk** of (A) different seed types succumbing to environmental causes of cache loss (e.g., rotting, fungus infection, or insect predation) and (B) all cached seeds becoming unavailable to a hoarder due to environmental causes of cache mortality. Seeds were buried in Auburn, Alabama in October 2020 and monitored for seed condition through one scatterhoarding season (through March 31, 2021, 162 days). Shaded areas represent 95% confidence levels.



Chapter 4. Pilferage risk and selective pilfering of scatterhoarded food in Auburn, Alabama

Animals that experience a food-scarce season, typically during winter, can supplement their diet by storing hundreds of food items around their home range that can be consumed at a later date. A form of this phenomenon is termed "scatterhoarding," where the food items can be hundreds of seeds that are buried at a shallow depth beneath ground litter and surface soil. To combat the risks of rot and germination of buried seeds, animals typically bury sound, dormant seeds or killed (i.e., through embryo excision) seeds. However, theft, or pilferage, is considered the largest risk to stored food; yet previous quantification of the magnitude and particular types of seeds pilfered has been at best haphazard. We investigated the relative pilferage risk of 842 artificially scatterhoarded seeds (whole mockernut hickory, *Carya tomentosa*; whole American beech, *Fagus grandifolia*; whole and excised white oak, *Quercus alba*; whole and excised water oak, *Quercus nigra*) buried in Auburn, Alabama from October 2020 – February 2021, and monitored until March 2021. Our study area contained hoarding populations of eastern gray squirrels (*Sciurus carolinensis*) and eastern chipmunks (*Tamias striatus*). Our buried seeds had a combined pilferage risk of 0.98 over 182 days, and the pilferage risks for individual seed types were all greater than 0.97. Whole water oak acorns were 1.39 times as likely to be pilfered than excised water oak acorns ($P < 0.01$), however, there was no difference in the pilferage rates of excised and whole white oak acorns ($P = 0.80$). Thus, we found evidence that animals are able to selectively pilfer the same seed types that are selected during the initial burial (whole, dormant seeds). Our findings

highlight the importance of the many pilferage reduction strategies documented in hoarding species and may indicate an advantage to having a diverse supply of hoarded foods that include lower-value seeds with lower pilferage risk.

4.1 Introduction

Scatterhoarding animals store food in many places within their home range for use at a later time, usually when food is harder to find (Morris 1962). Scatterhoarding is adaptive if hoarders experience a survival or reproductive benefit from having this extra food source during the food-scarce season, which for most animals is over winter (Sechley et al. 2014). However, scatterhoarding has many potential costs, including increased predation risk to the hoarder (Leaver 2004) and the energetic cost of finding and burying seeds. Additionally, any number of events may decrease the realized benefit of the behavior, including loss of stored food before recovery due to germination of seeds (Soné et al. 2002, Suselbeek et al. 2013), insect infestation or rot of seeds (Forget 1997, Suselbeek et al. 2013), and pilferage (theft by another animal, reviewed in Vander Wall and Jenkins 2003). Scatterhoarders reduce their loss of seeds to germination, insects, and rot by preferentially burying dormant, insect-free seeds (Smallwood et al. 2001, Weckerly and Nicholson 2017) and killing seeds to prevent germination (i.e., embryo excision, Fox 1982, Steele et al. 2001, Hou et al. 2010). Additionally, scatterhoarders have numerous ways to reduce pilferage of their stored food, such as increasing the distance between valuable seeds (Male and Smulders 2007), burying seeds in areas with higher predation risk for potential pilferers (Steele et al. 2014), and burying seeds deeper in moist soils to reduce their scent (Geluso 2005). Thus, knowledge of the exact rates of pilferage, and the factors that influence those pilferage rates is critical to understanding the adaptive value of scatterhoarding behaviors.

Estimates of pilferage rates experienced by hoarding species vary widely, with previous studies estimating pilferage rates at between 0.4 – 100% of hoarded food lost per day (reviewed in Vander Wall and Jenkins 2003). However, previous long-term seed fate studies focused on overall survival of seeds to the seedling stage, rather than pilferage rates explicitly (e.g., Brewer and Webb 2001, Theimer 2001, Haas and Heske 2005, Hou et al. 2010, García et al. 2014, Kuprewicz 2015) or estimated pilferage risk for only one type of seed (reviewed in Vander Wall and Jenkins 2003). Most studies of pilferage followed scatterhoarded food over a relatively short period (e.g., Forget 1997, Brewer and Webb 2001, Soné et al. 2002, Haas and Heske 2005, Delgado and Jacobs 2019). However, pilferage estimates from such short-term studies may not be applicable to a full season and are difficult to compare because pilferage risk can be impacted by many factors such as food availability during the study (Gálvez et al. 2009, Yi et al. 2019), the abundance of the animals using the food sources (Li and Zhang 2007), or other changes in pilferage risk throughout the season. Finally, different species of hoarders have different adaptations to cope with pilferage strategies used by coexisting species, so pilferage behavior and risks are also dependent on the other hoarding species in the community (Leaver and Daly 2001, Dittel et al. 2017, Wang et al. 2018). Thus, pilferage rates should be highly variable, and yet also contribute to the evolution of pilferage reduction behaviors within hoarding populations. Consequently, additional studies are needed to fully elucidate the rates of pilferage experienced by hoarders.

One factor that could be important for influencing pilferage rates is the value of different seed types to pilferers. Few studies have examined the selection of seeds being pilfered, though many studies have investigated the selection of seeds during the initial hoarding of seeds (Steele et al. 2006, Moore et al. 2007, Wang et al. 2013, Cao et al. 2018). For example, seeds with delayed germination (e.g., water oak, *Quercus nigra*; mockernut hickory, *Carya tomentosa*) are selected for hoarding over seeds that germinate soon after falling from the tree (e.g., white oak, *Quercus alba*) due to lower perceived risk of germination before recovery (Smallwood et al. 2001). Given that some seeds should be more valuable to pilferers than others (Vander Wall et al. 2019), and that hoarders often store seeds in risky locations to deter pilferage (Steele et al. 2014, Lichti et al. 2020), pilferers should benefit from being selective in which seeds to dig up, once located. Indeed, previous studies have found evidence that hoarders can determine the condition of buried seeds through scent, before digging up the seed (Sundaram et al. 2020, also see Chapter 3: Multiyear Supply). Thus, pilferers should have the ability and impetus to be selective about which seeds they steal; however, whether or not pilfers are selective about which seeds they steal has largely not been tested.

In this study, our objective was to determine the impacts of pilferage on experimentally scatterhoarded food buried in Auburn, Alabama, throughout an entire scatterhoarding season. We recorded pilferage rates for 6 types of seeds: whole mockernut hickory, whole American beech (*Fagus grandifolia*), excised water oak, whole water oak, excised white oak, and whole white oak. These seeds are all commonly used by scatterhoarders in our study area (personal observation, SBR). Squirrels prefer to eat, rather than bury, white oak acorns; however, they will excise them before burial to avoid losing this early germinating species to seedling growth (Steele et al. 2006). Water oak acorns are typically buried whole, due to being dormant during the fall (prime burial season), but we included excised water oak acorns because squirrels will excise them if the acorns are found after dormancy is broken (Smallwood et al. 2001). We explored pilferage by scatterhoarding eastern gray squirrels along with pilferage by potential cheaters (i.e., a species that scatterhoards few seeds but pilfers and moves seeds to a defended burrow: eastern chipmunks, *Tamias striatus*), in the study area. We tested the hypothesis that hoarders selectively pilfer seed types commonly selected during the hoarding process. We predicted that water oak and hickory seeds would more likely be pilfered than white oak and beech seeds, due to a penchant for hoarders to store dormant seeds. We also predicted that whole red oak acorns should more likely be pilfered than excised red oak acorns, given the low risk of germination in the species and the added value of whole seeds, while we expected to find the opposite result for white oak acorns due to whole white oak acorns being more susceptible to germination. Our overall goal in this study was to better understand the adaptive value of hoarding different types of seeds over a scatterhoarding season.

4.2 Methods

Study Area

We conducted our study in a small forest (4.5 ha) on the outskirts of Auburn University main campus in Auburn, Alabama (32.594°W, -85.489°N; about 220m a.s.l.), which consists of 2.5 ha of a closed-canopied American beech, oak, pine, and hickory forest with patches of thick understory (Chinese privet, *Ligustrum sinense*; greenbriar, *Smilax spp.*; numerous saplings of hardwood canopy species) and 2 ha of mixed, moderately-closed-canopy and open-canopy, mature oak, American beech, longleaf pine (*Pinus palustris*), and hickory with little to no understory due to mowing by Auburn University. The mast crop usually falls to the ground in our study area starting in September or October (personal observation, SBR), thus, marking the beginning of the scatterhoarding season. New vegetative growth, a common spring food for rodents (Thompson and Thompson 1980), typically signals the end of the scatterhoarding season in February or March. The mild climate during winter (mean 7.6 degrees Celsius in January, little to no frozen precipitation; NCEI 2019) provides conditions for some vegetative growth to persist during winter (partridge berry, *Mitchella repens*; chinaberry, *Melia azedarach*; Chinese privet, thorny olive, *Elaeagnus pungens*; southern magnolia, *Magnolia grandiflora*; unpublished data, SBR**)** and may provide a supplemental food source to scatterhoarders in our study area. We had previously documented a population of at least 30 scatterhoarding eastern gray squirrels in our study area (unpublished data, SBR**),** as well as a population of scatterhoarding and larderhoarding eastern chipmunks. Squirrels were observed throughout the study area, while chipmunks were mainly present in the dense canopied area. During previous studies of food hoarding behavior with these populations of squirrels and chipmunks, we found both species pilfered seeds to eat or recache in a scatterhoard or a larder (See Chapter 5: Belowground Cues).

Seed Collection and Preparation

In September 2020, we collected seeds from species in the study area that were likely to be hoarded by squirrels or chipmunks (mockernut hickory, American beech, water oak, and white oak). We only used sound (i.e., viable for hoarding) seeds in this study. All collected seeds were placed in a bucket of water and those that floated to the surface were removed, since the floating seeds were considered potentially rotten or had been eaten by insects (Allen et al. 2001), particularly weevils. Squirrels can identify weevil-infested seeds without any physical signs on the seed and typically do not bury these seeds (Steele et al. 1996). We also removed any seeds from our dataset that showed signs of weevils (exits holes in the seed coat) later in the study. To imitate the embryo excision strategy commonly used by hoarders to prevent germination (Steele et al. 2001), we attempted to remove the embryos from a portion of white oak and water oak acorns by drilling a small hole in the radicle end of each acorn (Xiao et al. 2009).

Field

We set up 15 (24 cm x 30 cm) plots during October 2020 throughout our study area. Seven plots were located in the moderate to open canopy portion of the forest with no undergrowth, while 8 plots were located in the dense canopied portion of the forest. The make-up of the 6 types of the 842 seeds used in the study were as follows: 165 whole mockernut hickory, 110 whole American beech, 176 excised water oak, 136 whole water oak, 120 excised white oak, and 135 whole white oak. We attempted to deploy all seeds using a fully-factorial, randomized-block design, however, towards the end of our deployment period, the condition of many seeds deteriorated in storage (e.g., white oak seeds germinated; many seeds showed presence of weevil-infestation) so we ended up deploying different numbers of each seed type. We planned to bury two of each seed type in each plot every ~4 weeks, October 2020 – February 2021. We could not deploy all seeds at the beginning of the study due to time constraints and logistical complications of monitoring such a large number of seeds each month. Each seed was deployed to a randomly selected cell within an 8 x 10 cell grid placed over the plot at deployment. The seeds were buried 1-2 cm below the soil surface in a randomly selected cell and were re-covered with any leaf litter present before burial. For a concurrent study, we had attempted to document seed survival when pilferage was prevented, so we had covered each plot with garden mesh to attempt to discourage pilferage of seeds, though the mesh appeared to have minimal effect on decreasing pilferage risk and thus provided us with the opportunity to explore pilferage throughout the scatterhoarding season. Additionally, when animals chewed through the mesh to pilfer seeds, it provided us with a direct cue of which seeds were stolen. Avian hoarders rarely pilfer seeds buried by rodents and the mesh likely helped further exclude birds from trying to steal the seeds, (reviewed in Dally et al. 2006).

Each month, we randomly selected 15 of each seed type (1 of each seed type per plot) to dig up and check for pilferage and other loss until March 2021, the end of the scatterhoarding season. A seed was recorded as pilfered if it was no longer present in the location where it was buried. Pilferage was also usually indicated by a visible hole in the mesh directly over the seed's cell and further digging in the soil beneath. If seeds were rechecked and determined to no longer be viable for hoarding (i.e., rotten or insect-infested), we removed those seeds from the plot. Results pertaining to these complete survival data were reported elsewhere (See Chapter 3: Multiyear Supply). If we suspected that seeds not selected for long-term monitoring had been pilfered (e.g., obvious hole in dirt, chewed mesh), we also dug up and checked those seeds.

Analysis

We used the "survival" package in Program R version 4.1.1 (Therneau 2021, Therneau and Grambsch 2000, R Core Team 2021) to calculate Kaplan-Meyer survival rates to the end of the scatterhoarding season (March 31, 2021) for all seeds and each seed type. To apply this analysis, we equated pilferage with "mortality" and unpilfered seeds were censored. We used the staggered entry method for survival rates because all seeds did not enter the study on the same day, and we assumed that all seeds survived at least one day after burial. If a seed was removed from a plot for reasons unrelated to pilferage (e.g., rot, fungus, insects), the seed was right-censored in the analysis on the last day the seed was known to be alive, or one day after burial if we could not estimate the last day known to be alive (i.e., seed was dead at first recheck). We also right-censored seeds that survived to the end of the study, and seeds with unknown fates due to construction in the area in March 2021. We converted survival rates to cumulative pilferage rates for all seeds and each seed type by subtracting the survival rates from 1. We standardized our pilferage rates to the length of a typical scatterhoarding season, 182 days (October – March).

We used mixed effects Cox Proportional Hazards regression (Cox PH) in the "coxme" package in Program R (Therneau 2020) to determine if the time to pilferage differed among seed types, which could indicate both an ability of pilferers to differentiate among seed types by scent and to select for certain seed types. As with pilferage rate calculations described above, we right-censored all seeds that were removed from the study via mechanisms other than pilfering, had unknown fates, or survived to the end of the scatterhoarding season. We included a random effect of the plot of each seed in our analysis to account for unmeasured habitat characteristics throughout the study area that could impact seed pilferage and survival (e.g., canopy cover, Steele et al. 2014; or soil moisture, Vander Wall 1995)

4.3 Results

We removed seeds from our dataset throughout our study that showed indications of weevil presence (small exit-hole in seed shell; 2 hickory nuts, 25 red oak acorns and 22 white oak acorns), resulting in a final dataset of 793 seeds used in analyses. Between October 2020 and March 31, 2021, 66.8% (n = 530) of all seeds were pilfered. However, 20.7% (n = 164) of seeds were lost due to other reasons (e.g., rot, insects, etc.). After right-censoring the data for these lost seeds, the estimated pilferage rate through the entire scatterhoarding season (182 days), for all of our cached seeds was 0.98 (0.97 –

0.99, 95% confidence limits [C.L.]), with each of the seed types having pilferage rates of at least 0.96 (Table 1, Figure 1). Whole water oak acorns were more likely to be pilfered than other seed types, including excised water oak (all comparisons $P < 0.01$, Table 2). Similarly, excised water oak was more likely to be pilfered than all other seeds, except the aforementioned whole water oak; plus, the difference between excised water oak and hickory was not statistically significant ($P = 0.33$). Hickory was more likely to be pilfered than beech, or either type of white oak (whole or excised; all $P < 0.04$; Table 2). Finally, we observed no statistical difference in the likelihood of pilferage between excised and whole white oak acorns ($P = 0.80$; Table 2). Differences among the remaining seed types also were not statistically significant (all $P > 0.20$; Table 2).

4.4 Discussion

Few studies have documented pilferage rates of a large supply of multiple seed types over a long period of time (Forget 1997, Brewer and Webb 2001, Soné et al. 2002, Haas and Heske 2005, Delgado and Jacobs 2019). Artificial pilferage studies such as ours have been used many times to determine short term pilferage rates for different seeds species within different hoarding communities (reviewed by Vander Wall and Jenkins 2003). A major advantage of an artificial pilferage study is the ability to monitor a large number of seeds for pilferage (e.g., 100 seeds, Vander Wall et al. 2019, 603 triads of caches, Leaver 2004; 793 seeds, this study; 2030 seeds, Cao et al. 2018). Given the high rate of pilferage in our study, the mesh we used to cover our plots did not appear to impact pilferage rates and, in fact, made it easier for us to determine which seeds were pilfered. Though we could not determine the species or individual identity of pilferers, studying behaviors within a community of known species is common for food hoarding studies (Moore et al. 2007, Wang et al. 2013, Cao et al. 2018). However, because we did not track seeds after pilferage events, we could not determine the final fate of the seeds. Hoarders are known to recache pilfered seeds (Vander Wall 2002), so it is possible that our estimate of pilferage represents the proportion of seeds that change ownership, rather than seeds that are removed from the food supply. Combining artificial pilferage studies with more time-intensive individual seed tracking methods (e.g., tin-tagging, Zhang et al. 2008; telemetric tags, Hirsch et al. 2012) could provide further information about pilferage rates within a community.

In this study, we found that water oak was the most frequently pilfered seed species in our study area. Furthermore, while pilferers did not differentiate between excised or whole white oak acorns, they did select whole water oak acorns over excised water oak acorns. The differences we found between the susceptibility to pilferage of different seed types suggests that hoarders can detect seed type and condition through olfactory cues before making the decision to dig up a seed. To our knowledge, only one other study (Vander Wall et al. 2019) has compared pilferage rates among seeds potentially perceived to have differing values to hoarders. In that study, the authors found that pilferage rates differed among four desert seed species of different sizes (singleleaf piñon pine, *Pinus monophylla*; desert peach, *Prunus andersonii*; antelope bitterbrush, *Purshia tridentata*; Utah juniper, J*uniperus osteosperma*), with heavier species more likely to be pilfered. By comparison, the most selected seed species in our study, water oak, was the third smallest of the four species we used, suggesting seed mass was likely not the factor driving perceived value between our seed species. Given the previously observed selection for dormant seeds over nondormant seeds as well as the higher pilferage rates for whole water oak acorns compared to excised water oak acorns in this study, we suggest that the perishability of seeds was the trait selected by pilferers in our study area. Indeed, pilferers are well-known to use scent to locate seeds buried by other hoarders (Vander Wall 2000) and can even distinguish between buried seeds that are still dormant versus those with broken dormancy (Sundaram et al. 2020). Thus, our study provides further evidence that scatterhoarders consider the value of seeds in their search for food to either eat or store.

Estimates of pilferage rates vary considerably among previous studies. Thus, Vander Wall and Jenkins (2003) standardized pilferage rates for various species to the percentage lost per day during each study. Our overall pilferage rate of 98% through the scatterhoarding season (182 days) translates to 2.1% lost per day, if one assumes that the pilferage rate was constant throughout the season. This estimate of daily loss is on the low end of pilferage rates for *Sciurus* species (eastern fox squirrel, *Sciurus niger*: 0.4 – 33.2%; eastern gray squirrel: 1.0 to >95%; *Sciurus vulgaris*: 36-96%; *Sciurus lis*: 4.6 – 21.7%; reviewed in Vander Wall and Jenkins 2003). However, all of these previous studies, except for one, were conducted for 3 weeks or less (the exception is Thompson and Thompson 1980 which studied eastern gray squirrel pilferage rates for 188 days and found a daily pilferage rate of 1.0%). Due to temporal variation in the environment (Vander Wall 2000, Dimitri and Longland 2022), food availability (Gálvez et al. 2009), and other species active in the area (Leaver and Daly 2001, Li and Zhang 2007), short-term studies of pilferage likely capture a snapshot of pilferage risk for that population, rather than providing a complete description of pilferage risk over time. For example, stored food items that are not pilfered shortly after burial might persist for long periods potentially because they are hidden better, their scent is masked, or they are in locations that pilferers avoid (e.g., see Figure 1). Our results suggest that is not the case. Rather, our results suggest that very few items make it through an entire scatterhoarding season without being pilfered at least once. Thus, pilferage is a critical factor influencing the benefits of scatterhoarding behavior.

Pilferers do not always eat the food they steal; they can also rebury it or ignore it after recovery, leading to seeds potentially changing owners many times before ultimately being eaten (Haifeng et al. 2017). Due to the high pilferage rate through the scatterhoarding season in our study area (0.98 pilferage rate), if a scatterhoarder did not add to their stored food supply by pilfering at similar rates to which food is stolen from them (i.e., reciprocal pilferage, Niu et al., 2020; Vander Wall & Jenkins, 2003), their stored food supply would be quickly depleted. In fact, under natural conditions, a scatterhoarder could quickly recover pilfered food if it was reburied nearby by the pilferer. Indeed, the competitive advantage gained from being a good pilferer could even cause being a good thief to become adaptive within populations with high amounts of pilferage (Vander Wall and Jenkins 2003). Alternatively, given that pilferers appear to select certain items over others, hoarders may benefit from storing a variety of items, as those items that are perceived to be of lower value to pilferers – and consequently ignored – may provide sufficient and reliable sustenance for the original hoarder should food become extremely scarce.

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4.6 Literature Cited

Brewer, S. W., and M. A. H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. Oikos 93:32–41.

Cao, L., B. Wang, C. Yan, Z. Wang, H. Zhang, Y. Geng, J. Chen, and Z. Zhang. 2018. Risk of cache pilferage determines hoarding behavior of rodents and seed fate. Behavioral Ecology 29:984–991.

Dally, J. M., N. S. Clayton, and N. J. Emery. 2006. The behavior and evolution of cache protection and pilferage. Animal Behaviour 72:13–23.

Delgado, M. M., and L. F. Jacobs. 2019. How squirrels protect their caches: Location, conspicuousness during caching, and proximity to kin influence cache lifespan. bioRxiv 738237.

Dimitri, L. A., and W. S. Longland. 2022. Pilfering of western juniper seed caches by scatter-hoarding rodents varies by microsite and canopy type. Integrative Zoology 17:192–205.

Dittel, J. W., R. Perea, and S. B. Vander Wall. 2017. Reciprocal pilfering in a seed-caching rodent community: Implications for species coexistence. Behavioral Ecology and Sociobiology 71.

Forget, P. M. 1997. Effect of microhabitat on seed fate and seedling performance in two rodent- dispersed tree species in rain forest in French Guiana. Journal of Ecology 85:693–703.

Fox, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. Evolution 36:800–809.

Gálvez, D., B. Kranstauber, R. W. Kays, and P. A. Jansen. 2009. Scatterhoarding by the Central American agouti: A test of optimal cache spacing theory. Animal Behaviour 78:1327–1333.

García, D., M. Bañuelos, and G. Houle. 2002. Differential effects of acorn burial and litter cover on Quercus rubra recruitment at the limit of its range in eastern North America. Canadian Journal of Biology 80:1115–1120.

Geluso, K. 2005. Benefits of small-sized caches for scatterhoarding rodents: Influence of cache size, depth, and soil moisture. Journal of Mammalogy 86:1186–1192.

Haas, J. P., and E. J. Heske. 2005. Experimental study of the effects of mammalian acorn predators on red oak acorn survival and germination. Journal of Mammalogy 86:1015–1021.

Haifeng, G., Q. Zhao, and Z. Zhang. 2017. Does scatter-hoarding of seeds benefit cache owners or pilferers? Integrative Zoology 12:477–488.

Hirsch, B. T., R. Kays, and P. A. Jansen. 2012. A telemetric thread tag for tracking seed dispersal by scatterhoarding rodents. Plant Ecology 213:933–943.

Hou, X., X. Yi, Y. Yang, and W. Liu. 2010. Acorn germination and seedling survival of *Q. variabilis*: Effects of cotyledon excision. Annals of Forest Science 67:1–7.

Kuprewicz, E. K. 2015. Scatter hoarding of seeds confers survival advantages and disadvantages to large-seeded tropical plants at different life stages. PLoS ONE 10:1–16.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. Behavioral Ecology 15:729–734.

Leaver, L. A., and M. Daly. 2001. Food caching and differential cache pilferage: A field study of coexistence of sympatric kangaroo rats and pocket mice. Oecologia 128:577–584.

Li, H., and Z. Zhang. 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). Forest Ecology and Management 242:511–517.

Lichti, N. I., H. J. Dalgleish, and M. A. Steele. 2020. Interactions among shade, caching behavior, and predation risk may drive seed trait evolution in scatterhoarded plants. Diversity 12:1–19.

Male, L. H., and T. V. Smulders. 2007. Hyper-dispersed cache distributions reduce pilferage: A laboratory study. Animal Behaviour 73:717–726.

Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. Ecology 88:2529–2540.

Morris, D. 1962. The behavior of the green acouchi (*Myoproctapratti*) with special reference to scatterhoarding. Proceedings of the Zoological Society of London 139:701–732.

National Centers for Environmental Information [NCEI]. 2019. Global summary of the month for Auburn, Alabama. https://www.ncei.noaa.gov/.

Niu, H., Z. Wang, G. Huang, C. Peng, Z. Zhang, and H. Zhang. 2020. Responses of a scatter-hoarding squirrel to conspecific pilfering: A test of the reciprocal pilferage hypothesis. Animal Behaviour 170:147–155.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Sechley, T. H., D. Strickland, and D. R. Norris. 2014. Causes and consequences of pre-laying weight gain in a food-caching bird that breeds in late winter. Journal of Avian Biology 45:85–93.

Smallwood, P. D., M. A. Steele, and S. H. Faeth. 2001. The ultimate basis of caching preferences of rodents, and the oak-dispersal syndrome: Tannins, insects, and seed germination. American Zoologist 41:840–851.

Soné, K., S. Hiroi, D. Nagahama, C. Ohkubo, E. Nakano, S. I. Murao, and K. Hata. 2002. Hoarding of acorns by granivorous mice and its role in the population processes of *Pasania edulis* (Makino) Makino. Ecological Research 17:553–564.

Steele, M. A., T. A. Contreras, L. Z. Hadj-Chikh, S. J. Agosta, P. D. Smallwood, and C. N. Tomlinson. 2014. Do scatterhoarders trade off increased predation risks for lower rates of cache pilferage? Behavioral Ecology 25:206–215.

Steele, M. A., L. Z. Hadj-Chikh, and J. Hazeltine. 1996. Caching and feeding decisions By *Sciurus carolinensis*: Responses to weevil-infested acorns. Journal of Mammalogy 77:305–314.

Steele, M. A., S. Manierre, T. Genna, T. A. Contreras, P. D. Smallwood, and M. E. Pereira. 2006. The innate basis of food hoarding decisions in gray squirrels: Evidence for behavioral adaptations to the oaks. Animal Behaviour 71:155–160.

Steele, M. A., G. Turner, P. D. Smallwood, J. O. Wolff, and J. Radillo. 2001. Cache management by small mammals: Experimental evidence for the significance of acorn-embryo excision. Journal of Mammalogy 82:35–4235.

Sundaram, M., A. E. Higdon, K. V. Wood, C. C. Bonham, and R. K. Swihart. 2020. Mechanisms underlying detection of seed dormancy by a scatter-hoarding rodent. Integrative Zoology 15:89–102.

Suselbeek, L., P. A. Jansen, H. H. T. Prins, and M. A. Steele. 2013. Tracking rodent-dispersed large seeds with Passive Integrated Transponder (PIT) tags. Methods in Ecology and Evolution 4:513–519.

Theimer, T. C. 2001. Seed scatterhoarding by white-tailed rats: Consequences for seedling recruitment by an Australian rain forest tree. Journal of Tropical Ecology 17:177–189.

Therneau, T. 2022a. A Package for Survival Analysis in R. R package version 3.4-0. https://CRAN.R-project.org/package=survival.

Therneau, T. M. 2022b. coxme: Mixed Effects Cox Models. R package version 2.2-18.1. https://CRAN.R-project.org/package=coxme.

Therneau, T. M., and P. M. Grambsch. 2000. Modeling Survival Data: Extending the Cox Model. Springer, New York. ISBN 0-387-98784-3.

Thompson, D. C., and P. S. Thompson. 1980. Food habits and caching behavior of urban gray squirrels. Canadian Journal of Zoology 58:701–710.

Vander Wall, S. B. 1995. Influence of substrate water on the ability of rodents to find buried seeds. Journal of Mammalogy 76:851–856.

Vander Wall, S. B. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behavioral Ecology 11:544–549.

Vander Wall, S. B. 2002. Chapter 13: Secondary dispersal of Jeffrey pine seeds by rodent scatterhoarders: The roles of pilfering recaching and a variable environment. *In* Seed Dispersal and Frugivory: Ecology, Evolution and Convervation. CABI Publishing.

Vander Wall, S. B., L. A. Dimitri, W. S. Longland, and J. D. M. White. 2019. Seed value influences cache pilfering rates by desert rodents. Integrative Zoology 14:75–86.

Vander Wall, S. B., and S. H. Jenkins. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology 14:656–667.

Wang, B., C. X. Ye, C. H. Cannon, and J. Chen. 2013. Dissecting the decision making process of scatterhoarding rodents. Oikos 122:1027–1034.

Wang, Z., B. Wang, X. Yi, C. Yan, L. Cao, and Z. Zhang. 2018. Scatter-hoarding rodents are better pilferers than larder-hoarders. Animal Behaviour 141:151–159.

Weckerly, F. W., and K. E. Nicholson. 2017. Experimental test of discrimination by squirrels for insect-infested and noninfested acorns. The American Midland Naturalist 12:412–415.

Xiao, Z., X. Gao, M. Jiang, and Z. Zhang. 2009. Behavioral adaptation of Pallas's squirrels to germination schedule and tannins in acorns. Behavioral Ecology 20:1050–1055.

Yi, X., M. Ju, Y. Yang, and M. Zhang. 2019. Scatter-hoarding and cache pilfering of rodents in response to seed abundance. Ethology 125:492–499.

Zhang, H., J. Cheng, Z. Xiao, and Z. Zhang. 2008. Effects of seed abundance on seed scatterhoarding of Edward's rat (*Leopoldamys edwardsi Muridae*) at the individual level. Oecologia 158:57–63.

Tables

Table 4.01. Pilferage rates for seeds buried October 2020 – March 2021 in Auburn, Alabama. Seeds (American beech, *Fagus grandifolia*; mockernut hickory, *Carya tomentosa*; excised and whole water oak, *Quercus nigra*; excised and whole white oak, *Q. alba*) were monitored monthly for survival. Pilferage rates were standardized at 182 days, the length of a common scatterhoarding season: October – March. C.L. = confidence limits

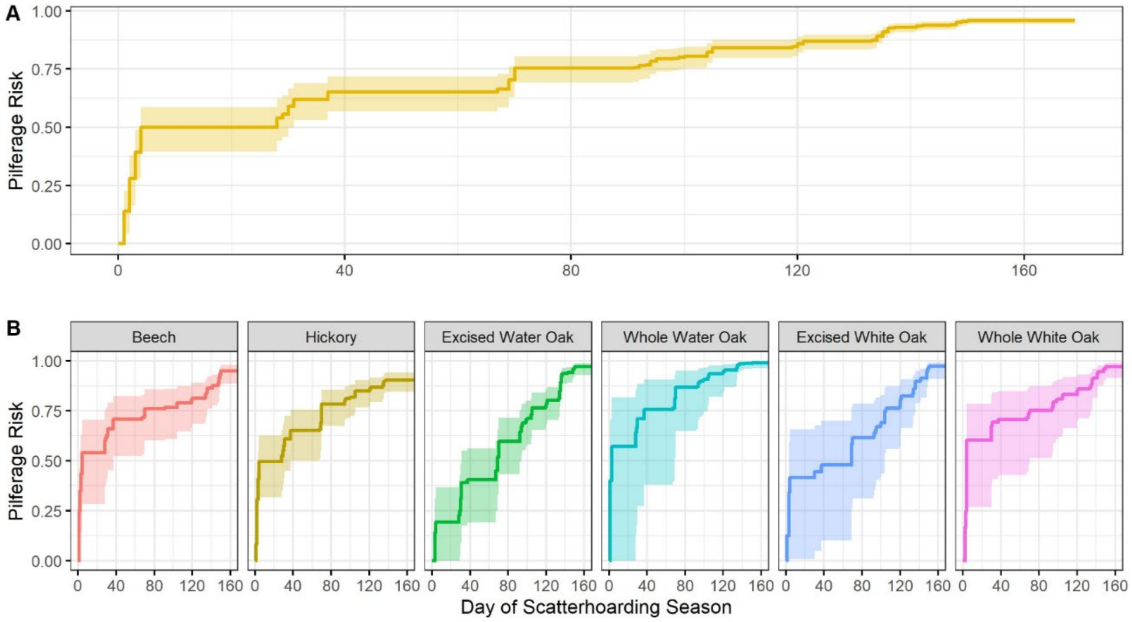
Seed Type	Pilferage Rate	95% CL
All	0.98	0.97 – 0.99
Beech	0.97	0.93 – 0.99
Hickory	0.96	0.92 – 0.98
Excised Water Oak	0.99	0.96 – 1.00
Whole Water Oak	0.99	0.98 – 1.00
Excised White Oak	0.99	0.95 – 1.00
Whole White Oak	0.99	0.95 – 1.00

Table 4.02. Effect of seed type on pilferage of seeds buried October 2020 – March 2021 in Auburn, Alabama. Seeds (American beech, *Fagus grandifolia*; mockernut hickory, *Carya tomentosa*; excised and whole water oak, *Quercus nigra*; excised and whole white oak, *Q. alba*) were monitored monthly for survival. OR = odds ratio, CL = confidence limits, * indicates statistical significance

Predictor		OR	95% CL	P-value	
Hickory	(vs. beech)	1.75	1.26 - 2.43	< 0.001	*
Whole water oak	(vs. beech)	2.78	2.04 – 3.88	< 0.001	*
Excised water oak	(vs. beech)	2.02	1.49 – 2.73	< 0.001	*
Whole white oak	(vs. beech)	1.19	0.85 – 1.66	0.30	
Excised white oak	(vs. beech)	1.24	0.88 - 1.75	0.20	
Whole water oak	(vs. hickory)	1.59	1.17 – 2.15	< 0.01	*
Excised water oak	(vs. hickory)	1.15	0.43 - 0.76	0.33	
Whole white oak	(vs. hickory)	0.68	0.49 - 0.94	0.02	*
Excised white oak	(vs. hickory)	0.71	0.51 – 1.00	0.04	*
Excised water oak	(vs. whole water oak)	0.72	0.55 – 0.96	< 0.01	*
Whole white oak	(vs. whole water oak)	0.43	0.31 - 0.59	< 0.001	*
Excised white oak	(vs. whole water oak)	0.45	0.32 - 0.62	< 0.001	*
Whole white oak	(vs. excised water oak)	0.59	0.44 - 0.80	< 0.001	*
Excised white oak	(vs. excised water oak)	0.62	0.45 - 0.84	< 0.01	*
Excised white oak	(vs. whole white oak)	1.05	0.74 - 1.47	0.80	

Figures

Figure 4.01. Cumulative pilferage risk of all cached seeds (A) and cumulative pilferage risk of different seed types (B). Beech (*Fagus grandifolia*), mockernut hickory (*Carya tomentosa*), water oak (*Quercus nigra*), and white oak (*Quercus* alba) seeds were buried in Auburn, Alabama in October 2020 and monitored for seed condition through the end of the scatterhoarding season (March 31, 2021). Oak acorns were either excised (embryos drilled out to mimic rodent hoarder behavior) or left whole. Shaded areas represent 95% confidence levels.



Chapter 5. Adaptations of scatterhoarders to seedlings as cues of belowground food

Many animals engage in scatterhoarding behavior, in which they store food, usually underground, around their home range for consumption during a period of food scarcity. These species experience fitness benefits from this behavior when they dig up and consume the buried food, and seedlings may be used as cues for germinating seeds below the plant. We investigated whether scatterhoarders use various characteristics of seedlings and their seeds as physical cues of the value of the seed. We tagged and buried 108 germinating white oak (*Quercus alba*, January 2022) and 68 germinating northern red oak (*Quercus rubra*, October 2022) acorns in a forest in Auburn, Alabama. Scatterhoarding eastern gray squirrels (*Sciurus carolinensis*) and eastern chipmunks (*Tamias striatus*) recovered white oak acorns more quickly during spring when the acorns' seedlings had longer leaves and taller stems (both $P < 0.05$), while northern red oak acorns were recovered more quickly during fall when the seedlings had a larger number of longer leaves (both $P < 0.05$). No seed or seedling characteristics significantly impacted dispersal of seeds during spring (all $P > 0.24$), while during fall hoarders were more likely to disperse seeds to a new location after recovery as root length increased ($P = 0.053$). Finally, we found that increases in radicle length increased the likelihood of seeds being eaten or buried (rather than ignored) for all of our seeds combined ($P = 0.05$). Thus, we found new evidence suggesting hoarders use physical cues from the seedling to find and recover the seed, disperse the seeds, and determine whether the seed is valuable or not. These findings indicate that masting species, such as oaks, are not safe from

predation after initial germination, which has important implications for how long seedlings are vulnerable to predation.

5.1 Introduction

Scatterhoarding is a very time- and energy-consuming activity of storing food for periods when little other food is available, typically winter (Morris 1962a). The scatterhoarding process involves considerable work, including foraging for the food, determining suitability for long term storage, and transporting and burying the food (Wang et al. 2013). During the recovery process, the animal must relocate the hoarded food using a combination of memory and visual or olfactory aids (Macdonald 1997, Kamil and Gould 2008, Li et al. 2018), followed by excavation. After recovery, the animal may experience the benefit of the caching process by eating the food item (Andersson and Krebs 1978) or the item can be recached (reburied) somewhere else until the next recovery effort (Zhang et al. 2014). Scatterhoarding can increase the fitness of the animals engaging in the behavior by providing food for young (Boutin et al. 2000, Derbyshire et al. 2018), increasing survival of the hoarder (Morrison et al. 2009), or increasing lifetime reproduction (Sechley et al. 2014). Given the potential implications of not scatterhoarding sufficient food or hoarding perishable food, scatterhoarders have developed behaviors that increase the likelihood that they benefit from stored food.

Throughout the process of scatterhoarding, hoarders may modify their behavior to account for the value of a seed being buried. For example, to reduce the risk of losing particularly valuable food to theft by other animals (i.e., pilferage), scatterhoarders may bury more valuable seeds in areas with higher predation risk to pilferers (Steele et al. 2011, 2015), or carry more valuable seeds farther away from potentially pilfering neighbors before burial (Gálvez et al. 2009b). Additionally, many scatterhoarding species preferentially hoard seeds with winter-long dormancy periods that can provide a viable food source through winter without germinating (Hadj-Chikh et al. 1996, Steele et al. 2006). Alternatively, perishable seeds without dormancy periods can be hoarded if the embryo is excised first, a behavior consisting of chewing the cotyledon out of the seed to kill it (Fox 1982). Eastern gray squirrels (*Sciurus carolinensis*), for example, will excise the embryos of nondormant seeds (e.g., white oak, *Quercus alba*) before burial to prevent losing that seed to germination. Food hoarders also preferentially store food that is free of insects or signs of rot to reduce the risk of spoilage (Smallwood et al. 2001, Weckerly and Nicholson 2017). Such knowledge of how scatterhoarders have adapted their behaviors to account for seed value in different situations helps scientists understand the evolution of scatterhoarding behavior. However, information is still needed on how scatterhoarders gather information about seed value.

Typically, scatterhoarders use a combination of olfactory cues and memory of cache locations to recover stored food they buried (Vander Wall 2000), while olfactory cues of stored seeds (Vander Wall 2000) and visual cues of a cache being made (Bugnyar and Kotrschal 2002, Steele et al. 2008) enhance the hoarder's ability to pilfer from other caches. However, evidence also indicates that scatterhoarders can recognize small seedlings as a visual cue of food belowground (Bossema 1979, Pyare and Longland 2000, Jansen et al. 2006, Kuprewicz 2015)**.** Given the importance of being able to recognize valuable seeds, scatterhoarders could have developed adaptations for associating characteristics of seedling growth with the value of the food below ground. Few studies have examined nutrition changes during the beginning stages of germination and seedling growth in acorns, though cotyledon seed weight of some species of scatterhoarded seeds decrease with increased seedling growth (Ovington and Macrae 1960, Jansen et al. 2006). Thus, seeds may become less valuable as seedling growth progresses, and scatterhoarders might use characteristics of the seedling to assess the nutrition left in the seed below. Indeed, Bossema (1979) found that European jays (*Garrulus glandarius*) used seedling characteristics, including stem height, as cues of which seeds below ground were still beneficial to dig up and eat. However, few other studies have quantified the seedling characteristics, such as stem height or leaf size, that are used as a signal of seed quality to scatterhoarders. As a result, a test is needed of whether scatterhoarders use seedling size, or other characteristics, as a cue of the relative benefit of a below-ground seed.

In this study, we investigated whether specific physical characteristics of the seedling (stem height, leaf number, leaf size, root length) were used by scatterhoarders as cues to nutritional changes in the underlying seed. We tested the hypothesis that scatterhoarders use seedlings as a visual cue of food belowground. We assumed that the nutritional value of a seed decreases with germination and seedling growth and thus we predicted that when encountering a germinating oak acorn with a seedling, scatterhoarders would be less likely to excavate, disperse, or use seeds as the seedling size increased. Investigating whether scatterhoarders perceive the benefit of a seed based on seedling characteristics helps provide more information about the complex behavior of scatterhoarding and how changes in food value impact animal behavior.

5.2 Methods

Study Area

We conducted this study on a 4.5-ha tract of woodland on the outskirts of Auburn University’s main campus in Auburn, Alabama (32.594, -85.489). Hickory (*Carya spp.*), oak (white oak and water oak, *Q. nigra*) and pine (longleaf pine, *Pinus palustris*; and loblolly pine, *P. taeda*) made up the canopy of the forest while the understory layer varied from open (under the mature oak and pine stands) to dense with invasive Chinese privet (*Ligustrum sinense*) and greenbriar (*Smilax* spp.). We primarily conducted our field work in an area with a closed canopy, open understory, and numerous snags and logs on the ground where we confirmed (through trapping and observations, SBR) that eastern gray squirrels and eastern chipmunks were present. Field work for this study was conducted 14 January – 14 March 2022 and 29 September – 1 November 2022. In previous research by two of the authors (SBR, TDS) at Lowndes Wildlife Management Area (about 145 km west of Auburn), eastern gray squirrels were observed still scatterhoarding food in late February (Wilson et al. 2023). Our study area is in the Fall Line Hills of the Southeastern Plains ecoregion (Griffith et al. 2001) with mean temperatures of 7.6 degrees Celsius in January and 26.7 degrees Celsius in July (NCEI 2019). Mean annual precipitation is 129.8 cm (NCEI 2019).

Acorn Collection

Only rot-free (hard-bodied), weevil-free (no exit holes) acorns were used in this study to increase the chances of a seed being hoarded (Steele et al. 1996). We collected northern red oak acorns in 2020, stored them at three degrees Celsius in a resealable bag with a moist paper towel until dormancy was broken (acorns cracked open and radicle began to emerge, Fox 1982). We deployed these acorns in September 2022, soon after dormancy was broken. We also collected white oak acorns when they became available in late October 2021 for deployment in January 2022. White oak acorns do not have a dormancy period, so we stored these acorns in a humid container immediately after collection to promote germination (Burns and Honkala 1990) and the seeds took 1 – 2 months for stems to emerge.

Acorn Germination and Tagging

Germinating acorns were each placed in an individual cell in one of four, 70-cell, covered, and vented germination containers with a small amount of potting soil to keep the seed moist. As the acorns progressed through germination, they were sorted into four grow trays based on approximate seedling size- none (no stem seen above the soil), small (short stem with no leaves), medium (small leaves starting to develop), and large (tall stem, leaves). The cells of each germination container were numbered and an equal number of acorns from each of the four trays were selected each day of deployment based on randomly generated cell numbers for each tray. As acorns were removed from the germination containers to be used for data collection, they were replaced with other acorns showing signs of initial germination (acorn shell split and tip of root was visible, Fox 1982) to ensure a large sample of acorns in various stages of germination was available throughout the study.

Prior to deployment in the field, we measured the mass (g), length (mm), and width (mm) of each acorn and various other measurements of seedling growth (length of epicotyl(s) in mm; length of roots in mm; length of leaves in mm; and the number of leaves). Mass of seeds included both the acorn and the seedling. We also marked each acorn with a unique code written on the shell with waterproof permanent marker. To tag acorns for ease of relocations, we poked a small hole into the acorn's shell and inserted a 12-cm length of wire fishing line with a numbered 4-cm x 1-cm aluminum tag (from a soda can) tied to the end. The wire was superglued into place within the acorn's shell. This 'tin-tagging' of seeds is commonly used to track hard mast that is manipulated and dispersed by scatterhoarders (Xiao et al. 2006). A piece of flagging was tied to each acorn's tag to aid in our recovery of the seed. Flagging has not been found to affect decisions made by scatterhoarders handling tagged acorns, other than aiding discovery (Hirsch et al. 2012). We performed preliminary acorn tagging and monitoring in the field in February 2021 to confirm that this method was acceptable for tracking seeds dispersed by rodents in our study area.

Field

Acorns in various stages of germination were tagged as described above and released in the field to monitor scatterhoarding activity (149 white oak acorns, 14 January – 14 March 2022; 68 northern red oak acorns, 29 September – 1 November 2022). All acorns were buried 2 – 3-cm below ground to mimic the scatterhoarding behavior of eastern gray squirrels in the study area (personal observation SBR). Each tagged acorn was located up to 5 times per week until it was handled by a squirrel. We recorded the fate of recovered (dug up) acorns as ignored (acorn was left in place after recovery, usually with teeth marks or other signs of handling), eaten (acorn shell pieces found), or stored (under leaf litter or soil in a new location). We also noted if acorns were transported before being handled. All stored acorns were checked to see if they were excised before burial (hole in seed coat and epicotyl chewed out, Fox 1982). If an acorn remained in the initial deployment location for over ten days of deployment, we recorded it as completely ignored.

Analysis

We considered the recovery process for scatterhoarded food to consist of 3 main behaviors: 1. the initial decision of digging up the seed, 2. handling the seed in situ or carrying it to a new location, and 3. the final behavior of ignoring, eating, or storing the seed. Therefore, we tested the impacts of seed and seedling characteristics on each step of this process. First, we ran a mixed effects Poisson regression using the "lme4" package in Program R (Bates et al. 2015, R Core Team 2021) to determine the impact of aboveground seedling characteristics (height of the tallest stem, leaf number, length of the longest leaf) on the number of days before squirrels recovered our buried acorns. We recorded the days until recovery of the seed as the number of days between when the seed was buried and the last day the seed was known to be buried. We assumed all seeds stayed buried for at least one day after deployment. For seeds that were never recovered, we recorded the total number of days they were buried. We included a random effect of Julian calendar day of deployment to account for any variation in behavior due to approaching the end of the scatterhoarding season. For each step within the recovery process, we tested for interactions between seed species and each of the seed or seedling measurements. If there were any significant interactions, we analyzed all of the data within the step for each seed species separately.

Next, for seeds that were dug up by scatterhoarders, we used a mixed-effects logistic regression to determine how visual cues of both the previously described aboveground seedling characteristics as well as the belowground seed characteristics (acorn length, width, mass, and root length) affected if the acorn was handled in situ or transported before further handling. We also included a random effect of Julian calendar day of deployment for the same reason described for the first model. Finally, we used logistic regression to determine how the perceived value each acorn was impacted by the aboveground seedling and belowground seed characteristics previously described. We defined valuable acorns as those that were eaten or stored and non-valuable acorns as those that were ignored.

5.3 Results

Deployment

We measured, tagged, and deployed 149 white oak acorns for hoarders to pilfer and handle during spring 2022, however 41 seeds ultimately showed evidence of weevils (i.e., exit holes in seed shells) and were removed from the study because hoarders typically do not bury weevil-infested seeds (Steele et al. 1996). Seventy-six of our 108 weevil-free acorns had at least one epicotyl and the tallest stem on each of these seeds was 74.96 ± 42.68 mm tall (mean ± standard deviation). Twenty-four seedlings had 2.54 ± 1.35 leaves and the longest leaf on each seedling was 25.81 ± 21.20 mm long. We also deployed 68 weevil-free northern red oak acorns during fall 2022 (Table 1). Twenty-five of these germinating acorns had at least one epicotyl and the tallest stem on each of these seeds was 94.01 ± 29.16 mm tall. Twenty-three seedlings had 6.35 ± 2.25 leaves and the longest leaf on each seedling was 56.36 ± 28.69 mm long.

Recovery

We found significant interactions between seed species and leaf number, stem length, and leaf length (all $P < 0.01$), therefore, we analyzed the effect of these seed and seedling characteristics on the days until recovery for each species separately. Of the 108 weevil-free white oak seeds we buried at the study area in spring 2022, 101 seeds were recovered by scatterhoarders. Hoarders recovered seeds 1.83 ± 1.97 days after deployment. About 76% ($n = 77$) of these white oak seeds were dug up by scatterhoarders after one day, while the longest lasting seeds ($n = 2$) were not recovered until 11 days after being released. The number of leaves (rate ratio [RR] = 0.67, 0.58 – 0.78, 95% confidence levels [C.L.]), length of the longest leaf (RR = 0.96, 0.95 – 0.98 95% C.L.), and height of the tallest stem (RR = 0.99, 0.99 – 0.99, 95% C.L.) were all significantly related to the time-to-recovery in univariate models (all $P < 0.001$, Table 2). However, we observed collinearity among all three variables in our model (variance inflation factor [VIF]: leaf number = 3.23, leaf length = 2.67, stem height = 1.50). In the multivariable model, with all three independent variables, we found that hoarders recovered white oak acorns more quickly with increases in height (cm) of the tallest stem (RR = 0.94, 0.91 – 0.98, 95% C.L., $P < 0.001$; Table 2) and as leaves grew longer (cm; RR = 0.74, 0.59 – 0.92, 95% C.L.; P = 0.01). Though no longer statistically significant in our multivariable model, estimates suggested that hoarders recovered acorns more slowly as the number of leaves on the seedling increased (RR = 1.12, 0.87 – 1.45, 95% C.L., P = 0.37).

During fall 2022, hoarders dug up 73% of our northern red oak acorns (n = 48) within one day of deployment and only 2 seeds were not recovered by hoarders after 13-14 days buried at our field site. In univariate models, only leaf length (cm) significantly impacted the number of days until seeds were recovered (RR = 0.92, 0.86 – 0.98, 95% C.I., P = 0.01; Table 2). However, as with our spring data, collinearity existed among our seedling measurements (VIF: leaf number = 5.53, leaf length = 3.95, stem height = 8.01). In our multivariable model, with these three independent variables included, we found that hoarders dug up our acorns more slowly (RR = 1.15, 1.04 – 1.27, 95% C.L.) as seedlings grew more leaves ($P < 0.01$), but acorns were recovered more quickly (RR = 0.81, 0.70 – 0.93, 95% C.L.) as the leaves grew longer (cm, $P < 0.01$). Stem height (cm) had no apparent relationship on time to recovery (RR = 0.98, 0.86 – 1.09, 95% C.L.; P = 0.74).

Dispersal

We found interactions between seed species and both seed mass and radicle length, so we analyzed the two species separately. Fifty-three of the 101 white oak acorns recovered by hoarders were carried to a new location during spring 2022. In univariate models, we found that an increase in seed mass increased the likelihood of the seed being dispersed (odds ratio [OR] = 1.34, 0.92 – 1.82, 95% C.L.), though this result was not quite statistically significant ($P = 0.06$). No other seed and seedling measurements had significant effects on the likelihood of a seed being dispersed after recovery (all $P > 0.17$, Table 3). Due to collinearity among our variables (all VIF > 1.23, Table 3), we kept all seven independent variables in our multivariable model and there were no significant effects of any of the seed or seedling measurements on the likelihood of seeds being dispersed (all $P > 0.24$, Table 3).

Of the 66 northern red oak acorns that were recovered by hoarders in fall 2022, 43 of these seeds were transported to another location. In univariate models, seed mass (OR = 0.76, 0.58 – 1.00, 95% C.L.; $P = 0.05$), radicle length (cm, OR = 0.66, 0.50 – 0.89, 95% C.L., $P < 0.01$), stem height (cm, OR = 0.90, 0.80 – 1.01, 95% C.L.; $P = 0.06$), number of leaves (OR = 0.85, 0.72 – 1.01, 95% C.L.; $P = 0.06$), and length of the longest leaf (cm, OR = 0.84, 0.71 – 1.01, 95% C.L.; $P = 0.06$) were all related to the likelihood of a seed being transported (Table 3). However, we detected substantial collinearity among our variables (VIF: leaf number = 3.57, stem length = 2.40, leaf length = 2.92, radicle length = 1.34, seed mass = 1.44). Due to this collinearity and all independent variables showing the same direction of effect, we only included these significant (or nearly significant) variables in our multivariable model. In this multivariable model, all p-values but that of radicle length lost significance (all other $P > 0.24$, Table 3). The likelihood of dispersal increased with increases in the number of leaves (OR = 1.02, 0.69 – 1.50, 95% C.I.) and stem length (cm, OR = 1.25, 0.86 – 1.84, 95% C.I.), though the p-values of both variables increased (both P > 0.23). Increases in leaf length (cm, OR = 0.77, 0.52 – 1.15, 95% C.I.), seed mass (OR = 0.95, 0.64 – 1.42, 95% C.I.), and the length of the radicle (cm, OR = 0.56, 0.29 – 1.02, 95% C.L.) decreased the likelihood of seeds being dispersed, though both leaf length and seed mass lost significance in our multivariable model (both P > 0.20, radicle length P = 0.053).

Final seed fate

We did not find any interactions between seed species and the seed or seedling measurements (all P > 0.56), therefore we combined all data (122 total seeds, Table 1) to determine the impacts of different measurements on the likelihood of seeds being used (eaten or buried) or ignored after recovery. Hoarders ignored 17% of seeds, ate 51%, and stored 5% (Table 1). We were not able to determine the fate of 44 seeds that were removed from their tags and carried away from the deployment location. In univariate analyses, we found that scatterhoarders were 0.24 (0.22 – 0.26, 95% C.L.) times as likely to use (eat or bury) seeds for each 1 cm increase in the width of the seed (P < 0.001, Table 4). As with our other models, collinearity was present among our variables (all VIF > 1.86, Table 4). Due to this collinearity and many of our variables showing opposite directions of effects, we included all seed and seedling measurements as independent variables in our multivariable model. In this model, seed width lost significance (cm, OR = 0.43, 0.03 – 6.75, 95% C.I., P = 0.54), though radicle length significantly increased the likelihood of seeds being eaten or buried (cm, OR = 1.45, 1.00 – 2.09, 95% C.I., P = 0.046). No other variables significantly impacted seed fate in this model (Table 4).

Due to the multicollinearity among many of our seed and seedling measurements, we performed principal component analysis for recovery behavior, dispersal behavior, and the final fate of seeds, though, these analyses did not improve our understanding of the results (See Appendix A).

5.4 Discussion

We did not find support for our hypothesis that scatterhoarders have adapted to seedling growth as a cue of belowground food nutritional value, as hoarders behaved opposite of what we expected; larger seedlings were typically recovered more quickly in both fall and spring. We had assumed that seedling growth would be correlated with decreases in the nutrients within the seed, and hence scatterhoarders would recover the smallest seedlings (i.e., the most valuable seeds) the fastest. Our results can be explained in a number of (non-mutually exclusive) ways: first, changes in nutritional value of seeds may not have been inversely correlated with seedling growth characteristics in our study; second, squirrels may have ignored (or been unaware of) nutritional condition of the seed; third, larger seedlings may have been easier for squirrels to find.

Seedlings growing in different conditions throughout an ecosystem (soil type, soil moisture, or amount of sunlight) could show different patterns of growth (e.g., taller stems in shade, shorter stems in sun) and seedlings in our study area could be exposed to enough different growing conditions that there is not a consistent type of growth associated with nutrients left in the seed (Guo et al. 2001, Perez-Ramos et al. 2010, Beals et al. 2022). This could lead to hoarders being exposed to seedlings that grow quickly, but do not have large changes in the nutrition of the seed early in the growth period. We assumed that values of seed nutrition perceived as valuable to hoarders (e.g., fat, Yadok et al. 2020; carbohydrates, protein, (Lichti et al. 2017) decreased at a noticeable rate early in the germination process, however we could not find any studies that had previously tested this relationship between seedling growth and seed nutrition. Our understanding of hoarder responses towards seedling growth could be enhanced with further study of the changes within the seed during germination process among hard masting species.

Another explanation for our results could be that larger seedlings do have lower value seeds, but that squirrels simply ignore the value of the seed in their decisions or otherwise that decision is context dependent. For example, in our study area, tall stems and long leaves encouraged recovery in spring but only long leaves encouraged recovery in fall, which could indicate that when scatterhoarded food is the main source of energy for hoarders (i.e., winter – spring), tall leaves could make the buried food more visible and accessible for recovery while during fall when food is abundant, larger leaves indicate a lower quality food item due to increased seedling growth. During winter and early spring when food is harder to find, slight difference in nutrition of seeds might not matter as much as having food to eat. For example, eastern gray squirrels have been found to eat lower quality food during winter when other higher quality foods are hard to find (Nixon et al. 1968, Wilson et al. 2020). These findings could also indicate that the behavior of using visual cues of seedlings could be plastic and these cues may be interpreted differently as the scatterhoarding season progresses.

Our finding that seedling characteristics can decrease the number of days before recovery provides evidence that seedlings can be used as a “flag” to guide hoarders to food located belowground. The use of seedlings as cues of belowground food has been noted in a variety of hoarding animals and the seed species they interact with: heteromyid rodents and Indian ricegrass (*Achnatherum hymenoides,* Pyare and Longland 2000), red acouchies (*Myoprocta exilis*) and African crabwood (*Carapa procera*, Jansen et al. 2006a), European jays and pedunculate oak (*Quercus robur*, Bossema 1979), spiny picket mice (*Heteromys desmarestianus*) and palm (*Astrocaryum mexicanum*, Brewer and Webb 2001) and Liaoning oak (*Q. wutaishanica*) and several rodent species (Zhang et al. 2022). However, prior to our study, seedling growth had been categorized rather than quantified as a continuous measurement from initial germination through large seedling (presence and absence of seedlings, Pyare and Longland 2000; 20 – 40 cm tall stem, Jansen et al. 2006a; 8 – 15 cm vs. 24 – 30 cm tall stems, Bossema 1979). To our knowledge, this use of seedlings as a visual cue of food to pilfer had not yet been demonstrated in eastern gray squirrels or eastern chipmunks.

We also found that seed and seedling characteristics had potential impacts on dispersal of seeds (positive, seed mass in spring; negative radicle length in fall). During spring, our finding that total mass of the seed had a positive effect on the decision to carry the seed to a new location is similar to many studies that suggest that larger seeds are more valuable, and more time and energy is invested in these seeds (Jansen et al. 2002, Wang and Chen 2009, Yi and Yang 2011, Wang et al. 2013, Lang and Wang 2016). During fall, the presence of a root could be the first indication of a seed beginning to spoil and the hoarder might then deem that seed as decreasing in value, and thus the seed is not worth the extra energy investment. Hoarders are known to invest more time and energy in seeds that are considered more valuable (Wang et al. 2013). Valuable seeds are often dispersed to a new location at least once to increase the distance from the source of food (Zhang et al. 2014), decrease the density of buried seeds owned by the hoarder (Kraus 1983), or to move the seed to a riskier location to prevent pilferage of that seed

(Steele et al. 2014). Pilferers might be using the mass of a seed as a cue of its value during spring, hence the behavior to disperse heavier seeds to new locations, whereas during fall, seeds with no or small roots are interpreted as more valuable.

Interestingly, we found a positive relationship between the root growth of the seedling and the propensity of hoarders to perceive seeds as valuable food (i.e., eat or store the seeds versus ignoring the seeds). Hoarders were more likely to eat or bury seeds with longer roots. Some species quickly grow taproots shortly after germination to transfer nutrients away from the seed that is susceptible to predation (such as white oak; Fox 1982). However, it is unlikely that hoarders sought out nutrient rich roots to eat, as the majority of our seeds' roots were chewed off and left at the spot of recovery. The final fate of seeds may have been more dependent on the hoarder's perceived costs (e.g., opportunity costs, predation risk) and benefits (energy gain from eating the seed) in that moment, rather than the condition or future value of the seed. We find it interesting, however, that seed mass impacted dispersal of seeds but did not impact whether the seeds were eaten or ignored, as would usually occur during the initial hoarding of a seed (Wang et al. 2013, Hou et al. 2021). Contrary to other studies that showed hoarders prefer to dig up seedlings with smaller leaves (Jansen et al. 2006) or shorter stems (Bossema 1979), we did not find an upper limit of seedling growth where hoarders ignored the seeds. In fact, our largest white oak seedling was eaten, and our largest northern red oak seedling was excised and buried. Indeed, we found ample evidence that eastern gray squirrels and eastern chipmunks will eat germinating seeds, which has been documented for few other species in prior studies (agouti, *Dasyprocta punctata*, Forget 1992; Japanese field mouse, *Apodemus argenteus* and large Japanese field mouse, *A. speciosus*, Soné et al. 2002; red acouchy, Jansen et al. 2006a; Siberian chipmunk, *Tamias sibiricus*, Deng et al. 2020)

Current research typically assumes that seeds are free from predation by scatterhoarders once the seed is past its initial germination stage and the seedling has begun to grow (Dracxler and Forget 2017, Bogdziewicz et al. 2020). However, our results indicate that seeds are not safe from predators immediately after germination and hoarders will eat seeds with large seedlings, potentially resulting in selection for acorns that quickly move seed resources to the seedling shortly after germination. Indeed, white oak acorns are known to transfer their nutrients to large taproots before growing a large stem (Fox 1982). This adaptation could help prevent seedling loss if the seed is removed by a predator (Fox 1982), as well as delay the appearance of the seedling cue for hoarders looking for food to recover. The majority of our seeds were removed from their seedlings before being dispersed. If the removed seedling was large enough, it could persist without further risk of predation by hoarders (Bossema 1979, Zhang et al. 2022). So, while small seedlings are still at risk of being removed prematurely from their seed (Bossema 1979), seedlings that grew fast enough could still escape from mortality. Thus, scatterhoarders may add a selection pressure for seedlings to grow quickly within the first several days after germination. Ultimately, from an evolutionary perspective, masting species can maximize their fitness if hoarders first disperse the seeds before germination and then germination progresses quickly so if a hoarder uses the seedling cue to recover the seed, the seedling can survive the encounter.

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5.6 Literature Cited

Andersson, M., and J. Krebs. 1978. On the evolution of hoarding behaviour. Animal Behaviour 26:707–711.

Bates, D., M. Martin, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67:1–48. doi:10.18637/jss.v067.i01.

Beals, K. K., A. E. Scearce, A. T. Swystun, and J. A. Schweitzer. 2022. Belowground mechanisms for oak regeneration: Interactions among fire, soil microbes, and plant community alter oak seedling growth. Forest Ecology and Management 503:119774.

Bogdziewicz, M., E. E. Crone, and R. Zwolak. 2020. Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. Journal of Ecology 108:1009–1018.

Bossema, I. 1979. Jays and oaks: An eco-ethological study of a symbiosis. Thesis, University of Groningen.

Boutin, S., K. W. Larsen, and D. Berteaux. 2000. Anticipatory parental care: Acquiring resources for offspring prior to conception. Proceedings of the Royal Society B: Biological Sciences 267:2081–2085.

Brewer, S. W., and M. A. H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. Oikos 93:32–41.

Bugnyar, T., and K. Kotrschal. 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: Is it “tactical” deception? Animal Behaviour 64:185–195.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Vol 2. Forest Service USDA, Washington, DC.

Deng, Y., J. U. Mengyao, and Y. I. Xianfeng. 2020. Exclusion of interspecific competition reduces scatter-hoarding of Siberian chipmunk Tamias sibiricus: A field study. Integrative Zoology 15:127–134.

Derbyshire, R., D. R. Norris, K. A. Hobson, and D. Strickland. 2018. Isotopic spiking and food dye experiments provide evidence that nestling Canada Jays (*Perisoreus canadensis*) receive cached food from their parents. Canadian Journal of Zoology 97:368–375.

Dracxler, C. M., and P.-M. Forget. 2017. Seed caching by rodents favours seedling establishment of two palm species in a lowland Atlantic forest remnant. Journal of Tropical Ecology 33:228–231.

Forget, P.-M. 1992. Seed removal and seed fate in Gustavia superba (Lecythidaceae). Biotropica 24:408–414.

Fox, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. Evolution 36:800–809.

Gálvez, D., B. Kranstauber, R. W. Kays, and P. A. Jansen. 2009. Scatterhoarding by the Central American agouti: A test of optimal cache spacing theory. Animal Behaviour 78:1327–1333.

Griffith, G. E., J. M. Omernik, J. A. Comstock, G. Martin, A. Goddard, and V. J. Hulcher. 2001. Ecoregions of Alabama. U.S. Environmental Protection Agency, National Health and Environmental Effects Research Laboratory, Corvallus, OR.

Guo, Y., M. G. Shelton, and B. R. Lockhart. 2001. Effects of light regimes on the growth of cherrybark oak seedlings. Forest Science 47:270–277.

Hadj-Chikh, L. Z., M. A. Steele, and P. D. Smallwood. 1996. Caching decisions by grey squirrels: A test of the handling time and perishability hypotheses. Animal Behaviour 52:941–948.

Hirsch, B. T., R. Kays, and P. A. Jansen. 2012. A telemetric thread tag for tracking seed dispersal by scatterhoarding rodents. Plant Ecology 213:933–943.

Hou, X., B. Zhang, M. A. Steele, N. Han, T. Feng, J. Wang, X. Chen, A. N. Xiaolei, and G. Chang. 2021. Seed traits and rodent community interact to determine seed fate: evidence from both enclosure and field experiments. Integrative Zoology 16:939–954.

Jansen, P. A., M. Bartholomeus, F. Bongers, J. A. Elzinga, J. den Ouden, and S. E. Van Wieren. 2002. The role of seed size in dispersal by a scatter-hoarding rodent. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation:209–225.

Jansen, P. A., F. Bongers, and H. H. T. Prins. 2006. Tropical rodents change rapidly germinating seeds into long-term food supplies. Oikos 113:449–458.

Kamil, A. C., and K. L. Gould. 2008. Memory in food caching animals. Pages 419–439 *in* R. Menzel and J. H. Byrne, editors. Learning and Memory: A Comprehensive Reference, Volume I Learning Theory and Behaviour. Amsterdam.

Kraus, B. 1983. A test of the optimal density model for seed scatterhoarding. Ecology 64:608–610.

Kuprewicz, E. K. 2015. Scatter hoarding of seeds confers survival advantages and disadvantages to large-seeded tropical plants at different life stages. PLoS ONE 10:1–16.

Lang, Z., and B. Wang. 2016. The effect of seed size on seed fate in a subtropical forest, Southwest of China. IForest 9:652–657.

Li, Y., D. Zhang, H. Zhang, Z. Wang, and X. Yi. 2018. Scatter-hoarding animal places more memory on caches with weak odor. Behavioral Ecology and Sociobiology 72:1–8.

Lichti, N. I., M. A. Steele, and R. K. Swihart. 2017. Seed fate and decision-making processes in scatter-hoarding rodents. Biological Reviews 92:474–504.

Macdonald, I. M. V. 1997. Field experiments on duration and precision of gray and red squirrel spatial memory. Animal Behaviour 54:879–891.

Morris, D. 1962. The behavior of the green acouchi (*Myoproctapratti*) with special reference to scatterhoarding. Proceedings of the Zoological Society of London 139:701–732.

Morrison, S. F., G. Pelchat, A. Donahue, and D. S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159:107–116.

Nixon, C. M., D. M. Worley, and M. W. McClain. 1968. Food habits of squirrels in southeast Ohio. The Journal of Wildlife Management 32:294–305.

Ovington, J. D., and C. Macrae. 1960. The growth of seedlings of *Quercus Petraea*. Journal of Ecology 48:549–555.

Perez-Ramos, I. M., L. Gomez-Aparicio, R. Villar, L. V Garcıá, and T. Maranon. 2010. Seedling growth and morphology of three oak species along field resource gradients and seed mass variation: A seedling age-dependent response. Journal of Vegetation Science 21:419–437.

Pyare, S., and W. S. Longland. 2000. Seedling-aided cache detection by heteromyid rodents. Oecologia 122:66–71.

Sechley, T. H., D. Strickland, and D. R. Norris. 2014. Causes and consequences of pre-laying weight gain in a food-caching bird that breeds in late winter. Journal of Avian Biology 45:85–93.

Smallwood, P. D., M. A. Steele, and S. H. Faeth. 2001. The ultimate basis of caching preferences of rodents, and the oak-dispersal syndrome: Tannins, insects, and seed germination. American Zoologist 41:840–851.

Soné, K., S. Hiroi, D. Nagahama, C. Ohkubo, E. Nakano, S. I. Murao, and K. Hata. 2002. Hoarding of acorns by granivorous mice and its role in the population processes of *Pasania edulis* (Makino) Makino. Ecological Research 17:553–564.

Steele, M. A., M. Bugdal, A. Yuan, A. Bartlow, J. Buzalewski, N. Lichti, and R. K. Swihart. 2011. Cache placement, pilfering, and a recovery advantage in a seed-dispersing rodent: Could predation of scatter hoarders contribute to seedling establishment? Acta Oecologica 37:554–560.

Steele, M. A., T. A. Contreras, L. Z. Hadj-Chikh, S. J. Agosta, P. D. Smallwood, and C. N. Tomlinson. 2014. Do scatterhoarders trade off increased predation risks for lower rates of cache pilferage? Behavioral Ecology 25:206–215.

Steele, M. A., L. Z. Hadj-Chikh, and J. Hazeltine. 1996. Caching and feeding decisions by *Sciurus carolinensis*: Responses to weevil-infested acorns. Journal of Mammalogy 77:305–314.

Steele, M. A., S. L. Halkin, P. D. Smallwood, T. J. McKenna, K. Mitsopoulos, and M. Beam. 2008. Cache protection strategies of a scatterhoarding rodent: Do tree squirrels engage in behavioral deception? Animal Behaviour 75:705–714.

Steele, M. A., S. Manierre, T. Genna, T. A. Contreras, P. D. Smallwood, and M. E. Pereira. 2006. The innate basis of food hoarding decisions in gray squirrels: Evidence for behavioral adaptations to the oaks. Animal Behaviour 71:155–160.

Steele, M. A., G. Rompré, J. A. Stratford, H. Zhang, M. Suchocki, and S. Marino. 2015. Scatterhoarding rodents favor higher predation risks for cache sites: The potential for predators to influence the seed dispersal process. Integrative Zoology 10:257–266.

Vander Wall, S. B. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behavioral Ecology 11:544–549.

Wang, B., and J. Chen. 2009. Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. Ecology 90:3023–3032.

Wang, B., C. X. Ye, C. H. Cannon, and J. Chen. 2013. Dissecting the decision making process of scatterhoarding rodents. Oikos 122:1027–1034.

Weckerly, F. W., and K. E. Nicholson. 2017. Experimental test of discrimination by squirrels for insect-infested and noninfested acorns. The American Midland Naturalist 12:412–415.

Wilson, S.B., R. A. Gitzen, S. S. Ditchkoff, and T. D. Steury. 2023. Behavioral Adaptations of Scatterhoarders to Seasonal Flooding. Canadian Journal of Zoology. Just-IN https://doi.org/10.1139/cjz-2023-0024

Wilson, S. B., T. D. Steury, R. A. Gitzen, and S. S. Ditchkoff. 2020. Fall and winter diets of eastern gray squirrels in a seasonally flooded ecosystem in Alabama. Southeastern Naturalist 19:771–780.

Xiao, Z., P. A. Jansen, and Z. Zhang. 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. Forest Ecology and Management 223:18–23.

Yadok, B., P. Forget, D. Gerhard, B. Aliyu, and H. Chapman. 2020. Seed nutrient content rather than size influences seed dispersal by scatterhoarding rodents in a West African montane forest. Journal of Tropical Ecology. 36:174–181.

Yi, X., and Y. Yang. 2011. Scatterhoarding of Manchurian walnut Juglans mandshurica by small mammals: Response to seed familiarity and seed size. Acta Theriologica 56:141–147.

Zhang, H., M. A. Steele, Z. Zhang, W. Wang, and Y. Wang. 2014. Rapid sequestration and recaching by a scatterhoarding rodent (*Sciurotamias davidianus*). Journal of Mammalogy 95:480–490.

Zhang, J., X. Yan, B. Dayananda, Y. Luo, and J. Li. 2022. Frequency-dependent predation and seedling fate: Effect of forest litter on regeneration of the *Quercus wutaishanica* seedling. Global Ecology and Conservation 38:e02233.

Tables

Table 5.01. Mass (g), height of the tallest stem (mm), and number of leaves on germinating acorns deployed in Spring 2022 (white oak, *Quercus alba*) and Fall 2022 (northern red oak, *Quercus rubra*) to be handled by hoarding rodents in Auburn, Alabama. Stem height and leaf number calculations include seeds without stems or leaves.

		n	Mass	Stem Height	No. Leaves
			Total Deployed		
Spring		108	4.90 ± 2.48	54.14 ± 49.49	0.56 ± 1.23
Fall		68	6.67 ± 2.10	34.56 ± 48.89	2.15 ± 3.29
			Recovered		
Spring	Yes	101	4.92 ± 1.56	56.60 ± 49.84	0.60 ± 1.27
	No	7	4.61 ± 1.49	18.65 ± 26.32	0 ± 0
Fall	Yes	66	6.69 ± 2.12	35.61 ± 49.25	2.21 ± 3.32
	No	2	0 ± 0	0 ± 0	6.07 ± 1.60
			Transported		
Spring	Yes	53	5.21 ± 1.58	51.32 ± 47.41	0.51 ± 1.20
	No	48	4.61 ± 1.49	62.41 ± 52.28	0.71 ± 1.34
Fall	Yes	43	6.69 ± 2.12	26.69 ± 47.85	2.21 ± 3.32
	No	23	7.46 ± 2.42	52.29 ± 48.47	3.30 ± 3.70
			Known Final Fate		
Spring	Ignored	8	4.69 ± 0.99	62.25 ± 70.49	0.75 ± 1.49
	Eaten	64	4.86 ± 1.67	58.10 ± 50.40	0.70 ± 1.39

	Stored	4	4.01 ± 0.86	62.96 ± 22.43	0.25 ± 0.50
	Ignored	21	7.06 ± 2.52	42.42 ± 48.04	2.62 ± 3.65
Fall	Eaten	21	7.27 ± 2.22	54.97 ± 56.00	3.24 ± 3.33
	Stored	4	27.90 ± 55.80	6.06 ± 1.03	1.75 ± 3.50

Table 5.02. Results from univariate and multivariate models analyzing the days until recovery (being dug up) by scatterhoarders for seed buried in Auburn, Alabama. Germinating seeds were tagged and measured for seedling growth (mm) before being buried in the field in spring 2022 (108 white oak, *Quercus alba*) and fall 2022 (and 68 northern red oak, *Quercus rubra*) for hoarders to dig up. RR = rate ratio, CI = confidence interval, VIF = variance inflation factor.

		Univariate			Multivariate			
	Coefficient	RR	CI	P-value	RR	CI	P-value	VIF
Spring	Leaf Number	0.67	0.58 – 0.78	< 0.001	1.12	0.87 – 1.44	0.37	3.23
	Stem Length	0.99	0.99 – 0.99	< 0.001	0.99	0.99 – 1.00	< 0.001	1.50
	Leaf Length	0.96	0.95 – 0.98	< 0.001	0.97	0.95 – 0.99	0.01	2.67
Fall	Leaf Number	0.98	0.93 – 1.03	0.45	1.15	1.03 – 1.29	0.01	5.53
	Stem Length	1.00	0.99 – 1.00	0.08	1.00	0.99 – 1.01	0.74	8.01
	Leaf Length	0.99	0.98 – 1.00	0.01	0.98	0.97 – 0.99	< 0.01	3.95

Table 5.03. Results from univariate and multivariate models analyzing the likelihood of seeds being dispersed by scatterhoarders in Auburn, Alabama. Germinating seeds were tagged and measured for seed size (mm, g) and seedling growth (mm) before being buried in the field in spring 2022 (101 white oak, *Quercus alba*) and fall 2022 (and 66 northern red oak, *Quercus rubra*) for hoarders to dig up. OR = odds ratio, CI = confidence interval, VIF = variance inflation factor

		Univariate			Multivariate			
	Coefficient	OR	CI	P-value	OR	CI	P-value	VIF
Spring	Leaf number	1.07	0.73 – 1.58	0.73	1.23	0.59 – 2.57	0.58	3.28
	Stem length	1.03	0.99 – 1.01	0.59	1.00	0.98 – 1.01	0.82	1.83
	Leaf length	0.90	0.95 – 1.03	0.60	0.96	0.90 – 1.03	0.29	2.68
	Root length	1.02	0.99 – 1.04	0.17	1.01	0.99 – 1.04	0.41	1.23
	Seed mass	1.34	0.98 – 1.82	0.06	1.34	0.82 – 2.18	0.24	2.52
	Seed length	1.14	0.89 – 1.45	0.30	1.07	0.66 – 1.75	0.78	2.02
	Seed width	1.25	0.90 – 1.73	0.17	0.96	0.71 – 1.31	0.81	1.58
Fall	Leaf number	0.85	0.72 – 1.01	0.06	1.02	0.69 – 1.50	0.92	3.57
	Stem length	0.99	0.98 – 1.00	0.06	1.02	0.98 – 1.06	0.24	2.40
	Leaf length	0.98	0.97 – 1.00	0.06	0.97	0.94 – 1.01	0.20	2.92
	Root length	0.96	0.93 – 0.99	< 0.01	0.94	0.88 – 1.00	0.05	1.34
	Seed mass	0.76	0.58 – 1.00	0.05	0.95	0.64 – 1.42	0.82	1.44
	Seed length	0.97	0.78 – 1.21	0.76	--	--	--	--
	Seed width	0.85	0.61 – 1.19	0.33	--	--	--	--

Table 5.04. Results from univariate and multivariate models analyzing the likelihood of seeds being used (eaten or buried) or ignored by hoarders in Auburn, Alabama. Germinating seeds (76 white oak, *Quercus alba* and 46 northern red oak, *Quercus rubra*) were tagged and measured for seed size (mm, g) and seedling growth (mm) before being buried in the field for hoarders to dig up. OR = odds ratio, CI = confidence interval, VIF = variance inflation factor

	Univariate			Multivariate			
Coefficient	OR	CI	P-value	OR	CI	P-value	VIF
Stem Length	1.00	0.99 – 1.01	0.74	1.00	0.98 – 1.02	0.95	3.44
Leaf Number	0.95	0.79 – 1.14	0.57	0.89	0.67 – 1.18	0.41	3.12
Leaf Length	0.99	0.97 – 1.02	0.60	1.01	0.97 – 1.05	0.61	2.42
Root Length	1.02	0.99 – 1.05	0.15	1.04	1.00 – 1.08	0.05	2.16
Seed Mass	0.91	0.70 – 1.17	0.44	0.76	0.51 – 1.11	0.15	3.70
Seed Width	0.87	0.86 – 0.87	< 0.001	0.92	0.70 – 1.21	0.54	2.36
Seed Length	1.04	0.84 – 1.29	0.70	1.14	0.88 – 1.48	0.31	1.86

Appendix A. Principal Component Analyses Results

Recovery

For all seeds released into the field in spring 2022, the first principal component (hereafter, PC) explained 77% of variation within the data and this PC represented a size component, particularly describing seeds with tall, large-leafed seedlings (Table S1). We included all three PCs as independent variables in a mixed-effects Poisson regression model to investigate the effect of these PCs on the number of days until seeds were dug up by hoarders. We included a random effect of the day of deployment in this model to account for changes in hoarder behaviors based on the progression of the scatterhoarding season. We found that hoarders recovered seeds with larger seedlings more quickly (PC1, RR = 0.68, 0.61 – 0.77, 95% C.I., $P < 0.001$). Seedlings with moderate stem height and a smaller number of large leaves were also recovered in fewer days (PC3, Table S1; RR = 0.63, 0.40 – 0.95, 95% C.I., Table S2).

For seeds released into the field in fall 2022, the first PC accounted for 87% of variation in our dataset and described seeds with tall stems and many, long leaves (Table S1). We included our three PCs in a mixed-effects Poisson regression model as described above. Similar to our spring results, large seeds were dug up more quickly (PC1, RR = 0.89, 0.80 – 1.00, 95% C.I., $P = 0.04$; Table S2). We also found that hoarders took longer (PC2, RR = 1.38, 0.99 – 1.91, 95% C.I.) to dig up seeds with small stems and very few, but large, leaves ($P = 0.05$; Table S1).

Dispersal

For white oak seeds recovered by scatterhoarders in spring 2022, the majority of the variation in the data (80%) was described by PC1 (42%), PC2 (24%), and PC3 (15%, Table S3). The first PC described small, lightweight seeds with very little seedling growth, PC2 described large, heavy seeds with very little seedling growth, and PC3 described seeds with very little root growth (Table S3). We include all seven PCs as independent variables in a mixed-effects logistical regression model to determine their effect on the likelihood of dispersal of seeds. As described above, we included a random effect of the deployment date of the seed. We did not find any significant effects of any of the seven PCs on the likelihood of seeds being dispersed (all $P > 0.11$, Table S4).

For northern red oak seeds recovered by scatterhoarders in fall 2022, the majority of variation in the data (80%) was described by PC1 (61%) and PC2 (19%, Table S4). PC1 was a size-based component and described larger seeds with large seedlings, while PC2 described large, heavy seeds with little seedling growth (Table S5). We ran a similar model as described for the spring dispersal data. Larger seeds (PC1) were less likely (odds ratio [OR] = 0.72, 0.53 – 0.96, 95% C.I.) to be dispersed ($P = 0.02$; Table S4).

Final Fate

In previous analyses, we did not find any significant interactions between the seed species and any of our seed or seedling measurements when analyzing the final fate of seeds, so we included all seeds with known fates in our principal component analysis (PCA). The majority of the variance within the data was explained by PC1 (49%) and PC2 (22%, Table S6). As with our previous PCAs for recovery and dispersal, the first PC was based on large seed and seedling size. The seeds described by PC2 were small, lightweight, but had larger roots and tall stems. We included the PCs in a mixed-effects logistic regression model to determine the effect of each PC on the likelihood that a seed would be used (eaten or buried) rather than ignored. We found increases in the likelihood of being used for seeds as described by PC2 (OR = 1.66, 1.11 – 2.48, 95% C.I., $P = 0.01$,

Table S7) and for seeds with small roots and long leaves (PC3, Table S6; OR = 1.69, 0.99 – 2.88, 95% C.I.)

Table S5.01. Loadings of principal component analysis describing germinating seeds measured for seedling growth then tagged and buried for scatterhoarders to dig up. White oak (*Quercus alba*, n = 108) seeds were released in spring 2022 and northern red oak (*Quercus rubra*, n = 68) seeds were released in fall 2022 in Auburn, AL.

	Spring			Fall		
	PC1	PC2	PC3	PC1	PC2	PC3
Stem Length	0.55	-0.79	0.26	0.60	-0.19	-0.78
Leaf Number	0.61	0.16	-0.78	0.58	-0.57	0.58
Leaf Length	0.58	0.59	0.57	0.56	0.80	0.23
Standard Deviation	1.52	0.67	0.47	1.62	0.54	0.30
Proportion of Variance	0.77	0.15	0.07	0.87	0.10	0.03
Cumulative Proportion	0.77	0.93	1.00	0.87	0.97	1.00

Table S5.02. Effects of principal components (PC) on the days until germinating seeds were dug up by scatterhoarders in Auburn, Alabama (spring 2022, white oak, *Quercus alba*, n = 108; fall 2022, northern red oak, *Quercus rubra*, n = 68). RR = rate ratio, LCL = lower confidence limit, UCL = upper confidence limit

		RR	LCL	UCL	P-value
Spring	PC1	0.68	0.61	0.77	< 0.001
	PC2	0.92	0.74	1.14	0.43
	PC3	0.63	0.42	0.95	0.02
Fall	PC1	0.89	0.80	1.00	0.04
	PC2	1.38	0.99	1.91	0.05
	PC3	0.59	0.31	1.12	0.10

Table S5.03. Loadings of principal component analysis describing germinating white oak (*Quercus alba*, n = 101) seeds dug up by scatterhoarders in **spring 2022**. Seeds were measured for seed and seedling characteristics before being tagged and released in the field in Auburn, AL.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Stem Length	-0.42	-0.33	-0.17	-0.48	0.58	-0.22	0.25
Leaf Number	-0.47	-0.35	0.14	-0.05	-0.24	-0.08	-0.76
Leaf Length	-0.40	-0.43	0.21	0.27	-0.32	0.40	0.52
Root Length	-0.14	0.01	-0.93	0.09	-0.16	0.28	-0.08
Seed Length	-0.39	0.43	0.14	0.39	0.55	0.40	-0.17
Seed Width	-0.28	0.53	0.12	-0.65	-0.35	0.27	0.08
Seed Mass	-0.44	0.36	-0.09	0.32	-0.22	-0.69	0.21
Standard Deviation	1.71	1.28	1.03	0.72	0.60	0.54	0.45
Proportion of Variance	0.42	0.24	0.15	0.07	0.05	0.04	0.03
Cumulative Proportion	0.42	0.65	0.80	0.88	0.93	0.97	1.00

Table S5.04. Effects of principal components (PC) on the likelihood a germinating seed was dispersed or handled in situ upon recovery by scatterhoarders in Auburn, Alabama (spring 2022, white oak, *Quercus alba*, n = 101; fall 2022, northern red oak, *Quercus rubra*, n = 66). OR = odds ratio, LCL = lower confidence limit, UCL = upper confidence limit

	Spring				Fall			
	OR	LCL	UCL	P-value	OR	LCL	UCL	P-value
PC1	1.11	0.79	1.56	0.53	0.72	0.53	0.96	0.02
PC2	1.42	0.92	2.20	0.11	0.80	0.47	1.38	0.42
PC3	1.37	0.85	2.19	0.19	0.86	0.35	2.07	0.73
PC4	1.13	0.57	2.25	0.71	0.64	0.25	1.59	0.32
PC5	0.98	0.41	2.33	0.96	2.87	0.64	12.88	0.16
PC6	0.63	0.23	1.72	0.36	0.31	0.08	1.24	0.09
PC7	1.59	0.45	5.57	0.46	0.25	0.02	3.49	0.29

Table S5.05. Loadings of principal component analysis describing germinating white oak (*Quercus rubra*, n = 66) seeds dug up by scatterhoarders in **fall 2022**. Seeds were measured for seed and seedling characteristics before being tagged and released in the field in Auburn, AL.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Stem Length	0.43	-0.30	0.15	0.07	0.26	0.03	0.79
Leaf Number	0.41	-0.32	0.19	-0.17	0.17	-0.68	-0.40
Leaf Length	0.37	-0.35	-0.11	0.66	-0.41	0.24	-0.25
Root Length	0.43	-0.05	0.06	-0.49	0.21	0.65	-0.31
Seed Length	0.24	0.65	0.43	0.45	0.35	0.02	-0.12
Seed Width	0.34	0.32	-0.85	0.03	0.20	-0.15	0.03
Seed Mass	0.38	0.40	0.15	-0.30	-0.73	-0.14	0.19
Standard Deviation	2.07	1.14	0.72	0.64	0.49	0.42	0.27
Proportion of Variance	0.61	0.19	0.07	0.06	0.03	0.02	0.01
Cumulative Proportion	0.61	0.80	0.87	0.93	0.96	0.99	1.00

Table S5.06. Loadings of principal component analysis describing germinating white oak (spring 2022; *Quercus alba*, n = 76) and northern red oak (fall 2022, *Quercus rubra*, n = 46) seeds that were known to be eaten, buried, or ignored after being dug up by scatterhoarders. Seeds were measured for seed and seedling characteristics before being tagged and released in the field in Auburn, AL.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Stem Length	0.37	0.50	-0.02	-0.30	-0.03	-0.58	0.44
Leaf Number	0.47	0.10	0.23	0.08	0.74	-0.01	-0.40
Leaf Length	0.38	0.28	0.54	-0.14	-0.49	0.46	-0.12
Root Length	0.23	0.45	-0.68	0.36	-0.19	0.16	-0.30
Seed Length	0.33	-0.41	-0.39	-0.72	-0.07	0.09	-0.21
Seed Width	0.37	-0.46	0.13	0.40	-0.39	-0.52	-0.23
Seed Mass	0.45	-0.30	-0.14	0.29	0.14	0.38	0.67
Standard Deviation	1.85	1.24	0.95	0.66	0.53	0.49	0.43
Proportion of Variance	0.49	0.22	0.13	0.06	0.04	0.03	0.03
Cumulative Proportion	0.49	0.71	0.84	0.90	0.94	0.97	1.00

Table S5.07. Effects of principal components (PC) on the likelihood a germinating seed was used (eaten or buried) or ignored by scatterhoarders in Auburn, Alabama (spring 2022, white oak, *Quercus alba*, n = 76; fall 2021, northern red oak, *Quercus rubra*, n = 46). OR = odds ratio, CI = confidence interval.

	OR	CI	P-value
PC1	0.87	0.69 – 1.09	0.21
PC2	1.66	1.11 – 2.48	0.01
PC3	1.69	0.99 – 2.88	0.05
PC4	0.75	0.36 – 1.54	0.42
PC5	1.61	0.69 – 3.71	0.26
PC6	1.10	0.42 – 2.87	0.84
PC7	1.69	0.57 – 5.03	0.34