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Cache decisions, competition, and cognition in the fox squirrel, *Sciurus niger*

by

Mikel M. Delgado

A dissertation submitted in partial satisfaction of the
requirements for the degree of
Doctor of Philosophy

in

Psychology

in the

Graduate Division
of the
University of California, Berkeley

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Summer 2017

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Abstract

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Doctor of Philosophy in Psychology

University of California, Berkeley

Lucia F. Jacobs, Chair

Caching is the movement and storage of food items by animals for future use. Caching facilitates survival during periods of scarcity, may reduce foraging time during future searches for food, and allows animals to take advantage of periods when available food exceeds current needs. Scatter-hoarding animals store one item per cache, and must employ cognitive strategies to protect their caches. These strategies include assessing the relative value of food items, carefully hiding food items, deceptive behaviors to thwart potential pilferers, and remembering each cache location. Such decisions should be driven by economic variables, such as the value of the individual food items, the scarcity of these items, and competition and risk of pilferage by conspecifics.

My dissertation begins with a general overview of the food-storing literature and the natural caching behavior of the scatter-hoarding fox squirrel (*Sciurus niger*). I then describe several experiments that explored the decisions fox squirrels make when storing food. A study examining how fox squirrels adjust effort assessing and caching food based on the food item's value (weight, perishability and nutritional content) using two different foods, hazelnuts and peanuts, is described in Chapter 2. Squirrels ($n = 23$) were observed during natural periods of food scarcity (summer) and abundance (fall). Assessment and investment per cache increased when resource value was higher (hazelnuts) or resources were scarcer, but decreased as experimental sessions continued. This study showed that fox squirrels' assessment and caching behaviors were sensitive to both daily and seasonal resource abundance.

Another important problem facing scatter-hoarding animals is how to maximize the retrieval of stored food items while minimizing the risk of pilferage by competitors. One defense against theft could be the spatial placement of caches. I describe a study examining whether the spatial distribution of caches is dependent on nut species in Chapter 3. I measured four key variables of the cache decision: distance and direction traveled, the use of distinct cache areas by nut species, and density of caches. Fox squirrels ($n = 48$) were tested in 50 sessions, and the geographical coordinates of over 900 cache locations were recorded. Results suggested that squirrels distribute caches using three heuristics: matching the distance traveled before caching to the value of the food item, systematically covering a caching area, and matching cache density to minimize pilferage risk to the highest valued food items. Squirrels spatially chunked their

caches by nut species, but only when foraging from a single location. This first demonstration of spatial chunking in a scatter-hoarder underscores the cognitive demand of scatter-hoarding.

I describe a final field study in Chapter 4. A pilot study revealed that there was a high level of pilfering (25%) among a population of fox squirrels. Nineteen fox squirrels cached 294 hazelnuts with passive integrated transponder tags implanted in them. Variables collected included assessment and cache investment and protection behaviors; cache location, substrate, and conspicuousness of each cache; how long each cache remained in its original location, and the location where the cache was finally consumed. polymer chain reaction (PCR) analysis of hair samples obtained from 14 of the subjects was used to determine relatedness among this group of squirrels, and its potential impact on behavior. Results suggest that cache protection behaviors and the lifespan of a cache are dependent on the conspicuousness of a cache. Squirrels may mitigate some of the costs of pilfering by caching closer to the caches of related squirrels than to those of non-related squirrels.

In Chapter 5, I describe a model of the antagonistic relationship between food storing animals and their competitors using agent-based simulations where caching, memory size, and pilfering co-evolve. During periods of food abundance and scarcity, individuals could consume or store found items, retrieve old caches, or pilfer others' caches. In the absence of pilfering, selection is strongest for longer memory. As pilfering increases, shorter memory may be more adaptive, because old caches are likely to be depleted. Contrary to common thought that social interactions enhance cognition, these findings demonstrate how competition may constrain rather than promote some cognitive abilities.

Finally, in Chapter 6, I argue that my research demonstrates that food assessment and cache investment strategies of fox squirrels represent a complex suite of behaviors. These behaviors allow squirrels to maximize the benefits of periods of excess food in the environment, while increasing the likelihood of retrieving nuts later, when food in the environment is scarce. Competition via pilfering influences these food-storing decisions and outcomes, and in some cases, may impair the cognitive abilities of food-storing animals. I discuss the overall implications of this work, and potential directions for future research.

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Table of Contents

List of Figures	vii
List of Tables	viii
Chapter 1: Introduction	1
1.1. General Introduction	1
1.2. The Scatter-hoarding Tree Squirrel.....	2
1.3. Storage of Food	3
1.4. Agent-based Modeling and Simulation (ABMS).....	4
1.5. Precis	5
Chapter 2: Fox squirrels match food assessment and cache effort to value and scarcity ...	7
2.1 Introduction	7
2.2 Methods.....	10
2.2.1. Study Site.....	10
2.2.2. Study Animals	10
2.2.3. Procedure	11
2.2.4. Statistical Analyses.....	12
2.3. Results	12
2.3.1. Assessment Behaviors	12
2.3.2. Travel Time	13
2.3.3. Investment in caches.....	14
2.3.4. Concealment of caches	15
2.3.5. Outcome.....	16
2.4 Discussion	17
Chapter 3: Where to bury a nut: The adaptive geometry of cache distribution	21
3.1. Introduction	21
3.2. Methods.....	23
3.2.1. Study Site.....	23
3.2.2. Study Animals	23
3.2.3. Procedure	24
3.3.4. Determining GPS Accuracy	26
3.2.5. Statistical Analyses.....	26
3.3. Results	27

3.3.1. Nut species, weight, source type, and sequence impact distance traveled from food source to cache.	27
3.3.2. Central-place foraging increases directionality of caching.	28
3.3.3. Squirrels cache higher-valued food items at lower density, except when food is presented from multiple sources and in pseudorandom order.	28
3.3.4. Squirrels organize caches by food type when centrally-sourcing food items.	30
3.4. Discussion	32
Chapter 4: Cache life: Factors related to how long nuts remain where squirrels buried them.....	36
4.1. Introduction	36
4.2. Experiment 1: Testing squirrel responses to stimuli	38
4.2.1. Methods.....	38
4.2.1.1. Study Site.....	38
4.2.1.2. Study Animals	38
4.2.1.3. Procedure	38
4.2.2. Results of Experiment 1	39
4.3. Experiment 2: Assessing pilferage in the field.....	39
4.3.1. Methods.....	39
4.3.1.1. Study Site.....	39
4.3.1.2. Study Animals	39
4.3.1.3. Procedure	40
4.3.2. Results of Experiment 2	40
4.4. Experiment 3: Field Study	41
4.4.1. Methods.....	41
4.4.1.1. Study Site.....	41
4.4.1.2. Study Animals	41
4.4.1.3. Experimental Stimuli.....	41
4.4.1.4. Procedure	41
4.4.1.5. Statistical Analyses.....	43
4.5. Experiment 3: DNA Collection and Analysis.....	43
4.5.1. Methods.....	43
4.5.1.1. Study Site.....	43
4.5.1.2. Study Animals	43

4.5.1.3. Procedure: Hair Collection	43
4.5.1.4. Procedure: Preparation of Hair Samples	44
4.5.1.5. DNA Amplification, PCR, and Sequencing	45
4.5.1.6. Statistical Analyses	45
4.5.2. Results of Experiment 3	48
4.5.2.1. Cache outcomes	48
4.5.2.2. Microsatellite analysis	48
4.5.2.3. Spatial distribution of caches	50
Discussion	54
Chapter 5: Pilfering imposes limits on the memory of food-storing animals	58
5.1. Introduction	58
5.2. Methods	59
5.2.1. The model	59
5.2.2. The population	59
5.2.3. The environment	60
5.2.4. Behaviors: Foraging, caching and pilfering	60
5.2.5. Genetic selection and reproduction	61
5.2.6. Implementation of the model	61
5.2.7. Data analysis	61
5.3. Results	61
5.4. Discussion	62
Chapter 6: Conclusions	65
References	70

List of Figures

Figure 2.1. Fox squirrel food assessment behaviors.	8
Figure 2.2. A representation of the hypothetical decision-making process in squirrels	9
Figure 2.3. The effect of trial number on assessment.	13
Figure 2.4. Time spent paw manipulating and covering caches by nut species and season.	14
Figure 2.5. Assessment and cache protection by trial.....	14
Figure 2.6. Mean time spent travelling, covering caches and number of ICs by condition and season.	15
Figure 2.7. Time spent caching and covering caches under competition.	15
Figure 2.8. Outcome by assessment.....	16
Figure 2.9. All cache decisions for each squirrel in the study by season and condition...	18
Figure 3.1. Distance (m) travelled from the food source to cache location by condition and nut species.	27
Figure 3.2. Correlation between weight (g) and distance traveled (m) by nut species.	28
Figure 3.3. Nearest Neighbor (NN) distance (m) by condition and nut species.	29
Figure 3.4. Percent of spatial overlap by cache species for each condition.....	31
Figure 3.5. Examples of cache distributions under different conditions.	32
Figure 4.1. Pilfering of caches made by the focal squirrel.	40
Figure 4.2. Hair collection procedures.....	44
Figure 4.3. Total cache time (seconds) in the presence of other squirrels.....	49
Figure 4.4. Cache investment and protection at different levels of cache conspicuousness.	50
Figure 4.5. The relationship between relatedness and distance between caches.	51
Figure 4.6. Distance traveled for each cache buried by each week of the experiment.	53
Figure 4.7. Polygons depicting the minimum bounding geometry for caches made by all squirrels for each week of the experiment.	54
Figure 5.1. Average memory length under different caching and pilfering rates.....	62

List of Tables

Table 3.1. Average nutrients acquired by nut species.	25
Table 3.2. Correlation between distance to cache and distance from nearest self-made cache.	30
Table 3.2. Correlation between distance to cache and distance from nearest cache made by a different squirrel in the study.	30
Table 4.1. Motifs and oligo sequences for twelve polymorphic microsatellite loci used in the study to determine relatedness among fox squirrels.	46
Table 4.2. Number of nuts cached by each squirrel, and average cache life (both mean and median) in days.	49
Table 4.3. Expected (H_E) and observed (H_O) heterozygosities at the twelve loci analyzed.	51
Table 4.4. Probabilities of relatedness between individuals in the study.	52
Table 4.5. Nearest Neighbor Distances throughout the experiment.	53

Chapter 1: Introduction

1.1. General Introduction

All species depend on the acquisition of energy to support reproduction and survival. Under natural conditions, this translates into foraging behavior to detect and consume edible foods (Abrams, 1991), competition for a given food source (Croy & Hughes, 1991), predation risk (Lima, Valone, & Caraco, 1985), and even an individual's genetics (Hunt et al., 2007) or learning ability (Rapaport & Brown, 2008). All animals must acquire food to survive, and at least thirty families of mammals and fifteen families of birds, including over 200 vertebrate species, also store, or cache, food items for future use (Sutton, Strickland, & Norris, 2016; Vander Wall, 1990).

Caching facilitates survival during periods of scarcity. It may also reduce foraging time during future searches for food, and can allow a food-storer to take advantage of periods where food in the environment exceeds current needs (Smith & Reichman, 1984; Vander Wall, 1990). Food-storing animals typically employ one of two strategies – either larder-hoarding or scatter-hoarding food items (Vander Wall, 1990). Larder-hoarders store many food items in a centralized location, and use aggression and vigilance to guard their hoards from theft (Vander Wall & Smith, 1987).

Scatter-hoarders store food items in different locations, usually one item per cache, and theoretically must employ cognitive strategies to increase the chance of retrieving their own caches, since individual caches cannot be physically protected from pilferers. These strategies potentially include memory for cache locations, as several scatter-hoarding species, including songbirds, corvids, and tree squirrels, can recall distinct cache locations, sometimes weeks after being cached (e.g., Clayton & Dickinson, 1998; Hitchcock & Sherry, 1990; Jacobs, 1992a; Kamil & Balda, 1985). Memory for cache locations gives the individual who stored the food items an advantage for harvesting those items over naïve individuals (Andersson & Krebs, 1978; Vander Wall & Jenkins, 2003).

Other species engage in deceptive behaviors while caching that may thwart potential pilferers, including pretending to cache in the presence of pilferers, or changing cache locations multiple times (e.g., Bugnyar & Kotrschal, 2002; Dally, Emery, & Clayton, 2004; Dally, Emery, & Clayton, 2006; Steele et al., 2008). Many scatter-hoarders engage in careful handling and hiding of food items, behaviors that they adjust specifically when in the presence of potential thieves (e.g., Delgado, Nicholas, Petrie, & Jacobs, 2014; Hopewell & Leaver, 2008; Preston & Jacobs, 2009; Vander Wall & Smith, 1987). The efficacy of these different behaviors in protecting caches is in many ways still an open and important question.

The complexity of scatter-hoarding behavior is in part due to the interaction between the environment (i.e., seasonal availability of food), qualities related to the food source (such as nutrition and handling time), the caching animal's abilities (memory and caching behaviors), and the social environment (including the amount and competence of competitors). Results from empirical studies, both from the lab and the field, and mathematical models have demonstrated that all of these factors play an important role in the food storing process.

From a squirrel's first encounter with a food item, until that item is finally eaten, lies a series of important actions or reactions that will influence whether that nut is retrieved,

stolen, or ultimately forgotten. Squirrels handle and assess food items, presumably to adjust their caching behaviors in a manner that offers additional protection to valuable items. Squirrels also make decisions about the spatial placement of caches that could affect how easily those caches are retrieved or stolen by others. Little is understood about these decisions and how they might impact cache outcomes.

The goal of my dissertation is to explore the different stages of the decision-making processes of fox squirrels while storing food under naturalistic conditions. I investigated these questions using a series of field experiments and a simulation model. First, I will review the natural history of the fox squirrel, some of the cognitive mechanisms related to scatter-hoarding behavior, and how agent-based modeling can help us better understand this behavior.

1.2. The Scatter-hoarding Tree Squirrel

Tree squirrels, including the fox squirrel, are diurnal rodents that do not hibernate and must meet their energetic needs by foraging throughout the year. The scatter-hoarding tree squirrels are not considered territorial, although they have a hierarchical social structure (Pack, Mosby, & Siegel, 1967). Squirrels are tolerant of other conspecifics and individuals frequently have overlapping home ranges (Gorman & Roland, 1989; Pack et al., 1967; Sharp, 1959; Taylor, 1966), and their density is impacted by the fragmentation of the landscape (Koprowski, 2005). Some co-nesting occurs, with young squirrels nesting with their mothers until they are weaned at three months, and adults sharing nests during cold weather (Steele & Koprowski, 2001).

Despite such tolerance, most squirrel encounters are aggressive (Koprowski, 1996; Thompson, 1978). Squirrels have a complex signaling repertoire they use for communication with conspecifics, including visual signals, olfactory cues, and vocalizations (Bakken, 1959; McCloskey & Shaw, 1977; Steele & Koprowski, 2001; Taylor, 1966; Taylor, 1977). Furthermore, squirrels behave as if they perceive other squirrels as both competitors at a food source and as potential pilferers of already stored food (Hopewell, Leaver, & Lea, 2008; Leaver, Hopewell, Caldwell, & Mallarky, 2007)

Squirrels are omnivorous, but nuts and seeds are their main food source (Steele & Koprowski, 2001). Their preferred diet includes the seeds of oak (*Quercus*), hickory (*Carya*), walnut (*Juglans*), and pine trees (*Pinus*). Squirrels are specially adapted to eat heavily-shelled nuts, but because handling and eating time of different nut species vary, squirrels will preferentially cache items that take longer to eat (Jacobs, 1992a; Moller, 1983; Preston & Jacobs, 2009).

Most studies of scatter-hoarding behavior in tree squirrels have focused on gray squirrels (*Sciurus carolinensis*) and the fox squirrel. These two species are sympatric in many areas of North America, and are similar in morphology and behavior, including how they handle and bury food (Steele & Koprowski, 2001). Fox squirrels tend to be larger, and less vulnerable to predation (Smith & Follmer, 1972). Compared to gray squirrels, they also tend to prefer more open, mixed habitats of mature pine and oak trees (Weigl, Steele, Sherman, Ha, & Sharpe, 1989), although habitat use between the two species will greatly overlap where they co-exist.

The fox squirrel of the University of California, Berkeley campus is relatively habituated to humans, allowing a detailed study of their cognition and behavior (e.g., Jacobs & Shiflett, 1999; Waisman & Jacobs, 2008). Despite this habituation, the squirrels

routinely bury food (Preston & Jacobs, 2009), show seasonal changes in caching behavior related to food availability (Delgado et al., 2014), and experience seasonal weight changes related to tree mast (Delgado & Jacobs, unpublished data). Thus, the free-ranging fox squirrel serves as an excellent model species for field studies of cognition and food-storing behavior in a naturalistic environment. This assertion is further supported by the fact that the morphology of the tree squirrel is very similar to that of their ancestors from 35 million years ago (Emry & Thorington, 1984)

1.3. Storage of Food

Many animal species cache food, including several birds, various small mammals and some large carnivores, such as leopards and hyenas (Smith & Reichman, 1984; Vander Wall, 1990). Seeds are the most commonly stored food item by non-human animals, but insects, small vertebrates, and other vegetation such as tubers are also commonly cached (Smith & Reichman, 1984). Even humans exhibit several forms of caching behavior, securing quantities of food for future use, hoarding unnecessary objects, and by placing money into bank accounts. The widespread presence of caching throughout the animal kingdom suggests this behavior is an adaptive strategy for many species.

Food hoarding likely evolved as a response to temporary changes in environmental food availability or nutritional needs. To persist in populations, there would have to be some fitness advantage to the food-storing animal over those who do not store food, and the behavior would have to have some level of heritability. Food storing could have originated as the tendency for an animal to leave food at a site that they later returned to; more elaborate caching or food-protection behaviors, such as concealing food items, could have followed (Vander Wall, 1990).

There are two styles of food storing: larder-hoarding is the storage of several food items in one location, typically defended by its creator; scatter-hoarding is the creation of several caches which have only small amounts of food (or even just one item) stored in each location (Smith & Reichman, 1984; Vander Wall, 1990). Most food-storing animals cache in one form exclusively, although some species, such as the red squirrel (*Tamiasciurus hudsonicus*), both larder- and scatter-ward depending on food availability, travel time, and competition (Hurly & Lourie, 1997; Hurly & Robertson, 1987; Hurly & Robertson, 1990). There is little evidence that either method of storing food is more efficient than the other in terms of the energetic costs of transporting food items or in preventing theft (Hurly & Robertson, 1987)

Hoarding style may be related to the patchiness of available food sources, such that when food is centrally sourced, larder-hoarding becomes more efficient in terms of travel time. For widely dispersed food items, caching each item close to where it was located would be more efficient, and would support a scatter-hoarding strategy (Hurly & Robertson, 1990). Some animals cache flexibly; Merriam's kangaroo rats (*Dipodomys merriami*) switched from primarily scatter-hoarding to larder-hoarding after repeatedly experiencing pilferage by competitors (Preston & Jacobs, 2001). Larder-hoarding may be dependent on an animal's ability to carry multiple food items at once, suggesting additional physical constraints (De Kort, Tebbich, Dally, Emery, & Clayton, 2006). These findings can inform us about some of the environmental pressures that may have led to the evolution of one type of food-storing, or the other, and why some animals may engage in both forms.

Stored food is likely detectable and attractive to competitors. One possible advantage of scatter-hoarding over larder-hoarding is that an individual will experience a smaller loss if another animal finds a cache (Brodin, 2010). Other strategies to reduce the effects of pilferage include increased vigilance, as seen in kangaroo rats caching under a competitive paradigm (Preston & Jacobs, 2001). After experiencing loss from pilferage, many animals will start caching in less-preferable areas, or avoid pilfered areas (Hampton & Sherry, 1994; Preston & Jacobs, 2005). Some animals store food in such a manner that avoids giving visual, acoustic or olfactory cues related to caches. For example, when being observed, jays tested in a laboratory setting prefer to cache in areas that are less well-lit, when given a choice of locations (Dally et al., 2004). Jays also choose a quieter substrate to cache in if competitors are within hearing distance (Shaw & Clayton, 2013). Chipmunks bury many of their seeds in ash, which was experimentally shown to reduce the detection of caches by pilferers, presumably by olfactory means (Briggs & Vander Wall, 2004). Many animals return to caches and rebury them in a different location, a strategy that would reduce cues for conspecifics, but may also interfere with the memory of the food storer for the new cache location (Dally, Clayton, & Emery, 2006). Animals may switch from caching to eating in order to reduce food loss if pilferage is high (Clary & Kelly, 2011).

Vander Wall and Jenkins (2003) suggest that pilferage may be reciprocal, and the losses due to pilferage are minimal, as those who are stolen from will pilfer themselves. Thus, caching food can be an evolutionary stable strategy (ESS), even if pilferage rates are quite high. A genetic algorithm model also demonstrated that in an environment where caching and pilfering co-exist, the population was resistant to cheaters, or individuals who only pilfered and never cached (Vander Wall & Jenkins, 2003). A logical conclusion is that as caching strategies evolved, so did pilfering strategies.

1.4. Agent-based Modeling and Simulation (ABMS)

Agent-based modeling and simulation (ABMS) is the creation of a computer environment where individual, autonomous agents interact with one another and their surroundings, and make decisions based on predetermined rules (Bonabeau, 2002; Macal & North, 2005; McLane, Semeniuk, McDermid, & Marceau, 2011; Tang & Bennett, 2010). Agents typically operate under a given set of rules based on probabilities of behaviors and direct interactions with other individuals in the environment.

ABMS has several applications, and has been used to model the spread of disease, fluctuations in the stock market, transportation systems, ecosystems, and the behavior of animals (Macal & North, 2005). Although typically computationally intensive, ABMS allows for the modeling of processes or behaviors that might be too complex to study in real-time, including evolutionary processes and large group decision-making.

Although ABMS has been used to model foraging, learning, and other social interactions in animals (Arbilly, 2015; Arbilly, Motro, Feldman, & Lotem, 2010; Bryson, Ando, & Lehmann, 2007), to date it has not been used as a means to model food-storing decisions or cache pilfering. Perhaps the most similar application has been the use of agent-based modeling to assess the cognitive arms race between producers, or animals who procure food, and scroungers, or those who take advantage of others' findings (Arbilly, Weissman, Feldman, & Grodzinski, 2014). Results supported the evolution of a general cognitive ability that persisted throughout the entire population, rather than

solutions that were specific only to producers, or only to scroungers. Much like scroungers rely on producers for their gains, pilfering cannot exist in an environment without food-storers. By using ABMS to model evolution, it is possible to explore whether certain traits are adaptive and can spread throughout the population, and to distinguish whether a trait's frequency in the population is due to genetic drift or selection.

In Chapter 5, I will present the results of an ABMS that allows a population of food-storing animals to forage, cache, pilfer from competitors, and retrieve previously cached food items. Each population evolved across 2000 generations, allowing for the exploration of how interactions between individuals can impact the evolution of memory.

1.5. Precis

In the five remaining chapters, I will outline four experimental results from field studies and a computational model, that explore the food-storing decisions of the scatter-hoarding fox squirrel. The final chapter summarizes the implications of the results and discusses several open questions for future research.

In the second chapter, I examine how fox squirrels adjust their caching effort based on the food item's value. Because squirrels are omnivorous, they routinely encounter food items of different levels of nutritional value, perishability, and handling time. In order to test how they adjust assessment and caching behaviors based on item value, seasonal changes and ephemeral food abundance, squirrels were presented with a series of two food types that varied in value, during natural periods of food scarcity and abundance. The results suggest that squirrels are sensitive to the abundance and value of food, and that they utilize food assessment behaviors to adjust specific caching behaviors.

The third chapter investigates how squirrels might use the spatial distribution of caches to maximize their retrieval and minimize theft. By presenting squirrels with differently valued food items, and different foraging conditions, and recording the geographical location of their caches, I demonstrate that cache placement is one in a series of important decisions made by squirrels while storing food. Squirrels matched the distance traveled for caching to the value of the food item, and cached items at a density that would minimize pilferage risk to the most valuable items. This study was also the first to provide evidence for spatial chunking in a mammalian scatter-hoarder.

Chapter 4 explores the placement and movement of caches, and how social interactions and relatedness between individual squirrels might impact caching behavior. Multiple field studies explored the relationship between social interactions and caching behaviors. I observed a high level of pilfering, and found that cache behaviors and the lifespan of a cache were dependent on the conspicuousness of a cache. Simultaneous microsatellite analysis using PCR (polymer chain reaction) assessed the level of relatedness between individuals in the study area. From this data, I determined that squirrels may mitigate some of the costs of pilfering by caching closer to the caches of related squirrels than to those of non-related squirrels, and protect caches by burying new caches close to their own previously made caches.

Finally, Chapter 5 describes an agent-based computational model of the antagonistic relationship between food-storing animals and their competitors using evolutionary simulations where caching, memory size, and pilfering co-evolved. The results suggest

that competition in the form of pilfering between individuals may shorten memory rates, but the effect may be mitigated when food-storing animals increase their caching rates.

Chapter 2: Fox squirrels match food assessment and cache effort to value and scarcity

2.1 Introduction

Food storing allows animals to take advantage of excess food in relation to current demand (Smith & Reichman, 1984), survive periods of scarcity, and reduce foraging time during future food searches (Vander Wall, 1990). Because food-storing animals either consume items immediately or delay consumption for the future, they are a natural candidate for the study of the evolution of economic decisions such as discounting. The successful retrieval of previously stored food caches should impart a significant fitness advantage to the storer (Andersson & Krebs, 1978). However, storing food is inherently riskier than eating it immediately as cached food may spoil, be forgotten, or be pilfered by others.

Unlike general foraging decisions (e.g., Stephens & Krebs, 1986) which have been broadly studied, the decision to eat or cache a food item is not as well understood. This may be because many motor movements of caching are innately programmed (Eibl-Eibesfeldt, 1963; Horwich, 1972). Yet even the expression of an innate program, such as a courtship display, must be allocated according to the costs and benefits of its expression in a particular context. Even if scatter-hoarding movements are expressed innately, how a scatter-hoarding animal decides to allocate time and energy to individual food items is significant.

Foragers may allocate responses to a food item in proportion to its value (Herrnstein, 1961) or may combine prior knowledge with current sampling of food items in a Bayesian manner (Valone, 2006). Food-storing animals should balance the benefits of cache investment with the risks of cache loss. They should adjust efforts to item value, their own physical condition, their current cache inventory, and the current economic climate (e.g., current food abundance and the competition for that food).

Food-storing decisions are part of a multi-step process that is sensitive to multiple aspects of food quality and the environment (Lichti, 2012; Moore, McEuen, Swihart, Contreras, & Steele, 2007; Preston & Jacobs, 2009; Wang, Ye, Cannon, & Chen, 2012). To adjust the cost-benefit ratio properly for a cache, the scatter-hoarder should assess the value of each item efficiently, minimizing the trade-off between speed and accuracy. The cost of such assessment has been notably absent as a variable in prior models of foraging. Models of food-storing behavior indicate that an animal's ability to obtain information about the future value of food can improve food-storing decisions (Gerber, Reichman, & Roughgarden, 2004).

Assessment of food items before consumption or storage is a common and important behavior in diverse species, including primates, fish and birds (Kislalioglu & Gibson, 1976; Langen, 1999; Langen & Gibson, 1998; Ligon & Martin, 1974; Melin et al., 2009; Rockwell, Gabriel, & Black, 2013). Western scrub-jays (*Aphelocoma californica*), Piñon jays (*Gymnorhinus cyanocephalus*) and Stellar's jays (*Cyanocitta stelleri*) use visual cues and handle food items to determine quality before eating, caching or rejecting seeds (Langen, 1999; Langen & Gibson, 1998; Ligon & Martin, 1974). White-faced capuchins (*Cebus capucinus*) will touch, bite, sniff and perform extended visual inspection of figs before deciding to eat or reject (Melin et al., 2009), and stickleback fish (*Spinachia*

spinachia) increase handling time and become more selective about prey items when satiated (Kislalioglu & Gibson, 1976). Food-storing animals should also use information gained from assessment to mitigate the energetic costs of caching by adjusting investment, e.g., time or effort spent caching, to item value.

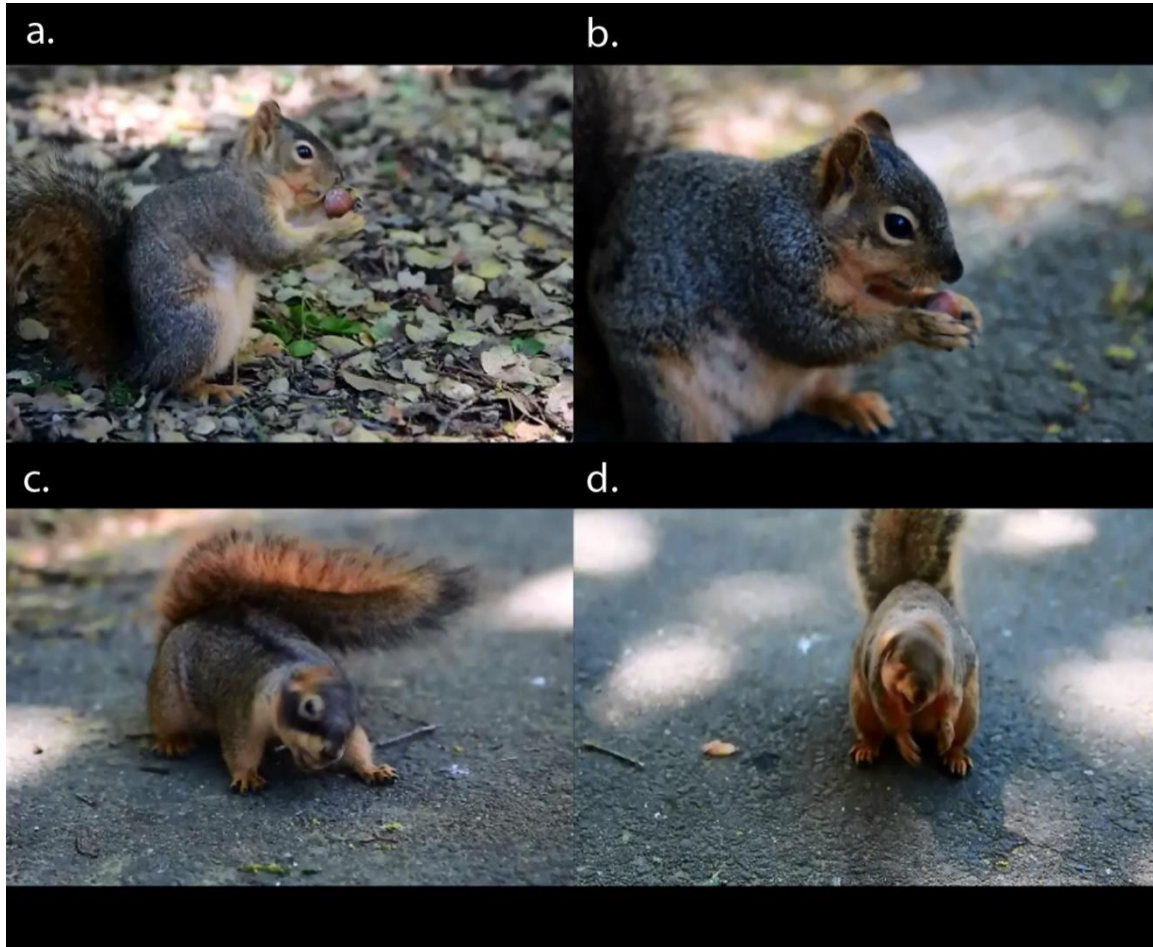


Figure 2.1. Fox squirrel food assessment behaviors. Squirrels paw manipulate a food item by rotating it in their mouth and paws (a, b). They secure the nut in their mouth and head flick, rapidly rotating their head back and forth (c, d).

The scatter-hoarding fox squirrel conspicuously spends time handling food items before both eating and caching. Squirrels first paw manipulate a food item, holding it loosely in their paws and rotating it in their mouth and then head flick, moving the head in a rapid rotation while holding the item in the mouth (Preston & Jacobs, 2009; Figure 2.1). Head flicking is highly correlated with heavier, less perishable food items, and with the subsequent caching, rather than eating these items (Preston & Jacobs, 2009). These unique behaviors likely assess the weight, probability of spoilage or other aspects of food quality (Preston & Jacobs, 2009; Thompson & Thompson, 1980).

After assessing a food item, tree squirrels either eat or cache it, often moving to a location away from the food source and conspecifics for either process (Kraus, 1983; Leaver et al., 2007; McQuade, Williams, & Eichenbaum, 2012; Schmidt & Ostfeld, 2008). Caching by tree squirrels begins with digging. Some squirrels perform an

incomplete cache (IC), where the squirrel digs but does not bury the nut, instead moving to another location to continue the cache sequence. The squirrel chooses a final cache location, and then tamps the nut with its front teeth to seat it more firmly into the ground. Finally, the squirrel uses its paws to collect items such as leaves and loose substrate to cover the cache. Squirrels vary individually in all aspects of this sequence including time spent traveling, how many ICs they perform, and time spent covering a cache (Hopewell & Leaver, 2008; Leaver et al., 2007).

In the present study, we tested the hypothesis that free-ranging fox squirrels would adjust their assessment and investment in food items according to both intrinsic and extrinsic variables related to scarcity (Figure 2.2). Fox squirrels experience seasonal fluctuations in food availability, since their largest food source is trees (e.g. oaks, hickories; Nixon, Worley, & McClain, 1968), which produce all their seeds only in late summer and early fall and at irregular annual intervals, i.e. mast. Fox squirrels typically cache in fall and winter and retrieve the caches through the spring (Thompson & Thompson, 1980) and even summer (Nixon et al., 1968). Cached food may increase in value over time as natural food becomes less abundant and energetic costs increase in the winter (Kotler, Brown, & Hickey, 1999). We predicted that squirrels would increase their assessment and investment behaviors in the summer, when food from trees is scarce and squirrel body weights tend to be low (Goodrum, 1972; Nixon, Hansen, & Havera, 1991; Short & Duke, 1971).

Fox squirrels may not only be sensitive to seasonal abundance of food, but might also respond to an experimental test session as an ephemeral environmental abundance. If squirrels strictly match effort to value on an item-by-item basis, then assessment and investment should not change over trials except based on other external variables (such as

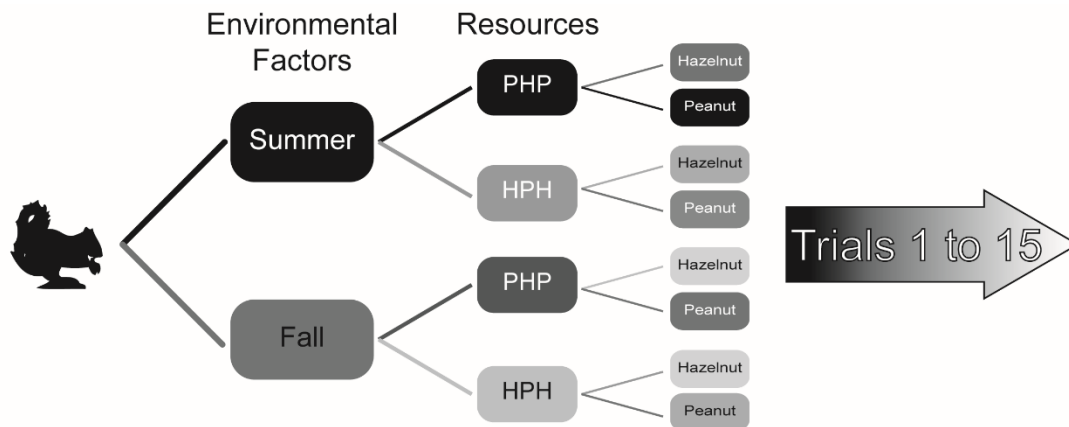


Figure 2.2. A representation of the hypothetical decision-making process in squirrels when assessing food items and investing in caches. Multiple factors (season, competition, current food availability and food type) influence assessment behaviors and cache protection strategies. The darker shades represent the conditions under which we predict food assessment would increase, relative to other factors. PHP represents the experimental condition where squirrels received five peanuts, then five hazelnuts, and finally five peanuts. HPH represents the experimental condition where squirrels received five hazelnuts, five peanuts, and then five hazelnuts.

nut species). However, if squirrels update their evaluation of food availability in the environment in a probabilistic or Bayesian fashion, we would expect that squirrels would decrease assessment and investment across trials, and adjust these behaviors depending on the proportion of higher-valued food items, decreasing assessment and investment when high-valued food items are more abundant within an experimental session.

Tree squirrels also modify foraging decisions in response to the value of the item (Brown, Morgan, & Dow, 1992; Lewis, 1982). We expected a greater assessment of heavier, thicker-shelled, and less perishable food items (hazelnuts) compared to peanuts. Squirrels travel farther to cache larger or heavier-shelled nuts (Moore et al., 2007), perhaps to reduce pilferage by dispersing caches at a lower density (Stapanian & Smith, 1978; Stapanian & Smith, 1984), or are more likely to move them to a more open area where predation risks may deter pilferers (Steele et al., 2014). We predicted that squirrels should invest more effort in hazelnut caches than peanut caches.

Finally, social pressures could affect a fox squirrel's perception of scarcity and influence its caching decisions. Eastern gray squirrels adjust caching behavior when facing competition, including more frequent digs and time spent on caches in the presence of other squirrels (Leaver et al., 2007; Steele et al., 2008). We expected that fox squirrels would increase both their assessment and investment behaviors in the presence of conspecifics, relative to caches made when no other squirrels were present.

2.2 Methods

2.2.1. Study Site

The study site was the University of California at Berkeley campus. The site has a diversity of native and non-native food- trees, which make up at least 46% of surveyed trees in the general testing area. There at least 149 coast live oak (*Q. agrifolia*), and 55 other oak trees; 55 pine trees (e.g. *Pinus pinea*, *Pinus ponderosa*); over 350 redwoods (*Sequoia sempervirens*), and smaller numbers of maple, hickory, walnut, hazelnut and beechnut trees (Cockrell & Warnke, 1976; John Radke, personal communication). These trees typically peak in their mast in late September or early October (Fowells & Schubert, 1956). Furthermore, the California Acorn Survey for the time period of 2008 – 2013 indicated that the mast for *Q. agrifolia* peaked in 2010 (Walt Koenig, personal communication; Koenig, Knops, Carmen, & Pearse, 2008-2013). Although we cannot estimate the number of acorns available to squirrels on the campus during testing, these factors indicate that the summer would have relative scarcity of food compared to the fall of this study.

2.2.2. Study Animals

This research project was approved by the Animal Care and Use Committee of the University of California, Berkeley. The fox squirrel, an introduced species on the Berkeley campus, is well habituated to humans, allowing detailed studies of their caching behavior, memory and other decision-making processes (Delgado & Jacobs, 2016; Jacobs & Shiflett, 1999; Preston & Jacobs, 2009; Waisman & Jacobs, 2008). Squirrels were individually marked with Nyanzol-D (American Color and Chemical Corporation, Charlotte, NC), applied from a distance by gently squirting the dye at the squirrels from a syringe. We maintained a database of marked squirrels to track individual identities.

The participants were 23 free-ranging, adult fox squirrels who were part of a larger pool of marked individuals. Ten squirrels (five female, five male) participated in the summer session, and 13 squirrels (six female, four male and three of unknown sex) participated in the fall session. Two squirrels began but did not complete the experiment (one in summer, one in fall).

2.2.3. Procedure

As quantifying assessment required precise measurements of both counts and durations of behaviors, we videotaped and coded all sessions. We recruited squirrels with calls or gestures. The first marked squirrel to approach the experimenters was chosen to be the focal squirrel for the session. One person served as the feeder and video recorder and the second experimenter recorded the number of conspecifics in the immediate area every five minutes. All sessions were recorded using a Canon FS300 handheld camcorder.

Sessions occurred during the summer from July 22 until August 3, 2010 and during the fall from November 4 to December 2, 2010. There were two experimental conditions for handing the focal squirrel a series of 15 nuts in the shell, one at a time. We assessed how squirrels responded to receiving a sequence of 15 nuts within one session, alternating between five peanuts (a low value, highly perishable, non-native legume) and five hazelnuts (native to California; a high calorie nut with a heavy shell, and less perishable). For simplicity, we refer to both food items as nuts. In Peanut-Hazelnut-Peanut (PHP), squirrels were given a series of five peanuts, then five hazelnuts and then a second series of five peanuts. In Hazelnut-Peanut-Hazelnut (HPH), squirrels were given five hazelnuts, then five peanuts, then five hazelnuts. Peanuts weighed between 2.0 to 3.0 g, and hazelnuts weighed between 2.5 and 3.5 g. Twenty-two of 23 squirrels were tested in both experimental conditions within a season; one squirrel was tested only in one condition (“Hawaii”, male).

To determine the relative value of hazelnuts to peanuts, we calculated what percent of total nut weight was edible content for 20 peanuts and 20 hazelnuts. We found that peanuts had, on average, 73.8% (SD: 2.49%) consumable matter, while hazelnuts were 42.0% (SD: 5.17%) consumable. Taking this into consideration, we calculated the ratio of the nutritional values of each food item for the two nut species using their average weight in the study (2.5 g for peanuts, 3.0 g for hazelnuts; United States Department of Agriculture, 2012). Although per gram, hazelnuts are higher in several nutrients, when analyzing per food item peanuts generally provide more calories, protein, carbohydrates, sugars, and polyunsaturated fatty acids. Peanuts and hazelnuts were similar in lipid content, and hazelnuts are higher in Vitamin E, B-6, and monounsaturated fatty acids). Hazelnuts in our study were slightly heavier than peanuts. Peanuts also have a soft, porous shell, which presumably makes them more susceptible to spoilage in comparison to hazelnuts.

We gave the focal squirrel the first nut of the series and then followed and videotaped them from a distance of 5 to 10 m, as they handled and either carried the nut to a cache location and completed the caching sequence, or ate the nut. After the squirrel was finished eating or caching, we gave it the next nut in the sequence. Sessions lasted between 10.58 and 47.58 minutes ($X + SD = 25.02 + 7.97$ minutes).

All videos of the sessions were coded using The Observer XT (Noldus, Leesburg, VA) and JWatcher 1.0 (D. Blumstein, <http://www.jwatcher.ucla.edu/>) by viewing videos at fifty percent speed. Files coded in JWatcher 1.0 were imported into The Observer XT for final analysis. There were five video coders, and inter-rater agreement on onset, timing and presence of behaviors ranged between 71.1 and 85.9%. We used a mutually exclusive coding scheme to record dependent variables. These included: the number of head flicks for each nut, the number of times and amount of time spent paw manipulating, time spent traveling until eating or caching, the number of incomplete caches before completing caching and the amount of time spent covering the nut. Paw manipulations could easily be discriminated from eating by observing when pieces of shell could be detected breaking away from the nut. If the squirrel ate the nut, we recorded the amount of time it took to finish consumption. We noted the outcome of every trial (eat or cache).

2.2.4. Statistical Analyses

All data were analyzed using mixed models in R 2.15 (R Foundation for Statistical Computing, Vienna, Austria) and JMP 10.0 (SAS Institute, Cary, NC; Bolker et al., 2009). These models allow for repeated measures and missing data points and account for individual variability while using fewer degrees of freedom. Unless otherwise noted, Generalized Linear Mixed Models (GLMM) with a zero-inflated Poisson distribution were used to examine outcome variables that were integer-valued counts of events (number of head flicks, paw manipulation bouts and ICs), using the “glmmAMDB” package in R (Skaug, Fournier, & Nielsen, 2006). Logistic regression was used for the binary variable outcome (eat or cache) using the “lme4” package in R (Bates, 2011; Cox, West, & Aiken, 2009). JMP 10.0 was used to analyze least squares mixed models to assess continuous variables (paw manipulation time, cache time, travel time, cover time), with all variables log-transformed except for cover time, which was square-root transformed. The alpha level for all analyses was set at 0.05.

We included squirrel identity as a nominal random effect in all models, and season, nut species, condition (PHP/HPH), trial number, and whether other squirrels were present (yes/no) were included as dependent variables in all models. Although we did not have a priori predictions as to how factors may interact to impact the assessment behaviors and caching decisions of squirrels, we examined all possible two-way interactions of main effects as an exploratory documentation of multi-factorial decision-making in a complex environment. We removed any insignificant interaction effects in a stepwise fashion. Only significant interactions and all main effects were included in the final model to explain the effects of the dependent measures on different aspects of caching behavior.

2.3. Results

Means (X) and standard errors (SE) are from raw data.

2.3.1. Assessment Behaviors

Squirrels performed fewer head flicks for peanuts than hazelnuts (peanuts, $X + SE = 0.71 + 0.05$; hazelnuts, $X + SE = 1.05 + 0.06$; $Z = 4.69$, $p < .001$). Squirrels showed a sharper decrease in head flicks across trials in the presence of other squirrels compared to when there were no squirrels around ($Z = -2.35$, $p = .019$; Figure 2.3).

Squirrels performed more paw manipulating bouts in the summer ($X + SE = 1.89 + 0.09$) than fall ($X + SE = 1.35 + 0.05$; $Z = -2.91, p = .004$) and spent more time paw manipulating in the summer ($X + SE = 5.03 + 0.46$ s) compared to fall ($X + SE = 2.30 + 0.14$ s; $F(1, 23.81) = 4.77, p = .039, r = .41$; Figure 2.4). Both paw manipulating bouts and time decreased as trials continued ($Z = -2.98, p < .001$). There was an interaction of nut species with season ($F(1, 545.2) = 9.42, p = .002, r = .13$), where the change in time spent paw manipulating was more extreme for hazelnuts in the summer (Figure 2.4). Time spent paw manipulating followed a U-shaped function for peanuts, and a more linear decline for hazelnuts across trials ($F(1, 544.1) = 5.32, p = .021, r = .10$; Figure 2.5).

To assess how paw manipulation was related to caching behavior, we re-analyzed the effect of the independent variables on paw manipulation only for the nuts that the squirrels cached. Squirrels spent less time paw manipulating hazelnuts ($X + SE = 2.31 + 0.16$ s) than peanuts ($X + SE = 2.91 + 0.23$ s) when caching ($F(1, 350.7) = 13.36, p < .001, r = .19$).

2.3.2. Travel Time

We defined travel time as the time the squirrel moved away with the food item until they stopped to eat the nut or started digging to cache. Travel time is a reasonable proxy for travel distance (utilizing GPS, correlating straight-line distance with time traveled; $r(835) = .47, p < .001$; unpublished data). Squirrels spent more time traveling to carry hazelnuts ($X + SE = 33.6 + 1.86$ s) than peanuts ($X + SE = 17.16 + 1.12$ s; $F(1, 559.9) = 123.51, p < .001, r = .42$) but showed some tendency to increase time for peanuts as trials continued, while decreasing time traveling for hazelnuts ($F(1, 562) = 9.67, p = .002, r = .13$). Squirrels spent more time travelling in condition HPH in the summer, but there were no differences between the two conditions in the fall ($F(1, 566.5) = 8.17, p = .004, r = .12$; Figure 2.6).

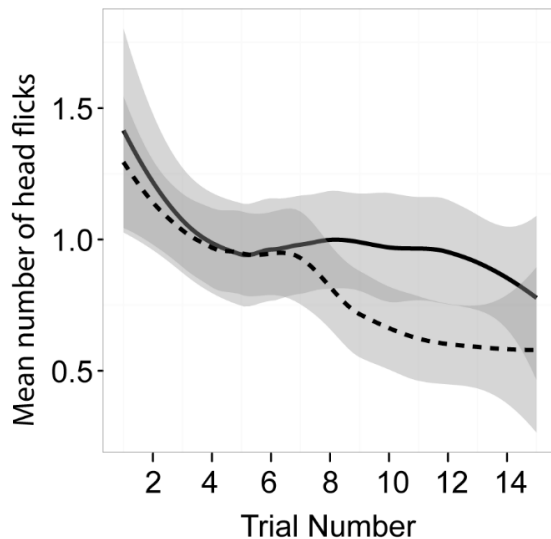


Figure 2.3. The effect of trial number on assessment. Squirrels showed a sharper decrease in head flicks across trials in the presence of other squirrels (dashed line) than when no other squirrels were present (solid line).

2.3.3. Investment in caches

Squirrels spent more time caching (from the first dig until the squirrel completed covering the cache) in summer ($X + SE = 41.67 + 5.27$ s) than in the fall ($X + SE = 21.17 + 1.71$ s, $F(1, 24.78) = 18.48$, $p < .001$, $r = .65$). Squirrels decreased the time they invested in caches from trial 1 to trial 15 ($F(1, 313.8) = 5.32$, $p < .022$, $r = .13$) but this effect was not the same for both nut species ($F(1, 313.1) = 4.23$, $p = .041$, $r = .11$; Figure 2.5). The total cache time for peanuts was initially higher than hazelnuts and decreased across

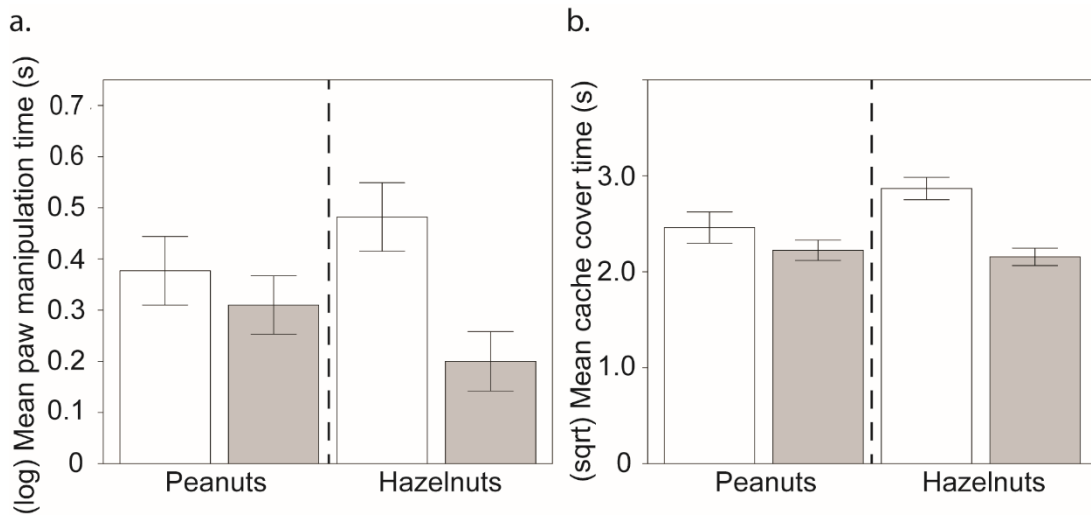


Figure 2.4. Time spent paw manipulating and covering caches by nut species and season. The increase in paw manipulations (a; in seconds, log transformed) and cache cover time (b; square root transformed) is more extreme for hazelnuts in the summer (□) compared to fall (■). Error bars show ± 1 SE.

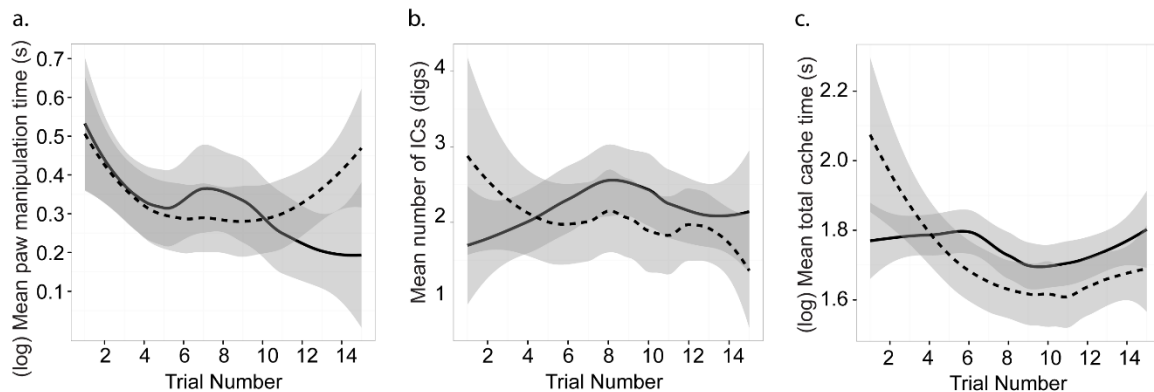


Figure 2.5. Assessment and cache protection by trial. The time squirrels spent paw manipulating (figure a) followed a U-shaped function for peanuts (dashed line), and a more linear decline for hazelnuts (solid line) across trials. Figure b (incomplete caches) shows an inverted U-shaped function for hazelnuts, with squirrels making more ICs toward the middle of sessions; ICs for peanuts decline across trials. The total cache time (c) for peanuts is initially higher than hazelnuts and decreases across trials; cache time for hazelnuts is relatively consistent across trials.

trials; cache time for hazelnuts was relatively consistent across trials. There was also an interaction of condition with presence of other squirrels ($F(1, 295.2) = 7.07, p = .008, r = .15$), where squirrels spent less time caching for condition HPH when no other squirrels were present (Figure 2.7).

2.3.4. Concealment of caches

Squirrels performed more ICs in the summer ($X + SE = 2.47 + 0.20$) than in the fall ($X + SE = 1.84 + 0.11; Z = -3.25, p = .001$; Figure 2.6). Squirrels made more ICs for hazelnuts ($X + SE = 2.16 + 0.12$) than peanuts ($X + SE = 1.93 + 0.14; Z = -2.59, p = .010$). Squirrels

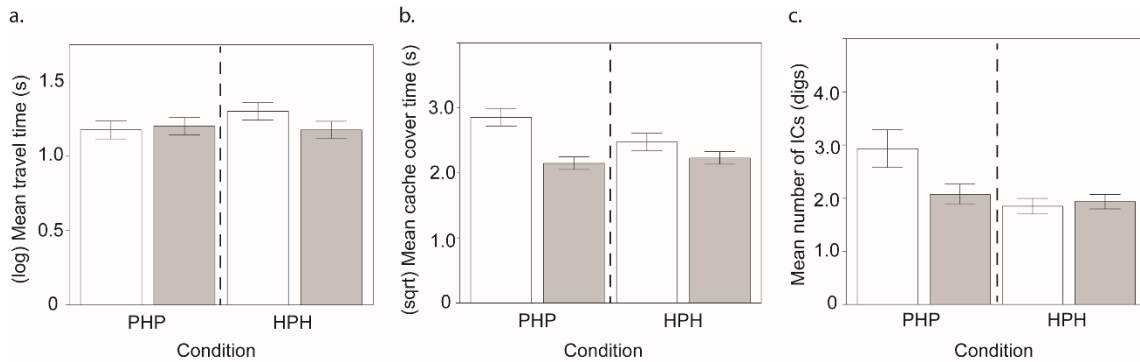


Figure 2.6. Mean time spent travelling, covering caches and number of ICs by condition and season. Squirrels spent more time travelling (a; log transformed) for Condition HPH (Hazelnut-Peanut-Hazelnut) in the summer (□) than fall (■). Squirrels spend more time covering caches (b) in Condition PHP (Peanut-Hazelnut-Peanut) in the summer, but there were no differences in cover time in fall based on Condition. Squirrels performed more ICs (c) for condition PHP in summer. Error bars show ± 1 SE.

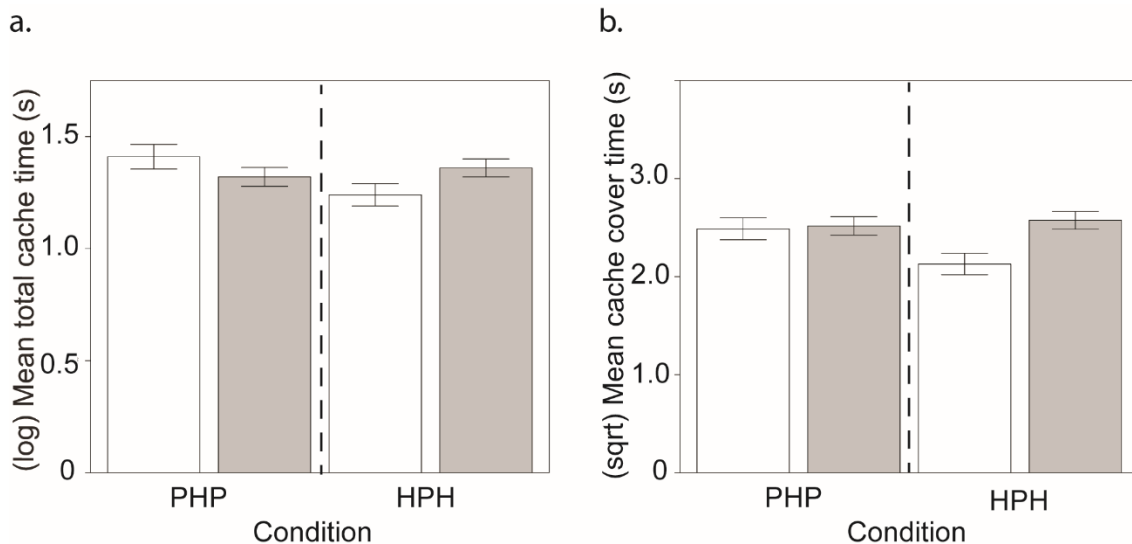


Figure 2.7. Time spent caching and covering caches under competition. Squirrels spend less total cache time (a) for condition HPH when no other squirrels were present (□). Figure b shows that squirrels spent more time covering caches for Condition HPH in the presence of other squirrels (■). Error bars show ± 1 SE.

made fewer ICs as trials continued ($Z = -3.04, p = .002$) and made fewer ICs in condition HPH ($X + SE = 1.98 + 0.11$) compared to condition PHP ($X + SE = 2.23 + 0.16; Z = -3.39, p < .001$). There was a significant interaction between trial and nut species ($Z = 3.16, p = .002$), with an inverted U-shaped function for hazelnuts, with squirrels making more ICs toward the middle of sessions; but ICs for peanuts declined across trials. Squirrels performed more ICs for condition PHP in summer ($Z = 2.47, p = .014$) compared to fall, but no such difference was found for condition HPH (Figure 2.6).

Squirrels spent more time covering caches in the summer (summer: $X + SE = 8.48 + 0.37$ s; fall $X + SE = 5.22 + 0.22$ s; $F(1, 22.74) = 10.37, p = .004, r = .56$; Figures 2.4 and 2.6) and when other squirrels were present (squirrels present: $X + SE = 7.13 + 0.25$ s; no squirrels: $X + SE = 5.10 + 0.27$ s; $F(1, 284.3) = 7.51, p = .007, r = .16$; Figure 2.7). Squirrels spent more time covering caches in condition PHP in the summer, but there were no differences in cover time in fall between conditions ($F(1, 301.3) = 9.70, p = .002, r = .18$). Squirrels also spent significantly less time covering caches for HPH in the presence of other squirrels ($F(1, 315.6) = 7.79, p = .006, r = .16$; Figure 2.7). Cache cover time was higher for hazelnuts in the summer, with a similar amount of time spent on peanuts and hazelnuts in the fall ($F(1, 313.1) = 7.44, p = .0067, r = .15$; Figure 2.4).

2.3.5. Outcome

Nut species ($Z = 5.70, p < 0.001$) and trial number ($Z = 8.04, p < 0.001$) were both significantly related to outcome, with squirrels being more likely to eat peanuts and to cache as trials continued. Squirrels were more likely to eat in the summer ($Z = 3.66, p < 0.001$) but the effect was dependent on nut species ($Z = 3.10, p = 0.002$). Squirrels cached almost all hazelnuts (99%) in the fall and most hazelnuts in the summer (76%), although they always ate more peanuts than they cached, with a more pronounced effect in the summer (78%) than the fall (59%).

Because squirrels head flick, paw manipulate, and carry food items whether caching or eating, we conducted a separate analysis to examine which assessment behaviors were related to the outcome. The observation of head flicks was associated with a greater

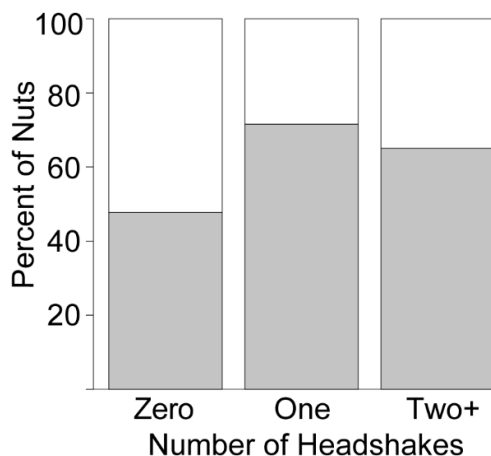


Figure 2.8. Outcome by assessment. The proportion of nuts eaten (□) or cached (■) based on the number of head flicks. Head flicks predicted a greater likelihood of caching nuts instead of eating them.

likelihood of caching ($Z = 3.13, p = 0.002$), with squirrels that did not head flick caching 48% of nuts, and squirrels that head flicked one or more times caching 69.8% of nuts received (Figure 2.8). Paw manipulation time was greater before eating outcomes than before caching outcomes ($Z = -4.09, p < 0.001$). Greater travel times were associated with the caching outcome ($Z = 7.97, p < 0.001$). The individual caching decisions of each squirrel in each condition and season are depicted in Figure 2.9.

2.4 Discussion

The primary goal of our study was to determine if squirrels adjust their food assessment and cache investment behaviors in response to factors indicating scarcity. Our results suggest that squirrels are monitoring scarcity at different temporal scales (micro and macro) and that they integrate all of these factors and both scales in each decision. This study is also the first examination of such a fine-grain analysis of food assessment behaviors in a wild scatter-hoarder.

Seasonal changes have predictable effects on environmental scarcity. In general, squirrels invested more per cache in the summer, when food is scarce in the environment. These caching behaviors also tended to be more variable and sensitive to the value of individual food items in the summer. For example, squirrels only increased paw manipulation time and time spent covering caches for hazelnut caches in the summer. Caching behavior becomes more stereotyped in the fall, and when large amounts of food are available, squirrels respond by caching as much and as quickly as possible, and perhaps with less deliberation and less regard for the value of individual items.

Similar patterns could be seen in squirrels' responses to smaller scale changes, i.e. within a session. Squirrels decreased paw manipulation time and bouts, cache time, and ICs as trials continued. The effect of trial number could reflect several possible factors, such as satiation, exhaustion, or behavioral discounting by decreasing investment in future rewards (Loewenstein, 1987). However, trial number influenced neither travel time nor how much time squirrels spent covering caches. As in other studies of scatter-hoarding rodents, factors in the environment may influence each step of the decision-making process in different ways (Lichti, 2012; Moore et al., 2007; Wang et al., 2012). The presence of other squirrels increased time spent covering caches, suggesting that squirrels created caches more carefully when social competition increased. However, squirrels also showed a rapid decline in assessment behaviors (head flicks) when conspecifics were present. This may be because assessment is costly, and a better strategy is to increase decision speed in the presence of others. Head flicking may be a signal of cacheable food and alert competitors to a potential food source, and reducing this signal in the presence of other squirrels could be a beneficial response.

In general, the influence of competition is moderated by the abundance of food (Hopewell & Leaver, 2008), which perhaps explains why the effect of conspecifics in previous studies of squirrels has not been consistent, and why condition and competition interacted in their influence on cache behaviors in the present study. Previous studies have shown that eastern gray squirrels face away from others when caching food items, decrease cache density (Leaver et al., 2007), increase travel time and spend more time covering caches for high-value food items when other squirrels are present (Hopewell & Leaver, 2008). In other studies, fox squirrels showed no influence of competition on

number of head flicks or digs when nuts were in the shell (Preston & Jacobs, 2009) and there was no effect of conspecific presence on digging in eastern gray squirrels (Hopewell & Leaver, 2008).

On the finest scale of behavioral resolution, our results show that squirrels are highly sensitive to differences in individual food items. Squirrels invested more in hazelnut caches and were more likely to head flick hazelnuts than peanuts, and food type was the only factor that influenced this behavior. Our results support previous findings that the head flick is a part of an assessment process related to nut quality, perishability, and weight (Preston & Jacobs, 2009). Perishability is an important determinant in whether a squirrel should eat or cache a nut (Hadj-Chikh, Steele, & Smallwood, 1996), especially given that peanuts, per food item, may have provided squirrels with more calories and were more likely to be eaten than cached. The increased tendency to cache rather than eat as trials continued may also be caused by the caloric intake from eating peanuts during the session.

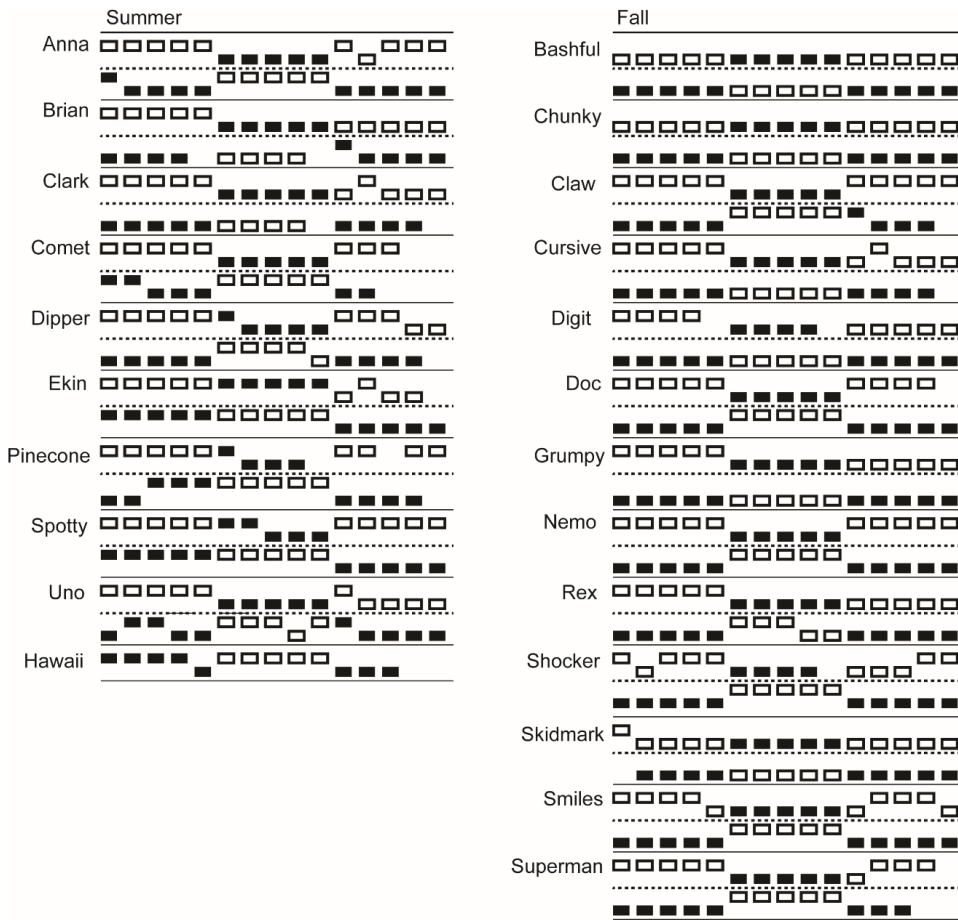


Figure 2.9. All cache decisions for each squirrel in the study by season and condition. The first row of each section for each squirrel represents peanuts (□) and hazelnuts (■) that were eaten, the second row represents nuts that were cached. The top section (above the dashed line) for each squirrel is Condition PHP, the bottom section is Condition HPH.

Increased time paw manipulating decreased the likelihood of caching. Before eating a nut, this behavior is likely related to finding the easiest location to break into the shell. Yet squirrels also paw manipulate before caching, suggesting that squirrels may use this behavior to assess its value, search for imperfections in the shell, or to determine how best to carry it to a cache site. Future research could experimentally vary nut quality, size, texture, and portability to identify the function of paw manipulations.

In summary, our results indicate that rather than being stereotyped and invariant as food storing has been described by behavioral economists (McClure, Laibson, Loewenstein, & Cohen, 2004), squirrels adjust assessment behaviors depending on the food item and whether they will eat or cache the nut, they travel different distances depending on food value, and they alter cache protection strategies depending on food type, season and competition. Interaction effects in this study suggest that squirrels weigh environmental variables differently and may respond to multiple factors in a Bayesian manner to quantify the likelihood of scarcity, as this population of squirrels does for spatial cues (Waisman, Lucas, Griffiths, & Jacobs, 2011). Future experiments could tease apart whether these cache protection strategies differ in efficacy, and how they interact to influence behavior.

We propose that these food assessment and cache investment behaviors represent flexible economic decisions in a non-human species. For example, we found that assessment and investment behaviors decreased consistently across trials. In humans, decreased decision time when purchasing items indicates two opposing causes: impulsive and irrational decision-making versus the effect of experience and expertise (Wood, 1998). In squirrels, reduced assessment could save time when a predictable source of food is available or there are competitors for food. Reduced investment across trials could be evidence for devaluation, or discounting, of food items as they continue to be available. For future studies, this could be tested by determining if a squirrel's decreased assessment and investment actually predicts lower survival of its caches, in particular those containing more valuable food items.

We temper the conclusions of our study by acknowledging that they are limited by some factors that cannot be controlled adequately in the field, including food and cache abundance and sample size. Our study only collected data in one summer and one fall of the same year, which limits the generalization of our results. Photoperiodic effects on brain and behavior must also influence seasonal changes in cache decisions (Burger, Saucier, Iwaniuk, & Saucier, 2013; Lavenex, Steele, & Jacobs, 2000b; Muul, 1969). Because the fate of caches is unknown, we do not know if these assessment and investment behaviors actually improved cache security and recovery. Yet the value of the present study is a demonstration that by capturing rich, detailed observations of the assessment and caching behaviors of free-ranging squirrels, the ecological and ethological factors impinging on economic decisions confirmed our a priori predictions, moreover in conditions that would be difficult, if not impossible, to replicate in a laboratory.

Our study lays the groundwork for future, more complex experimental designs with squirrels, as well as for comparisons with other food-storing and hoarding species. Laboratory pigeons (*Columba livia*), laboratory rats (*Rattus norvegicus*), and non-human primates are the most common subjects of behavioral economic studies. Based on our results and previous studies of foraging and food-storing behavior, we posit that the

human-habituated urban tree squirrel may be a better species than any of these as a model system to understand the interaction between extrinsic factors (such as resource availability and food value) and intrinsic factors (such as satiation and discounting) on the ecological function and evolution of economic decisions.

Chapter 3: Where to bury a nut: The adaptive geometry of cache distribution

3.1. Introduction

Scatter-hoarding animals face the formidable challenge of creating diverse, ephemeral cache distributions whose location they can remember accurately enough to retrieve later. To accomplish this, in addition to remembering the cache location (e.g., Clayton & Soha, 1999; Devenport, Luna, & Devenport, 2000; Jacobs & Liman, 1991; Kamil & Balda, 1985), scatter-hoarders also remember the contents of a cache, such as a black-capped chickadee (*Poecile atricapillus*) remembering whether a seed is shelled or unshelled (Sherry, 1984). Scatter-hoarders, such as the Western scrub jay, can also remember when a cache was made, a form of episodic-like memory (Clayton & Dickinson, 1998). Black-capped chickadees also demonstrated the ability to recall when and where perishable and non-perishable food items had been encountered (Feeney, Roberts, & Sherry, 2009).

As pilferage rates have been estimated to be up to 30% of daily stores, theft is a major cost to food-storing animals (Vander Wall & Jenkins, 2003). Scatter-hoarders create thousands of caches each year, and each cache is created with a single deposition in a different location. Thus, individual caches cannot be physically protected from theft (Vander Wall, 1990). Instead, scatter-hoarders utilize a suite of behaviors to minimize the theft of caches, both by conspecifics and heterospecifics (e.g., Andersson & Krebs, 1978; Dally, Clayton, et al., 2006; Hopewell et al., 2008; Leaver et al., 2007; Male & Smulders, 2007; Steele et al., 2008; Vander Wall & Jenkins, 2003).

Decisions regarding the location of each cache must incorporate trade-offs between returns on cache investment and at least three factors: the costs of the economic effort of caching, reducing theft by competitors, and the cognitive limitations of the caching individual. The economics of cache distribution have been well studied in scatter-hoarders. Many scatter-hoarding species carry larger, more valuable food items farther from the food source than smaller or less valuable food items before caching them (e.g., Delgado et al., 2014; Jokinen & Suhonen, 1995; Moore et al., 2007; Preston & Jacobs, 2009; Steele, Hadj-Chikh, & Hazeltine, 1996; Tamura, Hashimoto, & Hayashi, 1999; Waite & Reeve, 1993; Waite & Reeve, 1995). The prevalence of this behavior suggests that it provides some benefits to the caching animal, despite adding an energetic expense of increasing cache distance, and the opportunity cost of leaving an undefended food source in the presence of competitors.

A possible consequence of adjusting, by value, the distance an item is carried is that scatter-hoarders should cache more valuable items at lower density, as observed in fox squirrels, yellow pine chipmunks (*Tamias amoenus*), and gray jays (*Perisoreus canadensis*; Stapanian & Smith, 1984; Vander Wall, 1995b; Waite, 1988). Since pilfering tree squirrels are known to search longer in areas where nuts are found in high density, traveling away from a food source has a potential secondary benefit of reducing the likelihood that the area around the cache would be searched by a potential pilferer (Stapanian & Smith, 1984). But a heuristic to carry more valuable nuts farther from the food source is not likely a sufficient cache protection strategy if distance and density are independent. An animal could carry valuable nuts far but still cache them at a high density by burying them in close proximity to each other after being carried away.

Furthermore, the effects of cache density on pilferage rates are unclear. Changing the density of human-made caches did not influence pilferage rates in a study of gray squirrels (Kraus, 1983), with the caveat that human-made caches have been shown to be pilfered by squirrels at a higher rate than squirrel-made caches (Steele et al., 2011). Studies from other scatter-hoarding rodent groups are also inconsistent: loss of human-made scatter hoards to desert rodents (*Heteromyidae*; kangaroo rats and pocket mice) was effected by density (Daly, Jacobs, Wilson, & Behrends, 1992), yet there was little effect of density on pilferage of caches made by wild agoutis (*Dasyprocta punctate*; Galvez, Kranstauber, Kays, & Jansen, 2009).

Pilfering, however, is not the only challenge facing scatter-hoarders. For caching to be advantageous, efficient cache retrieval is essential, and that in turn requires spatial memory of cache locations. Many birds and mammals, including tree squirrels, demonstrate precise memories for the location of their caches, in some cases after several days or weeks (e.g., Hirsch, Kays, & Jansen, 2013; Jacobs, 1992b; Jacobs & Liman, 1991; Kamil & Balda, 1985; MacDonald, 1997; Sherry, 1984; Sherry, Krebs, & Cowie, 1981). Marsh tits (*Poecile palustris*) appear to retrieve caches in the reverse order in which they were made (Cowie, Krebs, & Sherry, 1981) and patterns of recovery could reduce economic effort and memory load, while increasing profitability (Vander Wall, 1990). Kraus (1983) has suggested that the directional biases in caching rodents is a heuristic to simplify cache distribution and may act as mnemonic for later retrieval. Directional food-storing behavior has also been observed in black-capped chickadees (Barnea & Nottebohm, 1995).

Hierarchically organizing caches by content should theoretically improve a scatter-hoarder's ability to accurately recall cache locations. This process is known as chunking, where a chunk is a collection of items that have commonalities and discriminability from other chunks (Gobet et al., 2001). Spatial chunking has already been demonstrated to improve spatial recall in laboratory rats retrieving three types of food rewards in a 12-arm radial maze. When food items of a certain type were consistently found in the same locations, the rats retrieved the rewards in order of food preference (Dallal & Meck, 1990; Macuda & Roberts, 1995), similar to the behavior of the black-capped chickadees (Sherry, 1984). The rats also retrieved preferred favored food items with fewer arm visits under these conditions (Dallal & Meck, 1990). If item type was switched but chunk integrity was maintained (i.e., food A was replaced with food B), rats retrieved preferred items in fewer visits compared to their performance when food type was randomly redistributed (Macuda & Roberts, 1995). Such a hierarchical memory representation has also been demonstrated in songbirds in their organization of song syllables to be learned (Williams & Staples, 1992). Although it has not been studied in scatter-hoarding animals, chunking could arguably be a useful tool for cache management.

A commonly studied scatter-hoarder, the fox squirrel, harvests tree seeds in a diverse temperate ecosystem, and they eat and cache many species of tree seeds (Landry, 1970; Steele & Koprowski, 2001). Squirrels evaluate each food item using assessment behaviors (e.g., paw manipulation, head flick; Preston & Jacobs, 2009) to determine the quality of food items, such as weight, integrity, and perishability. Food species and traits related to the nutritional content of a given food item are both linked to the decision whether to cache or eat a food item, the distance traveled to a cache location, the time spent digging before caching, and the time spent covering caches (Delgado et al., 2014;

Moore et al., 2007; Preston & Jacobs, 2009; Stapanian & Smith, 1984; Steele et al., 1996; Sundaram, Willoughby, Lichti, Steele, & Swihart, 2015).

One of the most important weapons in a scatter-hoarder's defense against pilfering should be the spatial placement of its caches. Scatter-hoarding animals create their own foraging patches for future use, which can be seen as a form of niche construction (Odling-Smee, Laland, & Feldman, 1996). The goal of the present study was to investigate the effects of food item value and presentation method on cache distribution decisions. Using free-ranging fox squirrels, we measured the influence of three possible constraints (cache effort, pilfering risk, and cognitive load) on these decisions. We offered squirrels four types of domestic food species (nuts or culinary nuts, hereafter referred to as nuts for simplicity: almonds, hazelnuts, pecans, and walnuts). We manipulated the order in which item type was encountered (either in runs or singly, in pseudorandom order), and the spatial distribution of the food source (from a central place or from multiple locations).

If squirrels only cache to match effort to value, then distance traveled should be related to the energetic returns of each food item. If squirrels are caching to minimize pilferage rates, they should assess food items on an individual basis, and the complexity of how food is presented should have little effect on caching behavior. Instead, caching behavior should reflect an attempt to decrease the nut density to prevent conspecifics from finding multiple caches that are close to each other. But if squirrels are deferring towards caching behaviors that reduce cognitive load, they may use strategies such as chunking to simplify remembering cache locations. By increasing the complexity of the presentation of food items, we anticipated that a chunking strategy and the robustness of other caching behaviors would be disrupted.

We tested the hypothesis that a scatter-hoarding fox squirrel employs a chunking strategy by allowing them to collect a series of four species of tree seeds, where both the location of the food source and the serial order of the nuts collected was systematically varied. We varied the complexity of the series to increase the cognitive load and measured the spatial overlap between caches of different nut species. We defined chunking as the creation of exclusive nut-species cache distributions that could not be explained by any other heuristic. We also predicted that chunking would vary with cognitive load, anticipating that organizing caches by species would be more difficult when food items were presented in pseudorandom order.

3.2. Methods

3.2.1. Study Site

The study was conducted on the University of California, Berkeley campus. The habitat encompasses open lawns, campus buildings and mature trees, including redwoods (*Sequoia sempervirens*), and coast live oak (*Quercus agrifolia*). The study area was approximately 0.1 km².

3.2.2. Study Animals

The subjects were part of a large pool of free-ranging, fox squirrels on the University of California, Berkeley campus. All squirrels were individually marked by spraying black dye (Nyanzol-D) onto their fur from a syringe while they were feeding. The research was

approved under a protocol submitted to the Animal Care and Use Committee of the University of California, Berkeley.

3.2.3. Procedure

All data were collected between June 29 and August 7, 2012; August 5 - 20, 2013; and February 21 through April 29, 2014, avoiding the fall season when caching behavior is most stereotyped (e.g., Delgado et al., 2014). Sessions occurred daily during the squirrels' period of highest activity (10:00 to 16:00). Squirrels were recruited for behavioral observation using auditory signals and visual gestures. The first marked squirrel that approached the experimenters was chosen as the focal squirrel for the session. Because some squirrels participated in multiple conditions, the order of condition was randomized and predetermined based on subject number. For squirrels who participated in multiple conditions, at least one week passed between sessions.

For each session, squirrels were handed a single nut at a time, in a series of 16 individual nuts of four species: almonds (labeled as A), *Prunus dulcis*; hazelnuts (H), *Corylus americana*; pecans (P), *Carya illinoensis*; and walnuts (W), *Juglans regia*. These species vary in weight, size, and perishability (see Table 3.1; Maness, 2014; University of California Agriculture and Natural Resources, 2010). To increase the likelihood of caching, all nuts were in the shell. Nuts were examined for integrity, weighed and assigned a unique code. We calculated the average amount of edible content per nut species by measuring the total weight and the kernel weight for 10-20 nuts of each species. The nutritional information for each nut species, per gram and by average nut weight and edible content is summarized in Table 3.1.

During the experiment, if a squirrel ate a nut instead of caching, the nut was replaced with one of the same type until the squirrel cached again. Squirrels were given one nut per trial, either in runs of 4 (RUNS; 4 nuts of same species, e.g., AAAAHHHHPPPPWWWW) or in a pseudorandom order (PSEUDO; 16 nuts, no species was given twice in a row, e.g., AWHPWHAPHWPAWHPA), using series generated by the website random.org. The order of presentation was randomized and predetermined, such that some squirrels received almonds first, some received hazelnuts first, and so forth.

Squirrels collected nuts under one of two spatial conditions: Multiple Locations (MULTI), where the squirrel would be given the next nut in the location it had just cached, and Central Location (CEN), where the squirrel had to return to a single location to collect the next nut. The MULTI condition allowed the squirrel to define their preferred cache area and allowed us to determine if squirrels would optimize differently if their travel costs were lower.

One experimenter served as the feeder, timer, and data recorder. They offered the squirrel the first nut in the sequence, and started a stopwatch when the squirrel picked up the nut. A second experimenter recorded the location of the start point using a handheld GPS (global positioning system) navigator (Garmin Etrex H or 10). To minimize any observer effect, as the squirrel cached the nut, experimenters maintained a distance of at least 5 to 10 meters from the squirrel.

After a squirrel completed caching the nut, they were given the next nut at their current location by the first experimenter. A third experimenter recorded the location of the cache (and next start point) with a handheld GPS. The second and third experimenters

Table 3.1. Average nutrients acquired by nut species.

	Almonds		Hazelnuts		Pecans		Walnuts	
	Per gram	Per nut	Per gram	Per nut	Per gram	Per nut	Per gram	Per nut
Average weight (g)	3.44	[3.09, 3.79]	3.22	[2.98, 3.44]	8.16	[7.43, 8.88]	11.75	[10.74, 12.77]
Average edible (g)	1.23	[1.06, 1.40]	1.36	[1.22, 1.51]	3.94	[3.36, 4.52]	5.28	[4.69, 5.88]
Average percent edible content	35.75	[33.33, 38.17]	42	[39.59, 44.42]	47.71	[44.08, 51.33]	44.79	[42.47, 47.12]
Water	0.05	0.06	0.05	0.07	0.04	0.16	0.04	0.21
Energy	6	7.38	6	8.16	7	27.58	7	36.96
Protein	0.21	0.26	0.15	0.20	0.09	0.35	0.15	0.79
Total lipid (fat)	0.49	0.60	0.61	0.83	0.72	2.84	0.65	3.43
Calcium, Ca	3	3.69	1	1.36	1	3.94	1	5.28
Iron, Fe	0.04	0.05	0.05	0.07	0.03	0.12	0.03	0.16
Magnesium, Mg	3	3.69	2	2.72	1	3.94	2	10.56
Phosphorus, P	5	6.15	3	4.08	3	11.82	3	15.84
Potassium, K	7	8.61	7	9.52	4	15.76	4	21.12
Sodium, Na	0	0	0	0	0	0	0	0
Zinc, Zn	0.03	0.04	0.02	0.03	0.05	0.20	0.03	0.16

then alternated recording cache locations. The first experimenter noted the waypoint coordinates, and the ID code of each nut cached. There were fifty sessions in Experiment 2 (RUNS-MULTI: N = 14; PSEUDO-MULTI: N = 14; RUNS-CEN: N = 17; PSEUDO-CEN: N = 15).

3.3.4. Determining GPS Accuracy

Although GPS is subject to measurement errors (the difference between the true location and the observed location; McKenzie, Jerde, Visscher, Merrill, & Lewis, 2009), location errors are considered independent and not accumulative, as errors in other methods of map-making, such as compass or pace length, may be (Oderwald & Boucher, 2003). GPS accuracy can be increased by averaging several waypoints in each location, which mitigates the effect of any extreme observations (Oderwald & Boucher, 2003). It should be noted that there is no consensus as to how many waypoints should be averaged to achieve high levels of accuracy but many sources, both commercial and academic, support that a greater number of waypoints increases accuracy and reduces the effect of any particular errant data point (D'Eon, 1995; Mancebo & Chamberlain, 2000; Oderwald & Boucher, 2003; Wilson, 2002). Throughout this study, we recorded at least 100 waypoints at each location.

Before and during this experiment, 75 sample distances were recorded to estimate GPS accuracy. GPS measurements were taken at known distances of 1, 3, and 5 meters. The distances between GPS points were analyzed using Fizzy Calc (www.fizzymagic.net). The difference between the known distance and the GPS estimate was calculated and absolute distances were used to obtain an estimate of the accuracy of the GPS receivers. The range of differences was 0.04 to 5.69 m and the mean difference between actual distance and recorded distance was 1.30 m (SEM 0.15 m). The 95% confidence interval for the true mean difference was between 1.04 and 1.65 m.

3.2.5. Statistical Analyses

All data were analyzed using ArcGIS version 10.3 (ESRI, Redlands, CA), JMP 12.0 (SAS, Cary, NC), and R version 3.2.1 (R Foundation for Statistical Computing, Vienna, Austria). Waypoints were entered into ArcGIS with the WGS 1984 Geographic Coordinate System, and with the State Plane NAD83 California Zone III projection.

Waypoints were adjusted in ArcGIS by creating a buffer of 1.65 m using the Data Analysis Buffer tool. This created a circular zone around each waypoint that likely held the true waypoint location for each cache. A polygon that incorporated all the buffered waypoints of interest was created for each squirrel's cache by nut species or by cache sequence. This provided four polygons by nut species (conditions RUNS and PSEUDO) or sequence within a run (the first four caches, second four caches, and so forth).

To assess the organization of caches, the polygons for each nut species and by runs for an individual squirrel were overlaid with the Union function in ArcGIS. This calculated the geometric intersection of the polygons, giving areas where there was no overlap, or overlap between two, three or four nut species or runs.

For statistical analysis, we used least squares mixed models and MANOVA in JMP, unless otherwise noted. We included squirrel identity as a random effect in all models to account for individual variability and repeated measures. As weight and nut species were highly correlated, with all nut species having significantly different weights from each

other ($F_{3, 826.9} = 4789.05, p < .001$), weight was not included in the models unless otherwise noted. Follow up pairwise comparisons were conducted using Tukey’s HSD or Wilcoxon Ranked Sum Tests.

3.3. Results

Five squirrels did not cache all 16 nuts: Eric (RUNS-MULTI) and Sparky (PSEUDO-MULTI) cached 14 nuts each; Skippy (RUNS-CEN) cached 9 nuts; Seed (RUNS-CEN) cached 10 nuts, and Berri (RUNS-CEN) cached 11 nuts.

3.3.1. Nut species, weight, source type, and sequence impact distance traveled from food source to cache.

Nut species, sequence position (1-16), sex, foraging type (MULTI or CEN), condition (RUNS or PSEUDO), and the interaction between foraging type and condition were included as fixed effects. Squirrels cached all nut species at different distances ($F(3, 868.1) = 64.43, p < .001$; Figure 3.1). There was no effect of condition on cache distance, $F(1, 73.8) = 2.18, p = .14$. Squirrels decreased distance as trials continued ($F(1, 870.2) = 15.10, p < .001, r = 0.13$), and male squirrels traveled farther to cache than female squirrels ($F(1, 38.54) = 14.14, p < .001, r = 0.52$). Squirrels traveled farther when food was presented in a central location rather than for multi-site foraging ($F(1, 103.2) = 12.87, p < .001, r = 0.33$). There was no interaction between condition and foraging type ($F(1, 455.2) = 2.51, p = .114$). The distances and confidence intervals by nut species, condition and foraging type are shown in Figure 3.1.

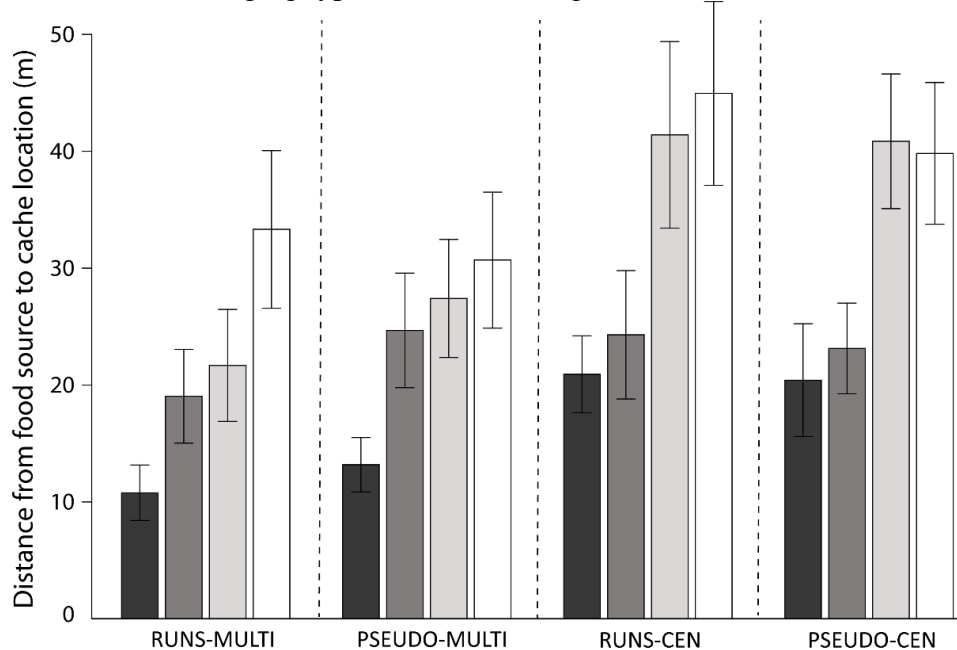


Figure 3.1. Distance (m) travelled from the food source to cache location by condition and nut species. Bars show means and 95% confidence intervals. Squirrels travel farther for heavier, higher quality nuts. Conditions: RUNS – nuts received in runs of 4 of the same nut type in a row; PSEUDO – nuts received in pseudorandom order; MULTI – nuts sourced from multiple locations; CEN – nuts sourced from one location. Nut species: ■ = Almonds, ■ = Hazelnuts, ■ = Pecans, □ = Walnuts.

Controlling for nut species, squirrels were also sensitive to the weight of the nut, travelling farther for heavier almonds ($r = 0.20$, $N = 231$, $p = .003$) and pecans ($r = 0.23$, $N = 238$, $p < .001$) compared to lighter nuts of the same species. Distance was not correlated with weight for hazelnuts or walnuts (Figure 3.2).

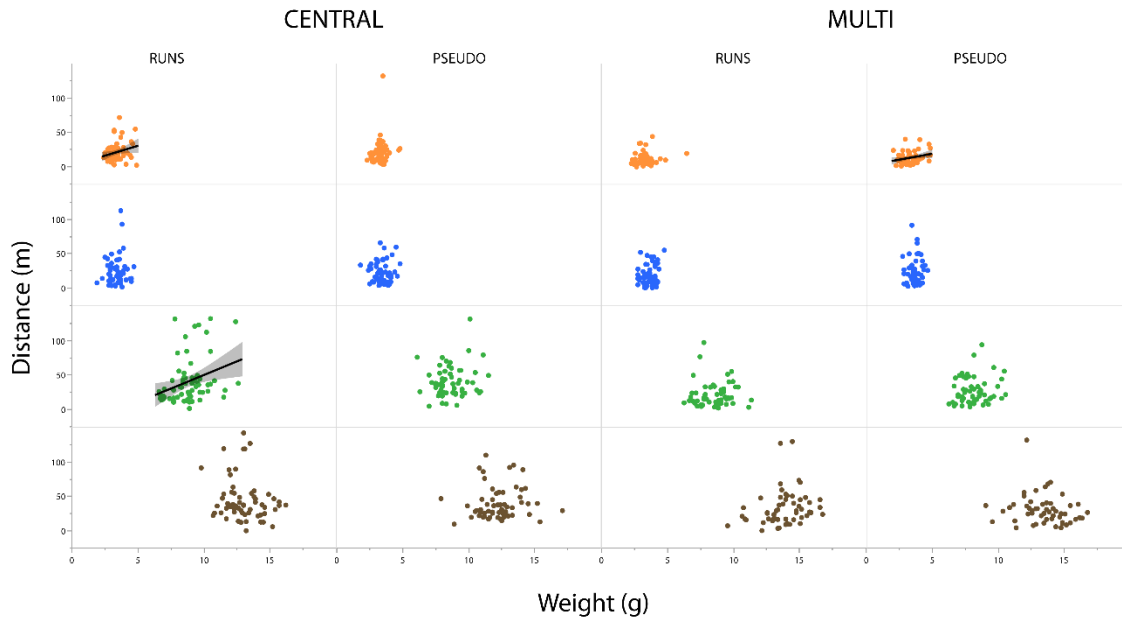


Figure 3.2. Correlation between weight (g) and distance traveled (m) by nut species. Squirrels traveled further for heavier almonds and pecans when compared to lighter nuts of the same species. Lines and 95% confidence intervals are depicted for statistically correlated results.

Nut species: ■ = Almonds, ■ = Hazelnuts, ■ = Pecans, ■ = Walnuts.

3.3.2. Central-place foraging increases directionality of caching.

A Rayleigh's test in R was conducted for each squirrel's caches to determine if they cached with a significant directional orientation. No squirrels in the MULTI condition (RUNS or PSEUDO) cached with a directional orientation (all $p > .10$). When foraging from a central location, nine squirrels cached with a significant directional orientation in condition RUNS-CEN. Six squirrels did not cache with a directional orientation. In condition PSEUDO-CEN, nine squirrels cached with a significant directional orientation and six squirrels did not.

3.3.3. Squirrels cache higher-valued food items at lower density, except when food is presented from multiple sources and in pseudorandom order.

Both sex and foraging type had an effect on the NN (nearest neighbor) distance for the entire cache session of 16 nuts, and male squirrels cached nuts at a lower density than female squirrels ($F(1, 50.38) = 17.19$, $p < .001$, $r = 0.50$). Squirrels cached nuts farther apart when centrally sourcing food items ($F(1, 54.29) = 4.44$, $p = .04$, $r = 0.27$). There was no effect of condition (RUNS vs PSEUDO), and no interaction between condition and foraging type. The average NN distance for all nuts was 10.6 m.

Male squirrels cached hazelnuts ($F(1, 13.83) = 5.41, p = .036, r = 0.53$) and pecans ($F(1, 24.13) = 8.92, p = .006, r = 0.52$) at a lower density than female squirrels. There was no effect of foraging type on NN distances for any almonds, hazelnuts, or walnuts. Pecans were cached at a lower density when centrally sourced, $F(1, 44.34) = 4.16, p = .047, r = 0.29$. Squirrels decreased cache density for almonds ($F(1, 29.97) = 6.44, p = .017, r = 0.42$), and hazelnuts ($F(1, 19.49) = 6.82, p = .017, r = 0.51$) in the pseudorandom condition (PR), and instead cached all nuts at a similar, lower density. Finally, there was an interaction effect between condition and foraging type on cache density for almonds and hazelnuts (almonds: $F(1, 35.59) = 6.94, p = .012, r = 0.40$; hazelnuts: $F(1, 23.26) = 6.80, p = .016, r = 0.48$) as seen in Figure 3.3.

When comparing NN distances of different nut species, a repeated measures MANOVA and pairwise Wilcoxon Signed Rank tests indicated that squirrels cached nuts at statistically different densities from each other ($F(3, 52) = 14.97, p < .001$). Almonds were cached at the highest density followed by hazelnuts, pecans, and walnuts, which were cached at the lowest density. Figure 3.3 summarizes these NN distances by condition and nut species.

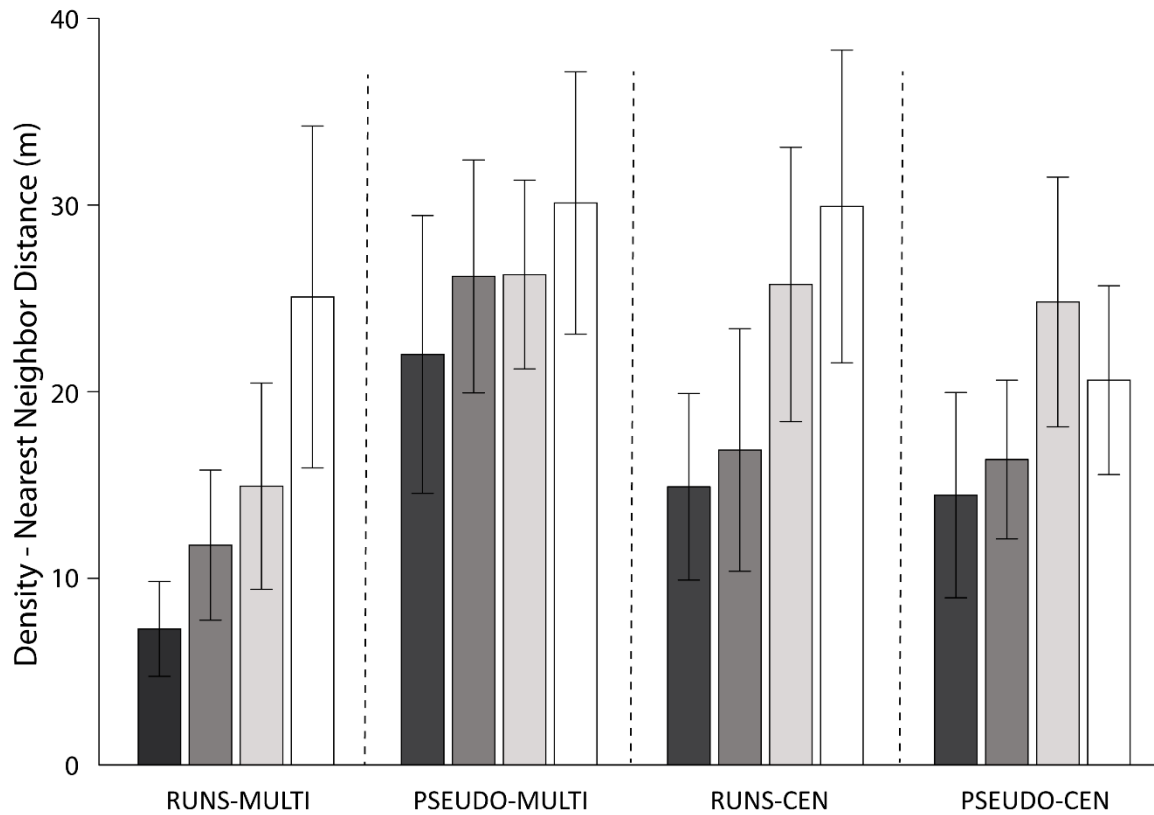


Figure 3.3. Nearest Neighbor (NN) distance (m) by condition and nut species. Bars show means and 95% confidence intervals. Squirrels cache heavier, higher quality nuts at lower densities except in PSEUDO-MULTI, where all nuts are cached at a similar, low density.

Nut species: ■ = Almonds, ■ = Hazelnuts, ■ = Pecans, □ = Walnuts.

To determine if differences in cache density could be maintained simply by traveling different distances based on nut species, we examined the correlation between distance traveled and the distance to the closest other nut for each cache, both for caches made by the same squirrel or the closest cache made by any other squirrel. A positive correlation would indicate that traveling a further distance to cache also indicated that that nut was likely to be cached at a further distance from other nuts. When food was centrally sourced, the distance traveled was related to distance from other self-made caches for most nut species, but this effect was less consistent when food was sourced from multiple locations (Table 3.2). Distance traveled was not an effective strategy for keeping caches away from those of other squirrels for most nut species, except in the RUNS-CEN condition (Table 3.3).

Table 3.2. *Correlation between distance to cache and distance from nearest self-made cache.*

	RUNS-MULTI	PSEUDO-MULTI	RUNS-CEN	PSEUDO-CEN
Almonds	.04	.20	.36*	.05
Hazelnuts	.28*	.13	.36*	.31*
Pecans	.57**	.13*	.34*	.42**
Walnuts	.09	.03	.38*	.55**

**p < .001, *p < .05

Table 3.3. *Correlation between distance to cache and distance from nearest cache made by a different squirrel in the study.*

		PSEUDO-MULTI	RUNS-CEN	PSEUDO-CEN
Almonds	.05	-.01	-.18	.07
Hazelnuts	-.31*	.12	.45**	.38**
Pecans	.01	.18	.54**	.07
Walnuts	-.05**	.25	.52**	.14

**p < .001, *p < .05

3.3.4. *Squirrels organize caches by food type when centrally-sourcing food items.*

Squirrels overlapped caches by nut species more in condition PSEUDO-MULTI than other conditions (Condition ($F(1, 32.09) = 30.28, p < .001, r = 0.70$), foraging type ($F(1, 51.8) = 9.11, p = .004, r = .39$), their interaction ($F(1, 35.1) = 54.53, p < .001, r = 0.78$); Figures 3.4 and 3.5). Because the overlap effect could also arise from other cache heuristics, such as a squirrel sequentially using different locales for the next few caches, we also examined how much squirrels overlapped their caches sequentially in groups of four rather than by species. Squirrels overlapped caches by nut less than by sequence when centrally foraging ($F(1, 48.51) = 19.90, p < .001, r = 0.54$; Figures 3.4 and 3.5). There was no effect of sex ($p = .72$).

A further examination of cache overlap based on how squirrels overlapped their caches sequentially in groups of four instead of based on nut species, showed that, squirrels overlapped caches by sequence more when centrally foraging ($F(1, 47.86) = 20.75, p < .001, r = 0.55$; Figure 3.5). We also tested whether this separation of caches by nut species when central foraging could be achieved by a simpler heuristic, such as adjusting

distance traveled from the food source based on nut size, for example, differentiating between the large nut species (pecans, average weight, $x = 8.16$ g; walnuts, $x = 11.75$ g) and the smaller nut species (hazelnuts $x = 3.22$ g; almonds, $x = 3.44$ g). A repeated measures ANOVA compared the overlap between smaller nuts with the overlap between larger nuts, and whether nut size interacted with condition. The distribution of large nuts overlapped with each other more than the distribution of small nuts (52.33% versus 11.59%) in condition RUNS ($F(1, 27) = 5.26, p = .030, r = 0.38$). In condition PSEUDO, the overlap between large nuts (23.1%) and small nuts (21.29%) was similar.

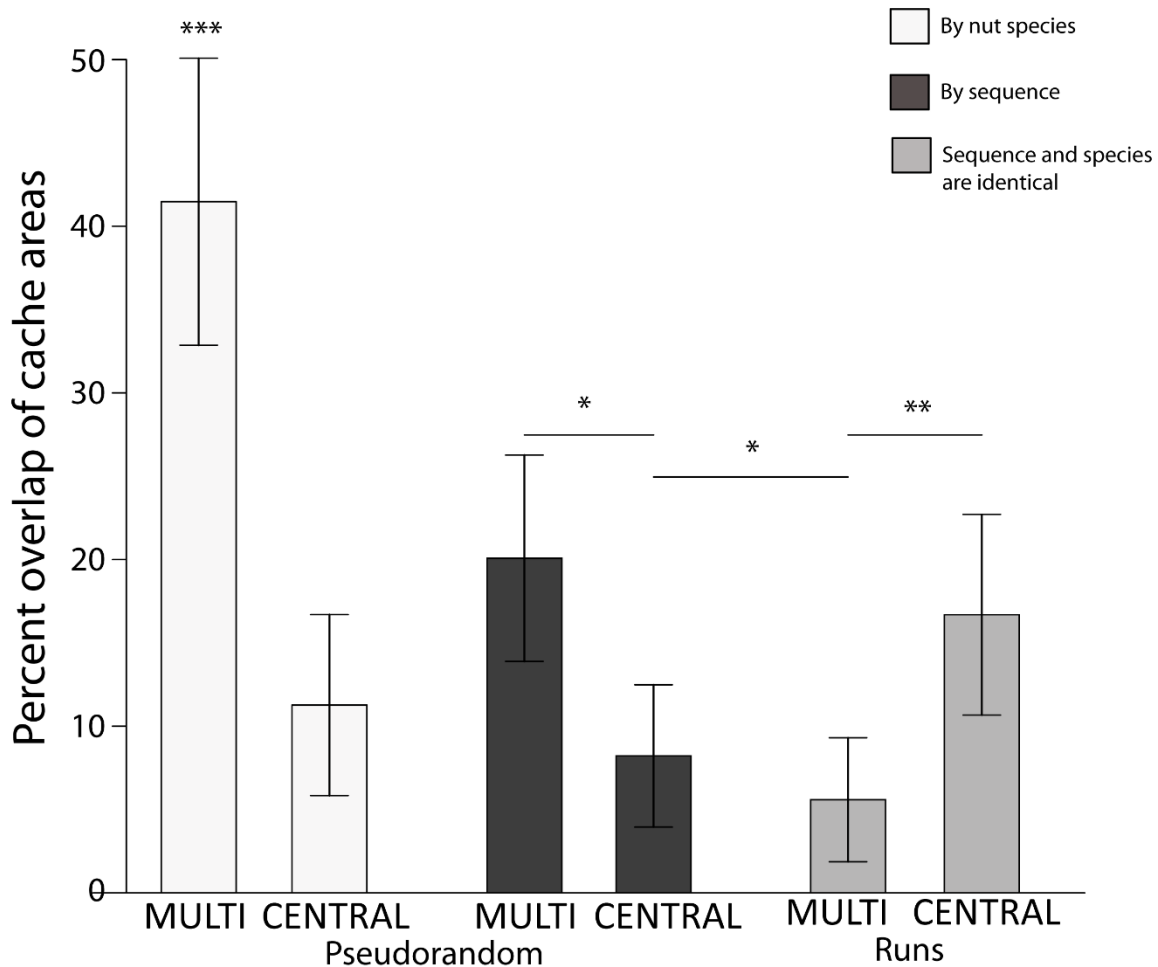


Figure 3.4. Percent of spatial overlap by cache species for each condition. Squirrels minimize overlap between nut species when central foraging regardless of order of presentation. Lower percent of overlap suggests more separation of caches by either species or sequence. Bars show means and 95% confidence intervals. Overlap is by nut species, or by sequential groups of 4 (nuts 1-4; nuts 5-8; nuts 9-12; nuts 13-16). Asterisks show statistical differences between cache types.

* $p < .05$

** $p < .001$

***statistically different from all other categories

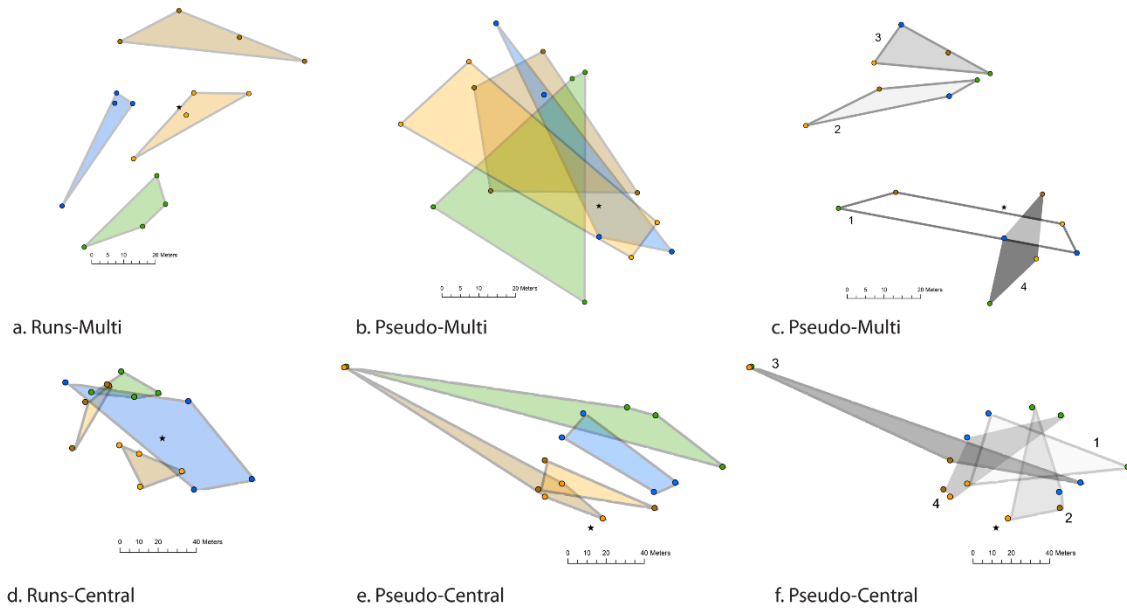


Figure 3.5. Examples of cache distributions under different conditions. Top row: Caches made by one adult female fox squirrel in the conditions RUNS-MULTI (a) and PSEUDO-MULTI (b, c). The low overlap between caches of different nut species can be explained by avoiding overlap with previous caches. Bottom row: Caches made by one adult male squirrel in conditions RUNS-CEN (d) and PSEUDO-CEN (e, f). Squirrels in these conditions organized caches by nut species rather than sequence. Numbers indicate the caching order in sequential runs of four.

Nut species: ■ = Almonds, ■ = Hazelnuts, ■ = Pecans, ■ = Walnuts

3.4. Discussion

In this study, we assessed the responses of fox squirrels to food items of different value, and how their presentation influenced their caching behavior. We detailed three aspects of their cache organization; one that is well established (distance traveled by value), one that has shown inconsistent patterns in previous studies (cache density), and one that is previously untested (chunking as a mechanism for cache organization). Our results suggest that squirrels use a systematic form of organization to cache nuts, which in some contexts may include a hierarchical cognitive representation of their caches, via chunking. Their cache organization was also impacted by food encounters that were more complex, either in the number of locations food was sourced from, or by presentation of food types in pseudorandom order.

The present study provides the first evidence that a scatter-hoarder could employ spatial chunking during cache distribution as a cognitive strategy to decrease memory load and hence increase accuracy of retrieval. When foraging from a central location, squirrels showed little overlap of caches by nut species, regardless of the order in which different food types were presented. Squirrels may thus be able to organize caches hierarchically by cache contents, i.e., spatially chunk cache locations, regardless of the order in which they have encountered different nut species under the natural conditions of a species-diverse deciduous forest.

Squirrels clearly discriminated between nuts based on type and quality, consistently travelling farthest from source to cache location for the heaviest nuts (walnuts), regardless of experimental condition. Our results support prior studies showing that tree squirrels travel farther for nuts of higher quality and nutritional value (D'Eon, 1995; Mancebo & Chamberlain, 2000; Oderwald & Boucher, 2003; Wilson, 2002).

We were interested in whether travel costs would impact behavior, as receiving nuts from a location close to a previous cache would reduce the travel costs induced by obtaining food from one source. When food was centrally sourced, squirrels traveled further overall, and adjusted distance by whether nuts were of low quality (almonds and hazelnuts) or high quality (walnuts and pecans, both members of the *Juglandaceae* family), using a more general heuristic to travel farther for high quality items. Squirrels may have traveled a shorter distance in the multiple source condition because they were already caching in a preferred area.

Squirrels typically cached more valuable nut species (pecans and walnuts) at a lower density than less valuable nut species (hazelnuts and almonds). Other studies of tree squirrels have also shown that squirrels cache higher-valued food items at lower densities (Moore et al., 2007; Stapanian & Smith, 1978). This finding can in large part be explained by caching higher-valued food items at a greater distance from the source (Hurly & Robertson, 1987), and in the current study, most nearest neighbor distances to other caches made by the same squirrel increased as distance from the food source increased (Table 3.2).

Squirrels did not adjust cache density to item value when nut species were presented pseudorandomly and from multiple locations. Instead, squirrels reduced the density of all caches. Under conditions where cognitive load is potentially higher, squirrels may find it easiest to density match to the most valuable food items, such that all items are cached at a similar, lower density, minimizing the risk of a competitor finding a high-valued nut if they discovered a lower-valued one nearby. In one study of mixed grids of cached nuts (walnuts and acorns), survival of nuts was decreased at high densities (Stapanian & Smith, 1984), so it may be beneficial for squirrels to adjust the overall density of caches to protect higher-valued food items.

Squirrels could achieve lower cache densities without constantly increasing distance by utilizing the full 360° around a food source. Yet when food was centrally sourced, most squirrels showed a preferred caching direction, suggesting that caching in a favored area may be more important to retrieval than overall cache density.

Prior models of cache dispersal have predicted that to maintain an optimal cache density, scatter-hoarders should carry the first cache the shortest distance and then increase or vary the distance traveled on subsequent caches (Clarkson, Eden, Sutherland, & Houston, 1986; Stapanian & Smith, 1984). Our current results and prior studies of fox squirrels (Delgado et al., 2014) also showed that squirrels traveled the farthest distance from the food source for early caches, and shortened the distance traveled for later caches. Such a pattern would be adaptive if the persistence of a food source is uncertain and earliest-made caches may be the only foods that will be harvested from a newly discovered food source. Caching early items farther would also ensure that some food is safe, i.e., cached at the lowest density, and if caching animals tend to recover later made caches first, as marsh tits do (Cowie et al., 1981), it could reduce the effort of short-term cache recovery.

Finally, and perhaps most importantly, the present study addressed for the first time whether a scatter-hoarder would spatially cluster its caches by food type, potentially to decrease memory load and increase accuracy of retrieval. When squirrels were encountering runs of nut species from multiple locations (RUNS-MULTI), they never overlapped more than two types of different nut caches. In the pseudorandom condition (PSEUDO-MULTI), all squirrels overlapped at least three cache types, and many overlapped four nut species. However, upon closer examination of the visualized data, squirrels appeared to be placing caches to prevent overlap with areas they had just used for caching in that session. Thus, cache non-overlap may have emerged from their use of a specific heuristic -- avoiding previously cached in areas -- not as a result of increased memory load disrupting their ability to organize their caches by nut species.

Conversely, when foraging from a central location, squirrels showed little overlap of caches by nut species, regardless of whether food was presented in runs or pseudorandom order. Thus, this provides the first evidence that squirrels could organize caches by their contents and not just by the order in which the food item was encountered. This behavior could be classified as spatial chunking, as seen in laboratory rats (Dallal & Meck, 1990). Future research should determine if chunking actually increases the accuracy of subsequent retrieval of these caches.

Because seed-bearing trees provide a superabundant food source, a caching squirrel that discovers this source may treat the chosen tree as a central place forager, bringing seeds in a preferred direction towards of its home range. When eating, squirrels often travel some distance from the food source, particularly in the face of competition (Delgado et al., 2014; Hopewell et al., 2008; Stapanian & Smith, 1984). But whether eating or caching, the distance travelled away from the food source will be influenced by the opportunity cost of leaving an ephemeral food patch to one's competitors for a long period of time. If the distance traveled is significant, returning to a central food source could be costlier than foraging from a new food source near where the squirrel cached or ate. However, in the current study, squirrels' cache responses to central place foraging appeared to be most effective for keeping caches away from those previously made by the cache owner or by other squirrels.

The results from this study point to a wealth of future questions about the cognitive demands of scatter-hoarding. Only a small percentage of a squirrel's caches survive through the winter (Cahalane, 1942; Thompson & Thompson, 1980), but there is little information about cache retrieval in the field, and these experiments did not determine if caches were removed by the animal who stored them. In captive rodents such as yellow pine chipmunks and Merriam's kangaroo rats, the cache owner has a retrieval advantage for cache recovery (Jacobs, 1992b; Vander Wall et al., 2006). Yet we lack any study of the fate of a cache, from caching to consumption, under natural conditions -- whether it is moved and if so, by whom, and when it is finally eaten. Many captive scatter-hoarders, such as Western scrub jays, captive squirrels and kangaroo rats, move caches in response to competition in the lab (Dally, Emery, & Clayton, 2005; Jacobs & Liman, 1991; Preston & Jacobs, 2001), and future work should address this in the field, in scatter-hoarding tree squirrels.

Finally, squirrels may be caching (including chunking) by item value, and this value may be derived from other factors as well as nut species, such as the weight of that individual nut. Although squirrels naturally encounter several different species of seeds,

there is also likely a range of variability of quality of seeds within one tree that a squirrel might be foraging in. This study also demonstrated that fox squirrels modulate the distance they will carry a nut of a certain species, carrying larger individual nuts significantly farther than smaller individual nuts of the same species. Our observation that squirrels, under certain conditions, categorize and respond to a nut as either large or small, also suggests that they could be organizing caches by even more subtle hierarchical structures than simply nut species.

In summary, our results showed that squirrels invested more in more valuable food items with more edible content and nutrition. They traveled farther when initially encountering items, and then behaved in a manner that allows them to uniformly distribute caches over a specific area. They reduced cache density based on individual value, but when centrally foraging, it is likely they do this by default by matching distance to value. When encountering food items of different types, as they might when foraging from multiple locations, squirrels appear to weigh density of caches based on the overall value of available food items. When centrally sourcing food, squirrels carried nuts in preferred directions, a method that allows them to avoid caching near their own previous cache locations, but not necessarily to avoid caching near the caches of other squirrels.

Squirrels adjusted caching behavior based on encounter order: they organized food by value when items were centrally sourced, and in a manner that potentially would reduce risk to the most valuable food items when sourced from multiple locations. Our results identify certain robust heuristics, and also suggest many avenues of future research to determine the fitness consequences of squirrels' decisions about where to bury a nut.

Chapter 4: Cache life: Factors related to how long nuts remain where squirrels buried them

4.1. Introduction

Scatter-hoarding animals cannot physically protect individual caches, and instead utilize several behavioral strategies that are hypothesized to offer protection for caches. These behaviors include assessing food items to appropriately allocate cache effort (e.g., Preston & Jacobs, 2009), caching out of sight of conspecifics (e.g., Dally et al., 2004), caching food items at low density (e.g., Male & Smulders, 2007), or at a great distance from the food source (Vander Wall, 1995a), or spending more time carefully covering caches (e.g., Leaver, Hopewell, Caldwell, & Mallarky, 2007). How these behaviors contribute to the survival and retrieval of these caches, or might reduce pilferage from conspecifics is still unknown. In fact, little is known about what factors do contribute to whether a cache is stolen, forgotten, or retrieved by the animal who cached it.

Many behavioral mechanisms that scatter-hoarding animals could use to protect caches have yet to be examined in detail, such as the adaptive use of food assessment. Several animal species display food assessment behaviors including squirrels, primates, birds and fish (Jablonski, Fuszara, Fuszara, Jeong, & Lee, 2015; Kislalioglu & Gibson, 1976; Melin et al., 2009; Preston & Jacobs, 2009). These behaviors help animals select higher quality food items, as demonstrated in scatter-hoarding Western scrub jays and Piñon jays, who use bill clicking and item handling to choose heavier seeds (Langen & Gibson, 1998; Ligon & Martin, 1974).

In the case of food-storing animals, assessment may provide information that allows for the adjustment of cache investments to the value of individual food items. Fox squirrels use two overt behaviors to assess food items, head flicks and paw manipulations. These behaviors may help squirrels assess the quality, weight, and perishability of food items before caching or eating them (Delgado et al., 2014; Preston & Jacobs, 2009). For example, fox squirrels are significantly more likely to cache than eat items after they perform a head flick (Delgado et al., 2014; Preston & Jacobs, 2009). Because many scatter-hoarding animals, including squirrels, jays, mice, and chipmunks, adjust cache distance to the value of food (e.g., Delgado et al., 2014; Jokinen & Suhonen, 1995; Moore et al., 2007; Tamura et al., 1999; Waite & Reeve, 1995), it follows that they should have some means of assessing individual food items to determine their value.

Several scatter-hoarding animals, including squirrels, are sensitive to the presence of other animals and adjust caching behaviors when competitors are present (Dally, Clayton, et al., 2006; Dally et al., 2005; Emery, Dally, & Clayton, 2004). Birds in the corvid and parid families eat food items and reduce the number they cache, or wait to cache until after competitors have left (Goodwin, 1956; James & Verbeek, 1984; Lahti & Rytönen, 1996; Leaver et al., 2007; Stone & Baker, 1989). Western scrub jays cache out of view or move their caches several times when conspecifics are present, presumably to reduce visual cues available to competitors (Dally et al., 2004; Dally et al., 2005). Eurasian jays (*Garrulus glandarius*) may even reduce acoustic information available to competitors by caching in quieter substrate (Shaw & Clayton, 2013), as other jays appear to use auditory information to locate and steal caches made by other jays (Shaw & Clayton, 2014). Scatter-hoarding tree squirrels also vary several behaviors in the presence of competitors:

the amount of time and effort spent traveling to a cache site (Delgado et al., 2014; Hopewell et al., 2008; Leaver et al., 2007), the number of holes dug before selecting a final cache location (Delgado et al., 2014; Steele et al., 2008), and time spent covering a cache site with available substrate such as dirt or leaves (Delgado et al., 2014; Hopewell & Leaver, 2008).

These behaviors suggest that there is a risk to the caching animal when burying food in the presence of competitors. Pilfering is assumed to be common, but because an animal who is pilfered from also likely pilfers from others, scatter-hoarding despite the risk of theft is considered a viable and stable strategy (Vander Wall & Jenkins, 2003).

Attempts to quantify the amount of pilfering have mainly assessed the rate of disappearance of human-made caches. In a three-week study of fox squirrels, results suggested pilfering rates of up to 9.4% per day, although a second study used shallower caches, and reported pilfering rates of up to 33% per day (Stapanian & Smith, 1984). Studies of congeneric eastern gray squirrels suggested that squirrel-made and human-made caches were removed from the ground at similar rates, although it was not known if the cache owner was also the cache retriever for squirrel-made caches (Thompson & Thompson, 1980). A more recent study of caches made by gray squirrels suggested that all were depleted in less than six days (Steele et al., 2014). However, another study demonstrated that by removing the caching animal from the area immediately after they cached (and thus mimicking predation), caches survived up to 27 days (Steele et al., 2011). This provided evidence that a caching animal holds some advantage in cache recovery, but tells us little about what factors led to the pilferage of nuts that were removed in the absence of the animal who originally stored them.

Reducing cache density has not shown consistent results in preventing pilferage. In some cases, the loss of human-made caches is reduced by decreasing density (Daly et al., 1992; Male & Smulders, 2008; Male & Smulders, 2007), but in other studies cache density has had little effect (e.g., Galvez et al., 2009). However, if cache density does increase pilfering, the impact of cache density or of caching close to the caches of other squirrels may be mitigated when pilferers are close relatives. Stapanian and Smith (1978) found that squirrels tended to cache in unique areas, and cached slightly closer to their own previous caches than to those made by other squirrels.

Food theft may be tolerated in animals with overlapping ranges because it is a form of reciprocal exchange that avoids the behavioral costs of cache defense, vigilance, and aggression (Stevens & Stephens, 2002). We currently know very little about the potential effects of kin selection on the pilferage of scatter-hoarded food in free-ranging tree squirrels. One study showed that related male-female and female-female pairs had closer range centers than those of unrelated squirrels. However, the same study found that within a restricted search area (a 50 x 50-m area around the food source), relatedness did not influence the proximity of caches made by different squirrels (Spritzer & Brazeau, 2003). Another study reported a low degree of relatedness within groups of fox squirrels, due to natal dispersal, which is influenced both by age and sex (Koprowski, 1996). Low relatedness would make the question of kin selection less relevant. Population density and dispersal patterns may be adapted to local conditions, however, and it is not clear what group relatedness would be in urban squirrels who are provisioned with food (Penner et al., 2013) or live in fragmented landscapes (Sheperd & Swihart, 1995), both which can impact dispersal.

Reciprocal theft tolerance among related food-storers has been demonstrated in larder-hoarding animals such as woodpeckers (*Melanerpes formicivorus*; Koenig, 1987) and beavers (*Castor canadensis*; Novakowski, 1967). Among scatter-hoarders, there could be fitness benefits in relaxing cache protection strategies in the presence of closely related individuals.

This study had several objectives. The first was to determine if levels of pilfering could be assessed in the field, including identifying specific individual squirrels who pilfer or move caches. If it was possible to observe pilfer events, and determine who was stealing from whom, further study into how behavioral and genetic factors could influence the outcome of caches would be justified.

The second goal was to determine the fate of squirrel-made caches, including how long caches remain where buried, and whether they are pilfered, re-cached, eaten or forgotten. An additional question was whether assessment or cache protection behaviors are related to the outcomes of buried nuts. Despite numerous studies of cache protection, there is little direct evidence that these strategies labeled as cache protection help animals recover their caches, or deter theft by others. I predicted that food assessment and cache protection behaviors should be related to a longer cache life.

The final objective was to examine the population dynamics and heterogeneity of squirrels in the study, including testing the hypothesis that cache proximity and pilferage tolerance could serve as a form of kin selection. Where theft did occur, I predicted there would be an increased likelihood of theft by offspring and other closely related individuals and higher tolerance of pilferage by closely related conspecifics.

4.2. Experiment 1: Testing squirrel responses to stimuli

In order to observe cache movements in the field, we painted 350 caching stimuli (intact hazelnuts) with two coats of yellow non-toxic acrylic paint (Sargent Art, Hazleton, PA). We first tested the squirrels' ability to discriminate between painted and unpainted hazelnuts to determine whether the paint might make it easier or more difficult for squirrels to locate cached nuts.

4.2.1. Methods

4.2.1.1. Study Site

The study was conducted outside of Tolman Hall on the University of California, Berkeley campus.

4.2.1.2. Study Animals

Eight free-ranging, marked fox squirrels participated in the study. The research was approved under a protocol submitted to the Animal Care and Use Committee of the University of California, Berkeley.

4.2.1.3. Procedure

Playground sand (Quikrete Cement and Concrete Products, Atlanta, GA) was placed in a 50.8 x 50.8 x 14-cm plastic container at a depth of approximately 5-cm. The container had a latch on one end that allowed the side to be lowered to allow easy access

into the box. The apparatus was divided into sixteen 12.7 x 12.7-cm quadrats, numbered from one to sixteen.

Data were collected between October 14 and November 5, 2014. We lured one marked squirrel at a time into the apparatus by calling to them and placing small pieces of peanuts nearby and on top of the sand. Once the squirrel was habituated to entering the apparatus, the peanut pieces were removed.

Four painted nuts, and four unpainted nuts were placed in quadrats chosen by a random number generator (random.com), such that no quadrat had more than one nut in it, and on any given trial, half of the quadrats contained a buried nut. Each hazelnut was covered with enough sand that it could not be detected visually. The focal squirrel was allowed to sniff around and dig in the sand, until it found a hazelnut. Some squirrels did not locate a hazelnut and left.

When a squirrel first located a hazelnut, the following data was recorded: the name of the squirrel, the quadrat the nut was removed from, and whether the nut was painted or unpainted. All squirrels that found hazelnuts carried them away and cached them. Between trials, all nuts were removed from the apparatus, the sand was stirred around to reduce olfactory cues, and nuts were placed in new locations as predetermined by random number generation.

4.2.2. Results of Experiment 1

Six squirrels completed at least 20 trials. A total of 118 trials were conducted. In 64 (55%) of the trials, the squirrel found a painted hazelnut first; in the remaining 54 trials, the squirrels found an unpainted hazelnut first. Using a binomial probability, this detection rate for painted nuts is not different from chance (binomial test, $p = .52$). From this result, we conclude that the painting of the nuts did not give off odor cues that would influence the difficulty or ease in locating cached nuts when compared to unpainted hazelnuts.

4.3. Experiment 2: Assessing pilferage in the field

The purpose of the pilot study was to determine whether pilferage between individual squirrels could be assessed in the field.

4.3.1. Methods

4.3.1.1. Study Site

The study was conducted on the University of California, Berkeley campus. This area is relatively open and flat, with oak, pine and other trees, lawns, ivy ground cover and campus buildings. The study area was approximately 0.09 km².

4.3.1.2. Study Animals

Twenty-three free-ranging fox squirrels who regularly frequented the study site participated in the study. All squirrels were individually marked with fur dye (Nyanzol-D, American Color and Chemical Corporation, Charlotte, NC). We chose one adult female (Flame) as the focal subject, because she was frequently seen foraging in the testing area. The research was approved under a protocol submitted to the Animal Care and Use Committee of the University of California, Berkeley.

4.3.1.3. Procedure

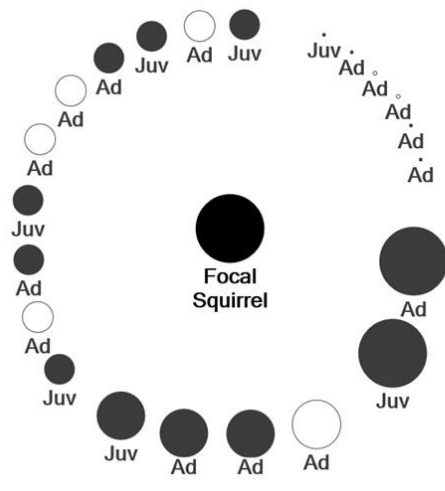
The study was conducted between the hours of 10:00 and 16:00 on each weekday from June 16th to July 25th, 2014. The caching stimuli were whole hazelnuts, in the shell, which had been painted bright yellow with two coats of non-toxic acrylic paint as in Experiment 1). The focal squirrel recognized the painted hazelnuts as food items, eating or caching all nuts.

On each morning of testing we dispensed up to 15 nuts, one nut at a time, and observed the focal squirrel while she either ate or cached the nut. The number of nuts dispersed was dependent on the presence of the focal squirrel. On some days, she left the study site before all 15 nuts were presented. If a nut was cached, we marked the number of the nut and the location of the cache on a paper map. We also took a GPS waypoint for each cache location. The focal squirrel cached 340 painted hazelnuts.

While nuts were dispersed, researchers noted which other squirrels could be observed in the area. Each day, after dispersing all nuts to the focal squirrel, we used binoculars to observe the squirrels in the study site for several hours each day. The yellow paint allowed for increased visibility of the food items while carried by squirrels. Because the nuts were painted, and all squirrels in the area were marked, when a squirrel was seen moving or eating a yellow hazelnut, we were able to note the identity of the squirrel carrying the painted nut. We also noted where nuts were re-cached.

4.3.2. Results of Experiment 2

During 125 hours of observation, 102 nuts were observed being moved by a squirrel. We observed the focal squirrel moving and either eating or re-caching 16 of these nuts. The remaining nuts were pilfered by other squirrels, suggesting an overall pilfering rate of at least 25 percent. Our observations suggested that although several individuals were



pilfering small amounts from the focal squirrel, some squirrels were more likely to pilfer nuts than others, with two squirrels pilfering 14 and 15 nuts respectively (Figure 4.1). For 22 caches (25% of stolen caches), nuts were pilfered within 20 minutes of being cached, allowing us to note the

Figure 4.1. Pilfering of caches made by the focal squirrel. Circles represent theft by either male ● or female ○ adult (Ad) or juvenile (Juv) squirrels. The size of circles represents number of nuts moved.

specific identity of that cache. Of the two squirrels that frequently stole nuts, one was a juvenile male often spotted in the same tree as the focal squirrel. Behavioral observations suggested this juvenile may have been the offspring of the focal squirrel.

4.4. Experiment 3: Field Study

The pilot data from Experiment 2 demonstrated that it was possible to quantify pilfering in the field, and to identify which squirrels are pilfering specific nuts. The purpose of the current study was to determine (1) what happens over the lifespan of a cache – how many times, where and when is a nut moved before it is finally eaten; (2) the influence of assessment behaviors on cache lifespan and outcomes; and (3) the effect of relatedness of caching behaviors.

4.4.1. Methods

4.4.1.1. Study Site

The study was conducted on the University of California, Berkeley in the same general area as the previous experiment. The study area was approximately 0.10 km².

4.4.1.2. Study Animals

Nineteen free-ranging fox squirrels who regularly frequented the study site participated in the study. All squirrels were individually marked with Nyanzol-D (American Color and Chemical Corporation, Charlotte, NC). The research was approved under a protocol submitted to the Animal Care and Use Committee of the University of California, Berkeley.

4.4.1.3. Experimental Stimuli

First, 350 hazelnuts were checked to determine that they had no cracks in their shell. A small hole was drilled in each nut using a Dremel Multipro 395 hand-held tool fitted with an 1/16" drill bit. A 12-mm 134.2 kHz pit tag (Biomark, Boise, ID) was placed in each nut, and the hole was filled with Elmer's wood glue. The surface of the nut was leveled when necessary by ensuring the hole was entirely filled with glue, and scraping away any excess glue. After the glue was dry, the nuts were painted with two coats of bright yellow paint (Sargent Art, Hazleton, PA). Due to experimental oversight, forty of the nuts were painted light green with the same brand of acrylic paint. After the nuts were dried, they were numbered 1 to 20 with a non-toxic marker, and placed in bags of 20 nuts each that were labeled alphabetically, such that each nut had a unique alphanumeric code (for example, A1, A2...B1, B2, etc.). All nuts were scanned with a BioMark HPR Plus reader to verify that their pit tag was functional. We weighed each nut, and entered each nut's alphanumeric code, pit tag code, and weight into a database.

4.4.1.4. Procedure

A total of 350 pit-tagged nuts were distributed to squirrels from February 11, 2016 until April 5, 2016, between 9:45 and 16:00 hours. On most days, 20 nuts were handed out (10 in the morning and 10 in the afternoon), dependent on weather, lab staffing, and squirrel participation.

A uniquely marked squirrel was solicited for each trial by an experimenter gesturing or calling to the squirrel. One experimenter videotaped all sessions with a Canon FS300

handheld camcorder, noting the squirrel, and alphanumeric code of the nut for each trial. The purpose of videotaping each cache was to record food assessment and cache investment behaviors. If a squirrel could not be easily filmed, experimenters dictated any change in behaviors when they could be observed.

A second experimenter gently tossed the nut on the ground toward the squirrel, and kept records of the subject, time, and the other squirrels present for each trial. The third experimenter scanned the nut at the start and end of the trial with the Biomark HPR Plus reader, which also collected GPS information for the start location and the final cache location.

The squirrel either cached or ate each nut. When the squirrel cached the nut, all experimenters followed the squirrel from a distance until the nut was cached. At that point, the third experimenter scanned the cache location to verify that the nut had been cached and could be detected. The location of the cache was drawn on a map, and the location of the cache was measured from at least two landmarks, noting both distance and bearing (determined by a handheld compass or cell phone compass application) from the landmarks.

Trials were repeated until 10 nuts were handed out for the session or until there were no squirrels available to participate. We alternated between different individual squirrels between trials if multiple subjects were available and willing to participate.

When not handing out nuts, experimenters observed the squirrels to note if there were any cache movements. We used the BioMark HPR Plus to search for previously cached nuts, initially scanning for all cached nuts that had a known location at least every two to three days. Other testing areas were scanned regularly using either the handheld HPR loop antenna, or with a portable antenna that had been mounted on a dolly with wheels to facilitate the rapid search of large, open areas where squirrels often cached. Constraints included weather, staffing, and the battery power of the pit tag reader.

We tracked nuts that had been stolen or re-cached, including their new locations, and if observed, who moved the cache. Cache life was defined as the number of days a cache stayed in its original location. We also recorded any nuts that were detected in a previously unknown location, and then checked those nuts routinely until they disappeared or were still present at the end of the experiment and assumed forgotten. Any new microchips that were detected six months after the end of the experiment were dug up to determine if they were still embedded in a nut or if the nut had been eaten.

All videos of the sessions were coded using The Observer XT (Noldus, Leesburg, VA). There were three video coders, and inter-rater agreement on onset, timing and presence of behaviors between the pairs of coders was high (agreement for coded videos ($n = 9$) averaged Cohen's kappa, $\kappa = .91$, range .75 to 1). The variables recorded for all cached nuts included: the number of head flicks for each nut, the amount of time spent paw manipulating, the amount of time spent digging, tamping, and covering the nut, and the amount of time the squirrel spent handling the nut, from initial receipt of the nut until the cache was completed.

One rater assessed the level of concealment of all cache events, whether open (the entire squirrel could be observed caching), partially concealed (more than half of the squirrel was covered by ivy or other plant matter), mostly concealed (less than half of the squirrel's body could be seen), or completely concealed (none of the squirrel could be observed while caching, such as if the squirrel was caching in a hedge). To determine

reliability, a second rater coded 60 of the cache events. Inter-rater agreement for the level of concealment of the cache was $\kappa = .84$.

GIS data was used to determine the distance traveled for each cache, and the proximity of an individual squirrel's caches to their own caches and those of other squirrels.

4.4.1.5. Statistical Analyses

All data were analyzed using mixed models in JMP 12.0 (SAS Institute, Cary, NC). All models included squirrel identity as a random effect. The alpha level for all analyses was set at 0.05 and Tukey's HSD tests were conducted for any pairwise comparisons.

The first model determined if there were effects of nut weight and assessment on distance traveled to cache. A second model examined the effects of assessment and investment behaviors, and social competition on cache life. The independent variables were number of headshakes, time spent paw manipulating, distance traveled, time spent on cache, concealment of cache, time spent digging, tamping, and covering the cache, and the number of other squirrels in the area. A third model was run to determine if squirrels adjusted investment behaviors (digging, tamping, and covering their caches) depending on the level of concealment of the cache location or the presence of other squirrels.

Spatial data were analyzed using ArcGIS version 10.3 (ESRI, Redlands, CA), and JMP 12.0 (SAS, Cary, NC). Waypoints were entered into ArcGIS with the WGS 1984 Geographic Coordinate System, and with the State Plane NAD83 California Zone III projection. I calculated the distance traveled for each cache, the proximity of each squirrel's cache to their own caches and all caches made by other squirrels.

4.5. Experiment 3: DNA Collection and Analysis

In order to assess the effects of relatedness on fox squirrel caching behaviors, hair samples were collected during the same testing period as the rest of the experiment.

4.5.1. Methods

4.5.1.1. Study Site

The study was conducted on the University of California, Berkeley campus in the same general area as the previous experiments. The study area was approximately .09 km².

4.5.1.2. Study Animals

Hair samples were collected from 14 of the free-ranging, marked fox squirrels who participated in Experiment 3. Hair samples were collected from an additional eight squirrels who were not in the field study. The research was approved under a protocol submitted to the Animal Care and Use Committee of the University of California, Berkeley.

4.5.1.3. Procedure: Hair Collection

Hair collection was based on methods previously described in multiple studies of free-ranging mammals (Finnegan, Hamilton, Perol, & Rochford, 2007; Reiners,

Encarnaç o, & Wolters, 2011). Squirrels were first desensitized to entering a Tomahawk Flush Mount Squirrel trap for food. Both doors of the trap were secured open with zip ties, so the trap would not be set off when an animal entered it. A 60.96 x 20.32-cm black strip of plastic was placed at the bottom of the trap to allow for easy baiting with small pieces of walnuts and peanuts. Once the squirrel entered the trap readily, the trap was set to collect hair.

Experimenters wore latex gloves during all handling of hair collection materials to reduce the risk of contamination. All equipment was sanitized between uses in the field or in the lab with rubbing alcohol. Five 3.58 x 13-cm strips of double-sided Ace brand heavy-duty carpet tape were placed on a piece of PVC tubing (20.32-cm long, diameter 4.11-cm). The tubing was suspended in a storage box by placing it over the center core of a multi-roll tape dispenser (Figure 4.2a). The storage box and a pair of sanitized tweezers were taken out to the field site.

A marked squirrel was recruited for hair collection. Other squirrels were kept away from the trap by tossing them peanuts. The release liner of the carpet tape was removed with tweezers and PVC tubing was inserted at one end of the trap. The tube was suspended by either a piece of wire affixed to both sides of the trap, or by the core of the tape dispenser (Figure 4.2b). The tube was suspended low enough that if a squirrel passed underneath it, their tail would touch the exposed tape. The squirrel was lured into the trap several times with walnut pieces, until an adequate number of hairs with follicles were collected from the tail. The tube was removed from the trap, and returned to the tape dispenser holder in the plastic storage container. The name and sex of the squirrel, and the date of collection were marked on a label on the container. The container was sealed and stored until hair samples could be processed.

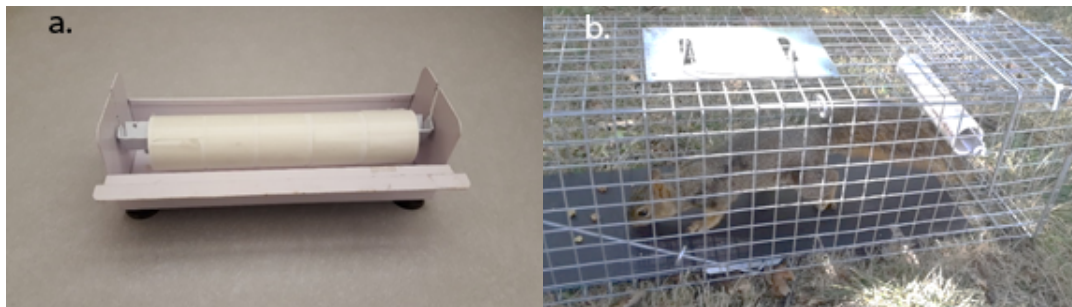


Figure 4.2. Hair collection procedures. (a) PVC tubing prepared for hair collection. (b) A marked fox squirrel in the trap baited for hair collection.

4.5.1.4. Procedure: Preparation of Hair Samples

Hair samples were later prepared for polymer chain reactions (PCR) in a clean environment where no other biological materials were handled. Experimenters wore gloves, a gown, a face mask and a hair net, which were all changed between samples. The surface was sanitized with Sanizide Germicidal Solution (Safetec, Buffalo, NY) and then a large piece of butcher paper was placed on the surface.

The tape dispenser with the hair sample was removed from the plastic storage container. The experimenter removed individual hairs from the tape, inspected them carefully for a follicle, and then cut the hair approximately 2 mm below the follicle. The follicles were placed in an individual Fisherbrand glass threaded 15 x 45-mm, 3.7 mL

vial (Fisher Scientific, Chicago, IL) containing ethanol (200 proof Ethyl Alcohol, Spectrum Chemical Mfg. Corp., Gardena, CA). Once an adequate number of hair follicles were collected (generally between 30 and 40 follicles, but fewer if the sample from the squirrel was scant), the tube was sealed and labelled with the squirrel's name and sex, and the date. In between processing samples, all materials were sanitized with rubbing alcohol, and any other materials (tape, butcher paper, hairs, gloves, gowns, etc.) were disposed of in an individual trash bag that was sealed.

4.5.1.5. DNA Amplification, PCR, and Sequencing

Genetic relatedness and diversity of 22 fox squirrels, 14 of whom participated in the current study, was inferred from PCR amplification and analysis of 12 microsatellite loci (Table 4.1). These markers were previously identified as polymorphous in fox squirrels (Fike & Rhodes Jr, 2009). Primers for the 12 loci were acquired from Sigma-Aldrich (The Woodlands, TX).

DNA from 5-10 hair follicles for each individual was extracted using standard methods via a DNEasy Blood and Tissue kit (QIAGEN, Valencia, CA). We amplified the DNA utilizing a polymerase chain reaction process in a BIO-RAD icycler thermal cycler (BIO-RAD, Hercules, CA).

Each 10- μ L reaction mixture contained 3 μ L of DNA material, 0.3 μ L each of the forward and reverse primer, 0.3 - 0.55 μ L MgCl₂ (adjusted for specific primer pairs, see Table 4.1), 0.25 μ L of dNTP, 1.0 μ L reaction buffer (Tango, Carlsbad, CA) and 0.12 μ L of Taq polymerase (Invitrogen, Carlsbad, CA). The forward primer for primer pairs was fluorescently labeled with either 6-FAM or HEX dye. PCR reactions were run through three steps: (1) denaturation at 95°C for 4 min; (2) 36 cycles of denaturation at 95°C for 45 s, annealing at 54-58°C (adjusted for specific primer pairs, see Table 4.1) for 30 s and elongation at 72°C for 45 s; and (3) final elongation at 72°C for 10 min.

Successful reactions were prepared for sequencing with 2 μ L of PCR product, diluted with 9.8 μ L of formamide and combined with 0.2 μ L of an internal size standard (LIZ 500, Applied Biosystems, Foster City, CA, U.S.A.). Fragments were determined via sequencing using a Thermo Fisher 3730 DNA Analyzer (Thermo Fisher, Waltham, MA). Base pair lengths were labeled using Geneious 10.1, with the Microsatellite Plugin 1.4 (Biomatters Limited, Newark, NJ).

4.5.1.6. Statistical Analyses

Pairwise relatedness between each pair of subjects in the study were estimated using the program ML-Relate 5.0 (Kalinowski, Wagner, & Taper, 2006), which calculates maximum likelihood estimates of relatedness and the most likely relationship between pairs of individuals. Expected and observed heterozygosity (the probability that an individual will be heterozygous at a given locus) were calculated using the “adegenet” package in R 3.3.0 (Jombart, 2008).

Table 4.1. Motifs and oligo sequences for twelve polymorphic microsatellite loci used in the study to determine relatedness among fox squirrels. Annealing temperature, magnesium chloride (MgCl₂) concentrations used during PCR, expected (H_E) heterozygosity as reported by Fike and Rhodes (2009).

Locus	Motif	Oligo sequence (5' to 3')	PCR Product (base pairs)	Annealing Temperature (°C)	MgCl ₂ (μL)	H _E
FO 06 - F	AC(9)	AGAATGGAAACTTAACCTAACTGTGG	218-222	57	.40	.632
FO 06 - R		CATTATTTTCGCAGGCTTTGG				
FO 11 - F	AG(22)	CCATTTATGAGGGAGGTAGGG	258-296	57	.40	.843
FO 11 - R		TTGAATCTGTAGATTGGGTAGTATGG				
FO 26 - F	GT(14)	TTTAGAGTCTCGGCTGCTATCC	346-354	57	.50	.561
FO 26 - R		GCTATGGAAACCAACCTAAGTGC				
FO 33 - F	AG(21)	ATTTCCCTGGGTTCAATTCC	149-171	54	.30	.850
FO 33 - R		GTGGTTGCTTCCATAATGAGG				
FO 35 - F	AC(12)	TTCGTATGCCCTCAGGTAGC	246-252	55	.40	.535
FO 35 - R		TCCATCCAAGGACATTACTGG				
FO 36 - F	CT(9)	TGGATTGCTTTAGTCCACTTG	106-122	55	.40	.601
FO 36 - R		AAATTAATGTTCTGCTGGTGTATAG				
FO 46 - F	AC(16)	TGTTCTTTTCCAAAGACCAA	214-224	57	.35	.238
FO 46 - R		CACAAGTTGGTGCCAAATCA				
FO 58 - F	CT(21)	CTCCTAATTAATTCAAAGGACAAGC	158-182	58	.35	.795
FO 58 - R		CCATGACCAAATTACTCAAAGC				
FO 62 - F	GT(19)	GAGCCAGGAACAAGGTAAAGC	198-208	57	.55	.689
FO 62 - R		CCTTCCTGGCAGTTATCACC				
FO 63 - F	CT(30)	CATAGTCACTTTCAAAGACTATTGATT	132-166	57	.30	.812
FO 63 - R		TTGATTATGGGATACTCTGTAATTC				
FO 65 - F	AC(14)	TTTGCTTTCTTCTCTTCTTCTGC	233-243	57	.45	.642
FO 65 - R		CCAACTGAACTATAAACCCAGACC				

Locus	Motif	Oligo sequence (5' to 3')	PCR Product (base pairs)	Annealing Temperature (°C)	MgCl₂ (μL)	H_{E1}
FO 67- F	CT(19)	CTTGAGGTTTCAGATCTCATGG	183-199	57	.45	.746
FO 67- R		AAATGATCAGCATAATTTCTCAGC				

4.5.2. Results of Experiment 3

4.5.2.1. Cache outcomes

A total of 292 nuts were cached. No video was obtained for three caches and some data was missing for these caches. Twenty nuts were eaten at the time they were distributed to squirrels, and 36 nuts had an unknown outcome because the squirrel could not be tracked until they ate or cached the nut.

The average lifespan of a cache was 38.38 days (Median = 4 days, range 0 to 482 days). The number of nuts cached and cache life by individual are depicted in Table 4.2. Four hundred and eighty-two days after the start of the experiment, 12 nuts remained in their original cache locations and were assumed forgotten. This suggests an overall forgetting rate of around four percent. An additional 18 nuts remained in new locations that they had been moved to at some point during the experiment, a further loss of six percent. Seven instances of pilfering and one recaching event (by the squirrel “Three”) were observed. Pilfering events between squirrels are noted in Table 4.4.

The only variable that was related to the length of time a cache stayed in its original location was the level of concealment ($F(3, 232) = 3.32, p = .021$) such that caches that were placed in mostly concealed areas had longer cache lives ($n = 39, M = 93.38$ days, 95% CI [40.92, 145.83 days], Median = 8 days) than caches placed in open ($n = 175, M = 32.80$ days, 95% CI [19.81, 45.77 days], Median = 4 days) or partially concealed areas ($n = 56, M = 21.30$ days, 95% CI [5.33, 37.27 days], Median 3.5 days). Caches placed in totally concealed areas had a lifespan of 26 days ($n = 20, 95\% \text{ CI } [-4.47, 56.47 \text{ days}], \text{ Median} = 5.5 \text{ days}$) and were not statistically different from other cache concealment categories.

Weight and the number of headshakes were weakly related to the distance from the food source that a squirrel traveled to cache, such that heavier nuts and more headshakes were associated with a longer distance traveled but the effect in both cases was not statistically significant (weight: $F(1, 275) = 3.14, p = .08$; headshakes $F(1, 75.78) = 2.91, p = .09$).

Finally, squirrels adjusted cache protection behaviors depending on the level of conspicuousness of the cache. They spent more time caching nuts when in open locations ($F(3, 269.4) = 3.76, p = .011$), or when other squirrels were present ($F(7, 265.2) = 2.72, p = .010$; Figure 4.3). Squirrels spent the most time digging ($F(3, 254.1) = 4.43, p = .005$), and covering their caches ($F(3, 256.5) = 13.68, p < .001$) when they cached in an open location, and spent the least amount of time on all cache protection behaviors (digging, tamping, and covering caches) when in a concealed location. See Figure 4.4.

4.5.2.2. Microsatellite analysis

The number of alleles per locus ranged from 3 to 16, and single locus heterozygosities ranged from 0.20 to 0.92 (Table 4.3), suggesting an overall high level of genetic diversity in the tested population. From 10000 randomized simulations performed in ML-Relate, a possible heterozygote deficiency was found at one loci ($F_{62}, p = .059$; Table 4.3). Observed heterozygosity was slightly higher than expected ($t_{11} = -2.09, p = .06$).

Based on estimates of the most likely relationships between individuals (unrelated, half siblings, full siblings or parent-offspring), there were likely six full siblings, five half

siblings, and three parent-offspring relationships between the fourteen individuals in the study for whom we had DNA samples (see Table 4.4).

Table 4.2. Number of nuts cached by each squirrel, and average cache life (both mean and median) in days.

Squirrel	Number of nuts cached	Average cache life (days) (SD)	Median cache life (days)
Biggie ^a	37	55.89 (115.75)	4
Billy Ray	3	18.00 (26.00)	4
Blake	18	28.89 (39.40)	11.5
Chubs ^b	23	91.65 (177.05)	5
Curly	1	24.00 (NA)	24
December	1	0.00(NA)	0
Fermata	7	23.57 (24.41)	22
Flame	16	26.31 (69.75)	4
Gwen	1	3 (NA)	3
Jewel	4	2.75 (3.50)	1
Joker	5	2.40 (1.14)	2
Mermaid	1	1.00 (NA)	1
Roger	21	21.29 (61.26)	5
Scarf	16	29.25 (63.69)	4
Squiggle ^c	43	41.40 (105.11)	4
Stool ^a	28	67.54 (136.01)	9.5
Stovetop	15	4.53 (5.83)	3
Teddy Bear	2	2.00 (1.41)	2
Three	47	24.57 (73.52)	3
Walter	3	2.33 (2.08)	3

^aForgot three caches

^bForgot four caches

^cForgot two caches

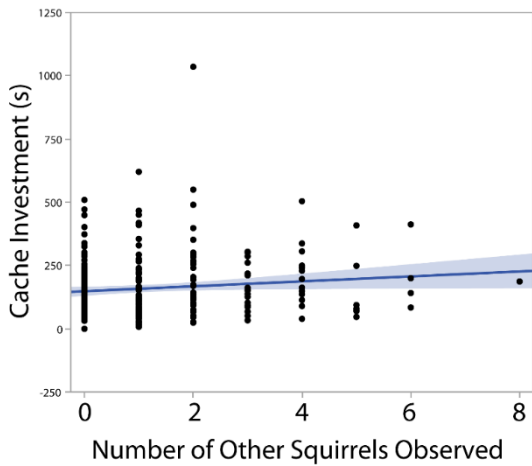


Figure 4.3. Total cache time (seconds) in the presence of other squirrels. Squirrels tend to spend more time caching as the number of competitors (other squirrels) increases.

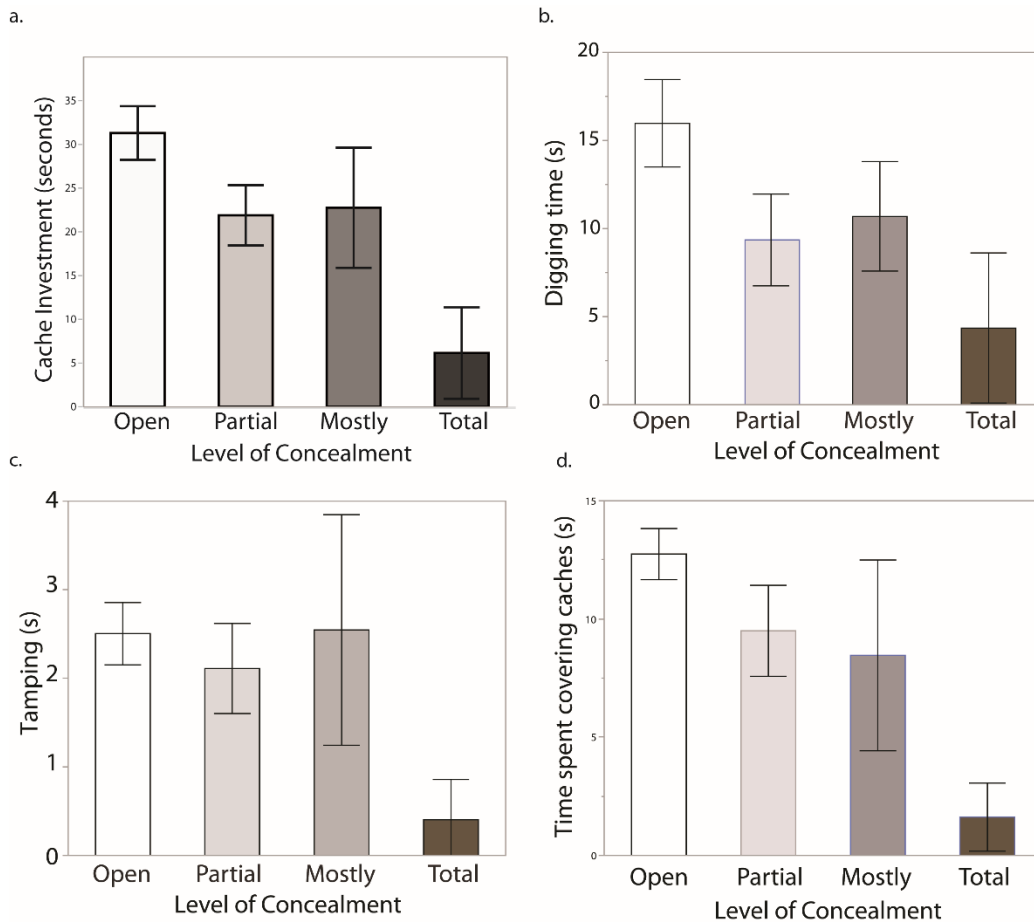


Figure 4.4. Cache investment and protection at different levels of cache conspicuousness. Squirrels spent more total time caching (a), more time digging (b), and more time covering (d) caches made in open locations compared to completely concealed locations. Squirrels spent the least amount of time tamping caches made in completely concealed locations.

4.5.2.3. Spatial distribution of caches

Geospatial data was used to assess the proximity of a squirrel's caches to their own caches, and to those of other squirrels, based on relatedness between individuals. When treated as a continuous variable, there was a negative linear relationship between probability of relatedness and cache distance ($F(1, 105) = 9.77, p = .002$, Figure 4.5a), but this effect was largely driven by the inclusion of the distance each squirrel tended to cache from their own other caches.

When assessed as a categorical variable (self, related, unrelated), there were differences between groups on average distance between caches ($F(2, 99.42) = 10.71, p < .001$). Squirrels tended to cache closer to their own caches ($M = 59.14$ m, 95% CI [44.87, 73.41]) than to those of other squirrels, particularly when compared to those of unrelated squirrels ($M = 91.28$ m, 95% CI [84.26, 98.3]). The average distance between related squirrels was $M = 81.93$ m, 95% CI [67.37, 96.49]. See Figure 4.5b.

Squirrels also tended to disperse their caches more as the experiment continued. The distance traveled from food source to cache increased during each consecutive week of

the experiment, ($F(1, 290) = 7.70, p = .006$, Figure 4.6). The density of nuts decreased as the experiment continued (Table 4.5), although squirrels continued to cache in the central area that they cached in during week 1 throughout the remainder of the experiment (Figure 4.7).

Table 4.3. Expected (H_E) and observed (H_O) heterozygosities at the twelve loci analyzed.

Locus	H_E	H_O
F06	0.64	1.00
F26	0.71	0.95
F11	0.92	1.00
F33	0.73	1.00
F35	0.71	0.59
F36	0.60	0.71
F46	0.71	0.95
F58	0.81	1.00
F62	0.34	0.20
F63	0.68	0.90
F65	0.64	0.86
F67	0.72	0.95

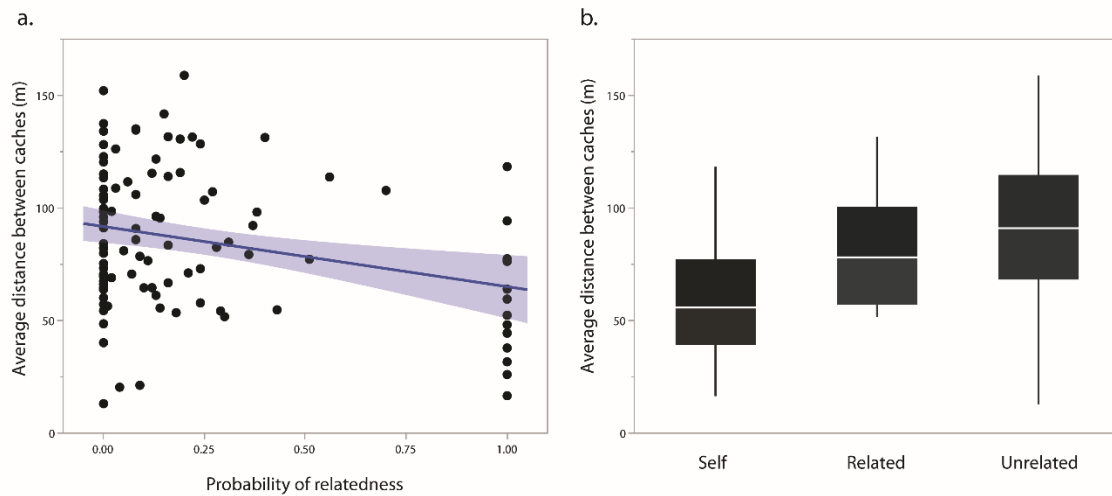


Figure 4.5. The relationship between relatedness and distance between caches.

Relatedness decreases distance between caches (a); squirrels tend to cache closer to their own previously made caches than to those of other squirrels.

Table 4.4. Probabilities of relatedness between individuals in the study.

	Biggie	Roger	Teddy	Fermata	Walter	Stool	Joker	Blake	Flame	Jewel	Three	Squiggle	Curly	Chubs
Biggie	1													
Roger	0.07	1												
Teddy	0.08	0.13 ^c	1											
Fermata	0	0.06	0.36 ^b	1										
Walter	0.19	0.03	0.11	0.13	1									
Stool	0.19	0.08	0.14	0	0.25	1								
Joker	0.01	0	0	0.08	0.20	0.13	1							
Blake	0.27	0	0	0.16	0	0	0.15	1						
Flame	0.51 ^b	0	0	0	0.02	0.05	0	0.70 ^b	1					
Jewel	0	0	0.09	0.31	0	0	0	0.56 ^a	0.43 ^a	1				
Three	0.29 ^b *	0.30 ^c	0	0	0.16	0.38 ^a	0	0	0.12	0	1			
Squiggle	0.28	0	0.10 [*]	0.12	0.24	0.37 ^b	0	0.08	0.24	0.16 [*]	0	1		
Curly	0	0	0	0.09	0	0	0	0.08	0.18	0.04	0	0.21 ^c	1	
Chubs	0.02 [*]	0 [*]	0	0	0	0.22 ^b	0.24 ^c	0.40	0.13	0.03	0	0.14 ^c	0	1

^aLikely parent-offspring relationship

^bLikely full-sibling relationship

^cLikely half-sibling relationship

*Pillfering event observed between these two individuals

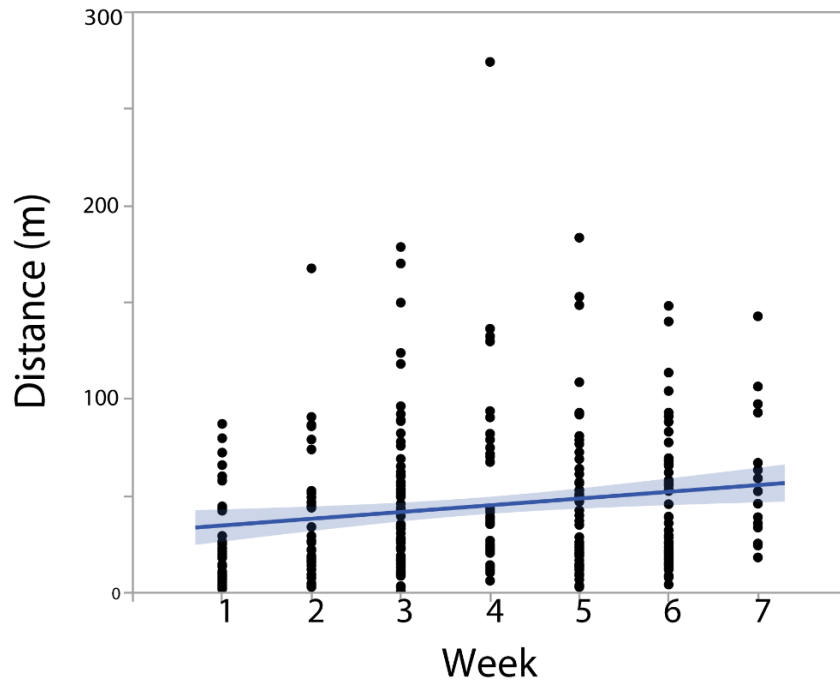


Figure 4.7. Distance traveled for each cache buried by each week of the experiment. Squirrels increased distance traveled from the food source as the experiment continued.

Table 4.5. Nearest Neighbor Distances throughout the experiment. NN ratios larger than one indicate nuts that were cached at a lower density than expected if randomly distributed. Observed distances between nuts tended to increase as the experiment continued.

Week	NN Ratio	Z-statistic	p-value	Observed distance (m)	Expected distance (m)
1	1.04	0.42	.680	8.43	8.13
2	.88	-1.34	.180	9.41	10.64
3	.88	-1.89	.060	10.48	11.87
4	.84	-1.71	.090	20.44	24.28
5	.80	-2.75	.006	19.37	24.20
6	2.03	1.15	.040	21.34	18.50
7	1.52	4.08	<.001	32.45	21.38

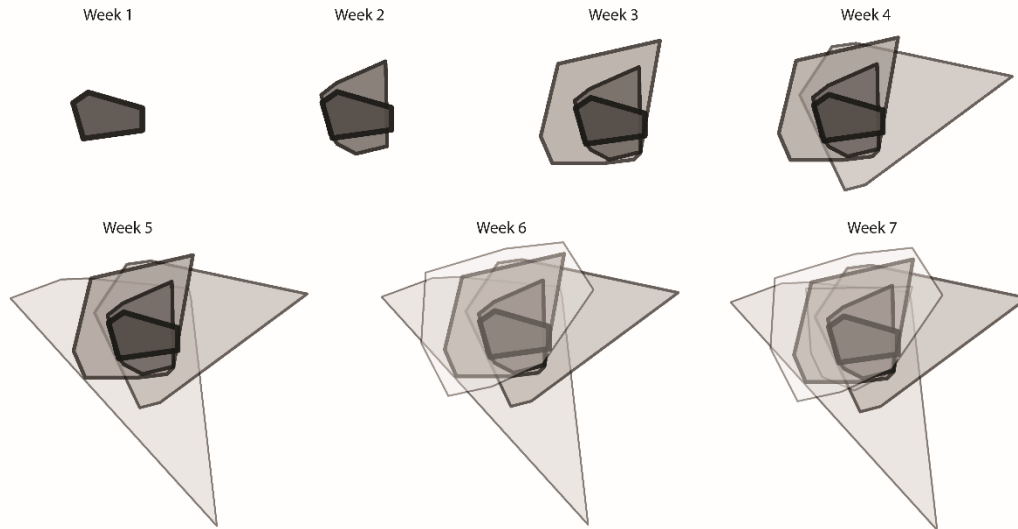


Figure 4.7. Polygons depicting the minimum bounding geometry for caches made by all squirrels for each week of the experiment. Squirrels utilized a larger area to cache in as the experiment continued, but also continued to cache in a core central area.

Discussion

The results of this study suggest that the most important factor contributing to the fate of caches made by fox squirrels, strictly measured as how long a cache remained in its original location, is the conspicuousness of the cache. Caches that were placed in open areas were moved sooner than other caches. Squirrels also spent more time digging, tamping and covering caches in open areas, compared to more concealed caches.

This study also supported previous findings that squirrels are sensitive to food item value and the social context when caching. Squirrels showed a tendency to travel further for heavier hazelnuts, even though the range of nut weights in this study was very small ($x = 3.94$ g, range 2.3 to 5.5 g). Several studies that have shown that tree squirrels tend to travel further for heavier nuts, nuts that provide more nutritional content, and nuts that are at lower risk of perishability (Delgado et al., 2014; Moore et al., 2007; Preston & Jacobs, 2009; Stapanian & Smith, 1984; Steele et al., 1996), and this study demonstrates that this may also happen on a very fine-grained scale, even when there are small differences in quality between food items.

Squirrels traveled further away from the food source to cache when greater numbers of competitors were present. They also showed some tendencies to cache closer to their own previously made caches, and closer to the caches made by related squirrels than unrelated squirrels. This supports that squirrels, although generally considered solitary (Steele & Koprowski, 2001) are sensitive to the social context they are caching within.

It has been assumed that the time squirrels spend covering caches is somehow related to preventing conspecific theft. Covering caches has been previously described as a method of disguising caches or as cache protection (e.g., Delgado et al., 2014; Hopewell & Leaver, 2008; Steele et al., 2008). The current study showed that more time covering caches was not a predictor of cache life and in fact the inverse may be true. Squirrels spent more time covering caches that were in open areas, and those caches also tended to

stay in place the shortest amount of time. In order to fully understand this effect, it would be necessary to assess the effect of substrate on covering time; it is possible that caches in open areas were placed in a more compact, tighter substrate that required more digging and covering than a looser soil.

If in fact caches are recovered by the squirrel who cached them, then cache covering may serve as protection. But even if the food-storing animal retrieves their own caches, the function of covering needs to be disentangled between different possible hypotheses. Covering caches could provide protection by creating scent cues or consolidating the memory of the food-storer, making retrieval easier for the caching animal. It could also provide protection by making it more difficult for a competitor to find and pilfer a cache.

However, in Experiment 1, 25% of pilfered nuts were stolen shortly after they were cached. This suggests that squirrels may be observing each other cache; in which case, spending more time covering could provide a signal to competitors that a nut is being buried, and give pilferers more time to observe the cache location. The function of cache covering behavior merits further exploration, but most importantly how the outcome of caches is related to covering behavior needs to be determined.

The results of this study demonstrated that pilfering between individual squirrels can be quantified in the field. Unfortunately, we were unable to observe many instances of pilfering or recaching in the final experiment. Given the results from the pilot study, this was surprising. However, in the pilot study, we only provided one squirrel with nuts to cache. This limited the area that needed to be observed, as the focal squirrel cached most of the nuts she was provided with in a central area. Provisioning her with nuts each day may have artificially inflated the pilfering rate by changing the caching behavior of only one individual in the study area.

Conversely, in the final study, because several squirrels were caching, the cache areas were distributed across a larger area of the testing area (Figure 4.7), which made observation difficult as the experiment continued. Furthermore, because we were providing squirrels with nuts in both the morning and afternoon, this limited our total observation time. Because many nuts were moved within a short period of time, the lack of pilfer and recache observations does not suggest that squirrels were not pilfering and recaching nuts; they just did so in times and places that were not being directly observed.

A previous study suggested that the experimental provision of food for squirrels could increase pilferage (Penner et al., 2013). Researchers first provided squirrels with ad libitum food in one plot, and did not offer food in a control plot. Later, pecans were buried at identical densities in both plots, and pilfering was statistically higher in the previously provisioned plot. We have not quantified how providing the squirrels with food in our study may have inflated pilferage; however, the current study did not include any provision of food prior to the experiment. During the study, squirrels were provided with nuts primarily where they were observed, thus the provisioning location frequently changed. No specific area of the study site should have been seen as more desirable for foraging or searching for previously made caches.

Squirrels buried the majority (almost 60%) of their caches in an open area, which suggests there may be some benefits to caching in an open area, such as ease of retrieval for short term storage. That said, five out of seven of the observed pilferage events were of nuts were originally cached in open areas. In a previous study (Steele et al., 2014), human-made caches under canopy were moved more than caches made in the open.

Based on the limited data we acquired in this study, fox squirrel caches in open areas may be pilfered more frequently. It is possible that since gray squirrels spend more time under canopy in comparison to fox squirrels (Steele & Koprowski, 2001), they were more likely to discover human-made caches under canopy than in the open.

In the current study, half of all cached nuts were moved within four days of being buried. That said, 25% of cached nuts had a life span longer than 20 days. A previous study of squirrel-cached acorns found that of 57 cached nuts, all were moved between one and six days after burial. No relationship was found between cache life and distance nuts were buried from cover. Because it is unknown in both studies if short lifespans are due to pilfering or recaching, it is difficult to say whether this life span is beneficial or detrimental to caching animals.

Approximately 10% of cached nuts remained in place a year after they were cached or re-cached. Based on observations of nuts that were dug up six months after the end of the experiment, they were likely no longer edible. Perhaps the squirrels could detect this and abandoned caches, or these forgotten caches may represent what percent of nuts is typically forgotten by food-storers. Cahalane (1942) found that fewer than two percent of nuts buried by fox squirrels were forgotten over the winter, but as he marked caches with stakes, he may have provided additional visual cues to the original food-storers or to pilferers that made these nuts easier to locate.

A key function of seed dispersers is to propagate tree species (Price & Jenkins, 1986; Sun & Zhang, 2013; Vander Wall, 1990), and squirrels have co-evolved with their food sources (Stapanian & Smith, 1978; Steele, Wauters, Larsen, & Forget, 2004; Vander Wall, 2010). Thus, some forgetting of cached nuts provides benefits to both the tree species, and the food storer, in terms of guaranteeing future food sources for kin. It is not possible to test the duration of memory for caches with human-made caches, and so pit-tagging of nuts provides an excellent methodology for further testing what percent of nuts may be forgotten by caching animals.

The microsatellite analysis of DNA collected for subjects in this study demonstrated that despite a fragmented habitat, human-made structures, and likely artificial supplementation of food, there is a similar level of genetic diversity among the study population as the populations of fox squirrels sampled in their native habitat (Fike & Rhodes Jr, 2009). We were able to use a non-invasive method to obtain hair samples from free-ranging squirrels that provided adequate DNA for sequencing and analysis. This analysis found expected levels of heterozygosity at 11 out of 12 loci.

More importantly, microsatellite analysis allowed me to explore how relatedness impacts caching behavior. Although I was not able to determine the relationship between probability of relatedness and likelihood of pilfering between individuals, results suggested that squirrels may cache nuts closer to caches made by relatives than unrelated squirrels. If squirrels are more likely to pilfer within or close to their caching territory, then this would suggest some form of kin selection could be at work. This could also prevent pilfering from non-related individuals. Given the small sample size, and the fact that the effect was small, we should interpret these results with some caution; further studies should examine this possibility in much more detail.

Ideally, this study would be replicated with fewer caching subjects and more time to observe individual cache movements. Alternatively, the focal squirrel could be rotated, testing just one individual at a time, to allow for a more fine-grained observations and

analysis of the relationship between caching behaviors, relatedness and cache fate. Ideally, hair samples would be collected from all participating squirrels in the study, in addition to sampling squirrels in other locations surrounding the test area, to better assess the level of dispersal among campus squirrels.

To summarize, this study established or validated several methods for testing the caching behavior and population dynamics of a group of free-ranging, scatter-hoarding tree squirrels. The results demonstrate the flexibility of squirrels when storing food, and show that they adjust behaviors according to several environmental and social factors. They also point to the need for a greater understanding of how these behaviors are related to the outcomes of caches that are stored for future use, a question that turned out to be much more challenging to answer than anticipated.

Chapter 5: Pilfering imposes limits on the memory of food-storing animals.

5.1. Introduction

Various animal species store food items for later retrieval, with storage periods ranging from just hours to months. Food storage is a means for taking advantage of excess food in the environment, a highly adaptive strategy in environments that experience periods of both food abundance and scarcity. Caching allows for both protecting food from spoilage, and for maintaining possession of food items in the face of inter- and intra-specific competition (Brodin, 2010; Vander Wall, 1990).

The diversion of food items to caching rather than immediate consumption has been shown to be, at least in some species, highly calculated. Items that spoil quickly are more likely to be consumed immediately rather than cached, or retrieved sooner than items that are better preserved when stored. For example, scrub jays are more likely to retrieve preferred wax worms instead of peanuts. However, when such a period of time has passed such that the worms are likely spoiled, they retrieve more cached peanuts (Clayton & Dickinson, 1998). Woodrats (*Neotoma cinereal*) and tree squirrels cache less perishable food items, and consume more highly perishable items (Hadj-Chikh et al., 1996; Post & Reichman, 1991). Tree squirrels are also more likely to store food items for a season of scarcity if the item's nutritional value is higher (e.g., Delgado et al., 2014; Hadj-Chikh et al., 1996; Smallwood & Peters, 1986).

It would seem, therefore, that food stores are an important part of a caching animal's diet. However, to take advantage of these stores, food-storers must overcome two challenges: remembering the locations of caches, and protecting stores from raids by competitors (Vander Wall, 1990). Both challenges are likely less of a burden for animals that primarily larder hoard such as red squirrels (*Tamiasciurus hudsonicus*; Hurly & Lourie, 1997), chipmunks (*Tamias striatus*; Vander Wall, Hager, & Kuhn, 2005), and red-headed woodpeckers (*Melanerpes erythrocephalus*; Doherty Jr, Grubb Jr, & Bronson, 1996), who store most food items in one location that can be physically defended. Conversely, the challenges are likely rather significant for scatter-hoarders, such as some squirrels and jays, who cannot defend individual caches.

Strategies to defend food from pilferers occur during the entire process of acquiring and storing food. Eastern gray squirrels perform cache-covering behaviors over empty cache sites to potentially deceive pilferers (Steele et al., 2008). Scrub jays cache out of sight of potential thieves (Dally et al., 2005), and re-cache previously stored food that conspecifics observed them caching (Emery & Clayton, 2001).

Despite these cache-protection strategies, pilfering remains a problem for food-storers, with field estimates of pilfering ranging from 30 to 80% (Clarke & Kramer, 1994; Vander Wall et al., 2006; Vander Wall & Jenkins, 2003). Theoretical analysis has shown that the defense strategies of food-storing animals, and counter strategies by pilferers, can lead to an evolutionary arms race of social cognition, where each side is trying to outsmart the other (Emery et al., 2004; Emery & Clayton, 2004). In light of these findings, it would seem that pilfering might shape not only food-storers' defenses, but also their cache retrieval strategies.

Field and lab studies suggest that food-storing animals remember the location of at least some of their caches, over long periods of time. Clark's nutcrackers (*Nucifraga columbiana*) remember cache locations up to 9 months later (Balda & Kamil, 1992), and nutcrackers, pinyon jays, and gray squirrels remember caches well up to two months (Bednekoff & Balda, 1996; Jacobs & Liman, 1991; MacDonald, 1997). Animals that live in harsher environments, and rely strongly on stored food, also have better memories (Pravosudov & Clayton, 2002).

In this study, we use evolutionary simulations to investigate how pilfering affects memory size of food-storing individuals. We evolve a population of food-storers in an environment where food availability changes over time, and show that in the absence of pilfering, individuals evolve to have a memory spanning almost their entire lifetime, recalling most of their past caches. Once pilfering is introduced, food-storers undergo selection for a short memory that only leads them to retrieve relatively recent caches, as old caches have likely been raided by conspecifics.

It remains unclear to what extent, if any, the memories of caching animals have been affected by pilferage. Previous models of food-storing behavior have mainly looked into sustainable rates of pilfering. It has been found that for caching to persist in the presence of pilfering, food-storing individuals should have a higher probability of recovering stored food items than pilferers (Andersson & Krebs, 1978). Alternatively, it has been suggested that pilferage would be tolerated if it is reciprocal (Vander Wall & Jenkins, 2003). Pravosudov and Lucas (2001) have shown that if caches do not last long (due to spoilage, forgetting or pilfering), animals are better off investing in fat reserves than in storing food. Pravosudov and Lucas also note that long-term memory should increase survival rate of food-storers, contrary to other models that found constraints on memory to be inconsequential to survival (Brodin & Clark, 1997; Smulders, 1998). However, these models did not specifically look at the potential effects of pilfering on memory length.

5.2. Methods

5.2.1. The model

We used an agent-based computer model to simulate a population of individuals who either cache, pilfer, or retrieve food, based on probabilities determined by their genotype, and receive a payoff based on these behaviors. We let memory for caches evolve in these populations. Individuals who accumulated higher payoffs had a higher chance of reproducing, thus increasing the frequency of their memory genotype in the population.

5.2.2. The population

We created a population (size $N = 100$) of individuals who had three behaviors probabilistically determined by their genes for caching/retrieving (CR), pilfering (P), and memory (M). The caching gene determined, on any given turn, the probability that an individual would either cache or attempt to retrieve a previously cached food item. The probabilities for caching were either 0.1, 0.5, or 0.9. The pilfering gene determined the probability (0, 0.1, 0.5, or 0.9) that an individual would attempt to pilfer a food item from a competitor. Populations were fixed to a single allele for CR and P genes (no mutation).

A third gene, the memory gene M , determined how long an individual's memory was (0, 1, 25, 50, 75 or 100 days), and therefore the oldest cached item they could attempt to

retrieve from their own cache. For example, an item cached 80 days earlier could be retrieved by an individual with the allele coding for 100 days long memory ($M = 100$) but not by an individual carrying any of the other alleles. The first generation in all populations carried only the $M = 0$ allele (no memory), and it was subject to mutation in subsequent generations (see below).

5.2.3. *The environment*

Each generation, G , experiences two phases, or seasons: one season with abundant food, where food encounters occurred at probability $p_1 = .75$, and one season during which food was scarce, where food encounters occurred at probability $p_2 = .25$. Each phase lasted 50 days (d).

5.2.4. *Behaviors: Foraging, caching and pilfering*

Each individual had four opportunities (Ops) per day to encounter a food item. An individual had to forage to meet a daily energetic requirement fulfilled by one food item, encountered at probability p_1 , before they could engage in other behaviors. Once an individual found and consumed one food item, the value of that food item (F_v) was added to the individual's payoff. The individual was then considered satiated for the day.

In the first season, once satiated, individuals first chose by binomial probability set to .50 (random) to either engage in a behavior, or do nothing. For squirrels who were not selected to engage in a behavior, the encounter ended. Individuals who were assigned to a behavior would either forage and cache, or pilfer and cache. If an individual found a food item while foraging, that item was cached and stored in a memory matrix in a location matched to the individual and day.

The probability of pilfering and caching stolen items was set by the pilfering allele (e.g., 0.1, 0.5, 0.9). If the individual was assigned to pilfer rather than forage, they would search through all other squirrels' previously made caches and choose one item at random to steal. That food item was eaten, and removed from the other squirrel's memory matrix. The value of that food item (F_v) was added to the pilfering squirrel's memory matrix. If there were no food items to be stolen or retrieved, the turn ended.

In the second season, food encounter rate was reduced to $p_2 (< p_1)$. Each individual, at any given turn, could either forage, retrieve previously cached nuts, or pilfer, depending on probabilities set by the caching and pilfering alleles (e.g., 0.1, 0.5, 0.9). Based on these probabilities, individuals were assigned '1' or '0' for caching and pilfering. If the individual was assigned '0' for both caching and pilfering, they were assigned to forage for food. If the individual was not satiated, and they found a food item while foraging, that item was consumed and its value was added to the squirrel's payoff. Otherwise, found food items were ignored.

If the individual was assigned '0' for caching and '1' for pilfering, they would search through all other squirrels' previously made caches and choose one item at random to steal. If the squirrel was not satiated for the day, that food item was eaten, and removed from the other squirrel's memory matrix. The value of that food item (F_v) was added to the pilfering squirrel's payoff. If the squirrel was satiated for the day, they would ignore found food items. If there were no food items available to pilfer, the squirrel did not receive any points or recache any food items.

If the individual was assigned ‘1’ for caching and ‘0’ for pilfering, they could search in their own memory matrix for a previously cached food item, in the search space determined by their memory allele. If they were not satiated for the day, that food item was eaten, and removed from their own memory matrix. If they were satiated, found food items were recached and stored in the memory matrix in a new location matched to the individual and day. If no food items were available in the squirrel’s memory matrix, they could not eat or recache any items.

Finally, if the individual was assigned a ‘1’ for both cache and pilfer, their behavior (pilfer or retrieve) on that turn was determined by binomial probability of .50. They would either pilfer and recache or retrieve and recache, as previously described. If there were no food items to be stolen or retrieved, the squirrel did not receive any points or recache any food items.

5.2.5. Genetic selection and reproduction

At the end of the second season, individuals were ranked according to their payoff. The top-earning 50% of individuals were selected to reproduce asexually (Arbilly, Motro, Feldman, & Lotem, 2011), with each individual producing two offspring with identical memory alleles. The parental generation was then eliminated, so that population size remained constant. Once a new generation was produced, mutation in the memory gene occurred at a rate $\mu = 1/N$. Mutants were randomly assigned a memory allele (1, 25, 50, 75 or 100). Evolution was allowed over 2000 generations, and each permutation of the model was run for 100 replications.

5.2.6. Implementation of the model

The model was written and run in Matlab 2015a (Mathworks, Natick, MA). Models were run utilizing the University of California, Berkeley Savio Institutional/Condo Cluster and the NSF Extreme Science and Engineering Discovery Environment (XSEDE; Towns et al., 2014).

5.2.7. Data analysis

Evolved memory lengths for each combination of pilfering and caching rates were determined by calculating weighted averages. The frequency of each allele in the population for the last 100 generations of each run were multiplied by that allele’s value. For example, if the last 100 generations averaged zero individuals possessing the 0, 1, and 100 alleles, and averaged .05 individuals with an allele for a memory of 25, .01 individuals with an allele for memory length 50, and 99.94 individuals with memory length 75, the weighted average for that run was calculated as $(0*0 + 0*1 + .05*25 + .01*50 + 99.94*75 + 0*100 = 74.97$. The average of the weighted values for all runs was calculated to determine the average memory length at each level of caching and pilfering.

5.3. Results

When there was no pilfering in the population, alleles coding for longer memory were favored by selection. The average memory length in the population was 80.9 ± 1.7 days when caching rate was low (0.1), and 90.4 ± 1.2 days when caching rate was high (0.9; see Figure 5.1). When pilfering was included in the model, selection for long memory

was reduced and there was an interaction between pilfering and caching rates (Figure 5.1). When pilfering was zero or low (0.1), there was little effect of cache rate on memory length. When pilfering was medium (0.5) or high (0.9) probability, the effect of pilfering on memory was dependent on the amount of caching. At low rates of caching, memory was short; at high rates of caching, memory was longer, yet shorter than when there was little or no pilfering in the environment.

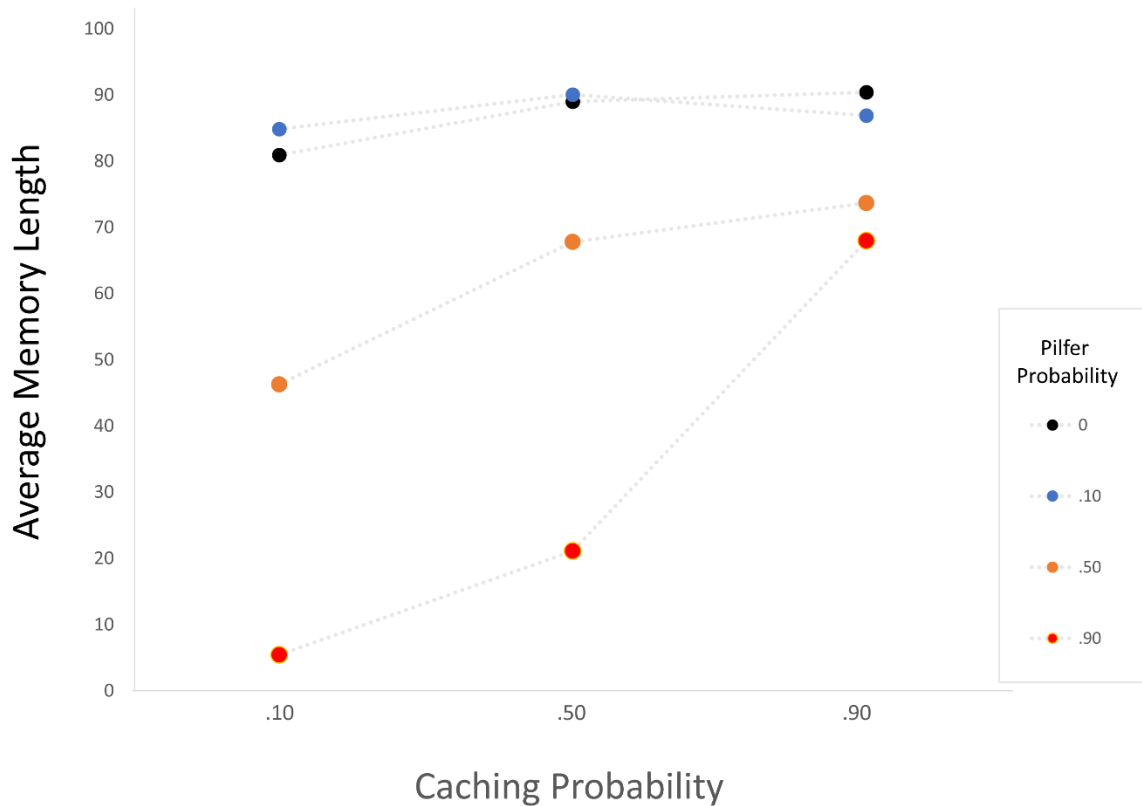


Figure 5.1. Average memory length under different caching and pilfering rates. Memory length is a weighted average based on average frequency of memory length alleles in the population. Memory is longest at high rates of caching and low rates of pilfering.

5.4. Discussion

Results of our computer simulations show that in the absence of direct competition (e.g., 0 and 0.1 pilfer probability in Fig 5.1), food-storing animals evolve a relatively long memory, regardless of how much food is actually being stored (0.1 to 0.9 caching probability). However, food-storing animals often face competition: field studies show that pilfering is common among scatter-hoarding animals (Clarke & Kramer, 1994; Vander Wall et al., 2006; Vander Wall & Jenkins, 2003). But Vander Wall and Jenkins' model (2003) demonstrated that as long as pilfering is reciprocal, a stable system of food-storing behavior can emerge. Their model included probability of larder-hoarding versus scatter-hoarding and likelihood of physically defending caches from pilfering, and did not specifically examine the effects of pilferage on memory.

In our model, we introduced pilfering into the environment to allow individuals to at times steal from competitors rather than forage from the available food in the environment, or to search for their own previously buried food. However, this search was constrained by the individual's memory. Once we introduced pilfering into our simulated populations, long-term memory was less advantageous. At higher rates of pilfering, selection favored alleles coding for shorter memory than when pilfering was low.

The effect of high rates of pilfering on memory was partially mitigated by an increased level of caching; meaning that if animals stored an adequate amount of food, there was positive selection for longer memory compared to when caching was low and pilfering was high. A high caching rate meant that individuals could still successfully retrieve food items they had previously cached when memory was longer.

If animals are pilfered from at high rates, it would follow that the benefits of caching might eventually be outweighed by the costs (Luo et al., 2014). Rather than cease caching, empirical studies have found that many food-storing animals increase caching rates in the presence of high rates of pilfering (Huang, Wang, Zhang, Wu, & Zhang, 2011; Luo et al., 2014). This effect was stronger in larder-hoarding animals who had been completely pilfered, but the results suggest that pilfering serves as a stimulus that increases food storing behavior.

On each turn, behaviors were determined by the probability of caching and pilfering, and individuals could not pilfer and cache within the same turn. When the probability of caching was equal to or higher than the probability of pilfering, then the effects of pilfering were reduced, because individuals would likely be pilfering on fewer turns, allowing for more successful retrievals. When the probability of caching or retrieving was lower than pilfering, more individuals would pilfer on their turns, depleting the stores of other squirrels in the population, and making a longer memory less useful. Essentially, when stores are depleted, there is little use in having a memory for them and searching in pilfered locations.

Even when pilfering was absent or very low in the model, populations rarely evolved a perfect memory. Why wouldn't food-storing animals evolve a perfect memory? Smulders (1998) created a model that suggested that memory *must* be long-term to impact retrieval of stored food items. Pravosudov and Lucas (2001) also found that both pilfering and forgetting led to decreased survivorship of individuals in their model. Thus, memory loss or a short-term memory should cause problems for food-storing individuals.

Recent neurobiological studies point to potential reasons for such limitations on memory as were found in our model. Neurogenesis primarily occurs in the dentate gyrus of the hippocampus, the area of the brain known to be critical for spatial memory (Kee, Teixeira, Wang, & Frankland, 2007), and may serve multiple functions, both generating new synaptic connections, while potentially weakening existing ones (Frankland, Köhler, & Josselyn, 2013). This weakening of older connections may cause interference with retrieval of older memories (Yau, Li, & So, 2015).

Stereological studies found a relationship between the size of the CA1 subfield of the hippocampus and the fall caching season in male eastern gray squirrel, but failed to find a relationship between overall cell proliferation in the hippocampus and season (Lavenex, Steele, & Jacobs, 2000a; Lavenex et al., 2000b). In chickadees, neuronal recruitment in the hippocampus increases in the fall, but the new neurons are short-lived, and no overall change in the number of neurons is observed at different times of the year (Barnea &

Nottebohm, 1994; Barnea & Nottebohm, 1996). The relationship between neurogenesis, memory, and caching behavior is therefore complicated, but suggests that limitations on memory such as that found in our model are not unexpected.

In the natural environment, some forgetting of caching propagates food-bearing trees (Price & Jenkins, 1986; Sun & Zhang, 2013; Vander Wall, 1990). However, the current model did not provide any long-term benefits to the population for forgetting caches. A likely explanation is that low pilfering rates may have reduced the need for a perfect memory, and could have made the majority of retrievals successful independent of memory length. This could have prevented strong selection for a perfect memory.

As many food-storing animals manage their caches by frequently moving them, a bias toward short-term memory in the natural environment could serve other functions: first, it could confuse potential pilferers who may have observed the original cache event and second, it may update the memory of the cache owner, in a sense extending the life of that cache. Future models can explore more explicitly how re-caching food may update memory or thwart pilfering, as well as how different pilfering strategies (such as locating the caches of other squirrels via observation versus olfactory search) effect memory length.

Length is not the only potentially important aspect of memory. Agent-based models could be used to directly test different types of forgetting and remembering, such as retrograde and anterograde interference, or episodic memory. In the case of retrograde interference, individuals would be more likely to remember recent caches; anterograde interference would make it harder for individuals to remember more recent caches. Models of the effect of episodic memory could add “what, where, when” information to see what costs and benefits there might be to having more detailed memory in a fluctuating and competitive environment.

All individuals in our model had the opportunity to both cache and pilfer food. There were no individuals who could adopt a pure producer or scrounging strategy (e.g., Barnard & Sibly, 1981). Additional models can explore how mixed populations would evolve and whether a pure pilfering strategy could persist in an environment where other individuals have different caching and pilfering rates.

Our results suggest that the evolution of cognitive strategies that aid cache retrieval in food-storing animals are dependent on both caching and pilfering rates. The model presents a simple environment with very few assumptions or costs. Although this model does not present the complexity of the natural caching environment, it demonstrates a proof of concept: caching animals likely have some (but not perfect) memory for their stores, and that in an environment with reciprocal pilfering, an imperfect memory is all you need to succeed.

Chapter 6: Conclusions

The goal of this dissertation work was to advance our understanding of the food-storing decisions made by scatter-hoarding animals. To that end, I conducted several field studies with the scatter-hoarding fox squirrel, testing several aspects of their food-storing behavior, including food assessment, cache placement, and pilferage. The fox squirrel is an excellent study species for this work as they are commensal with and easily habituated to humans, and still driven by the evolutionary pressures that shaped them millions of years ago (Emry & Thorington, 1984). The results spanning the studies described in this dissertation support the hypothesis that the food-storing behavior of the fox squirrel is complex and flexible, yet operating under multiple simple and fixed rules that help the squirrel maximize the retrieval of caches.

In Chapter 2, I demonstrated that fox squirrels show sensitivity to the absolute and relative value of food items. Fox squirrels can identify properties of a food item that might make it intrinsically valuable, such as its perishability, weight, or nutritional content. The unique food assessment behaviors of tree squirrels, the head flick and paw manipulation, allow squirrels to determine this value. They also can evaluate food items relative to previously received food items, and to the likelihood of food encounters based on seasonal fluctuation in food availability. Overall squirrels consistently invested more time and effort into the caches of higher valued food items.

Squirrels routinely eat and cache the seeds of many species of trees, including hickories, oaks, walnuts, hazelnuts and beechnuts (Steele & Koprowski, 2001). This varied diet may be a factor in the evolution of their food assessment behaviors, as squirrels adjust the distance traveled to cache and the density of caches based on the food's type, weight, quality, and nutritional value (Delgado et al., 2014; Moore et al., 2007; Preston & Jacobs, 2009; Stapanian & Smith, 1984; Steele et al., 1996). Such behaviors demonstrate the squirrels' sensitivity to subtle differences in the quality of individual food items. In fact, these behaviors appeared to be more prominent in the study described in Chapter 2, where food items were alternated, than in Chapter 4, where the food items remained consistent. It is possible that unexpected changes in food quality may stimulate these behaviors more than just the presentation of food items. When squirrels repeatedly encounter the same type of food item, they may habituate and perform less assessment.

This line of work could be expanded to include a wider range of natural food items to determine the function of these different assessment behaviors – for example, the paw manipulation may serve for judgment of both quality and efficient transport strategy, given that food items may vary in how easy they are to carry based on size, shape and shell texture. Experimentally manipulated food stimuli could control for weight, while varying size; control for size, while varying weight; or provide different levels of tractability. Parsing out these variables will help us understand which properties are most important to the assessment process.

Future studies should further explore the potential process of devaluation of or habituation to food item value that we found evidence for in this study. Squirrels decreased the effort placed into caching individual items as trials within a session continued, which may suggest a form of habituation, or discounting behavior where squirrels devalued food items that were abundant. This reduction in effort could also be an effect of fatigue, but the results of the study in Chapter 2 suggests that fatigue is not

the cause, because when squirrels switched from receiving peanuts to hazelnuts, assessment and investment behaviors increased. Future research should directly test the differences in the level of habituation or decreased investment when only receiving food items of one type, or by presenting squirrels with differently valued food items in separate sessions.

Tree squirrels are an excellent model species for many aspects of economic decision making. Delay discounting is a decline in the perceived value of a reward based on the time until its anticipated receipt, and is considered an indirect measure of impulsivity (Madden & Johnson, 2010). Humans and many other humans tend to prefer smaller, sooner rewards, over larger, delayed rewards. Squirrels and other caching animals routinely delay rewards by caching food. However, storing food is inherently riskier than eating it; animals must invest energy in caches which may spoil or be pilfered by others. Animals do not always survive long enough to eat the food they stored, or may forget caches. Because squirrels are constantly balancing the costs of effort and competition, their decisions during foraging and caching can reveal how they perceive the value of food items based on several factors, such as predictability of rewards, energy needs, and individual tendencies toward impulsivity (Madden & Johnson, 2010; Stephens & Krebs, 1986).

The spatial placement of caches as a potential mechanism to deter theft has been a subject of many studies. However, how this behavior might aid retrieval has not been the focus of caching studies. Chapter 3 provided the first evidence that squirrels may use the cognitive mechanism known as chunking, by organizing their caches spatially by type or value. This finding is new and potentially important and future studies could explore this effect with a larger sample of subjects. A larger number of food items per session would also allow for more detailed spatial analyses to see if this result is robust.

Squirrels also showed two modes of cache density adjustment depending on how food was foraged, but both modes potentially serve to minimize risk to high-valued items. When food was centrally foraged, squirrels adjusted density to value, which they could have achieved primarily by adjusting distance to value. When food was foraged from multiple locations, they distributed items in such a way that equalized their investment in all items. They did so by caching all food items at a lower density. This could serve to protect higher-valued items that would be at risk if cached too close to lower-valued items.

Some models of caching suggest that animals should deposit early-made caches close to a source, then place subsequent caches at either increasing or alternating distances from the food source (Clarkson et al., 1986; Stapanian & Smith, 1978). Studies of rock squirrels (*Otospermophilus variegatus*) and Merriam's kangaroo rats demonstrated that they cache nuts close to the food source, but move them within a few days of caching, a process described as rapid sequestration (Jenkins & Peters, 1992; Zhang, Steele, Zhang, Wang, & Wang, 2014) Contrary to previous findings and model predictions, the fox squirrels in studies described in Chapters 2 and 3 dispersed initial food items at a greater distance from the food source, and tended to decrease the distance traveled for subsequent caches. One key question that remains is whether this decreased distance as caching continues is because fox squirrels engage in less recaching than other scatter-hoarders, if recaching is dependent on initial distance traveled, or if this behavior occurs

for some other reason. Answering this question is dependent on conducting more long-term studies of the fate of caches.

Such an exploration of cache fate was one of the goals of the field study in Chapter 4. Other goals were to quantify the level of pilfering among a group of squirrels and to determine the effect of relatedness on caching behavior. Finally, I hoped to test how food assessment and caching behaviors were related to the outcome of caches. Unfortunately, this study was complicated at times by frequent rain, equipment failure, and an unexpected result: a lack of observed pilfering events.

After observing a 25% pilfering rate in the pilot study of one caching squirrel, I anticipated we would see a comparable amount of pilfering with a larger group of squirrels. Because the final field study involved a larger number of caching individuals, it became difficult to observe many of the areas where squirrels had cached while simultaneously running the experiment. The methodologies used in this study (tagging nuts, utilizing video, and incorporating geospatial data) could be repeated on a smaller number of focal squirrels, or by rotating which individual squirrel is caching during any given time period, rather than presenting cacheable items to several different individuals during the same experimental session. I believe such methodologies would provide better results.

The study successfully correlated some caching behaviors, such as the amount of concealment during caching, with the lifespan of a cache. In general, squirrels appear to prefer to cache in open or partially concealed areas, locations that were correlated with shorter lifespan. It remains to be tested whether caching in these observable areas increases pilfering, or is inconsequential due to rapid sequestration and recaching. The negative correlation between behaviors that had previously been described as cache protection, such as time spent covering caches, and the length of time a cache remained in place is an interesting result. We need to know if short-term caches are pilfered or recached by the original food-storing animal in order to better understand this finding.

Repeating this study with several different food types, such as those used in Chapter 3, would also allow an exploration of the interaction between food value, food assessment and caching behaviors, and cache lifespan. Since squirrels invest more time and effort in caches of larger and more valuable nuts, it is important to know if those caches also remain in place longer.

Finally, we found some weak support for the use of cache placement, and presumably tolerance of pilferage, as a form of kin selection. Squirrels appeared to cache closer to the caches made by related individuals than unrelated individuals. Due to the small sample size, and the small effect size, this experiment and these results would need to be replicated to feel confident about this finding.

This research would have been bolstered by collecting hair samples from a larger number of individuals. I was unable to obtain hair samples from all participants in the caching study. Given more time and resources, I would have collected hair samples from squirrels in other areas of the campus at several timepoints in order to assess gene flow (Moncrief, 1993; Signorile et al., 2014). A previous study found 100% natal dispersal in a group of fox squirrels living on a campus in Kansas (Koprowski, 1996). Given that all participants in the study in chapter 4 were adults, it appears that there may have been less dispersal in the squirrels in the research location described in this dissertation work than previously observed in other studies.

The introduction of agent-based modeling of a dynamic series of caching-pilfering interactions, as described in Chapter 5, is another important contribution to the food-storing literature. By keeping the environment very simple, the model clearly demonstrates that in the absence of other factors, competition reduces the memory capacity of food-storing animals. This contradicts the notion of caching and pilfering being strictly an evolutionary arms race where animals out-compete each other by evolving counterstrategies that thwart competitors (Emery et al., 2004; Emery & Clayton, 2004).

Although competition shortened memory, this finding does not by any means negate the social intelligence hypothesis, the theory that a complex social environment enhances cognition (Whiten & Byrne, 1988). Instead, it suggests the potential importance of forgetting or refinement of memory (Bannon, 2006; Storm, 2011). If an animal's caches have likely been stolen, it may be a better strategy to forage or pilfer from another animal, or search for more recently made caches, than to search for older caches which are no longer there.

Because food-storing interactions are so complex, there are several variables that could be included in future agent-based models to expand on this work. For example, food assessment and caching behaviors could be incorporated into the model, to test competing hypotheses. It is possible that there is a cost to food assessment and cache covering, such as by cueing conspecifics to the presence of food. If so, is that cost mitigated by the acquisition of information that helps the caching animal make better decisions about how much time and energy to invest in cache protection strategies? If caching behaviors, such as digging and covering, lead to better encoded memory for cache events, would that increase retrieval in a competitive environment? Models could help us better quantify the potential costs and benefits of investing in these behaviors.

Models could also incorporate spatial information to further explore the findings of Chapter 3 and Chapter 4. Simulations could be run with different costs and benefits to adjusting cache density, to help us understand how a mnemonic device to help an individual recall their caches might affect the ability of a pilferer to wipe out a set of cache stores. If scatter-hoarders do cache closer to the food stores of relatives, is a reciprocal pilfering relationship beneficial or harmful to an individual's fitness? Is it worth the additional energy of searching for caches outside of one's territory to pilfer from non-related competitors, or does reciprocal pilferage provide adequate kin selection?

Previous research has shown that repeated pilfering does not stop animals from investing in caching. To the contrary, studies that experimentally removed all caches that a variety of scatter-hoarding rodents had buried found increases in caching rates (Huang et al., 2011; Luo et al., 2014). The authors of these studies suggest that pilfering may stimulate hoarding behavior. In the model described in Chapter 5, individuals had only a set number of behaviors they could perform each day. A model could allow animals to freely interact and behave, at a metabolic cost of each behavior performed. This could test what environmental conditions, such as food abundance, would allow caching in the face of increased pilfering to result. For example, what is the usefulness of searching for and caching additional nuts if there is a lost opportunity cost of not utilizing that time to pilfer from others?

To conclude, the results of my research illustrate the complexity of the decision-making and cognition of food-storing animals. Using field studies, genetic analyses, and modeling led to a body of work that suggests that the value of food items and social interactions are likely universally critical to food-storing decisions. These findings challenge the notion that food-storing is a rigid, stereotyped behavior (McClure et al., 2004) and instead suggest that all aspects of decision-making by omnivorous, scatter-hoarding animals must take several factors into account: resource availability, food quality, competition, cognitive constraints, and perhaps even accounting for the needs of offspring or other relatives. The work in this dissertation answers some questions, but illustrates the richness of the many fascinating questions about food-storing behavior that still remain to be investigated.

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