Canadian Journal of Zoology

Article

Behavioral adaptations of scatterhoarders to seasonal flooding

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Abstract

Scatterhoarder responses to factors that influence stored food (i.e., flooding) is important given the strong reliance on hoarded food for survival. We examined how eastern gray squirrels (*Sciurus carolinensis*, Gmelin 1778) have adapted to a seasonally flooded ecosystem in Alabama. Our study area was dry September–November and flooded the rest of the year. We predicted squirrels would respond to flooding by storing food in areas that stay dry during winter, seasonally shifting to dry habitat, or decreasing the amount of hard mast in their winter diet. We also examined previously reported survival differences between the dry and flooded seasons. During the dry season, 72% of acorns were buried in areas that later flooded. Habitat use did not change significantly during the flooded and dry seasons; however, squirrels used habitat that stayed dry during flooding to a greater degree during non-flood seasons. The amount of hard mast in the diet did not change significantly between the dry and flooded seasons. However, squirrels were more likely to die during the flooded season ($P = 0.02$). We did not find any behavioral adaptations to seasonal flooding. Further research is needed to fully understand the effects of fluctuating environmental conditions on scatterhoarders.

Key words: *Sciurus carolinensis*, scatterhoarding, flooding, habitat selection, diet, survival

Introduction

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 and typically occurs before a food-scarce season (Smith and Reichman 1984; Brodin 1994; Zhang et al. 2008). Food hoarding exists in two forms, scatterhoarding and larderhoarding, with the appropriate strategy for a species depending on competition for cached food and the ability of the animal to defend that food (Vander Wall et al. 2005). Scatterhoarders bury food items in many caches throughout their home range, do not actively defend these caches, and experience high levels of interspecific and intraspecific competition for their stored food (Morris 1962; Vander Wall et al. 2005). Larderhoarding, however, is used by territorial species that actively defend their cached food, which is stored in a few locations in their home range (Hurly and Lourie 1997; Vander Wall et al. 2005). Further, many species use a combination of both larderhoarding and scatterhoarding strategies (e.g., eastern chipmunk, *Tamias striatus* (Linnaeus, 1758), Clarke and Kramer 1994; Merriam's kangaroo rats, *Dipodomys merriami* Mearns, 1980, Murray et al. 2006). 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 (and in the case of larderhoarding, defending) 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, the behavior should provide benefits to the hoarding individuals in the population.

Environmental factors affect use (and hence the benefits) of stored food for species that rely on hoarding. For example, though most scatterhoarding species rely on memory to find their own hoarded food (Lavenex et al. 1998), they do use olfaction to locate and steal food hoarded by others (Vander Wall 1991; Dally et al. 2006), and environmental conditions can influence these senses. For example, yellow pine chipmunks (*Tamias amoenus* Allen, 1980) 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). Similarly, winter conditions can also impact the use of stored food. 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*). If a hoarding population persists where they cannot access their stored food overwinter, this may indicate a shift in diet away from preferred foods during winter (Halonen et al. 2007). However, for scatterhoarding rodents, foods found during winter (e.g., vegetative growth, fungus, and bark) are not typically as nutritious as the nuts and seeds stored by the hoarders. Animals relying on more non-stored foods through winter may have worse body conditions and be more prone to predation or disease (Nilsson and Persson 1993). 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; Lens et al. 1994; Geluso 2005), but this hypothesis has rarely been tested.

Flooding is another environmental factor that could affect scatterhoarding behavior. Flooding over winter is a problem faced by scatterhoarders in many hardwood forests present in temperate riparian zones. Because many scatterhoarders store hard mast in the fall and use this stored food during winter, those living in floodplains during winter experience reduced access to recover and eat their 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 (e.g., switching to storing food in cavities and on roots rather than burying; Van der Meer et al. 2008), shift and enlarge habitats used (Hubbs and Boonstra 1998), or shift diets away from less available resources (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, and this loss of food could reduce overwinter survival. Thus, more information is needed on how scatterhoarders alter their behavioral strategies to compensate for potential lost mast due to various environmental conditions.

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 (see Wilson 2018). Eastern gray squirrels (*Sciurus carolinensis* Gmelin 1788) were used as the focal species because they exclusively 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; Wilson et al. 2020). Eastern gray squirrels commonly inhabit hardwood areas that flood during the winter in the southeastern United States, and this flooding could result in reduced area available for recovering scatterhoarded food. We studied a population of eastern gray squirrels on a central Alabama study area that floods every winter. In a previous research at this study area, we found that eastern gray squirrels were still eating hard mast species during winter (Wilson et al. 2020) and survival was similar to other hunted squirrel populations (Wilson et al. 2019). We explored behavioral adaptations that may allow the squirrels to survive in this seasonally flooded ecosystem. 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, and (3) reducing the amount of hard mast in their diet during the flooded season. Additionally, we further examined squirrel survival during the flooded and dry seasons. Understanding how squirrels respond to environmental factors (e.g., flooding) that affect their stored food is beneficial for understanding the evolution of scatterhoarding behavior.

Materials and methods

Study area

At the time of this study, the Lowndes Wildlife Management Area (LWMA; 16S 0523811 3580684) consisted of 6800 ha of planted hardwood (*Quercus* spp.), planted pine (*Pinus* spp.), wildlife food plots, and bottomland hardwood swamp in Lowndes County, Alabama, in the Southeastern Floodplains and Low Terraces ecoregion (Griffith et al. 2001). The land was 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 was managed to support populations of game species, such as white-tailed deer (*Odocoileus virginianus* (Zimmermann 1780)), waterfowl, Mourning Dove (*Zenaida macroura* (Linnaeus, 1758)), squirrels (*Sciurus* spp.), and Wild Turkey (*Meleagris gallopavo* Linnaeus, 1758). The annual hunting season for gray and fox squirrels (*Sciurus niger* Linnaeus, 1758) was mid-September through the first week of March during all years of this study. The scatterhoarding season for this area typically began in October (when seeds fell from the trees) and continued through late February–early March (when vegetative growth appeared in the tree canopies; Wilson, pers. obs.). Mean temperatures were 8 °C in January and 27 °C in July, with 135 cm of precipitation annually (NCEI 2018).

We selected a 15.43 ha core study area within LWMA consisting of about 2 ha of mature pine and about 13 ha of mature bottomland hardwood swamp for our research, based on suitable habitat and the presence of eastern gray squirrels in the area. Dominant canopy species included water oak (*Quercus nigra* L.), willow oak (*Quercus phellos* L.), southern red oak (*Quercus falcata* Michx.), sweetgum (*Liquidambar styraciflua* L.), and loblolly pine (*Pinus taeda* L.) with American hornbeam (*Carpinus caroliniana* Walter) and red maple (*Acer rubrum* L.) present in the understory. We observed flooding in a majority of the bottomland hardwood swamp for the majority of each year, due to the close proximity to the Alabama River and associated wetlands.

Field methods

To assess the extent of flooding on our study area throughout the year, we walked along the water line in the core study area after each major rain event between November 2016 and March 2017, using a handheld GPS to map how flooding fluctuated during the scatterhoarding season. We used ArcMap (Version 10.5.1, ESRI 2017) to create polygons of flooded land within the core study area and recorded the percentage of land that was flooded at each discrete point in time when the water level data were collected. Flooding was assumed to stay the same between each major rain event as we did

Can. J. Zool. **101:** 743–753 (2023) | dx.doi.org/10.1139/cjz-2023-0024

not observe any major differences in flood waters while in the field every day (Wilson, pers. obs). We defined the flooded season as the period when flooding covered >50% of the core study area. Based on observations of similar amounts of flooding throughout other years of our study, for analysis purposes, we assumed the extent of flooding was the same each year. Gage height for a nearby United States Geological Survey (USGS) monitoring station at the Alabama River supports our assumption that this area floods every winter, though these data are too coarse to describe the exact timing and lengths of the flood season in our study area every year (USGS 2022).

We trapped eastern gray squirrels July 2015–2016 using Tomahawk live traps (Hazelhurst, WI, USA; Collapsible Squirrel Trap Model 202) placed on the ground under and around any trees with dreys (i.e., stick nests in trees) or other signs of squirrels (e.g., chewed pine cones or holes in the leaf litter indicating scatterhoarding activity). We transferred each trapped squirrel to a cloth handling bag, anesthetized the animal with isofluorane, and then fitted the squirrel with a very high frequency (VHF) radio-telemetry collar (Advanced Telemetry Systems M1640, Isanti, MN, USA) and color-coded ear tags to allow for future visual identification of individual squirrels. See Wilson et al. (2019) for further details on trapping methods. Methods were approved by Auburn University Institutional Animal Care and Use Committee (Protocol #2014–2555) and the required trapping permits were obtained from the Alabama Department of Conservation and Natural Resources.

Prediction 1: scatterhoarding habits

We deployed radio-tagged acorns prior to and during the 2016–2017 flooded season to observe hoarding strategies used by eastern gray squirrels in the face of flooding. We attached VHF radio-telemetry transmitters (Advanced Telemetry Systems A2414, Isanti, MN, USA) to viable northern red oak (*Quercus rubra* L.) acorns (Steele et al. 2011), purchased from Acorno (Winooski, VT, USA, www.acorno.us), and placed the radio-tagged acorns individually throughout the core study area from October 2016 to February 2017 in areas where multiple squirrels were known to be present. We inserted transmitters in a small hole drilled through the top of the acorn and then filled the hole with hot glue with the antennae sticking out of the acorn (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). An average of 10.47 (standard deviation (SD) = 3.66) acorns were in the field at one time with an average of 4.04 (SD = 3.46) new acorns being deployed each day. Each acorn was placed at least 3 m away from other currently deployed, tagged acorns. Upon acorn consumption, we continuously redeployed transmitters on new acorns until battery failure of the transmitter.

Each radio-tagged acorn was monitored by a motion-detecting camera to identify the species that handled the seed for either caching or consumption as well as identify any squirrels that handled seeds by their colored ear tags (Tamura et al. 1999; Gálvez et al. 2009; Hirsch et al. 2013). We tracked tagged acorns daily via homing in on the radio-telemetry signal to record new locations after acorns were handled by animals. We categorized fates of acorns as buried (stored under the soil surface), cached (stored in or underneath an item or substance that was not soil), or eaten. If we tracked a tagged acorn in a burrow, we assumed the acorn had been larderhoarded by a mouse, as described by Tamura and Shibasaki (1996). If cached or buried, we replaced the tagged acorn with an untagged acorn to allow us to re-use the tagged acorn without decreasing that animal's hoarded food supply. A small portion of acorns in scatterhoarded locations were monitored by a motion-detecting camera to determine if the acorn was recovered before flooding occurred. Care was taken to disturb the cache site as little as possible to prevent creating any cues of a scatterhoarded acorn for a competitor (Duncan et al. 2002).

To determine whether squirrels were taking into account future flood conditions when scatterhoarding food, we fit a resource selection function comparing locations of acorns buried during the 2016 dry season (11 September 2016 to 29 November 2016; Manly et al. 2002) to an equal number of randomly selected points across the core study area. The area from which random points were selected was created by taking the longest distance an acorn was carried from its point of deployment (85.48 m) and using ArcMap to create a buffer of that distance around each radio-tagged acorn deployment location. Each radio-tagged acorn was assigned one random location that was considered available for that acorn to be scatterhoarded. We then identified whether each used or random point was under water during the flood season and conducted fixed conditional logistic regression (using the "clogit" function in the survival package in Program R; R Core Team 2016; Therneau and Grambsch 2000; Therneau 2021) to examine whether locations of buried acorns and random locations had similar likelihoods of being under water during the flooded season.

Prediction 2: habitat use

To examine potential changes in habitat use between the flooded season and the dry season, we followed telemetry signals to the location of each collared squirrel 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. Due to the volume of hunting in this area, squirrels were highly elusive, and we seldom could visually locate collared animals. We were able to track telemetry signals to a specific tree and assumed the squirrel was at that location. If we tracked the squirrel to a tree and then heard the animal move away in the tree canopy, we recorded the location the squirrel was at before they responded to our presence. We used a case-control habitat use analysis to determine differences between used and available habitat during the three flooded seasons and the two dry seasons (Keating and Cherry 2004). The habitat of used locations was compared to points randomly generated in ArcMap. We defined the available area for habitat use using the extent of observed locations of collared squirrels in combination with physical features (trees bordering the swamp, dirt roads, Tounzen et al. 2012) that bounded this area. For each collared squirrel, observed used locations were combined with an equal number of random locations. Methods for determining if locations were dry or flooded during flooding were the same as described for scatterhoarding habits.

We used the glmer function from the lme4 package (Bates et al. 2015) in Program R to run mixed-effects logistic regression models to determine effects of the covariates (winter flood conditions, flood season) on the habitat selection of eastern gray squirrels. A random effect of individual squirrel was included to account for varying numbers of locations across squirrels. We also tested for an interaction between flood season (flooded or dry) and winter flood conditions of locations to assess if selection for (or against) habitat that flooded was influenced by whether it was the flood season or not.

Prediction 3: diet

To determine any differences in the contribution of hard mast to the diet between the flooded and dry seasons, we examined the stomach contents of eastern gray squirrels harvested from LWMA and donated to this project by hunters in the 2015–2016 flooded season, 2016 dry season, 2016–2017 flooded season, and 2017–2018 flooded season. We recorded the proportion of each food item in each squirrel's stomach (based on differences in texture and color) and sent samples of these food items to Jonah Ventures (Boulder, CO, USA) for genetic analyses. See Wilson et al. (2020) for further description of sequencing methods used to identify foods eaten by these squirrels. We conducted a Fisher's exact test to determine if there was a significant difference between the amount of hard mast eaten in the dry season compared to the flooded seasons.

Survival

During relocations of squirrels described in habitat use methods, we also assessed survival of each squirrel. Our collars did not have mortality signals; so after locating the squirrel, if we determined a telemetry signal was coming from a tree, we assumed the squirrel was alive. We recorded the squirrel as dead when we located a collar with or without remains nearby, as no previously collared squirrels were recaptured without a collar and 12 squirrels were recaptured still wearing their collar after up to 341 days (median = 18 *d*). These methods are reported in more detail by Wilson et al. (2019).

Our previous analyses reported differences between fall and winter survival (Wilson et al. 2019) while for this study, we included all mortalities during the flooded season (November or December through August) to further elucidate differences in survival between the flooded and dry seasons. We used Cox proportional hazards regression (survival package in Program R; Therneau and Grambsch 2000; Hosmer et al. 2008; Therneau 2015) to analyze previously reported data (Wilson et al. 2019) to assess differences in survival of eastern gray squirrels between the dry season and the flooded season (flooding covers >50% of core study area; Nixon et al. 1968; Korschgen 1981). We used the same squirrels in our analyses as we described previously in Wilson et al. (2019).

Table 1. Water levels in the 15.43 ha core study area at Lowndes Wildlife Management Area, AL, were recorded the lowest in November 2016 and the highest in late January 2017. Flooding is shown as the percentage of the core study area that was covered in water at the date of data collection.

Date	Area flooded (ha)	Flooding (%)
10 November 2016	0.01	0.07
17 December 2016	8.60	55.71
4 January 2017	9.87	63.97
24 January 2017	13.30	86.19
10 March 2017	13.23	85.70
23 March 2017	8.49	55.01

Results

Flooding was assessed six times; the lowest water level was recorded in November 2016 with the highest recorded in late January 2017 (Table 1). Flood conditions were the 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 (S. B. Wilson), flooding levels and timing at this site were similar between the two winters in this study. Dry seasons occurred from 12 September 2015 to 27 October 2015 and from 12 September 2016 to 29 November 2016 when flooding covered <1% of the core study area, while 55%–86% of the core study area was flooded from 25 July 2015 to 11 September 2015; from 28 October 2015 to 11 September 2016; and from 30 November 2016 to 21 April 2017 (flooded seasons, Table 1). Once the flood season began, the amount of flooding throughout the study area varied; however, the flood line in the area where we recorded scatterhoarding habits did not change drastically after the first flood event due to the steep change in elevation from the flood zone to the dry land (Wilson, pers. obs.).

Prediction 1: scatterhoarding habits

Of the 114 radio-tagged acorns deployed during the 2016 dry season, 29 were buried, 3 were cached aboveground or larderhoarded in burrows by mice (*Peromyscus* spp.), 12 acorns were eaten (4 by gray squirrels; 1 by a raccoon, *Procyon lotor* (Linnaeus, 1758); 7 by unknown species that were not captured on camera), and 16 acorns were ignored by animals (Table 2). No tagged acorns were stored above the soil surface by squirrels. Of the 11 acorns that were monitored with cameras after burial, 1 acorn was recovered 11 days after burial while the remaining 10 acorns were not recovered before flooding occurred 15–26 days after they were buried. Our original tagging method of gluing the transmitter to the outside of the acorn resulted in 50 acorns having tags removed by the

Can. J. Zool. **101:** 743–753 (2023) | dx.doi.org/10.1139/cjz-2023-0024

Table 2. Fates of northern red oak acorns (*Quercus rubra*) tagged with radiotelemetry transmitters and released in a seasonally flooded area on Lowndes Wildlife Management Area from October 2016 to February 2017. Acorns were primarily handled by eastern gray squirrels (*Sciurus carolinensis* Gmelin 1778). Data presented as percentage (*n*) of seeds released during each month. The study area was completely dry from October to November, while most of the land then flooded from December to February.

	Month of seed deployment				
Seed fate	Oct.	Nov.	Dec.	Jan.	Feb.
Buried	18.2 (2)	55.1 (27)	33.3 (9)	26.1 (6)	0 (0)
Cached aboveground	9.1 (1)	2.0 (1)	0 (0)	0 (0)	14.3 (1)
Larderhoarded	9.1 (1)	0 (0)	7.4 (2)	0 (0)	0 (0)
Eaten	63.6 (7)	10.2 (5)	22.2 (6)	13.0 (3)	28.6 (2)
Ignored	0 (0)	32.7 (16)	37.0 (10)	60.9 (14)	57.1 (4)

animal before handling the seed. After switching to drilling a hole in the acorn, inserting the transmitter, and filling the hole with hot glue, only 1 acorn had the tag removed before handling. During the flooded season, 15 acorns were buried, 3 were cached or stored in burrows, 11 were eaten, and 28 were ignored. Additionally, 19 acorns were transported, but the transmitters died before we could relocate them; therefore, these acorns were excluded from further analyses. Scatterhoarding of tagged acorns was greatest during November 2016 and tagged acorn handling by squirrels decreased beginning in January 2017 (Table 2).

Before flooding occurred in December 2016, 20 of 29 scatterhoarded tagged acorns (72.41%) were buried in areas that would later be flooded (Fig. 1). Buried acorns were carried an average ($\bar{X}$) of 20.63 m (SD = 18.63, $n = 29$) before being buried an average depth of 28.00 mm (SD = 21.59, $n = 7$). Depth was not initially measured until we observed a difference in the depths acorns were buried in dry soil that stayed dry versus damp soil that later flooded, resulting in only seven measurements during the dry season. During the dry season, there was no significant difference between the average distance acorns were carried before being buried in areas that later flooded ($\bar{X} = 23.02$ m, SD = 17.86, $n = 21$) versus areas that stayed dry during flooding ($\bar{X} = 15.30$ m, SD = 20.26, $n = 8$; *t*-test, $t_{[14]} = -0.98$; $P = 0.34$). However, there was a significant difference in the average depth acorns were buried in damp soils that would later become flooded ($\bar{X} = 45.25$ mm, SD = 2.50, $n = 4$) versus dry soils that stayed dry during flooding ($\bar{X} = 5.00$ mm, SD = 0, $n = 3$; *t*-test, $t_{[3]} = -32.2$; $P < 0.001$).

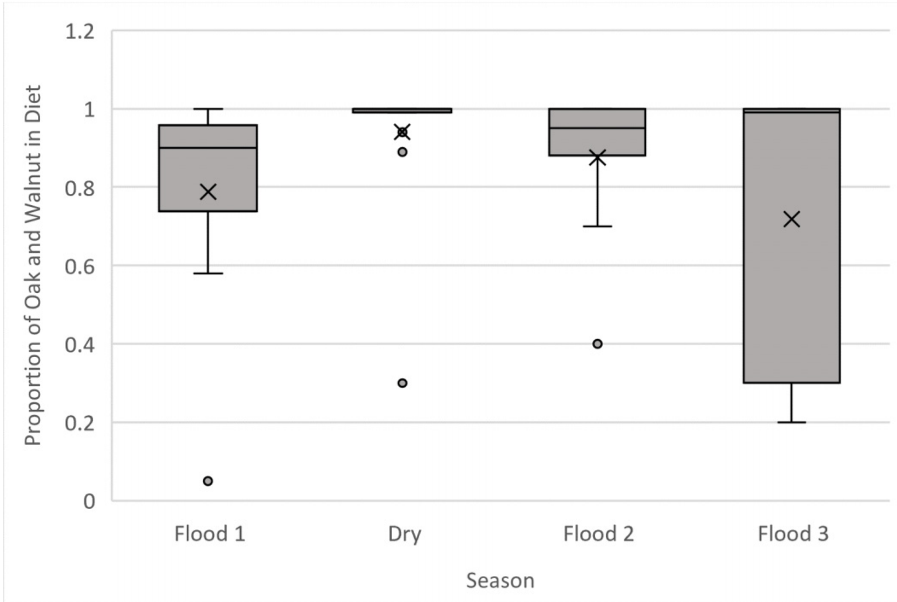
Additionally, our resource selection function indicated that during the dry season, squirrels were 2.75 times as likely (odds ratio; 0.88–8.64, 95% confidence limits (CL)) to bury acorns in soils that later flooded as soils that stayed dry during winter, though this relationship was not statistically significant ($P = 0.08$). Squirrels buried an additional 15 radiotagged acorns during the flooded season, with 13.33% ($n = 2$) of those also later ending up underwater. In total, 50% ($n = 22$) of all tagged acorns buried from October 2016 to February 2017 were eventually located under water during the winter and were unavailable for retrieval by squirrels through the end of the study in April 2017.

Fig. 1. Twenty-one out of 29 northern red oak acorns (*Quercus rubra*) scatterhoarded by eastern gray squirrels (*Sciurus carolinensis* Gmelin 1778) during the dry season (white circles, October 2016 to November 2016) later became susceptible to flooding beginning December 2016 (patterned area) at Lowndes Wildlife Management Area, AL. Deployment locations of acorns are indicated by gray triangles. Base map credit: Maxar, Microsoft. Map projection: NAD 1983 UTM Zone 16 N.

Prediction 2: habitat use

Between 24 July 2015 and 19 July 2016, 47 squirrels were collared. Locations from 37 squirrels were included in habitat use analyses; 10 additional squirrels were removed from

Fig. 2. Proportion of eastern gray squirrel (*Sciurus carolinensis* Gmelin 1778) diet found to consist of oak (*Quercus* spp.) and walnut (Juglandaceae) species. Squirrels were collected during the 2015–2016 flood season (Flood 1, $n = 10$), 2016 dry season (dry, $n = 15$), 2016–2017 flood season (Flood 2, $n = 11$), and the 2017–2018 flood season (Flood 3, $n = 5$) at Lowndes Wildlife Management Area in central Alabama.



analyses due to death occurring before the individuals were relocated. From these 37 squirrels, we collected 596 locations. 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 habitat use during flooded or dry seasons and whether the habitat floods was not statistically 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 the flooded and dry seasons 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 winter than areas that later became flooded (3.40–5.96, 95% CL; $P < 0.001$). Comparatively, during the flooded 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

We collected 10 eastern gray squirrels from bottomland hardwoods during the 2015–2016 flooded season, 15 squirrels during the 2016 dry season, 11 squirrels during the 2016–2017 flooded season, and 5 during the 2017–2018 flooded season. Overall, we identified 17 visually different food items eaten by these squirrels (5 food items present only in dry season, 8 food items present only in flooded season, and 4 food items present in both; Wilson et al. 2020). We conducted DNA analysis on the two visually different food items that showed up prominently in squirrels' stomachs during both the dry season and flooded season. Other items supplemented these two foods, but few made up the majority of the stomach contents. We found these two food items were oak (*Quercus* spp.) and walnut (*Juglandaceae*). Every squirrel collected had eaten either oak or walnut, with 73.07% of all stomach contents consisting of oak or walnut. Oak and walnut made up 94.08 ± 18.05% ($\bar{X}$ ± SD) of all foods eaten during the dry season and 81.73 ± 24.31% of all foods eaten during the flooded seasons. We did not find a significant difference in the amount of oak and walnut eaten in the dry season compared to the flooded seasons (Fig. 2, $P = 0.12$, Fisher's exact test). See Wilson et al. (2020) for further description of fall and winter diet for this population of eastern gray squirrels.

Survival

We collared 47 eastern gray squirrels in our core study area (Wilson et al. 2019). We lost the radio-telemetry signal of eight squirrels and are not able to confirm their fate. Of the remaining 39 radio-collared squirrels, we confirmed 34 mortalities and 5 squirrels were still alive at the end of the study in April 2017 (Wilson et al. 2019). Although 19 squirrels died during a flooded winter, 23 squirrels survived at least one 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 right-censored (Wilson et al. 2019). We found

Can. J. Zool. **101:** 743–753 (2023) | dx.doi.org/10.1139/cjz-2023-0024

squirrels were 4.63 times as likely to die during the flooded season (1.40–15.35, 95% CL) as the dry season ($P = 0.02$).

Discussion

Prediction 1: scatterhoarding habits

The results of our study did not support our prediction that squirrels would scatterhoard acorns in areas that do not flood during winter. Flooding rendered a large number of the tagged acorns buried by eastern gray squirrels (50%) unavailable for recovery during winter, when food hoarders are thought to rely on their stored food source to survive (Morrison et al. 2009), suggesting this population has not adapted their scatterhoarding habits to the loss of food due to flooding. Though scatterhoarders are known to re-cache buried seeds several times before consumption (Wang et al. 2014), only one of the 11 buried tagged acorns that we monitored with cameras was recovered before flooding (11–26 days after initial burial of acorns). Typically, seeds are recovered, and potentially recached, within a week after burial (Steele et al. 2011); so we do not believe the squirrels were moving their hoarded seeds out of the flood zone after initial burial.

Here are several previous studies documenting behavioral adaptations of scatterhoarders to the loss of stored food for other species. For example, animals that experienced high rates of pilferage increased their scatterhoarding effort (Huang et al. 2011; Niu et al. 2020) and avoided burying food in those areas in the future (Hampton and Sherry 1994). Scatterhoarding avian species have been shown to use different foraging sites during caching and recovery seasons due to the presence of snow and ice restricting access to certain areas during winter, similar to the effect of flooding in our study (Tomback 1980; Brodin 1994; Lens et al. 1994). Though the squirrels in our study area did not appear to respond to loss of hoarded food due to flooding, we did find squirrels that buried acorns deeper in flood zone areas with wetter soils than in areas with drier soils, which is evidence of an adaptation to reduce pilferage within our squirrel population. Burying seeds 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 that counteracts the lure of the strong scent (Vander Wall 1993*b*, 1995; Geluso 2005). Thus, our results suggest that the squirrels have behaviorally 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

The results of this study did not support our prediction that eastern gray squirrels would shift their home ranges and use different habitat during the dry and flooded seasons. While we predicted that squirrels would shift to dry land during the flooding season, we found that squirrels seemed to select flooded land even more during the flood season than during the dry season (although differences were not statistically significant). The results suggest that an important resource for the squirrels may be more abundant or considered greater quality in the flooded areas compared to the dry areas. For example, gray squirrels typically prefer nesting in hardwood species, rather than the mature pine that dominated the upland area of our core study area that stayed dry during the flooded season (Edwards and Guynn 1995; Cudworth and Koprowski 2011). In fact, Arizona gray squirrel (*Sciurus arizonensis* Coues, 1867) nests were found at greater densities in riparian hardwood stands compared to the upland pine-oak stands (Cudworth and Koprowski 2011).

Home range size is known to fluctuate with the availability of resources for many species (Corriale et al. 2013); so comparing the sizes of individual homes ranges rather than just habitat selection may have provided a better understanding of how squirrels utilize their habitat during flooding. For example, Willow Tits (*Parus montanus* (Conrad von Daldenstein, 1827)) showed scatterhoarding adaptations to winter snow and ice and hoarded food during fall in future winter foraging sites (Brodin 1994). However, Black-capped Chickadees (*Poecile atricapillus* (Linnaeus, 1766)) learned from short-term cache loss to avoid caching in certain locations but still used the entire experimental enclosure for foraging and recovery attempts (Hampton and Sherry 1994). Both seasonal prey availability (Wang et al. 2010) and seasonal habitat variation (Baschuk et al. 2012) have also been found to impact habitat selection in non-hoarding species (Wang et al. 2010).

Additionally, travel across the landscape by squirrels is not inhibited by the presence of flooding; so behaviors other than foraging, such as mating chases, escape from predation, or nesting in the hardwoods, could have impacted the use of trees in flooded areas. Eastern gray squirrels typically breed throughout the flooded season (January–September, Nixon and McClain 1975); so mating chases could also have led squirrels into flooded habitats. With high predation rates during winter at LWMA (Wilson et al. 2019), our squirrels might have shown a preference for the more spread out, dense canopy structure of mature oak that existed in the flooded areas. Although squirrels in our study area did not appear to choose habitat based on the availability of scatterhoarded food in those areas, there is likely another factor causing them to show different patterns during the flooded and dry seasons.

Prediction 3: diet

Previously, we have shown that squirrels in this population were eating hard mast species year-round (Wilson et al. 2020). After further investigation of the diet of this population, our prediction that squirrels would reduce the amount of hard mast in their diet during the flood season was not supported. We did observe a small decrease in the proportion of the diet that was hard mast during the flooding season, but differences were small (~13%) and not statistically significant. Eastern gray squirrels on LWMA may not show adaptations to the loss of their buried food to flooding because they are able to find ways to maintain their access to important mass (Wilson et al. 2020). On LWMA, there are small areas of dry land available for recovering scatterhoarded seeds during the flooded season, which could have accounted for the presence of hard mast species in the diet during flooded winter months. However, we could not confirm which part of plants were eaten, and the presence of hard mast species may reflect consumption of either scatterhoarded mast or new vegetative growth. In fact, 24 of the squirrels we collected to represent the flooded season diet were collected in late February, when new growth was observed in the oak trees at LWMA (Wilson, pers. obs.; Wilson et al. 2020). Eastern gray squirrels are known to take advantage of this early spring food resource and many other studies have documented flowers and buds of oak and walnut species as common components of the spring diet (Brown and Yeager 1945; Nixon et al. 1968; Korschgen 1981; Thompson and Thompson 1980). 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 (Wilson, pers. obs.; Wilson et al. 2020). While eastern gray squirrels can opportunistically alter their diets during spring and summer (Spritzer 2002), all populations of this species have been found to rely on hard mast as a major part of their diet during fall and winter (Goodrum 1940; Brown and Yeager 1945; Nixon et al. 1968; Thompson and Thompson 1980; Korschgen 1981; Spritzer 2002; Wilson et al. 2020). 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 (Korschgen 1962; Nixon et al. 1968; Thompson and Thompson 1980).

Survival

Lastly, using data from our previous study on LWMA (Wilson et al. 2019), we examined squirrel survival in more depth pertaining to the flood seasons, rather than focusing on comparing fall and winter survival. We found that squirrels were more likely to die during the flooded season than during the dry season. Additionally, we had previously found that survival decreased in relation to the amount of the study area that was flooded (Wilson et al. 2019). Other studies have also found a link between flooding and increased mortality for rodents (Madsen and Shine 1999; Thibault and Brown 2007), though the species in these studies did not use the tree canopies to travel around flooded areas, such as eastern gray squirrels do. Similar to the effect of ice formation decreasing access to food for tundra voles (*Microtus oeconomus* (Pallas, 1776)), flooding likely reduces the amount of nutritious food available during winter, resulting in greater susceptibility to predation (either through increased time spent foraging, Anholt and Werner 1998; or decreased body condition, Wirsing et al. 2002). Indeed, squirrels in our study area ate a greater amount and greater variety of non-hard mast food items than previously recorded for the species during winter (Wilson et al. 2020) and we recorded a large number of mortalities due to predation during the flooded season (Wilson et al. 2019). However, our population of squirrels also had an overall survival rate of 0.25 at 365 days, which is similar to other hunted populations of eastern gray squirrels (see Table 1 in Wilson et al. 2019). See Wilson et al. (2019) for further discussion of our squirrel population's survival compared to previous studies of eastern squirrel survival.

General discussion

We did not find support for our hypothesis that individuals relying on stored food during winter would show behavioral adaptations to flooding. Additionally, in concurrent research, we have found that these squirrels still eat hard mast during the flooded winter (Wilson et al. 2020) and annual survival rates are as expected for a hunted population (Wilson et al. 2019). Considering squirrels in our core study area lost 72% of their food stored during the dry season to future flooding and did not respond in a way that increased food resources during the food scarce winter, the results of our research suggest that this squirrel population may not rely solely on scatterhoarded food to survive Alabama's mild winters.

Hard mast species of plants were found in the stomachs of squirrels collected during the flooded winter season, though we are unable to identify that as seeds or scatterhoarded food (Wilson et al. 2020). 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 a sufficient amount of hard mast may have been available in the dry habitat (pine with some hardwoods) during the winter. If squirrels in our study area did not scatterhoard food during winter, due to loss from flooding, they may not survive a mast failure year when hard mast is not available on the ground through winter. Thompson and Thompson (1980) reported another population of eastern gray squirrels that still exhibited scatterhoarding behavior even though hard mast was on the ground through winter and recovered stored mast only made up 27.1% of the hard mast eaten during winter. Thus, even though our population only had access to 38% of acorns it stored during the dry season, such supplies may be enough to provide the benefits necessary for scatterhoarding behavior to persist in the population. Further, little information exists on how long seeds stay sound and edible once stored underground. Perhaps scatterhoarding in this population is a strategy used as a fallback during years of mast failure, when mast will not continue to be available throughout the winter, and during good mast years, the behavior simply provides a supplement food to other available sources of hard mast.

For scatterhoarding to exist in a population, the behavior should garner some benefit, typically believed to be in the form of winter survival or breeding-season body condition (Andersson and Krebs 1978; Morrison et al. 2009; Sechley et al. 2014). We did not record any measurements on body condition of individuals as we could not reliably re-trap squirrels before and after the scatterhoarding recovery season. Perhaps fitness of our squirrels was impacted by better body condition going into the spring breeding season in those animals that were able to rely on stored food rather than heavily relying on supplemental foods (Wilson et al. 2020). Alternatively, scatterhoarding behavior may be genetically ingrained in the species based on seasonal changes in photoperiod or temperature (Barry 1976) and the costs of this behavior may not be as extensive as previously assumed (Lichti et al. 2017). However, preliminary analysis from research con-

Can. J. Zool. **101:** 743–753 (2023) | dx.doi.org/10.1139/cjz-2023-0024

ducted by two of our authors suggests that it is not the case: geographic variations in climate can impact investment in scatterhoarding behavior in eastern gray squirrel populations across the United States (unpublished data, Wilson, TDS). 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 balance the major costs of scatterhoarding with benefits in these environments is important to understanding how scatterhoarding is maintained in these populations.

Acknowledgements

This research was made possible through funding from the Alabama Department of Conservation and Natural Resources. We thank the Santos Lab at Auburn University for generously allowing us to use their lab and supplies for DNA analyses. Several technicians, undergraduate researchers, and local hunters assisted with data collection for this project. We are very grateful for the assistance of J. Petty in collecting many of the squirrels used for diet analysis and N. Sandoval for her willingness to help in the field whenever needed.

Article information

History dates

Received: 3 February 2023
Accepted: 1 April 2023
Accepted manuscript online: 23 May 2023
Version of record online: 13 June 2023

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request. Thesis available at http://hdl.handle.net/10415/6231.

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Competing interests

The authors declare there are no competing interests.

Funding information

This research was supported by the Alabama Department of Conservation and Natural Resources (account No. 363922 - ADCNR-WILD PIGS-15; 363947 - ADCNR-WILD PIGS-16; 363970 - ADCNR-WILD PIGS-17).

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