The Ecology of Scatterhoarding in a Flooded Ecosystem

by

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Abstract

Food hoarding is a strategy typically used by species that experience times with little food readily available. Scatterhoarders store single food items in many locations throughout their home range before the food-scarce season and do not actively defend these caches before recovery during the food-scarce season. In the southeastern United States, flooding during winter is a problem faced by scatterhoarders due to a decrease in dry land available for cache recovery. Understanding how scatterhoarders respond to factors that could influence their supply of hoarded food, such as seasonal flooding, is important given the strong reliance on hoarded food to overwinter survival. We examined diet, hoarding behavior, habitat use, and survival of eastern gray squirrels (*Sciurus carolinensis*) in a seasonally flooded ecosystem on Lowndes Wildlife Management Area (WMA) in central Alabama. We predicted squirrels would respond to flooding by: storing food during fall in areas that stay dry during winter, seasonally shifting to dry habitat, changing their winter diet, or dying. During the dry season, over 72% of acorns were buried in areas that later flooded. Habitat use did not change during flooding periods; in fact, squirrels selected for habitat that stayed dry during flooding to a greater degree during non-flood seasons, although not significantly so. Diet did not change between the dry fall and flooded winter. We also found squirrels were 7.70 times as likely to die during the flood season (2.28-25.96, 95% C.L.) as the dry season and

mortality was 1.30 times as likely (0.26-6.38, 95% C.L.) for each 10% increase in the proportion of the study area that was flooded (both $p = 0.001$). Thus, this eastern gray squirrel population did not appear to show any behavioral adaptations to seasonal flooding. Further research is needed to fully understand the effects of fluctuating environmental conditions on scatterhoarding behavior and what management considerations should be taken into account for populations living in these conditions.

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Chapter 1: Literature review of previous studies

Evolution of food hoarding

For species that depend on temporally-limited food sources, food hoarding is a common strategy to combat temporary decreases in available food. Hoarding provides a steady supply of food energy and typically occurs before and during seasons with less readily available food (Smith and Reichman 1984, Brodin 1994*a*, Zhang et al. 2008*b*). For food hoarding to have evolved, the hoarder must experience increased fitness compared to individuals that do not hoard, (Andersson and Krebs 1978, Smulders 1998, Male and Smulders 2008). More specifically, the benefit of increased access to food must exceed the energetic costs of collecting, hiding, and defending the food stores (Andersson and Krebs 1978). Even in the presence of cheaters (nonhoarders that benefit from hoarded food without paying the associated costs), hoarding will continue to be selected for in a population as long as it increases the fitness of the hoarder relative to that of the nonhoarder (Andersson and Krebs 1978, Smulders 1998).

The two types of food hoarding are larderhoarding and scatterhoarding. Larderhoarding occurs when an individual stores food in one or few locations and actively defends its stores (Vander Wall et al. 2005). Larders are susceptible to being quickly depleted if the owner is unable to adequately defend it (Vander Wall et al. 2005). Larderhoarding species are generally those that do not experience intense inter- or intra-

specific competition for their food (Vander Wall et al. 2005). Alternatively,

scatterhoarding is characterized by many items of food buried or hidden far from one

another (Morris 1962). Species categorized as scatterhoarders usually only cache 1 or a

few food items per cache location (Lu and Zhang 2005, Xiao and Zhang 2006, Tuck

Haugaasen et al. 2010, Rusch et al. 2013*a*, Wang et al. 2013) in order to decrease thief

efficiency and reduce the effect of pilferage (retrieval by an individual that did not create

the cache) on their food stores (Geluso 2005, Thayer and Vander Wall 2005). This

strategy can result in food being cached short term (few days to few weeks; e.g.,

northwestern crow *Corvus caurinus*, James and Verbeek 1985) or long term (weeks to

months; e.g., eastern gray squirrel *Sciurus carolinensis*, Thompson and Thompson 1980),

depending on the period of time during which available food is scarce. Some species,

such as eastern chipmunks (*Tamias striatus*; Clarke and Kramer 1994), yellow pine

chipmunks (*Tamias amoenus*; Vander Wall et al. 2005), and large field mice (*Apodemus*

speciosus; Lu and Zhang 2005), exhibit behaviors characteristic of both larderhoarding

and scatterhoarding. These species either seasonally switch to scatterhoarding or use

scatterhoarding as a supplemental strategy when it is more difficult to defend the larder

(Clarke and Kramer 1994, Lu and Zhang 2005, Vander Wall et al. 2005). For a species to

use both food hoarding strategies, there must be advantages to the addition of

scatterhoarding to their usual larderhoarding behavior, such as taking less time to cache a

single item away from the larder or lessening the effects of pilferage of the larder (Sherry

et al. 1982, Clarke and Kramer 1994, Vander Wall et al. 2005, Rusch et al. 2013*a*).

Though hoarding has proven to be a sufficient strategy to cope with seasonal food scarcity, there are also associated costs. Both hoarding and recovery efforts take up a large amount of time that could be spent on other activities necessary for survival, such as eating, resting, and watching for predators (Tamura et al. 1999, Perea et al. 2011). After all the time and energy spent burying food, there is no guarantee that this food source will still be available when needed (Stapanian and Smith 1978). Seeds could rot, germinate, be pilfered, or become otherwise unusable. Yet, hoarding has evolved independently in different ecosystems globally (eastern gray squirrels *Sciurus carolinensis* in temperate deciduous forest vs. musky rat kangaroo *Hypsiprymnodon moschatus* in tropical rainforest), further demonstrating that the benefits must outweigh the costs in many situations (Dennis 2003, Tuck Haugaasen et al. 2010). There have been few attempts to quantify the benefits of hoarding for an individual or a population, other than showing it is relied on as a supplemental food source in many species (Thompson and Thompson 1980, Brodin 1994*a*, Lens et al. 1994). For many species, the proportion of stored food in the diet is unknown.

Scatterhoarding: Creation, management, and recovery of the cache

There are many aspects to take in to account when describing the caching and recovery efforts of a scatterhoarder. Scatterhoarders split their hoarded food between many places but should still show consistency in caching strategies to take advantage of the benefits of such strategies. The value of a strategy tends to differ among species and depends on environmental conditions (both present and future; Brodin 1994, Lens et al. 1994, Geluso 2005), preferred food qualities (Gálvez et al. 2009), competition (Petit et al.

1989, Preston and Jacobs 2005), size of the hoarder (Rusch et al. 2013*a*, Wang et al. 2013), and morphology of the hoarder (Petit et al. 1989). These challenges for hoarding and recovery are faced by all scatterhoarding species, therefore these species should all have developed similar strategies to cope with these challenges (Wang et al. 2013).

Caching decisions

Several characteristics of the food being handled affect the decisions made in the food hoarding process. This decision making process has 3 levels before caching may occur: 1. Ignore or manipulate; 2. Eat or remove to a determined distance; 3. Eat or cache (Wang et al. 2013). Seed dormancy schedules, tannin content, nutrition content, and seed size are all important factors in this process. For example, acorns in the red oak group (RO; e.g., southern red oak *Quercus falcata*, willow oak *Quercus phellos*, etc.) are preferentially cached by eastern gray squirrels over acorns in the white oak group (WO; e.g., chestnut oak *Quercus montana*, white oak *Quercus alba*, etc.) due to delayed germination until after the cache needs to be recovered, while WO acorns sprout the same season they fall from the tree (Lewis 1982, Smallwood et al. 2001, Wood 2005, Steele et al. 2006, Xiao et al. 2008). Thus, eastern gray squirrels (*Sciurus carolinensis*) cut out the embryos (embryo excision) of any WO acorns they cache, in order to prevent germination while in the cache (Fox 1982, Smallwood et al. 2001). Smallwood et al. (2001) found that germinating RO acorns also had embryo excision performed before germination, providing evidence for the theory that seeds with longer dormancy periods are more likely to be cached.

Many researchers believe high tannin content of RO acorns to be a major reason why they are cached rather than eaten when found. RO acorns have higher tannin concentrations than WO acorns (5-15% vs <2%, respectively; Chung-MacCoubrey et al. 1997, Smallwood et al. 2001) Seeds with higher tannin content are thought to have a longer storage life due to tannins being a natural deterrent for insect damage to the seed (Chung-MacCoubrey et al. 1997, Smallwood et al. 2001, Wang and Chen 2012). Most studies have produced results supporting the theory that animals should prefer to cache foods with increased tannin amounts while eating those with less (Barthelmess 2001, Xiao et al. 2008). But knowing that tannins bind to and make proteins indigestible for animals, researchers looked at the effects of tannins in eastern gray squirrels and found individuals fed solely RO acorns experienced protein deficiency, weight loss, and other physiological impacts (Chung-MacCoubrey et al. 1997, Dixon et al. 1997). Chung-MacCoubrey et al. (1997) suggested squirrels can only consume large amounts of RO acorns when other foods are also available. This raised the question of why squirrels cache RO acorns for winter survival when they cannot feed solely on food with such high tannin concentrations without experience negative effects. A few studies have been conducted to test the hypothesis that tannin contents degrades over time while buried, but none found this to be true (Dixon et al. 1997, Smallwood et al. 2001, Wood 2005). This is a topic that has not yet been resolved.

Nutrition content of a seed also affects how it is handled, along with how far it is dispersed. High nutrient content (in the form of peanut powder added to the seed) increased the probability a seed would be eaten or cached, rather than ignored, with

nutrient contents greater than 20-30% having a greater chance at being eaten rather than cached (Wang et al. 2013). High nutrient content seeds that are cached are considered valuable and transported further away before burial than lower nutrient content foods (Moore et al. 2007, Gálvez et al. 2009). Large seeds are generally assumed to have more nutrients, so many studies have focused on the effects of seed size on hoarding efforts. Some have found intermediate seed size to be more likely to be manipulated (Wang et al. 2012, Rusch et al. 2013*a*) while others found large seeds to be considered more valuable (Cheng et al. 2005, Xiao and Zhang 2006, Zhang et al. 2008*a*, Gálvez et al. 2009). Other contrasting studies found that all but the smallest seeds were removed (Wang et al. 2013) and larger seeds were less likely to be manipulated (Blate et al. 1998, Rusch et al. 2013*b*). These contradicting results may be due to preferences of many different species being tested and different sizes being labeled as small, intermediate, or large. But depending on the size of the animal being tested, a "large" seed for a small species, such as a mouse, may be considered a "small" seed for a larger species, such as a squirrel. More research should be conducted to see if different size species respond similarly to seeds that are a certain proportion of their body size, rather than trying to compare a set seed mass across all species.

Characteristics of the cache

Though specific months of the year may differ, seasons of caching and recovery correlate with seasons of food availability and food scarcity, respectively (Thompson and Thompson 1980, Brodin 1994*a*, Barthelmess 2001, Zhang et al. 2008*b*). Food is usually manipulated by scatterhoarders anywhere within 3-14 days after becoming available,

depending on the species and type of food included in the study (Dennis 2003, Xiao and

Zhang 2006, Xiao et al. 2008, Zhang et al. 2008*b*, Tuck Haugaasen et al. 2010). Seed size

and animal size have been found to effect the ideal maximum distance an item will be

dispersed (Cheng et al. 2005, Wang et al. 2012). Even within a species, there is a wide

range of dispersal distances observed (i.e. 1-62m, Japanese squirrels *Sciurus lis*, Tamura

and Shibasaki 1996; 0-168m, Japanese squirrels, Tamura et al. 1999). Mean distances for

caching and eating usually are not found to be different (Xiao and Zhang 2006).

Commonly, caching occurs within a mean of 20 m from the food source, but there is a lot

of variation within and among studies (Vander Wall 1995*a*, Tamura and Shibasaki 1996,

Tamura et al. 1999, Devenport et al. 2000, Dennis 2003, Lu and Zhang 2005, Xiao and

Zhang 2006). Dispersal distances also change depending on the dominance status of an

individual. Some studies have found aggressive species cache closer to feeding stations

(Petit et al. 1989) and younger subordinate individuals are forced to cache further from

their foraging areas (crested tit *Lophophane cristatus*; Lens et al. 1994), while other

studies recorded dominant males storing food higher in the tree than all others were

allowed (willow tit *Parus montanus*; Brodin 1994).

The potential competition a population is exposed to may have an effect on ideal

site selection for stored food (James and Verbeek 1985*b*, Petit et al. 1989). Some animals

tend to cache in more sheltered areas, such as near plants, woody debris, or tree bases in

order to decrease the risk of predation or provide themselves with landmarks to assist

with recovery (Steele et al. 2008, Tuck Haugaasen et al. 2010). The distance to the

nearest cache (nearest-neighbor distance; NND) is also a factor taken into account before

selecting a location. Like many aspects when it comes to scatterhoarding, this is another cache characteristic that depends on the population and the pressures it has experienced through competition for stored food. Nearest-neighbor distance has been measured at 13.39 m (Stapanian and Smith 1978) for surviving artificial caches in squirrels while another population had a median of 3.00 m between their cache location (Leaver et al. 2007). Even in a single population of yellow pine chipmunks (*Tamias amoenus*), NND ranged from 0.18-36.3 m, with a mean of 1.4-4.9 m, depending on the individual (Vander Wall 1995*a*). Dominance within a population also affects how far apart food is stored, though this has only been observed in the New Zealand robin (*Petroica australis*) where dominant males group their caches together while females had to scatter them further apart (Van Horik and Burns 2007).

Optimal cache density theory is the idea that the survival of buried food increases as cache density decreases so there must be a certain density that promotes the survival of the largest amount of stored food (Stapanian and Smith 1978). Optimal NND for a population should also create a cache density that maximizes the amount of stores that will remain in ground until recovery begins by the hoarder. The assumption is that animals pilfer one buried cache and then search the area around it for more buried food that can be pilfered (Stapanian and Smith 1978). Larger NND should result in less success when performing an area search. A few studies have found evidence supporting this theory (Stapanian and Smith 1978, Gálvez et al. 2009). However, Kraus (1983) tested artificial caches in grids spaced 2, 4, 6, and 8 meters apart and found all of these were pilfered within 3 days, which would be detrimental to any hoarder that did not store

for very short periods of time. Surviving artificial caches in a study conducted by Stapanian and Smith (1978) were 13.39 meter apart, so it is possible that Kraus (1983) simply did not test at a large enough grid. Galvez et al. (2009) found spacing between caches increased when food was scarce, possibly another attempt by the hoarder to protect their buried food by restricting the success of area searches. Nonterritorial animals might find it difficult to follow this theory, because they would not know how far their own caches are from the caches of other hoarders (Kraus 1983).

Scatterhoarders usually cache food within their own home range even when transporting food far away from the source (Clarke and Kramer 1994, Soné and Kohno 1999). In order to fully utilize all available space and further attempt to prevent pilferage, caches should be placed uniformly throughout the entire home range (following the optimal density theory), to avoid aggregations of food that would be easily stolen during an area search. While Lu and Zhang (2005) did find large field mice do not place caches randomly, hoarders do not necessarily use all areas of their home range equally. For example, eastern gray squirrels use a small section of the 360 degree arc around a resource (Kraus 1983) or have exclusive burial areas around their den tree (Stapanian and Smith 1978). Yellow pine chipmunks cache a load of seeds in a tight cluster and distribute different loads to different areas (Vander Wall 1995*a*). State of dominance of an individual also effects where they hoard food within the population. As previously noted, in some species, the dominant individuals hoard food away from the rest of the dominance and age classes, while other species force the younger individuals to hoard

food away from the rest of the group (Brodin 1994*a*, Lens et al. 1994, Van Horik and Burns 2007).

Present and future environmental conditions also affect how and where a cache is made. Many scatterhoarding mammal species use olfactory senses in order to pilfer or recovery food (Devenport et al. 2000, Rusch et al. 2013*a*). Because seeds with high water content seem to have a stronger scent (Vander Wall 1995*b*, Geluso 2005) and seeds absorb water from surrounding substrate (Vander Wall 1995*b*, 2000), soil moisture is very important in determining the depth at which to bury an item. There is an influence of cache depth on how many artificial caches are discovered (Vander Wall and Jenkins 2003, Vander Wall et al. 2003) as well as a negative effect of soil moisture on risk of pilferage. This would lead to the assumption that scatterhoarders should dig deeper holes in moist soil and shallower holes in dry soil. Several studies have tested the effect of soil moisture on the ability of animals to find caches (Vander Wall 1993*a*, 1995*b*, Geluso 2005, Rusch et al. 2013*a*), as well as depth (Vander Wall and Jenkins 2003, Vander Wall et al. 2003). Vander Wall (2000) found soil moisture did not affect recovery rates but naïve scatterhoarders were able to find many more caches in wet conditions than in dry conditions. Lens et al. (1994) hypothesized that scatterhoarders could be expected to show different hoarding strategies for distinct wet and dry seasons to lower pilferage risk based on the current conditions. But no studies have given animals the option of equally preferable wet and dry areas to scatterhoard, to test for an interaction between depth buried and soil moisture. Geluso (2005) attempted to test for differences of effect of depth in dry soil and moist soil, but only buried seeds at 12 mm and 24 mm, and did not

find a difference. Twenty-four millimeters may not have been deep enough to show a difference since some species regularly bury deeper than that (Devenport et al. 2000, Dennis 2003, Jenkins and Devenport 2014). Vander Wall (1995*b*) also tested the effect of moist vs dry soil, but buried all artificial caches at the same depth, 1.5 cm. Most of the present studies have also used enclosure experiments to test these characteristics of scatterhoarding, instead of measuring what happens in natural conditions to decrease the risk of pilferage.

Scatterhoarders should also consider future conditions and seasonal changes in foraging sites when scatterhoarding, in order to increase their chances of encountering food stores after the seasons change. In areas where heavy snow is present in the winter, this should be accounted for when hoarding food. Snow decreases the likelihood that landmarks will be present for easy recognition of cache sites, as well as increases the energy necessary to recover the cache through deep snow. Several researchers have hypothesized that scatterhoarders should account for future environmental conditions when hoarding food or questioned how animals know what winter will hold (Petit et al. 1989, Brodin 1994*a*, Lens et al. 1994, Geluso 2005). Clark's nutcrackers (*Nuifraga columbiana*) utilized two strategies when considering recovery during future snowfall (Tomback 1980). First, this species stores food on open slopes that do not accumulate heavy snow, which allows the food to be easily accessed by the nutcrackers but also attracts rodent pilferers (Tomback 1980). Second, the safer but more energy costing place to store food is the terrain near trees that does accumulate lots of snow during the winter but discourages rodent pilferers (Tomback 1980). Conversely, Petit et al. (1989) found

nuthatches and chickadees did not store food in places that would be protected from potential ice or snow. Some birds risk greater predation during the fall in order to hoard in trees they will be foraging in during the winter (willow tit *Poecile montanus*, Brodin 1994; crested tit (*Lophophanes cristatus*), Lens et al. 1994). Further research is needed to determine what types of environmental changes are taken into account by scatterhoarders, or what adaptations have been made in species that do not account for winter conditions.

Cache depth in natural situations depends on the species recovery technique and competition pressures. Since birds do not rely on smell to find caches underground, they generally wedge food into branches, moss, or tree trunks (Petit et al. 1989). Some bird species rely heavily on memory to find caches and bury caches to reduce the amount of pilferage from other bird species (Tomback 1980, James and Verbeek 1985*b*, Petit et al. 1989). White-breasted nuthatches (*Sitta carolinensis*) experience greater interspecific competition in areas where they forage so use cryptic caches as well as covered the cache in an attempt to prevent pilferage (Petit et al. 1989). In the same study, tufted titmice (*Parus bicolor*) and black-capped chickadees (*Parus atricapillus*) did not cover their caches because they did not experience the same level of competition for stored food (Petit et al. 1989). Many mammal species bury their caches just below the soil surface (Cahalane 1942, Tamura and Shibasaki 1996, Xiao and Zhang 2006), while others bury up the 3 cm deep (Devenport et al. 2000, Dennis 2003, Jenkins and Devenport 2014).

Though memory is more commonly known for its place during recovery, it is also used during the food storing and maintenance process. Central American agoutis (*Dasyprocta punctate*) utilize memory to revisit a previously buried cache; either to

refresh memory of the location or to monitor survival of the cache from pilferage and germination (Hirsch et al. 2013). Caching near landmarks, such as shrubs, trees, or logs, has been suggested as a way to assist memory in knowing where to place new caches or during cache maintenance (Steele et al. 2008, Tuck Haugaasen et al. 2010). However, thirteen-lined ground squirrels purposely bury food as far from any object as they can (Devenport et al. 2000), while musky rat-kangaroos (*Hypsiprymnodon moschatus*) bury at random with no pattern of association or avoidance with any objects in their habitat (Dennis 2003). Yellow pine chipmunks (Vander Wall 1995*a*) and coal tits (*Periparus ater;* Male and Smulders 2007) use memory of previous cache locations, rather than visual cues, to place new caches.

Functional purpose of recaching

In many early scatterhoarding studies, when a cache was emptied, the food item was not followed any further and no longer considered a part of the food supply (Cahalane 1942, Thompson and Thompson 1980, Zhang et al. 2008*a*, Gálvez et al. 2009). But researchers have since been able to more easily follow caches, concluding that it is fairly common for hoarded food to be dug up and recached (Tamura and Shibasaki 1996, Xiao and Zhang 2006, Xiao et al. 2008, Tuck Haugaasen et al. 2010, Wang et al. 2012). Several studies have found food items stored in up to 5 different locations before being eaten (Vander Wall and Joyner 1998, Perea et al. 2011) with Jansen et al. (2012) reporting Central American agoutis recached seeds as many as 36 times.

Little is known about the functional purpose of recaching. Recaching has previously been suggested as being the result of an item being pilfered and restored by the pilferer (Vander Wall and Jenkins 2003). During the food hoarding season, pilferers would probably benefit more from adding the stolen food to their own stores, rather than eating it at the moment of discovery (Tuck Haugaasen et al. 2010). Recaching could also be a result of the original hoarder conducting regular cache maintenance to check survival of the cache or refresh their memory of its location (Hirsch et al. 2013). The hoarder could be moving their stored food to refresh their memory of location (Vander Wall and Jenkins 2003). Another common reason recaching occurs is when food is quickly buried near a dense food source and then later redistributed further from the source (Sherry et al. 1982). For example, when Zhang et al. (2008*a*) concluded that larger seeds were recovered faster, this may have just been the result of the hoarder moving high value large seeds to safer locations. Many questions remain in regards to the meaning of recaching and the effects this has on the food stores of individuals. More research is needed in determining how often individuals spend time readjusting their food stores rather than leaving them until recovery.

Pilferage and pilferage reduction strategies

Pilferage is a major problem faced by scatterhoarders due to not actively defending their food stores. Many scientists have attempted to evaluate the pilferage levels of wild populations of scatterhoarders by creating artificial caches and checking periodically to determine if they have been removed (reviewed in Vander Wall and Jenkins 2003). Since no scatterhoarders have direct knowledge of the placement of these

caches, any that are removed are considered pilfered. Often, high pilferage rates result (Stapanian and Smith 1978; 52.8-65.5%, Swartz et al. 2010; 84.6%, Thompson 1978; 95% Kraus 1983; 87.6-100%, Haugaasen and Tuck Haugaasen 2010), which leads to the question of how scatterhoarding can be an adaptive trait when a majority of stored food is stolen. Pilferage level is another characteristic that can differ according to species. Thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) retrieved very few artificial caches, suggesting that pilferage is not a strategy that this species relies on for utilization of stored food (Devenport et al. 2000).

Often, pilferage is measured as a static characteristic of a community, while there are several conditions that can affect the pilferage risk that a cache faces. Commonly, pilferage rates are less during seasons when more food is available and then increase when more individuals are trying to recover buried food (Gálvez et al. 2009, Haugaasen and Tuck Haugaasen 2010). During the food abundant season, areas with less available food would have lower pilferage levels because fewer individuals are in those areas, but this effect would not be present when food is less available overall (Gálvez et al. 2009). As discussed previously, pilferage risk may also increase with increasing soil moisture, such as after heavy rain or during a wet season (Tuck Haugaasen et al. 2010). Measurements involving pilferage should be separated to look for differences between seasons, weather events, and other aspects that may show different levels of pilferage risk throughout the scatterhoarding season.

Given that pilferage is a potentially detrimental problem, scatterhoarders have developed many different strategies to try to reduce the amount of pilferage they

experience. Eastern gray squirrels alter their hoarding strategies in the presence of other

squirrels in order to make it less obvious where their food has been stored (Leaver et al.

2007, Hopewell and Leaver 2008, Steele et al. 2008). Merriam's kangaroo rats

(*Dipodomys merriami*) do not perceive other species as a pilferage threat, but do change

where they hoard after experiencing pilferage (Preston and Jacobs 2005). Many species

rely on cryptic cache locations to ensure caches are less easily found (Petit et al. 1989)

along with caching away from the food source (Brodin 1994*a*, Lens et al. 1994, Tamura

et al. 1999) or in areas with greater predation risk (Steele et al. 2014). Researchers have

found that when faced with complete or high amounts of pilferage, individuals will spend

more energy caching food to replace the stolen food (Lu and Zhang 2005, Male and

Smulders 2007). Animals are also able to recognize and avoid areas that have greater

rates of pilferage (Hampton and Sherry 1994, Preston and Jacobs 2005). Least chipmunks

(*Tamias minimus*) have even developed a strategy of coating their caches in bolus which

hardens after drying and significantly reduces pilferage once buried (Jenkins and

Devenport 2014).

   With scatterhoarders putting so much energy into protecting their hoards, the

question still remains about why reported pilferage rates are so high and if these

accurately describe natural pilferage activity. Thompson and Thompson (1980) noted that

observed recovery effort of squirrels matched the trend in decreasing artificial caches still

intact and concluded that pilferage rates obtained in this manner should be representative

of the rate experienced by the animals. Further research is necessary to compare artificial

pilferage rates to actual pilferage rates in a wild population to test for the accuracy of this

method. When attempting to gain a measurement for a wild population, it is necessary to differentiate between a pilferage event and a cache maintenance event by the hoarder. This is difficult to do and might be why artificial caches are usually relied upon as an appropriate measurement of pilferage levels.

Recovery of the cache

Caching periods transition to recovery periods once available food had declined and stored food must be utilized as a main source of energy (Thompson and Thompson 1980, Brodin 1994*a*, Zhang et al. 2008*b*, Tuck Haugaasen et al. 2010). In North America, recovery is categorized by the onset of winter (Thompson and Thompson 1980), while in more tropical climates it could be brought on by a dry season (Haugaasen and Peres 2007, Tuck Haugaasen et al. 2010). From the time of hoarding, caches stay intact 1-24 hours for short-term hoarders (Sherry et al. 1982, Clarke and Kramer 1994) and 1 week-1 month for long term hoarders (Tamura and Shibasaki 1996, Tuck Haugaasen et al. 2010). However, Steele et al. (2011) reported eastern gray squirrels (long term hoarders) recovering caches after less than 24 hours in an urban habitat with a high density squirrel population, so variations do exist depending on the population. Often there are a small amount of caches that remain intact for several months, sometimes never being recovered before the study ends (Cahalane 1942, Tamura and Shibasaki 1996, Tuck Haugaasen et al. 2010).

In several studies reporting recovery rates, they are either relying on artificial pilferage rates (Cahalane 1942, Clarke and Kramer 1994, Haugaasen and Tuck

Haugaasen 2010) or are not considering the possibility of recaching when taken from the original hoard location (Thompson and Thompson 1980, Devenport et al. 2000). Due to use of radio telemetry techniques in seed dispersal studies, other studies have been able to track the amount of time between hoarding and being eaten after multiple recaching events (Tamura and Shibasaki 1996, Tamura et al. 1999, Tuck Haugaasen et al. 2010). But obtaining true recovery rates would require uniquely tagged individuals to distinguish between hoarder versus pilferer, which Tamura et al. (1999) attempted to do. In this study, they monitored 9 hoarded walnuts and successfully captured photos of squirrels retrieving 5 of these (Tamura et al. 1999). Three of the 5 were dug up by the hoarder while the other 2 were pilfered (Tamura et al. 1999). While this is the type of information needed in regards to this topic, such a small sample size does not allow for strong conclusions to be made about individual recovery or pilferage rates. In 2012, Jansen et al. were able to identify 16 individual Central American agoutis involved in the hoarding and recaching of 116 seeds. They found that less than 1 out of every 6 caches was recovered by the original hoarder, including recached, pilfered seeds (Jansen et al. 2012). Since this study was focusing on recaching as an agent for long distance dispersal, there was little analysis of the pilferage data other than proving that reciprocal pilferage was evident in this population and many seeds were recached rather than eaten upon discovery. They also attribute such large amount of pilferage and recaching to the high density of the agouti population on the study site. Using the same methods as Jansen et al. (2012), further delving into pilferage and recovery rates in populations of other species of varying densities is possible and needed.

Recovery of a cache is also hindered/reduced by interspecific pilfering, either other scatterhoarders or species, such as deer, which just happen upon the buried food during their regular foraging activities. Ants consume seed buried under leaf litter (Haugaasen and Tuck Haugaasen 2010, Tuck Haugaasen et al. 2010) while wood mice (*Apodemus sylvaticus*) may eat up to 30% of cached seeds (Tamura et al. 1999). Mammals are able to pilfer food stored by birds, while birds cannot reciprocate without observing the storage location due to not having a strong sense of smell (Thayer and Vander Wall 2005). Larderhoarding rodents may steal cached food and store it in a burrow, therefore taking it out of the original hoarders potential food supply (Tamura and Shibasaki 1996, Xiao and Zhang 2006). Importantly, both white-tailed deer (*Odocoileus virginianus*) and wild pigs (*Sus scrofa*) can have hard mast in their stomachs during the winter and spring, when most mast is already buried in caches (Korschgen 1962, Wood and Roark 1980, Focardi et al. 2000), suggesting that these animals may be "stealing" cached mast from scatterhoarders. As wild pigs continue to expand their range throughout the United States, they have the potential to greatly affect the amount of stored food available to scatterhoarders during the winter. However the effects of this decrease in cached food on the diets of scatterhoarding species during the fall, winter, and early spring when hard mast is a staple in the diet is unknown.

Long term scatterhoarding rodents as well as birds in the *Corvidae* family (e.g., crows, jays, nutrcrackers, etc.) utilize spatial memory during the process of recovering their caches (McQuade et al. 1986, Jacobs and Liman 1991, Brodbeck 1994, Herz et al. 1994, Clayton and Cristol 1996, Bednekoff et al. 1997, Macdonald 1997, Devenport et al.

2000). While some researchers hypothesize that memory is used to return to the general

area of a cache and olfaction is used to locate the specific cache location (Cahalane 1942,

McQuade et al. 1986, Rusch et al. 2013*a*), a study involving artificial caches in close

proximity to real caches have resulted in only the real cache being recovered (Devenport

et al. 2000). Devenport et al. (2000) also found that scent of the seed or the substrate

around the seed did not have an effect on accurate recovery attempts. Evidence also

suggests that while birds in the *Paridae* family (tits, titmice, chickadees) are long-term

hoarders, they do not have the same vast long-term memory as Corvids which have a

stronger reliance on stored food for winter energy (Bednekoff et al. 1997, Brodin 2005).

This could be due to a few ecological differences between the two families. Parids store

food within their home range by wedging it into tree bark and may rely on discovering

stored food while foraging in the winter rather than remembering cache locations (Petit et

al. 1989, Brodin 1994*a*, 2005, Lens et al. 1994). This is different than Corvids which

travel large distances to bury food for winter survival and would have less of a chance of

finding cached food while foraging in winter (Brodin 2005). Whether other differences in

scatterhoarding strategies are due to ecological differences between species is unknown.

Does the hoarder have the recovery advantage?

For scatterhoarding to be adaptive, the hoarder must be able to ultimately recover

a larger proportion of their stored food than any other individual (Andersson and Krebs

1978). Given the extent of pilferage in most scatterhoarding populations (Vander Wall

and Jenkins 2003) and the incredible amount of recaching (Jansen et al. 2012), it is still

unknown how much of an advantage hoarders are able to have. Any amount of survival

benefit should be enough for scatterhoarding to continue to be selected for in a population, though this benefit has never been directly looked at. A majority of past studies involving hoarding have focused on the aspects of making the cache, protecting it from pilferage, and mechanisms that are used for recovery. Though these things all improve an individual's change of recovering their food, making a conclusion based on this information would involve great assumptions.

Recently, more researchers have tried to gain enough evidence to prove that the hoarder has the advantage. Steele et al. (2011) and Vander Wall et al. (2006) concluded this advantage does exist, after they removed individual hoarders and recorded a much longer period before recovery of their caches than when the hoarders were returned to the site. This indirect evidence is not enough to conclusively say that the hoarder recovers a greater proportion of its food. Those caches still could have been pilfered, or recached by the hoarder once returned to the site and then pilfered. Reciprocal pilferage is also an important aspect that may make up for an individual not being able to recover enough of what it originally buried (Vander Wall and Jenkins 2003). A scatterhoarder may steal enough food to make up for any food that is stolen from it. Further research is needed to follow the entire path of a seed, identify all individuals involved in its survival, and determine how much buried food a scatterhoarder is able to ultimately recover compared to what it originally buried and the amount pilfered from its food stores.

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Chapter 2: Behavioral adaptations of scatterhoarders to winter flooding that affects their stored food

Scatterhoarders store single food items in many locations throughout their home range for consumption during times when available food is scarce. In the southeastern United States, flooding during the food-scarce winter is a problem faced by scatterhoarders due to a decrease in land available for cache recovery. Understanding how scatterhoarders respond to factors that could influence their stored food, such as flooding, is important given the strong reliance on hoarded food to overwinter survival. We examined how eastern gray squirrels (*Sciurus carolinensis*) have adapted to a seasonally flooded ecosystem in Alabama. We predicted squirrels would respond to flooding by: storing food in areas that stay dry during winter, seasonally shifting to dry habitat, or changing their winter diet. Finally, if no behavioral responses were shown, we expected low winter survival. During the dry season, over 72% of acorns were buried in areas that later flooded. Habitat use did not change during flooding; in fact, squirrels selected for habitat that stayed dry during flooding to a greater degree during non-flood seasons, although not significantly so. Diet did not change between the dry fall and flooded winter. Squirrels were also 7.70 times as likely to die during the flood season (2.28 – 25.96, 95% confidence limits) as the dry season and mortality was 1.30 times as likely (0.26 – 6.38, 95% CL) for each 10% increase in the proportion of the study area that was flooded (both $P = 0.001$). Thus, this eastern gray squirrel population did not appear to show any

behavioral adaptations to seasonal flooding. Further research is needed to fully understand the effects of fluctuating environmental conditions on scatterhoarding behavior.

Key words: eastern gray squirrel, flooding, food hoarding, habitat selection, survival

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For species that depend on temporally variable food resources, food hoarding is a common strategy to combat seasonal decreases in available food. Hoarding provides a steady supply of food energy and typically occurs before food-scarce seasons (Smith and Reichman 1984, Brodin 1994*a*, Zhang et al. 2008). Food hoarding exists in two forms, scatterhoarding and larderhoarding. Scatterhoarding consists of scattering buried food items throughout a home range (Morris 1962), while larderhoarders store food in 1 or a few locations in their home range (Hurly and Lourie 1997). The strategy that is used by a species depends on competition for the food being cached and the ability of the animal to defend it once stored (Vander Wall et al. 2005). For hoarding to persist in a population, the benefits of the behavior, in terms of increased access to food during periods of limited availability, should exceed the costs of collecting and storing food (Andersson and Krebs 1978). Hoarding and recovering food items are energy- and time-consuming activities, and any time spent engaging in hoarding behavior cannot be spent watching for predators, reproducing, or resting (Tamura et al. 1999, Perea et al. 2011). However, hoarded food often is essential to long-term survival (Barkalow Jr. et al. 1970, Wrazen and Svendsen 1978, Wrazen and Wrazen 1982, Kuhn and Vander Wall 2009). Therefore, if hoarding is present in a species, it should provide major benefits to the individuals in the population.

Environmental factors have been shown to affect use (and hence the benefits) of stored food for species that rely on hoarding. For example, most scatterhoarding species rely on olfaction in some way to locate hoarded food (Vander Wall 1991, Dally et al. 2006), and environmental conditions can influence these senses. Ash from recent fires

was shown to inhibit chipmunks' (*Tamias* sp.) ability to follow scent to a cache (Briggs and Vander Wall 2004). Similarly, yellow pine chipmunks (*Tamias amoenus*) are able to find and pilfer more seeds when seeds and soils are wet, while dry conditions greatly hinder the use of olfaction to locate seeds in other scatterhoarders (Vander Wall 1991, 2000). Alternatively, frozen ground in colder climates can decrease the number of days available for hoarders to cache seeds underground and limits the ability to recover caches until temperatures have warmed again; snow cover also increases the cost of searching for buried caches (Thompson and Thompson 1980, Vander Wall 1993*a*). Many researchers have hypothesized that scatterhoarders should exhibit behaviors that counteract the effects of seasonal changes in the environment when hoarding food (Petit et al. 1989, Brodin 1994*a*, Lens et al. 1994, Geluso 2005), but few of these behavioral mechanisms have been tested. Thus, more information is needed on how scatterhoarders alter their behavioral strategies to compensate for potential lost mast due to various environmental conditions.

Flooding is another environmental factor that could affect scatterhoarding behavior. Flooding over winter is a common problem faced by scatterhoarders in many hardwood forests present in the southeastern United States. Since many scatterhoarders store hard mast in the fall and use this stored food during winter, those living in floodplains during winter experience reduced area available for recovery of cached food. Scatterhoarders may cope with flooding during the food scarce season in a variety of ways. For example, they may alter where or how they store mast in response to flooding. In a flooded bog in Malaysia, scatterhoarders stored food in tree cavities and on tree

roots, rather than burying in the substrate, suggesting that scatterhoarding species may adapt their food hoarding habits in the presence of seasonal flooding (Van der Meer et al. 2008). Alternatively, a shift in habitat use may occur during flood events to take advantage of dry areas where food may still be available. Indeed, small mammal species have been found to increase their home range size in response to less available food (Hubbs and Boonstra 1998). Finally, scatterhoarders that live in flooded areas may make a dietary shift away from hard mast during the winter. For example, when preferred white spruce (*Picea glauca)* cones were unavailable, red squirrels (*Tamiasciurus hudsonicus*) switch to hoarding abundant mushrooms (Fletcher et al. 2010). Ultimately, individuals that do not show behavioral adaptations to flooding will likely lose a large portion of their buried food in the winter due to rising water levels, which could result in increases in over-winter mortality. Thus, understanding how scatterhoarders respond to factors that influence the supply of hoarded food, such as seasonal flooding, is critical given the strong reliance on hoarded food to overwinter survival.

In this study, we tested the hypothesis that individuals relying on scatterhoarded food over winter would use behavioral adaptations to overcome the loss of their hoarded food due to seasonal flooding. Eastern gray squirrels (*Sciurus carolinensis*) were used as the focal species because they scatterhoard hard mast during the fall and are thought to rely on this stored mast to obtain the energy needed to survive winter (Goodrum 1940, Brown and Yeager 1945, Nixon et al. 1968, Thompson and Thompson 1980, Korschgen 1981, Spritzer 2002). This species commonly inhabits hardwood areas that flood during the winter and this flooding likely results in reduced area available for recovering

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scatterhoarded food. We studied a population of eastern gray squirrels from July 2015 – April 2017 on a portion of Lowndes Wildlife Management Area, in central Alabama, that floods every winter. There is limited evidence pertaining to how scatterhoarding behavior changes in areas with differing amounts of available dry land during the hoarding season and the season when stored food is utilized. We predicted that squirrels would respond to winter flooding by: 1. storing food during fall in areas that do not flood during winter, 2. seasonally shifting their home ranges and habitat use to areas that do not flood, 3. seasonally shifting their diet to include foods other than hard mast during winter and early spring when flooding occurs. Finally, we predicted that if squirrels did not engage in 1 of the 3 predicted behavioral adaptations, they would experience an increase in mortality during periods of flooding. Understanding how squirrels respond to environmental factors (i.e. flooding) that affect their stored food is beneficial for understanding the evolution of scatterhoarding behavior.

MATERIALS AND METHODS

Study Area

The Lowndes Wildlife Management Area (LWMA; 16S 0523811 3580684) consists of 6,800 ha of planted hardwood, planted pine, green fields, and bottomland hardwood swamp in Lowndes County, Alabama, in the southeastern floodplains and low terraces ecoregion (Griffith et al. 2001). The land is leased to Alabama Department of Conservation and Natural Resources Division of Wildlife and Freshwater Fisheries by the U.S. Army Corps of Engineers through cooperation with the Alabama Forever Wild Land

Trust. The LWMA is managed to support populations of game species, such as white-tailed deer (*Odocoileus virginianus*), waterfowl, mourning dove (*Zenaida macroura*), squirrels (*Sciurus* spp.), and wild turkey (*Meleagris gallopavo*). The annual hunting season for gray and fox squirrels (*Sciurus niger*) is mid-September through the 1st week of March. Mean temperatures are 8 degrees Celsius in January and 27 degrees in July, with 135 cm of precipitation annually (NCEI 2018).

We selected a core study area consisting of 2 ha of mature pine and 13 ha of mature bottomland hardwood swamp for trapping of gray squirrels. Dominant canopy species included water oak (*Quercus nigra*), willow oak (*Quercus phellos*), southern red oak (*Quercus rubra*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*) with musclewood (*Carpinus caroliniana*) and red maple (*Acer rubrum*) present in the understory. Large portions of the core study area exhibited seasonal flooding each winter from the adjacent Alabama River and associated wetlands.

Field Methods

To assess the extent of flooding of the study area throughout the year, the water line around the core study area was walked with a handheld GPS after each major rain event between November 2016 and March 2017. Flood conditions were most extreme in January 2017 but standing water remained over the majority of the area through the end of the study in April 2017. Based on personal observations in the field, flooding levels and timing at this site were similar between the 2 winters in this study. Delineation of flooded and dry seasons was based on personal observation of conditions in the field. Dry

conditions were present September – October 2015 and September – November 2016. Throughout the rest of both years, various levels of flooding occurred throughout the study area.

Eastern gray squirrels were trapped July 2015 – July 2016, with trapping effort concentrated during July of each year, using Tomahawk live traps (Hazelhurst, WI; Collapsible Squirrel Trap Model 202) baited with corn. Traps were placed on the ground under and around any trees with dreys (stick nests in trees) or other signs of squirrels, opened at sunrise, checked regularly, and closed at sunset. Trapping effort was concentrated in 2 areas on either side of the study area where capture success was greatest. Once trapped, each animal was transferred to a cloth handling cone and affixed with 2 unique color-coded ear tags (Figure 1, Brodin 1994, Steele et al. 2011). Isofluorane was used to anesthetize the squirrel before it was fitted with a very high frequency (VHF) radio-telemetry collar (Advanced Telemetry Systems M1640, Isanti, MN). Each squirrel was released at the trapping site after recovering from drug exposure. Methods followed guidelines of the American Society of Mammalogists (Sikes et al. 2016) and were approved by Auburn University Institutional Animal Care and Use Committee (Protocol #2014-2555).

Prediction 1: Scatterhoarding Habits

To examine where squirrels stored mast, radio-tagged acorns were deployed prior to and during the 2016 – 2017 flood season to observe hoarding strategies used by gray squirrels in the face of flooding. VHF radio-telemetry transmitters (Advanced Telemetry

Systems A2414, Isanti, MN) were attached to viable northern red oak (*Quercus rubra*) acorns (Steele et al. 2011), purchased from Acorno (Winooski, VT, www.acorno.com), and placed throughout the core study area October 2016 – February 2017. Transmitters were inserted in a small hole drilled through the top of the acorn, then the hole was filled with hot glue with the antennae sticking out of the acorn (Figure 2; Pons and Pausas 2007). Other studies of acorn tagging have found that similar acorn tagging methods do not affect the caching behaviors of the animals (Soné and Kohno 1999, Tamura et al. 1999, Hirsch et al. 2013). Upon acorn consumption, transmitters were continuously re-deployed on new acorns until battery failure.

Each radio-tagged acorn was monitored by a motion camera to identify the species (and possibly individual) that handled the nut for either caching or consumption (Tamura et al. 1999, Gálvez et al. 2009, Hirsch et al. 2013). Tagged acorns were tracked daily to record the new location after being handled. Fates of acorns were categorized as "buried", "cached", or "eaten", with buried acorns being those stored under the soil surface, while cached acorns were those stored in or underneath an item or substance that was not soil, such as a log. If cached or buried, the tagged acorn was replaced with an untagged acorn to allow researchers to re-use the tagged acorn without decreasing that animal's hoarded food supply. Care was taken to disturb the site of hoarding as little as possible to prevent creating any cues of a cached or buried acorn for a competitor or creating evidence of tampering for the hoarder (Duncan et al. 2002). If found in an underground burrow, the acorn was assumed to have been larderhoarded by a mouse, as described by Tamura and Shibasaki (1996).

To determine whether squirrels were taking into account future flood conditions when scatterhoarding food, a resource selection function was estimated for food buried during the dry season (September 11, 2016 – November 29, 2016; Manly et al. 2002). Locations of buried acorns represented "used" locations and an equal number of randomly generated points were selected from the study area to represent "available" locations. The "available" area was created by taking the longest distance an acorn was carried from its point of deployment (85.48 m) and using ArcMap (ESRI 2017) to create a buffer of that distance around all radio-tagged acorn deployment locations. The buffered area was cropped to fit inside the habitat defined as available to squirrels during the dry season (see habitat use methods; Figure 3). This created an area likely to be available for hoarding of any tagged acorn we put out.

As a predictor variable in our resource selection function, we used whether or not a "used" or "available" location would be underwater during the peak of the flood season or not. We used the "glm" function in Program R (R Core Team 2016) to run logistic regression models to determine effects of flood conditions on the likelihood of a location being "used" relative to "available" locations.

Prediction 2: Habitat Use

To examine potential changes in habitat use between the flood season and the dry season, collared squirrels were located 1 – 3 times per week from the time they were collared until they were no longer able to be followed, or until the telemetry period ended in April 2017. We used a case-control habitat use analysis to determine differences

between used and available habitat during 3 flood seasons (25 July, 2015 – 11 September, 2015; 28 October, 2015 – 11 September, 2016; 30 November, 2016 – 21 April, 2017) and 2 dry seasons (12 September, 2015 – 27 October, 2015 and 12 September, 2016 – 29 November, 2016; Keating and Cherry 2004). The previously noted telemetry locations were determined to be "used" habitat, while points randomly generated in ArcMap (ESRI 2015) denoted "available" habitat. Care was taken to generate random available points in the area with habitat used by collared squirrels but not likely containing habitat only used by uncollared squirrels. Two sides of the core study area were bordered by dirt roads which squirrels were known to rarely cross so those were used as part of the constrained area (Tounzen et al. 2012). The other side of the core study area was swamp, so the boundary was created based on the presence of trees close enough to be used by squirrels and still within the area used by collared squirrels (Figure 3). Each squirrel with used points was assigned an equal number of available points to account for the number of times each collared squirrel was located. Methods for determining conditions during flooding were the same as described for scatterhoarding habits.

To conduct our analysis, the "glmer" function from the "lme4" package was used in Program R (Bates et al. 2015, R Core Team 2016) to run mixed-effects logistic regression models to determine effects of the covariates on the habitat of eastern gray squirrels. A random effect of squirrel was included to account for some squirrels having more locations than others, so the results were not biased towards the habitat selection characteristics of those individuals. We tested for an interaction between flood season

(flooded or dry) and winter flood conditions of locations to determine within season and flood season effects of winter flooding.

Prediction 3: Diet

To test for shifts in diet of squirrels, we used eastern gray squirrels harvested from LWMA and donated to this project by hunters in the 2015 – 2016 flood season, 2016 dry season, and 2016 – 2017 flood season. Collected squirrels were weighed, stomachs were removed, and then stomach contents were weighed. The proportion of each food item in the stomach was visually estimated to the nearest 10%. Extractions of DNA from multiple samples of each food item were conducted using a Qiagen DNeasy Plant Mini Kit (Qiagon, Hilden, Germany).We used matK primers for the amplification of our DNA samples with polymerase chain reaction (PCR). Our forward primer was matK-xf: TAATTTACGATCAATTCATTC; while our our reverse primer was matK-MALP: ACAAGAAAGTCGAAGTAT (Ford et al. 2009, Dunning and Savolainen 2010). We followed a standard PCR recipe and thermocycling program for the matK marker (Ford et al. 2009, Dunning and Savolainen 2010). Amplified samples were sent to the Genomics and Sequencing Laboratory at Auburn University for sequencing. Once the samples had been sequenced, we used the program Sequencher (Gene Codes Corporation, Ann Arbor, Michigan) to view the chromatographs of each food item. Sequences obtained from chromatographs were then identified down to the lowest taxon using the online BLAST database (National Center for Biotechnology Information, Bethesda, Maryland).

Prediction 4: Mortality

During relocation described in habitat use methods, we also assessed survival of each squirrel. Due to the volume of hunting in this area, squirrels were highly elusive and we seldom could visually locate collared animals. If a signal was determined to be in a tree, the squirrel was assumed to be alive. If a squirrel was found dead, we attempted to identify cause as predation, hunter, or unknown. Death was assumed to be due to predation if the remains were scattered haphazardly around the site, the body was damaged, signs of the predator were found (tracks, scat, hair, etc.), or if there were signs of mortality (collar with blood, large amounts of squirrel fur, etc.). Squirrels were recorded as killed by hunters if they were returned or reported by the hunter. No squirrels were recaptured without a collar, so if a collar was found open with no remains nearby they were assumed to have been taken by a hunter: if a collar was found closed with no remains, it was recorded as predation. Squirrels were recorded as unknown mortalities if they were found with no obvious cause of death.

Cox proportional hazard regression ("survival" package in Program R; Therneau and Grambsch 2000, Hosmer et al. 2008, Therneau 2015) was used to assess differences in survival between the dry season and the flood season (flooding covers >50% of core study area; Nixon et al. 1968, Korschgen 1981). If the date of mortality could not be determined, the squirrel was not included in analyses. Squirrels that were still alive at the end of the study (April 21, 2017) or whose whereabouts were unknown due to collar failure were censored in this analysis. The effect of flooding was determined by creating a time-varying covariate split up into monthly steps corresponding to proportions of the

study area that were known to be flooded each month. We also included a second season variable (fall, winter, spring; see Chapter 3 for details) to separate the effect of flooding on survival from the effect of calendar season.

RESULTS

Between 24 July, 2015 – 19 July, 2016, 47 squirrels were collared (27 males and 20 females). Flooding was assessed 6 times; the lowest water level was recorded in November 2016 with the highest recorded in late January 2017 (Figure 4).

Prediction 1: Scatterhoarding Habits

Of the 43 radio-tagged acorns deployed during the dry season, 29 were buried, 2 were cached aboveground or larderhoarded in burrows by mice (*Peromyscus* spp.), 11 were eaten by gray squirrels, and 1 was eaten by a raccoon (*Procyon lotor)*. Observed scatterhoarding activity was greatest during October and November 2016 and tagged-acorn handling by squirrels decreased beginning in January 2017.

Before flooding occurred in December 20, 21 of 29 acorns (72.41%) were buried in areas that would later be flooded (Figure 5). Buried acorns were carried 20.63 ± 18.63 m ($\bar{X} \pm SD$, $n = 29$) before being buried an average depth of 28.00 ± 21.59 mm ($\bar{X} \pm SD$, $n = 7$). Depth was not initially measured until we observed a difference in the depths acorns were buried in soil that stayed dry versus soil that later flooded, resulting in only 7 measurements during the dry season. There was no significant difference between the average distance acorns were carried before being buried in areas that later flooded ($\bar{X} = 18.76$ m, $SD = 10.41$, n = 21) versus areas that stayed dry during flooding ($\bar{X} = 36.45$ m,

SD = 39.13, n = 8; t-test, t_{20} = -1.20; P = 0.18). However, there was a significant

difference in the average depth acorns were buried in areas that would later become

flooded ($\bar{X}$ = 45.25 mm, SD = 2.50, n = 4) versus areas that stayed dry during flooding ($\bar{X}$

= 5.00 mm, SD = 0, n = 3; t-test, t_3 = -32.2; P < 0.001). Additionally, our resource

selection function indicated that during the dry season, squirrels were 1.60 times as likely

(odds ratio; 0.52 – 4.96, 95% CL) to bury acorns in soils that flooded as soils that stayed

dry during winter, though this relationship was not statistically significant (P = 0.40).

Squirrels buried an additional 15 radio-tagged acorns during the flood season, with

13.33% of those later ending up underwater. In total, 52.27% (n = 23) of all tagged

acorns buried from October 2016 – February 2017 were eventually located underwater

during the winter and unavailable for retrieval by squirrels through the end of the study in

April 2017.

Prediction 2: Habitat Use

Locations from 37 squirrels were included in habitat use analyses; 10 additional

squirrels were removed from analyses due to death occurring before the individuals were

relocated. From these 37 squirrels, 596 locations were collected. However, we collected

121 locations from squirrels that had dispersed outside of our core study area into areas

where flood patterns were not recorded; these locations were not included in habitat

analyses. No squirrels dispersed during flooding or appeared back in the core study area

after flooding if they had previously left the area. Once the telemetry data was

constrained to the core area, 475 locations from 34 squirrels remained for use in the

habitat analyses, which were paired with 475 random "available" locations.

In our analyses of habitat selection, we found that the interaction between flooded or dry seasons and whether the habitat floods was not significant ($P = 0.10$), suggesting that squirrels do not select for habitats that flood differently between the two seasons. However, we analyzed the effect of flooding separately for each season in order to better elucidate how squirrels select for habitats that flood. During the dry season, squirrels were 4.50 times as likely to use areas that stayed dry during the winter than areas that later became flooded ($3.40 - 5.96$, 95% CL; $P < 0.001$). Comparatively, during the flood season, we found that squirrels were only 2.64 times as likely to be found in areas that stayed dry during flooded conditions ($2.26 - 3.09$, 95% CL; $P < 0.001$).

Prediction 3: Diet

Forty-two squirrels were collected for diet analysis, with 14 collected during the $2015 - 2016$ flood season, 18 during the 2016 dry season, and 10 during the $2016 - 2017$ flood season. The average stomach mass was 15.82 ± 12.39 g ($\bar{X} \pm SD$, n = 38) and the average squirrel mass was 434.88 ± 78.59 g ($\bar{X} \pm SD$, n = 34). Four squirrels were not included in stomach mass measurements because the stomach was shot during collection, and squirrel mass was not measured during the necropsies of the 1st 8 squirrels. Two squirrels included in analyses had completely empty stomachs (1 in flood season, 1 in dry season). Overall, there were 17 different food items eaten by these squirrels (5 items present only in dry season, 8 items present only in flood season, 4 items present in both).

DNA analysis was conducted on the two food items that showed up prominently in stomachs from both the dry season and flood season (Figure 6, Figure 7). Other items

supplemented these two but few made up a majority of the stomach contents. On average, almost 60% of all stomach contents were either "Food A" or "Food B", and only 20.51% of squirrels had not eaten either "Food A" or "Food B". "Food A" occurred in 19 stomachs, accounting for $70 - 100\%$ of stomach contents in 5 animals in flood season. "Food B" occurred in 19 stomachs, accounting for $70 - 100\%$ of stomach contents in 13 animals in both seasons. Six squirrels had eaten both "Food A" and "Food B".

Prediction 4: Mortality

Throughout this study, 47 eastern gray squirrels were collared, including 27 males and 20 females. The fate of 8 of these squirrels was unknown because the radio-telemetry signal was lost. Thirty-four squirrels were confirmed to be killed (22 by predation, 9 by hunters, 3 unknown deaths) and 5 were still alive at the end of the study in April 2017. Although 19 squirrels died during a flooded winter, 23 squirrels survived at least 1 flooded winter during this study. The 42 squirrels that had definite dates of death, dispersal, or lost signal were used in Cox proportional hazards regression, with 14 of these squirrels being censored.

When analyzed separately, both calendar the extent of flooding (1.30, odds ratio; $1.12 - 1.52$, 95% CL; $P = 0.001$) and calendar season ($P = 0.001$; See Chapter 3) significantly effect survival. However, when including both variables in the model to determine the effect of flooding after accounting for the effect of season on survival, the effects of both season and flooding lost significance ($P = 0.25$ and $P = 0.24$, respectively). Further investigation revealed collinearity existed between season and

flooding because a majority of the squirrels died during winter and spring, when flooding is most extreme, while very few squirrels died during the dry fall season. Though this collinear relationship prevented us from teasing apart the effect of winter from the effect of flooding on survival, we still found squirrels were 1.16 times as likely to die for each 10% increase in the proportion of the study area that was flooded (0.90 – 1.50, 95% CL) in this model accounting for the effect of season. See Chapter 3 for further survival analyses results pertaining to this population.

DISCUSSION

In our study, squirrels did not appear to show behavioral adaptations to seasonal flooding; none of our predictions of behavioral changes in anticipation and response to flooding were supported. Rather, squirrels seemed to simply have a greater mortality rate as flood water increased in the area.

Prediction 1: Scatterhoarding Habits

Squirrels did not adjust their scatterhoarding habits by burying acorns in areas that would be available during the flood season. Prior to flooding, only 27.6% of acorns were buried in areas where they would be available once flooding occurred. Ultimately, the population lost 52.3% of all acorns buried during this study due to flooding. In fact, while our results were not statistically significant, squirrels were more likely to bury acorns in areas that flooded than would be expected if burial location was random. While some species do take into account future winter conditions while scatterhoarding (Tomback 1980, Brodin 1994*b*, Lens et al. 1994), animals in those studies all utilize different

foraging sites during the winter than during the scatterhoarding season. If our study squirrels really were choosing muddy areas (any location that would later become flooded) to bury acorns, the behavior could be a selection for easier soil to dig in during the severe drought of fall 2016. Burying acorns deeper in wet soil is a well-known pilferage avoidance strategy used by scatterhoarders; while soil with more moisture increases the ability of scatterhoarders to pilfer by following the scent to the buried acorn, digging a deeper hole in wet soil counteracts the lure of the strong scent (Vander Wall 1993*b*, 1995, Geluso 2005). This suggest that the squirrels have adapted to loss of food in wet areas due to pilferage but not loss of food in these same areas due to flooding.

Prediction 2: Habitat Use

Squirrels did not shift habitat during the flood season, but rather stayed year-round in areas that would stay dry during flooding. In fact there was a trend for squirrels to avoid flood areas less during the flood season.

Prediction 3: Diet

Squirrels did not switch to eat foods other than acorns for a majority of their nutrition during the flooded winter season. There are no previous studies mentioning eastern gray squirrels relying on foods other than hard mast during the winter (Nixon et al. 1968, Thompson and Thompson 1980, Spritzer 2002). In our study, viable acorns present on the ground throughout the winter combined with mortality attributed to flooding may have resulted in decreased intraspecific competition for buried acorns, in addition to those still readily available on the ground. In more northern areas, buds and

flowers were not found in gray squirrel diets until spring (beginning of April; Brown and

Yeager 1945, Nixon et al. 1968, Thompson and Thompson 1980), though these food

sources appeared in our study area in early February and were potentially included in the

diet at that time. Ultimately, there did not appear to be a portion of the year when

squirrels were not able to find seasonal foods typically eaten by this species (Nixon et al.

1968, Thompson and Thompson 1980, Korschgen 1962).

Prediction 4: Mortality

Squirrels were significantly more likely to die during the flooding season, and

mortality increased with the extent of flooding. Eastern gray squirrels use the same

foraging and scatterhoarding areas year-round (Flyger 1960) and therefore may not

anticipate a difference in where they will be foraging, even when flooding changes which

areas are available for winter foraging. The consequence of flooding is in a large loss of

food stored for the winter once flooding begins. Winter food availability in this flooded

ecosystem during all but above average mast years likely mimics that of a poor or failed

mast crop. Squirrels are known to experience decreased survival rates during years of

poor mast crop production (Nixon and McClain 1969, Nixon et al. 1975, Koprowski

1991).

General Discussion

In this study, our hypothesis that individuals relying on stored food during winter

would show behavioral adaptations to flooding was not supported. Considering these

squirrels lost 72% of their stored food to flooding and did not respond in a way that

increases food resources during the food scarce winter, results of this study suggest that this squirrel population does not appear to rely solely on scatterhoarded food to survive Alabama's mild winters. Acorns were found in the stomachs of squirrels collected during the flooded winter season, though we are unable to identify those as scatterhoarded acorns. We caution, however, that our field work was conducted during years with good acorn crops where acorns were available on the ground until spring, so it is possible there was a sufficient amount of food available in the dry habitat (hardwoods and pine) during the winter. If squirrels in our study area do not rely on scatterhoarded acorns during winter, due to loss from flooding, they may not survive a mast failure year when acorns are not available on the ground through winter. Another population of eastern gray squirrels, living in a cultivated cemetery, still exhibited scatterhoarding behavior even though hard mast was on the ground through the winter and recovered stored mast only made up 27.1% of the hard mast eaten during that winter (Thompson and Thompson 1980). For scatterhoarding to exist in a population, there must be some benefit gained (Andersson and Krebs 1978). It is possible scatterhoarding is a strategy utilized by eastern gray squirrels as a fallback during years of mast failure, when mast will not continue to be available throughout the winter, and during good mast years it simply provides a supplement food to other available food sources. Further research is needed to fully understand the effects of fluctuating environmental conditions on scatterhoarding behavior, especially for animals that do not live in climates that allow for year-round available food. Specifically, knowledge of how these animals are balancing the major

costs of scatterhoarding with benefits in these environments is important to understanding how scatterhoarding is maintained in these populations.

ACKNOWLEDGMENTS

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FIGURE LEGENDS

Figure 1. Eastern gray squirrels (*Sciurus carolinensis*) were given unique color-coded ear tags for individual identification at Lowndes Wildlife Management Area, AL, July 2016 – April 2017.

Figure 2. Very high frequency (VHF) radio-transmitters were inserted into northern red oak acorns (*Quercus rubra*) and tracked to determine where they were scatterhoarded by eastern gray squirrels (*Sciurus carolinensis*), October 2016 – February 2017 at Lowndes Wildlife Management Area, AL.

Figure 3. The area determined to be available for habitat selection (yellow) by eastern gray squirrels (*Sciurus carolinensis*) in the 15 ha core story area on Lowndes Wildlife Management Area, AL, July 2015 – April 2017 was determined by using 2 existing roads and the presence of trees in flooded areas. Area available for scatterhoarding (white) by squirrels during the dry season was determined by using the longest distance any acorns was carried before being buried and created a buffer of that distance around all initial locations of acorns that were later buried. This buffered area was then cut down to only include habitat previously defined as available for habitat selection.

Figure 4. Water levels in the core study area at Lowndes Wildlife Management Area, AL, were recorded lowest in November 2016 (no flooding present) and highest in late January 2017. Dry habitat is represented by the area inside each polygon.

Figure 5. Twenty-one out of 29 acorns scatterhoarded by eastern gray squirrels (*Sciurus carolinensis*) during the dry season (October 2016 – November 2016) later became susceptible to flooding at Lowndes Wildlife Management Area, AL.

Figure 6. Eastern gray squirrels (*Sciurus carolinensis*) taken from Lowndes Wildlife Management Area, AL during the **dry season** (September – November 2016) were assessed for the amount of "Food A" and "Food B" present in their stomachs at the time of death.

Figure 7. Eastern gray squirrels (*Sciurus carolinensis*) taken from Lowndes Wildlife Management Area, AL during 2 **flood seasons** (November 2015 – August 2017, December 2017 – April 2018) were assessed for the amount of "Food A" and "Food B" present in their stomachs at the time of death.
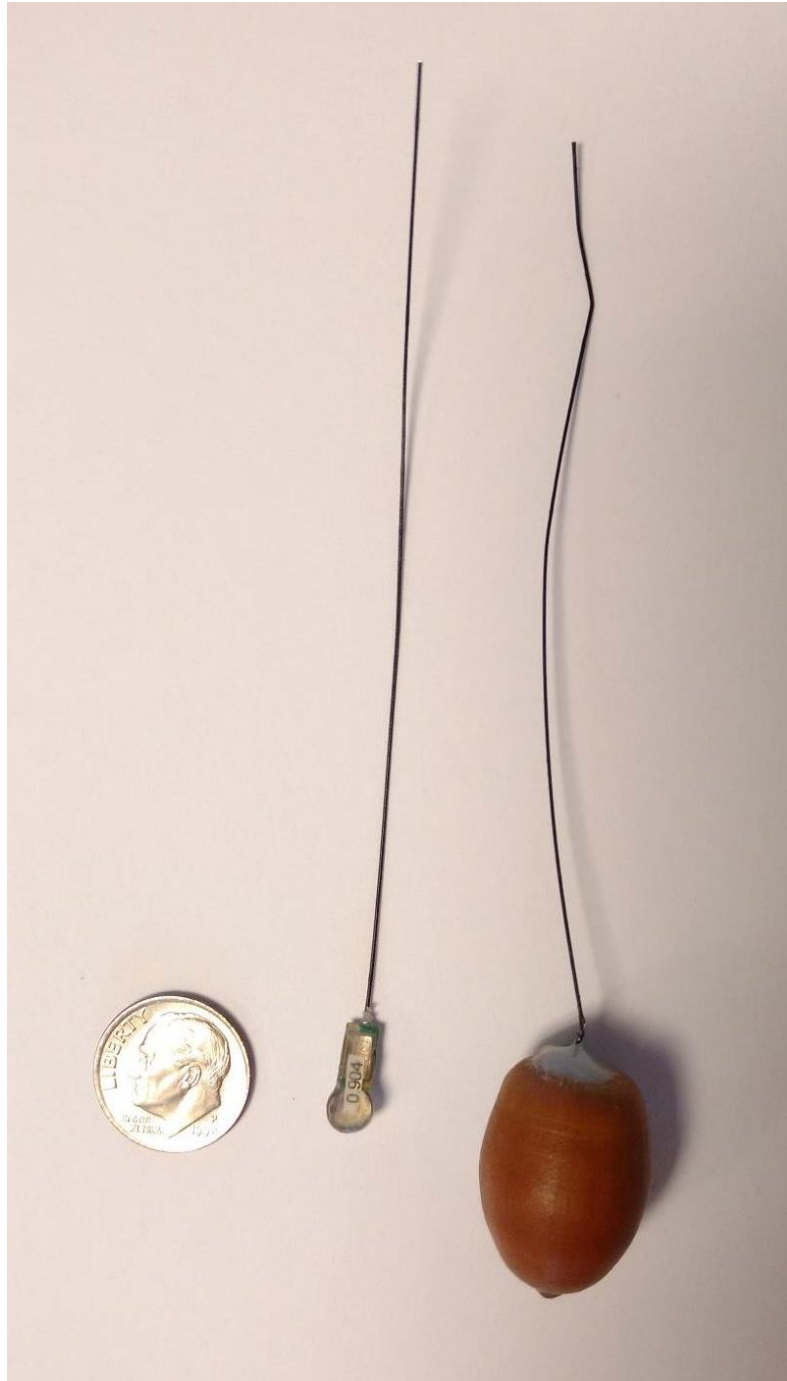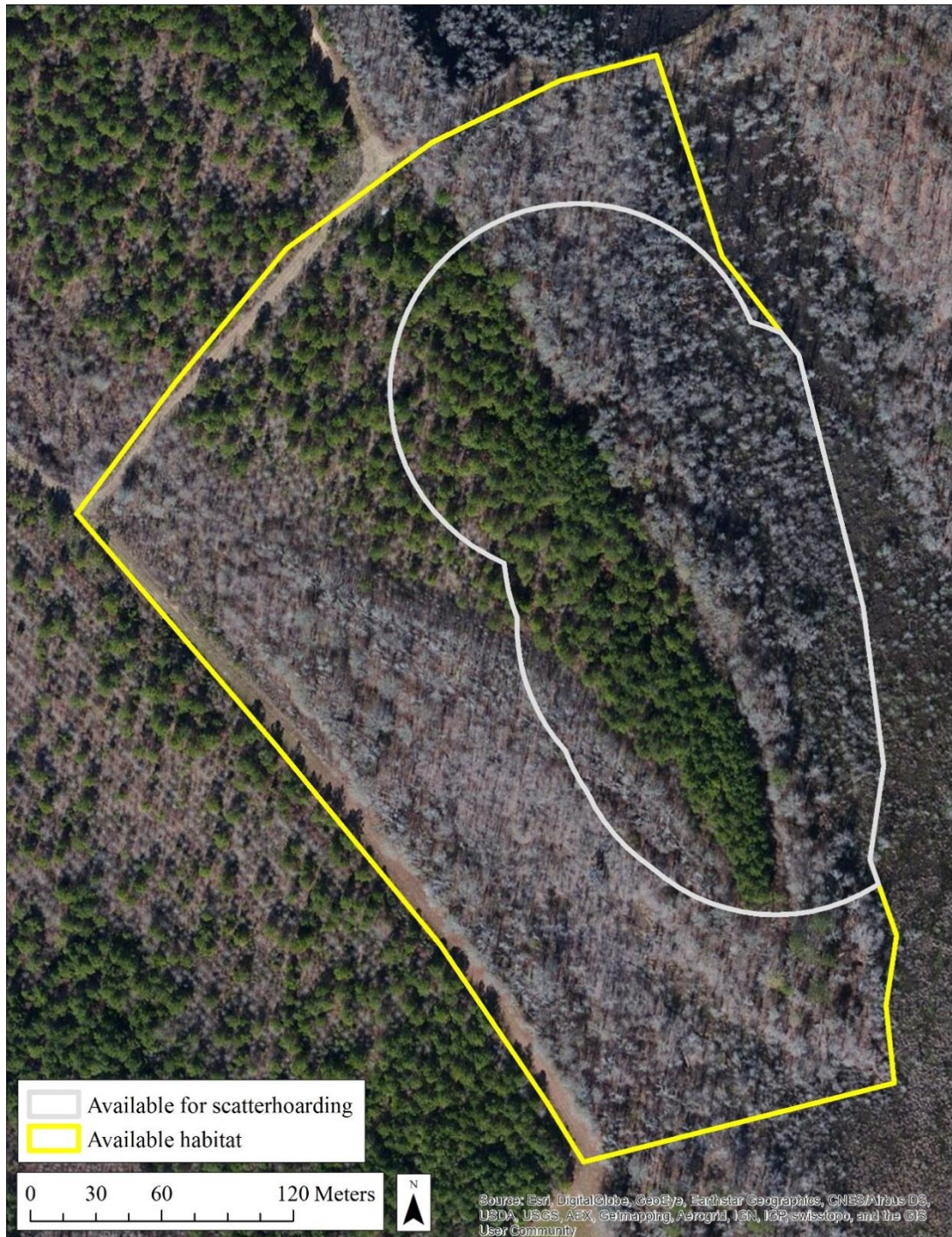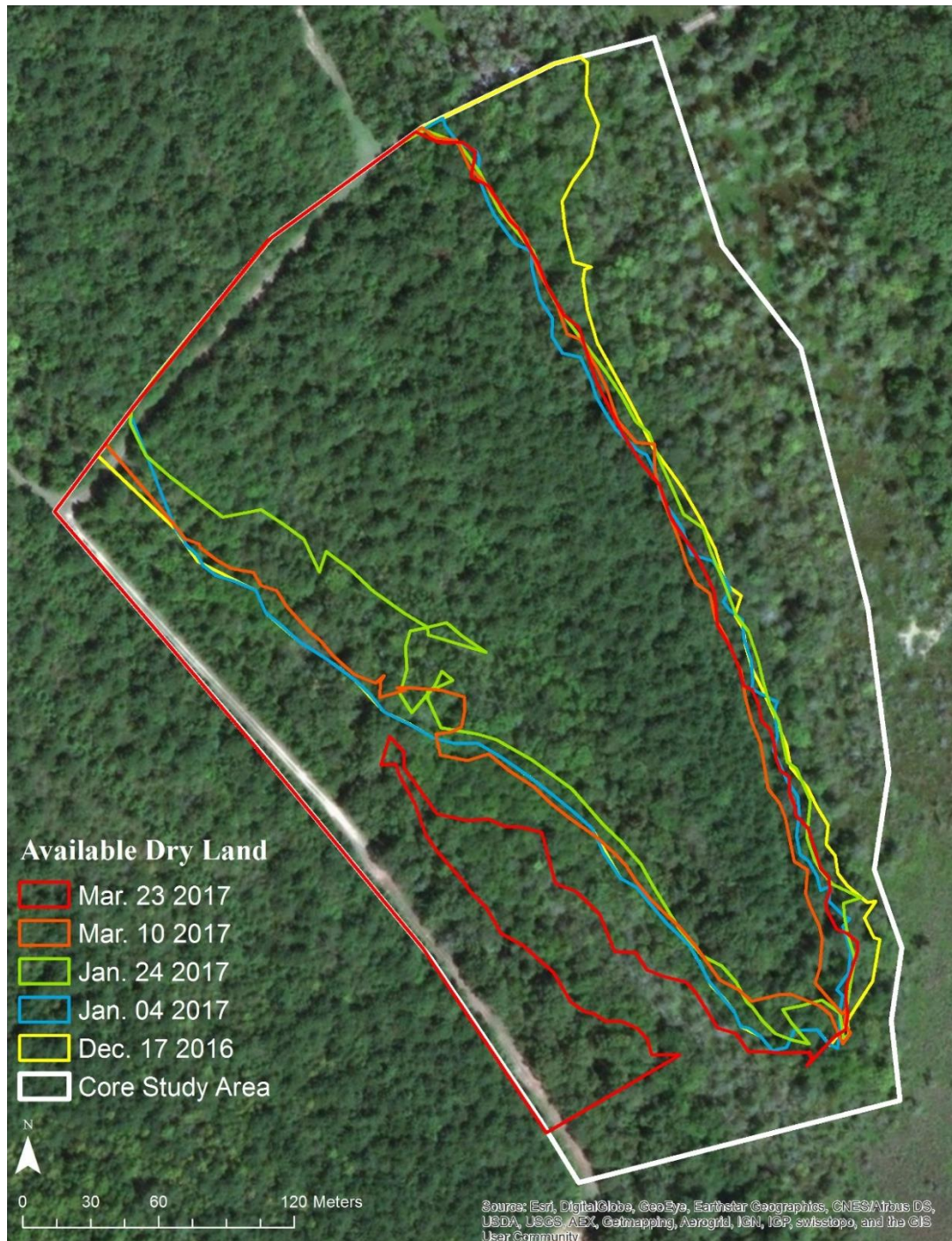
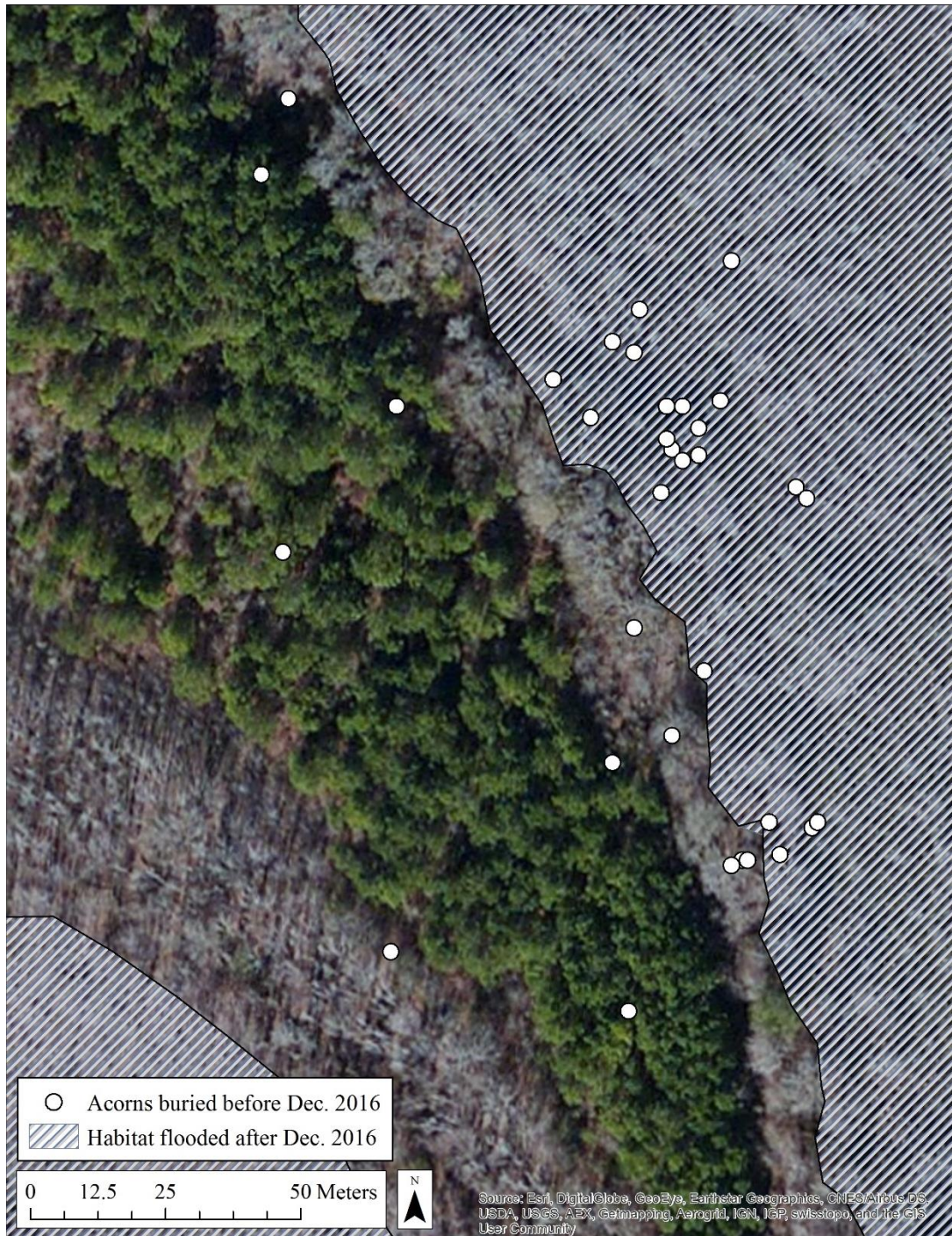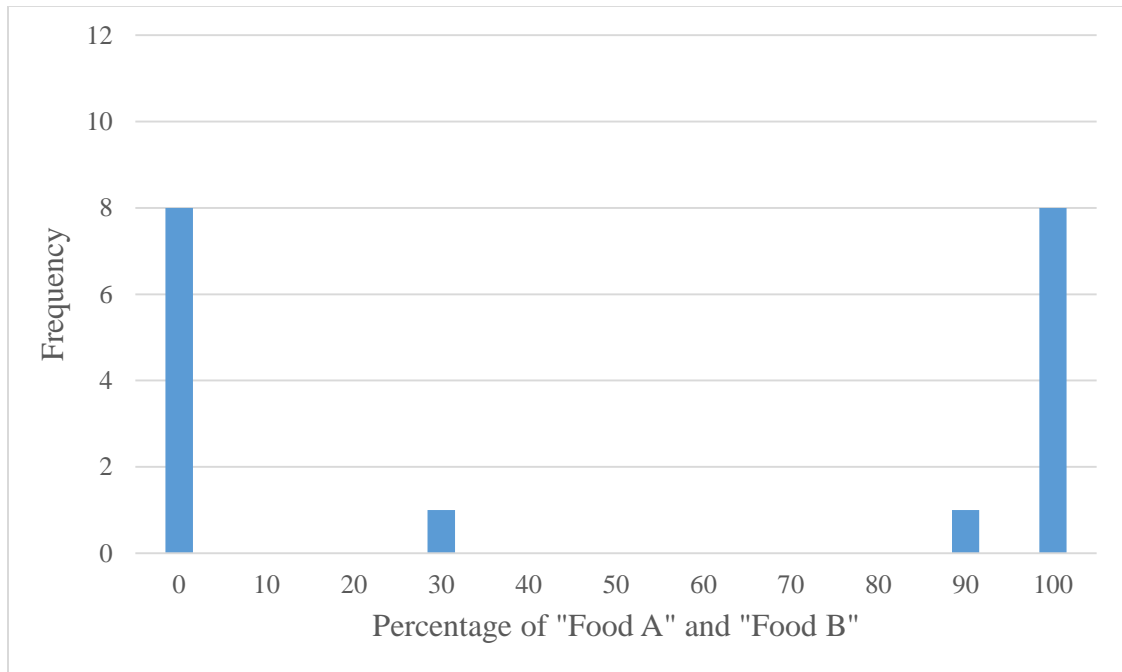**FIGURES**

Figure 1.

Figure 2.

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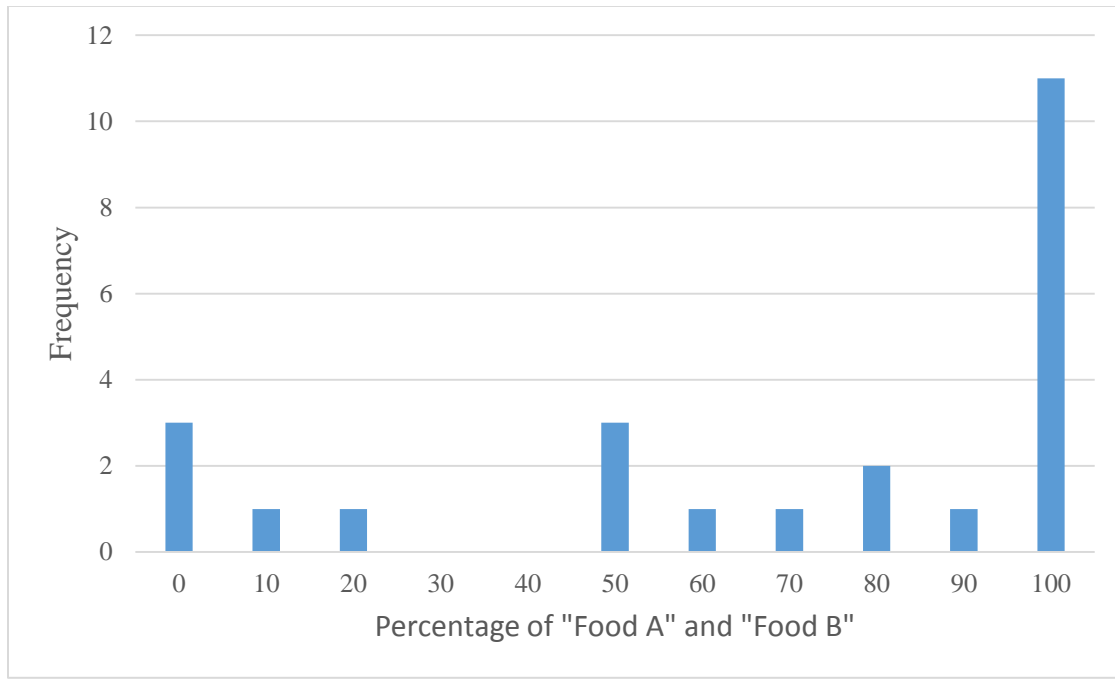
Figure 7.

Chapter 3: Eastern gray squirrel survival in a hunted, seasonally flooded ecosystem

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Squirrel Survival in a Flooded Ecosystem. *Wilson et al.*

Eastern Gray Squirrel Survival in a Hunted, Seasonally Flooded Ecosystem

Abstract: Though the eastern gray squirrel (*Sciurus carolinensis*) is a popular game species throughout its range, little is known about environmental factors that may affect its survival. We investigated survival and predation of a hunted population of eastern gray squirrels on Lowndes Wildlife Management Area in central Alabama from July 2015- April 2017. This area experiences flooding conditions starting in November and ending September of the next year, which could influence individual survival. The Kaplan-Meier survival estimate at 365 days for all squirrels was 0.25 (0.14-0.44, 95% CL) which is within the range for previously studied eastern gray squirrel populations (0.20-0.58). There was no significant difference between male (0.13; 0.05-0.36, 95% CL) and female survival (0.37; 0.18-0.75, 95% CL, $P = 0.16$). Survival was greatest in summer (1.00) and fall (0.65; 0.29-1.0, 95% CL) and least during winter (0.23; 0.11-0.50, 95% CL). We did find squirrels were more likely to die during the flood season and

mortality risk increased as flood extent throughout the study area increased. Over 60% of mortalities were due to predation, which is comparable to other *Sciurus* species. When managing populations of eastern gray squirrels, it is important to consider the effect of environmental factors, such as flooding, on survival.

To understand the dynamics of wild animal populations, one must have knowledge of the various demographic rates of the population, including reproduction, recruitment, and survival. Theory suggests that the growth rate of populations is most influenced by changes in survival, especially at early ages (Caswell 2001). Indeed, previous studies have confirmed that population dynamics are heavily influenced by that demographic parameter in a variety of species (e.g., lynx *Lynx canadensis*, Steury and Murray 2004; big brown bat *Eptesicus fuscus*, O'Shea et al. 2011; wandering albatross *Diomedea exulans*, Weimerskirch and Jouventin 2017). Thus, the successful management of wildlife populations requires a thorough understanding of animal survival, and the factors that influence it. Yet for many species, such information is lacking.

Despite being a commonly hunted species found in mature hardwood stands throughout the eastern United States (Fischer and Holler 1991, Koprowski 1994), little is known about the survival of eastern gray squirrel (*Sciurus carolinensis*) or factors that influence survival rates. Although studies of predation rates are lacking, a few studies have examined the overall survival of this species, with estimates of annual survival

ranging from 0.20 to 0.58 (Table 1). These rates are relatively low and variable compared to other tree squirrels (fox squirrel *Sciurus niger*, 0.69 Conner 2001, 0.49 Prince et al. 2014; Abert's squirrel *Sciurus aberti*, 0.78 Dodd et al. 2003). Previous studies also examined a few factors that influence survival and found some evidence for effects of sex, whether or not the species was hunted, and variation in food supply (Mosby 1969, Barkalow Jr. et al. 1970, Nixon et al. 1975). Survival may be more similar between sexes in hunted versus unhunted populations because individuals with greater activity levels, such as males during the breeding season, are more likely to be caught by an opportunistic predator, whereas hunters also focus their attention on less active squirrels in the canopy. However, previous studies of eastern gray squirrel survival used capture-recapture methods, failing to distinguish between dispersal and mortality and thus were unable to confirm death (and its cause) for a true description of survival (Longley 1963, Mosby 1969, Barkalow Jr. et al. 1970, Nixon et al. 1975, Thompson and Thompson 1980). Cleary, more information is needed on survival of the species and the conditions that influence that demographic.

Annual and seasonal variation in food supply appears to be an important factor affecting mortality of eastern gray squirrels (Nixon and McClain 1969, Nixon et al. 1975). Eastern gray squirrels scatterhoard hard mast during the fall, presumably to rely on this stored mast to gain the nutrition needed to survive winter months, when food typically is scarce (Goodrum 1940, Brown and Yeager 1945, Nixon et al. 1968, Thompson and Thompson 1980, Korschgen 1981, Spritzer 2002). Indeed, populations of this species appear to experience greater survival rates during years of good mast

production (Barkalow Jr. et al. 1970, Nixon et al. 1975). However, in much of the southeastern United States, winter flooding is prevalent in bottomland hardwoods occupied by eastern gray squirrels. Seasonal flooding could reduce the amount of scatterhoarded food available during the winter and result in lower survival rates (Nixon and McClain 1969, Barkalow Jr. et al. 1970, Nixon et al. 1975). Similarly, increased foraging time due to this lack of available stored food in flooded areas would result in greater risk of predation during the winter (Magnhagen 1988, Anholt and Werner 1998, Yoder et al. 2004). However, there is little to no information available about annual survival or seasonal variation in survival in eastern gray squirrel populations inhabiting seasonally flooded areas.

In this study, we examined annual and seasonal survival rates and predation for a population of eastern gray squirrels in a hunted, seasonally flooded ecosystem in Alabama. We expected that survival would be least during the winter season each year, due to the effect of flooding on stored food during that time. We also examined sex-specific survival, expecting similar survival rates between males and females in this hunted population.

STUDY AREA

This study was conducted at Lowndes Wildlife Management Area (LWMA; 16S 0523811 3580684), which consists of 6,800 ha of planted pine, young hardwoods, green fields, and mature hardwood swamp in central Alabama. Management at LWMA focuses on improving habitat conditions for populations of game species such as wild turkey (*Meleagris gallopavo*), white-tailed deer (*Odocoileus virginianus*), mourning dove

(*Zenaida macroura*), and various waterfowl. Mid-September through the first week of March each year is the annual hunting season for gray and fox squirrels. This land was leased to Alabama Department of Conservation and Natural Resources Division of Wildlife and Freshwater Fisheries (ADCNR) by the U.S. Army Corps of Engineers through cooperation with the Alabama Forever Wild Land Trust. Annual precipitation is 135 cm with mean temperatures of 8 degrees Celsius in January and 27 degrees in July (NCEI 2018).

Within LWMA, We chose a core study area of 15 ha (13 ha of mature bottomland hardwood swamp, 2 ha of mature pine) to focus our trapping efforts for eastern gray squirrels. The habitat in this area had willow oak (*Quercus phellos*), southern red oak (*Quercus rubra*), water oak (*Quercus nigra*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*) in the canopy with red maple (*Acer rubrum*) and musclewood (*Carpinus caroliniana*) forming the understory. Large portions of the core study area exhibited seasonal flooding each winter from the adjacent Alabama River and associated wetlands and is located in the southeastern floodplains and low terraces ecoregion (Griffith et al. 2001).

METHODS

Field

We trapped eastern gray squirrels using Tomahawk live traps (Collapsible Squirrel Trap Model 202; Hazelhurst, WI) baited with corn July 2015-July 2016, with more focused trapping effort during July of both years. We set traps on the ground in

areas with signs of squirrel activity or under trees with dreys (leaf nests). Traps were

opened by sunrise, checked regularly, and closed at sunset. We focused our trapping

efforts within the core study area where new squirrels were consistently trapped. Once

trapped, each squirrel was transferred to a cloth handling bag and affixed with 2 uniquely

colored ear tags (Brodin 1994, Steele et al. 2011). Each squirrel was anaesthetized with

Isoflurane before being fitted with a very high frequency (VHF) radio-telemetry collar

(Advanced Telemetry Systems M1640, Isanti, MN). After recovering from drug

exposure, each squirrel was released at the site of capture. Methods were approved by

Auburn University Institutional Animal Care and Use Committee (Protocol #2014-2555)

and collection permits were obtained through ADCNR before data collection began.

Each collared squirrel was located by homing in on the animal using VHF radio-

telemetry during daylight hours 1-3 times per week from the time they were collared until

21 April 2017. Due to the volume of hunting in this area, squirrels were highly elusive

and collared animals were seldom visually located. The squirrel was assumed to be alive

if a signal was determined to be in a tree. If a squirrel was found dead, we attempted to

identify the cause of mortality as a hunter, predation, or unknown. Mortalities were

attributed to hunters if the squirrel was returned or reported by the hunter. No squirrels

were recaptured without a collar, so if a collar was found open (nut no longer in place or

collar was cut off) with no remains nearby, the animal was assumed to have been taken

by a hunter, while if a collar was found closed (nut still in place) with no remains, it was

recorded as predation. Death was also recorded as due to predation if the remains were

not scattered haphazardly, there were signs of mortality (collar with blood, large amounts

of squirrel fur, etc.), there was damage to the body, or signs of the predator were found (tracks, scat, hair, etc.). Predation was classified as avian if the squirrel was found decapitated, a common feeding strategy of owls (Mendall 1944, Glue 1977, Bocheński et al. 1993, Hamer et al. 2001). Mammalian predators were attributed to the mortality if the squirrel's body was cached (under leaf litter or in a burrow), few remains were left or they were scattered in piles about 10 m from the kill site, or if bite marks were found on the collar (Epstein et al. 1983, Marks and Marks 1987). Mortality was recorded as unknown if the squirrel was found with no obvious cause of death.

To assess the severity of flooding in the core study area throughout the flood season, water levels were recorded by walking around flooded areas with a handheld GPS after all major rain events November 2016-March 2017. Flood conditions were most extreme during January 2017 while standing water remained in a majority of the core study area through the end of the study in April 2017. Delineation of dry and flood seasons was based on personal observation of conditions at the study area. The dry season was determined to be from September-October 2015 and September-November 2016. Duration of the flood season and flooding levels at this site were similar between the 2 years in this study, based on personal observations in the field.

Data Analysis

Kaplan-Meier survival estimates were calculated for all squirrels combined, males and females separately, and seasonally using the "survival" package in Program R (Therneau and Grambsch 2000, Therneau 2015, R Core Team 2016). If the date of

mortality could not be estimated, the individual was not included in analyses. Squirrels

that were still alive at the end of the study (21 April, 2017) or whose whereabouts were

unknown due to collar failure were censored in this analysis. All survival rates calculated

during this study were annualized to allow comparison to other studies without

sacrificing data. Cox proportional hazard regression was used to assess differences in

survival between seasons (summer, fall, winter, spring) and sexes (Hosmer et al. 2008).

The effect of flooding was also modeled by creating a time varying covariate with time

split up into monthly steps corresponding to proportions of the study area that were

known to be flooded each month. Results were considered significant if $P \leq 0.05$.

RESULTS

Throughout the study, 47 eastern gray squirrels were collared, including 27 males

and 20 females. The fate of 8 of these squirrels was unknown because the radio-telemetry

signal was lost. Thirty-four squirrels were confirmed dead (2 by avian predators, 10 by

mammalian predators, 10 by unknown predators, 9 by hunters, and 3 unknown deaths)

and 5 were still alive at the end of the study in April 2017. The longest lived squirrel

survived the entire study, 2.5 years.

The survival rate estimate for this population of gray squirrels at 365 days was

0.25 (0.14-0.44, 95% CL; Figure 1). The estimated survival rate for males at 365 days

was 0.13 (0.05-0.36, 95% CL) and for females was 0.37 (0.18 − 0.75, 95% CL), though

this difference was not found to be statistically significant ($P = 0.16$). Though we had

data for 7 discrete seasons, we found no difference in survival rates for the same season

across years (fall: $P = 0.36$; winter: $P = 0.95$; spring: $P = 0.95$), so we combined data

across years for each season. No deaths occurred during either summer 2015 or summer 2016. Survival during fall (0.65; 0.29-1.0, 95% CL, at 365 days) was significantly greater than survival during winter (0.23; 0.11-0.50, 95% CL, at 365 days; $P = 0.001$), but neither fall nor winter were statistically different from spring (0.64; 0.40-1.0, 95% CL, at 365 days; $P = 0.06$ and 0.19, respectively). We found that squirrels were 7.70 times as likely to die during the fall (2.28-25.96, 95% CL) as the winter ($P = 0.001$). Due to collinearity, after accounting for the effect of season on survival, we found squirrels were 1.16 times as likely to die (0.90-1.50, 95% CL) for each 10% increase in the proportion of the study area that was flooded ($P = 0.001$). See Chapter 2 for further explanation on the collinear relationship between season and flooding.

DISCUSSION

Our survival estimate of 0.25 for this hunted population of eastern gray squirrels on Lowndes Wildlife Management Area was similar to other hunted populations. Survival of hunted populations is more varied than unhunted populations with 2 studies estimating annual survival to be less than 0.30 (0.27, Longley 1963; 0.20, Nixon et al. 1975), while a third study found survival to be 0.52 (Mosby 1969). In areas where hunting was prohibited, only 4 studies of eastern gray squirrel survival have been conducted, with estimated annual survival rates ranging from 0.46 to 0.58 (Longley 1963, Mosby 1969, Barkalow Jr. et al. 1970, Thompson 1978; Table 1). Over the course of our study, 19% of our collared squirrels were taken by hunters. Predation was the cause of 65% of all mortalities of eastern gray squirrels throughout this study, which is at the upper end of the contribution of predation to total mortality for fox squirrels (*Sciurus*

niger, 64.3%; Mccleery et al. 2008), western gray squirrels (*Sciurus griseus*, 63.0%; Vander Haegen et al. 2013), and Arizona gray squirrels (*Sciurus arizonensis*, 37.5%; Cudworth and Koprowski 2014). No studies have examined predation rates in eastern gray squirrels.

We found support for our expectation that there would be no difference in survival of males and females in this hunted population. Only 2 previous studies on eastern gray squirrels tested for a sex-specific difference for survival. Nixon et al. (1975) found no difference in a hunted population (0.20 males, 0.21 females) and Barkalow Jr. et al. (1970) found females had greater survival than males in an unhunted population (0.44 males, 0.59 females). One additional study examined survival at both a hunted site and an unhunted site and found survival to be very similar between males and females under both conditions (hunted: 0.52 males, 0.52 females; unhunted: 0.57 males, 0.58 females) though they did not test for a statistical difference in sex-specific survival (Mosby 1969).

With a winter survival rate of 0.25, our expectation that survival would be least during the flood season was supported. Squirrels were more likely to die during the flooding season and mortality increased with the extent of flooding. Mortality was also more likely in the flood season than in the dry season. In other research, we found that this population lost over half of their scatterhoarded food due to flooding during the 2016-2017 flooded winter season (see Chapter 2). Thus, lower survival during the flood season was likely caused by a decrease in attainable food. Other studies have found similar patterns to ours when environmental conditions limit access to available food. Specifically, squirrels are known to experience decreased survival rates during years of

poor mast crop production (Mosby 1969, Nixon and McClain 1969, Nixon et al. 1975, Koprowski 1991). Winter food availability in this flooded ecosystem during all but above average mast years likely mimics that of a poor or failed mast crop.

When managing a hunted population of squirrels, it is important to consider how fluctuating environmental conditions may affect survival rates. Winter is typically a season with little to no food available for these animals and changes in food availability can affect their survival. Hunting mortalities must not exceed that which the population can replace the next breeding season. Reevaluating hunting limits may be necessary depending on available food or conditions of squirrel habitat.

ACKNOWLEDGMENTS

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TABLES

Table 1. Eight previous studies have recorded annual survival of the eastern gray squirrel (*Sciurus carolinensis*).

	Study	Location	Annual Survival		
			All	Males	Females
Hunted	Mosby 1969	Virginia	0.52	0.52	0.52
	Longley 1963	Minnesota	0.27	---	---
	This study	Alabama	0.25	0.13	0.37
	Nixon et al. 1975	Ohio	0.20	0.20	0.21
Not Hunted	Mosby 1969	Virginia	0.58	0.57	0.58
	Barkalow Jr. et al. 1970	North Carolina	0.52	0.44	0.59
	Longley 1963	Minnesota	0.48	---	---
	Thompson 1978	Ontario	0.46	---	---

Figure 1. Survival of 47 radio-collared eastern gray squirrels (*Sciurus carolinensis*) was assessed from July 24, 2015-April 17, 2017 on Lowndes Wildlife Management Area, Alabama. Dashed lines indicate 95% confidence limits.