Fall and Winter Diets of Eastern Gray Squirrels in a Seasonally Flooded Ecosystem in Alabama

Sarah B. Wilson[1,*], Todd D. Steury[1], Robert A. Gitzen[1], and Stephen S. Ditchkoff[1]

Abstract - As scatterhoarders, *Sciurus carolinensis* (Eastern Gray Squirrel) usually rely on food they buried during fall to survive cold winter months. However, the range of this species includes areas of the southeastern United States where winter flooding commonly restricts access to buried food during the recovery season. In this study, we investigated the effects of winter flooding on the diet of Eastern Gray Squirrels in bottomland hardwood forests of west-central Alabama. We examined the diet of 42 Eastern Gray Squirrels through DNA analysis of stomach contents collected during fall (September–November) 2016 and winter (December–February) 2015–2016, 2016–2017, and 2018–2019. Eastern Gray Squirrels ate 21 different types of plants, with 6 principal foods (>1% of any squirrel's stomach contents) during fall and 12 principal foods during winter. Throughout both seasons, Juglandaceae (walnut) and *Quercus* spp. (oak) were the most important foods and together made up 94.1% of the fall diet and an average of 78.6% of the winter diet. In contrast to other studies, we found more varied diets during winter (12 primary foods eaten) than fall (6). Additionally, a majority of the plant types consumed during winter at our study area were not hard-mast plants, and many had not been previously recorded as part of the diet of the Eastern Gray Squirrel. Our results suggest Eastern Gray Squirrels cope with reduced availability of scatterhoarded food due to winter flooding by increasing the diversity of foods they eat to include more herbaceous plants.

Introduction

Hard mast is widely accepted to be the critical component of the winter diet of *Sciurus carolinensis* Gmelin (Eastern Gray Squirrel; Feldhamer et al. 2003, Vander Wall 1990). Late spring through late summer, Eastern Gray Squirrels are opportunistic foragers, eating tree buds, flowers, leaves, and most other vegetative matter available (Nixon et al. 1968, Thompson and Thompson 1980). However, during the fall and winter months, when this vegetative growth is absent, Eastern Gray Squirrels appear to depend on hard mast as the staple of their diet (Brown and Yeager 1945, Goodrum 1940, Korschgen 1981, Nixon et al. 1968, Spritzer 2002). Eastern Gray Squirrels scatterhoard hard mast during fall (Morris 1962), presumably so that they can rely on this stored food to survive the winter months (Korschgen 1981, Nixon et al. 1968, Thompson and Thompson 1980). However, the degree of reliance on scatterhoarded hard mast over winter is poorly understood, especially in some regions. Previous studies describing Eastern Gray Squirrel diet in hardwood stands have been conducted in Ontario (Thompson and Thompson 1980), Illinois (Brown and Yeager 1945), Missouri (Korschgen 1981), Ohio (Nixon et al. 1968),

[1]School of Forestry and Wildlife Sciences, Auburn University; 602 Duncan Drive, Auburn, AL 36849. [*]Corresponding author - swilso8@clemson.edu.

Manuscript Editor: Karen Powers

Texas (Goodrum 1940), and Florida (Spritzer 2002), leaving much of the range of the species in the southeastern United States unstudied. Given the longer growing season, warmer winter temperatures, and thus increased availability of vegetation over winter in the Southeast, hard mast may not be as critical for winter survival of Eastern Gray Squirrels in that region.

In addition to a potentially decreased need to rely on hard mast over winter, Eastern Gray Squirrels in many areas in the southeastern United States—such as in bottomland hardwood stands—must cope with seasonal flooding as well as flooding due to extreme weather events that may cause stored hard mast to be unavailable. Eastern Gray Squirrels in many regions usually depend on their ability to find hard mast on the ground during winter (Brown and Yeager 1945, Nixon et al. 1968, Spritzer 2002). Yet in a bottomland forest in Alabama, for example, Eastern Gray Squirrels buried 72% of radio-tagged acorns in areas that were unavailable for recovery during winter due to flooding, and no radio-tagged acorns were stored above ground (Wilson 2018). Presumably, Eastern Gray Squirrels compensate for decreased availability of stored hard mast during flooding by either shifting their diet to eat food items other than hard mast or by supplementing their diet with smaller amounts of many foods that may be available during winter. Thus, Eastern Gray Squirrels living in southeastern floodplains will probably have different fall and winter diets than those living in drier hardwood stands with full access to their scatterhoarded food.

In this study, we investigated the composition of the diet of Eastern Gray Squirrels in a seasonally flooded, bottomland hardwood swamp in central Alabama. We assessed reliance on stored hard mast in flooded areas, in contrast to previous studies of diets of Eastern Gray Squirrels from dry hardwood or *Pinus* spp. (pine) stands (Brown and Yeager 1945, Goodrum 1940, Korschgen 1981, Nixon et al. 1968, Spritzer 2002). Additionally, this study was the first to use genetic methods to determine foods eaten by Eastern Gray Squirrels, allowing a more comprehensive look into the diet of this species.

Field-site Description

At the time of this study, Lowndes Wildlife Management Area (LWMA; 32.362973°N, 86.746934°W) consisted of 6800 ha of forested wetlands (~85%) and upland habitat (~15%) (Mitigation Implementation Plan for LWMA; US Army Corps of Engineers, Lowndesboro, AL, unpubl. data) in Lowndes County, AL, in the southeastern floodplains and low terraces ecoregion (Griffith et al. 2001). Habitat types included immature planted *Quercus* spp. (oak), natural and planted pine, food plots for game species, and bottomland hardwood swamps of various ages. Eastern Gray Squirrels were mainly found in the bottomland hardwood stands that flooded seasonally due to proximity to the Alabama River. Dominant canopy species in these bottomland hardwood areas included *Quercus nigra* L. (Water Oak), *Quercus phellos* L. (Willow Oak), *Quercus rubra* Michx. (Southern Red Oak), *Liquidambar styraciflua* L. (Sweetgum), and *Pinus taeda* L. (Loblolly Pine) with *Carpinus caroliniana* Walter (Musclewood) and *Acer rubrum* L. (Red Maple) present in the understory. The fall mast crops of 2015 and 2016 were large enough that mast remained available on the ground throughout fall and winter, despite the presence of many mast-eating species such as *Maleagris gallopavo* L. (Wild Turkey), *Odocoileus virginianus* Zimmerman (White-tailed Deer), *Sus scrofa* L. (Wild Pig), *Sciurus niger* L. (Fox Squirrel), and Eastern Gray Squirrel (SB.. Wilson, unpubl. data). We did not observe the 2017 and 2018 mast crops.

Large portions of the study area exhibited seasonal flooding each winter from the adjacent Alabama River and associated wetlands. Previous research at LWMA documented extensive flooding with the lowest water level (dry floodplains; 23.81-m flood stage at nearby Robert F Henry Lock and Dam) recorded in October and the highest water level (38.71-m flood stage) recorded in early January (USGS 2019, Wilson 2018). Mean temperatures are 8° C in January and 27° C in July, with a mean precipitation of 3.38 cm during the fall dry season and 16.05 cm during the winter flooded season (NCEI 2020).

Methods

Data collection

Eastern Gray Squirrels were donated to the study by local hunters during the squirrel-hunting season (September 12–March 7; ADCNR 2020) from bottomland hardwood areas prone to flooding on LWMA during winter 2015–2016, fall 2016, winter 2016–2017, and winter 2018–2019. We categorized September–November as fall and December–February as winter. During necropsies, we weighed intact stomachs then counted and visually estimated the proportion of each distinct food item inside the stomach to the nearest 10%, based on unique colors and textures of food items (Korschgen 1981). For a majority of the food items, we were able to tell which food items were the same across stomachs, but we were not able to distinguish between different parts of the plant. Next, we collected samples of each unique, distinct food item in the stomachs and stored the samples in vials of 95% ethanol in a freezer at -18 °C until further analysis.

We sent all food samples to the company Jonah Ventures (Boulder, CO) for genetic analysis using polymerase chain reaction (PCR). We chose to use this technique because it has previously been shown to be a very powerful tool for determining food items in the diet (Dell'Agnello et al. 2019). Extractions of DNA from multiple samples of each food item were conducted using a Qiagen DNeasy PowerSoil HTP 96 Kit (Qiagon, Hilden, Germany). Jonah Ventures used trnL primers for the amplification of DNA samples with PCR. The forward primer was trnL-c: CGAAATCGGTAGACGCTACG; while the reverse primer was trnL-h: CCATTGAGTCTCTGCACCTATC (Taberlet et al. 2007). Each 25-µL PCR reaction was mixed according to the Promega PCR Master Mix specifications (Promega catalog # M5133, Madison, WI), which included 0.4 µM of each primer and 1 µl of gDNA. DNA was PCR amplified using the following conditions: initial denaturation at 94 °C for 3 minutes, followed by 40 cycles of 30 seconds at 94 °C, 30 seconds at 55 °C, and 1 minute at 72 °C, and then a final elongation at 72 °C for 10 minutes. Amplified samples were sent to the Texas A&M Sequencing Center

(College Station, TX) for sequencing. Sequences were then identified down to the lowest possible taxon using the Usearch v11.0.667 (Edgar 2010). We labeled any food items that could not be identified to at least family as "unknown".

Analysis

We categorized food items as principal (>1% of any Eastern Gray Squirrel's stomach contents), secondary (between 0.5% and 0.9%), and trace (<0.5%) components of fall and winter diets (Korschgen 1981). We also used the aggregate percentage method to account for the amount of each food eaten by Eastern Gray Squirrels (Martin et al. 1946). We used saturation curves to determine if we had adequately sampled a sufficient number of Eastern Gray Squirrels in each season to capture every primary item in the diet. Specifically, we randomly sampled 1 squirrel from our pool of squirrels and enumerated the number of primary items in that squirrel's diet. We then randomly sampled another squirrel from our pool of remaining animals and enumerated the total number of primary items in the diet of both squirrels. We continued this process of selecting a remaining squirrel from the pool and enumerating the total number of primary items in the diet of all selected squirrels until every squirrel was selected from the pool. We then fit the Michaelis–Menton equation for enzyme kinetics to the data:

$$Y = aX / b + X,$$

where Y was the total number of primary items in the diet of the selected squirrels, X was the number of selected squirrels, and a was the asymptotic number of primary items in the diet. The coefficient b determined how quickly primary items are added to the count as the number of squirrels selected increased. We used the nls function in R (version 3.6.1; R Foundation, Vienna, Austria) to fit the function to the data. We repeated the process of randomly selecting squirrels, building the data, and fitting the model 10,000 times to generate confidence intervals on the value of a. We determined what proportion of a, the true number of primary items in the diet, we had achieved from our sample.

Results

We collected 44 Eastern Gray Squirrels from bottomland hardwoods during winter 2015–2016 (n = 12), fall 2016 (n = 16), winter 2016–2017 (n = 11), and winter 2018–2019 (n = 5). Two specimens had completely empty stomachs (1 in winter 2015–2016 and 1 in fall 2016) and were excluded from analyses. Of the remaining 42 specimens, we found an average of 1.67 ± 0.82 (mean ± SD) visually distinct food items in each stomach, and stomachs weighed 15.79 ± 12.42 g. We visually identified 23 unique food items.

Sequencing results indicated that Eastern Gray Squirrels consumed 21 types of plants (Table 1), less than the number of unique food items we visually identified, and that each Eastern Gray Squirrel ate 3.21 ± 1.95 (mean ± SD) plant types, a hihger average than we detected through visual estimations. Walnut and oak were the major food items throughout both seasons, although Eastern Gray Squirrels ate much more walnut during fall and increased their consumption of oak during winter (Table 2). Every Eastern Gray Squirrel we collected ate walnut (*n* = 13), oak (*n* = 11), or both (*n* = 18) in primary amounts. When Eastern Gray Squirrels consumed only 1 of these types of food, walnut and oak accounted for 97.69 ± 8.32% and 64.70 ± 33.04% of their stomach contents, respectively. Eastern Gray Squirrels that had eaten both oak and walnut tended to have a greater proportion of walnut (55.36 ± 32.08%) than oak (29.66 ± 26.49%) in their stomachs. All Eastern Gray Squirrels that only consumed walnut did not eat other food items, but 67% of the squirrels that only ate oak had supplemented their diet with *Fagus grandifolia* Ehrh. (American Beech), Ulmaceae (Elm family), *Stellaria* sp. (chickweed), or *Campsis radicans* Seem. (Trumpet Vine). Five Eastern Gray Squirrels ate less than 50% of combined walnut and oak, instead eating large amounts of elm, pine, or American Beech. When eating both walnut and oak, 89% of Eastern Gray Squirrels ate 43.02 ± 35.62 % (mean ± SD) more walnut than oak.

Table 1. Foods eaten by *Sciurus carolinensis* (Eastern Gray Squirrel) at Lowndes Wildlife Management Area in Alabama, expressed as the percentage of squirrels that had eaten each type of food. Data were collected in 2015–2017 and 2019.

Food item	Winter 2015–2016 (*n* = 11)	Fall 2016 (*n* = 15)	Winter 2016–2017 (*n* = 11)	Winter 2019 (*n* = 5)	All (*n* = 42)
Juglandaceae (walnut)	54.5	100.0	90.9	40.0	78.6
Quercus spp. (oak)	100.0	46.7	72.7	100.0	73.8
Acer spp. (maple)	45.5	26.7	54.5	-	35.7
Ulmaceae (elm)	27.3	6.7	27.3	80.0	26.2
Pinus spp. (pine)	9.1	26.7	9.1	40.0	19.0
Fagus grandifolia (American Beech)	63.6	-	9.1	-	19.0
Fagaceae (beech and oak)[C]	54.5	-	9.1	-	16.7
Myristicaceae or Order Dicranales (moss)[CD]	9.1	-	9.1	40.0	9.5
Poaceae (grass)	9.1	6.7	9.1	-	7.1
Asteraceae (aster)[BD]	9.1	-	-	20.0	4.8
Vitis rotundifolia (Muscadine)	-	13.3	-	-	4.8
Unknown plant[AC]	-	6.7	9.1	-	4.8
Juniperus sp. (juniper)[CD]	-	-	-	40.0	4.8
Stellaria spp. (chickweed)[D]	9.1	-	-	-	2.4
Nothoscordum bivalve (Britton Crowpoison)[D]	-	-	9.1	-	2.4
Proboscidea louisianica (Ram's Horn)[D]	-	-	9.1	-	2.4
Melia azedarach (Chinaberry)[CD]	9.1	-	-	-	2.4
Campsis radicans (Trumpet Vine)[D]	-	-	9.1	-	2.4
Pisum sativum (Garden Pea)[CD]	9.1	-	-	-	2.4
Aesculus sp. (buckeye)[C]	9.1	-	-	-	2.4
Vicia tetrasperma (Lentil Vetch)[CD]	9.1	-	-	-	2.4

[A]Unknown included foods that were not identified to family or were identified as a plant that is not found in the southeastern United States.
[B]Food that were considered secondary components to the diet and were between <1.0% and >0.5% of any squirrel's stomach contents.
[C]Foods that only made up trace amounts (<0.5%) of any squirrel's stomach contents.
[D]Foods that were previously undocumented in the Eastern Gray Squirrel diet.

Our saturation curves indicated the true fall diet of our Eastern Gray Squirrels likely included 8.12 (median; 95% CI = 4.70–61.47) primary food items, while the winter diet had 12.59 (median; 95% CI = 7.85–26.76) primary food items. A Mann–Whitney U test indicated that the estimated asymptotes were significantly different ($U = 7.63 \times 10^7$, $P < 0.0001$). *Vitis rotundifolia* Michx. (Muscadine), consumed by 1 squirrel in primary amounts and 1 squirrel in trace amounts, was the only species that was eaten during fall but not winter, whereas several foods were only eaten during 1 winter season (Table 1). We identified 12 principal, 1 secondary, and 8 trace components of the winter diet (Table 1). Primary foods eaten in winter by more than 1 Eastern Gray Squirrel in the average order of importance included: oak, walnut, elm, American Beech, and *Acer* spp. (maple) (Table 2). Poaceae (grass), chickweed, *Nothoscordum bivalve* (L.) (Britton Crowpoison), *Proboscidea louisianica* (Mill.) Thell. (Rams Horn), and Trumpet Vine were all consumed in primary amounts by just 1 Eastern Gray Squirrel each. The only secondary addition to the winter diet was Asteraceae (aster). We also identified 7 primary, 0 secondary, and 1 trace components of the fall diet (Table 1). Primary foods eaten by more than 1 Eastern Gray Squirrel during fall in the order of importance included: walnut, oak, and pine (Table 2).

We documented 10 plants eaten by Eastern Gray Squirrels that have not been mentioned by previous studies: Britton Crowpoison, aster, *Juniperus* sp. (Juniper), Myristicaceae or Order Dicranales (Moss), chickweed, Ram's Horn, *Melia azedarach* L. (Chinaberry), Trumpet Vine, *Pisum sativum* L. (Garden Pea), and *Vicia*

Table 2. Foods eaten in primary amounts by *Sciurus carolinensis* (Eastern Gray Squirrel) at Lowndes Wildlife Management Area in Alabama, expressed as the aggregate percentage of each food item making up the diet. Data were collected in 2015–2017 and 2019. Only food items that made up >1% of foods eaten by any individual in this population of squirrels were included in this table. Other foods were only eaten in secondary or trace amounts by very few squirrels and were not considered important parts of the diet.

Food item	Winter 2015–2016 (*n* = 11)	Fall 2016 (*n* = 15)	Winter 2016–2017 (*n* = 11)	Winter 2019 (*n* = 5)	All (*n* = 42)
Juglandaceae (walnut)	19.33	84.56	67.72	19.25	55.29
Quercus spp. (oak)	56.37	9.52	20.03	52.49	29.66
Ulmaceae (elm)	0.08	0.08	2.72	28.10	4.11
Fagus grandifolia (American Beech)	14.21	-	0.84	-	3.94
Acer spp. (maple)	2.37	0.68	3.66	-	1.82
Pinus spp. (pine)	0.03	4.43	-[A]	0.03	1.59
Stellaria spp. (chickweed)	2.80	-	-	-	0.73
Poaceae (grass)	-	-[A]	2.52	-	0.66
Vitis rotundifolia (Muscadine)	-	0.65	-	-	0.23
Nothoscordum bivalve (Britton Crowpoison)	-	-	0.45	-	0.12
Proboscidea louisianica (Ram's Horn)	-	-	0.10	-	0.03
Campsis radicans (Trumpet Vine)	-	-	0.10	-	0.02

[A]Eaten by 1 squirrel in trace amounts that contribute <1% to the diet.

tetrasperma (L.) Schreb. (Lentil Vetch). We were unable to identify which parts of these plants were eaten. Chickweed was a primary food (30.8% of stomach contents) for the 1 Eastern Gray Squirrel that ate it, while Britton Crowpoison was a secondary food for a second squirrel (4.9%) and Ram's Horn (1.1%) was a secondary food for a third squirrel. All other newly documented food items were only found in trace amounts (Table 1).

Discussion

Our results agreed with previous studies concerning the importance of hard mast species in the winter, as oak and walnut were the most important food sources for Eastern Gray Squirrels in our study area during both fall and winter (Korschgen 1981, Nixon et al. 1968, Spritzer 2002, Thompson and Thompson 1980). However, we found more Eastern Gray Squirrels ate walnut during fall (100% in our study, 56% in Nixon et al. [1968]) and there was a much greater proportion of hickory in the fall diet than previous studies (84.5% in our study, 22% in Korschgen [1981], 16.86% in Thompson and Thompson [1980], and 0% in Spritzer [2002]). Muscadine was the only food we found eaten during fall but not winter, which is in agreement with previous studies, likely because this plant fruits during fall. (Brown and Yeager 1945, Goodrum 1940, Korschgen 1981). Pine was another plant group that was eaten by many of the Eastern Gray Squirrels in our study during fall, as documented by other studies (Spritzer 2002, Thompson and Thompson 1980), but we found pine was also eaten in trace amounts during winter. Overall, these Eastern Gray Squirrels within bottomland hardwood forests were eating many of the same things as other populations reported in previous studies, but some plants occurred in the diet during different times of the year for the LWMA.

We observed some differences from other studies that could be due to flooding in our study area. First, although walnut and oak were the major food items for Eastern Gray Squirrels, the squirrels in our study consumed a greater diversity of food items during winter than previously reported (60% of foods were not hard mast in this study, 50% in Korschgen [1981] via microscopic examination of stomach contents, 37.5% in Thompson and Thompson [1980] via observations, and 0% in Nixon et al. [1968] via microscopic examination of stomach contents; in all cases items were counted by family when compared to our study). Flooding in our study area rendered over 72% of scatterhoarded acorns unavailable during the recovery season, and squirrels did not move out of flooded habitat during the flooded season (Wilson 2018), so the squirrels likely did not have access to the same amount of cached hard mast during winter as other studied populations. Second, we also found a greater variety of plants were eaten during winter compared to fall, while a more varied fall diet has previously been reported for Eastern Gray Squirrels (12 primary items in winter vs. 6 in fall in this study, 11 vs. 17 in Nixon et al. [1968], 5 vs. 12 in Korschgen [1981], 8 vs. 9 in Thompson and Thompson [1980], and 1 vs 4 in Spritzer [2002]). Once winter flooding started in November, most scatterhoarded seeds as well as mast still on the ground became covered in water and inaccessible to the squirrels until at least February (Wilson 2018). Though the effects of flooding on scatterhoarding were only studied in 1 small area by Wilson (2018), the large decrease in dry land due to flooding was consistent with flooding seen throughout the rest of the swampy areas of LWMA where Eastern Gray Squirrels were found (S.B. Wilson, pers. observ.). Thus, Eastern Gray Squirrels appeared to have coped with flood conditions by varying their winter diet.

Due to our use of genetic analyses for identification of food items in the stomachs of Eastern Gray Squirrels, we were not able to determine what part of the plant was being eaten. We were also unable to observe squirrel consumption of food items or foraging behavior. Though we found Eastern Gray Squirrels during winter had consumed parts of plants that produced hard mast, Eastern Gray Squirrels could have been eating new growth rather than stored mast due to the effects of extreme flooding on their ability to access buried food (Wilson 2018). The consumption of vegetative growth of mast trees has been recorded by other studies (Brown and Yeager 1945, Nixon et al. 1968). Most of our winter collections were done during February when spring growth had already started in the study area (S.B. Wilson, unpubl. data). We had defined winter months based on periods used by other studies (Korschgen 1981), but our study may have actually captured the early spring diet of Eastern Gray Squirrels in this flooded area due to our warmer climate with short winters, and in that case samples from December or January would be needed to determine a true winter diet. Additionally, other plant types eaten during February, such as chickweed and aster, were observed as leafy material in the stomach, indicating the Eastern Gray Squirrels were indeed eating vegetative growth.

Eastern Gray Squirrels did have access to limited amounts of dry ground or small islands throughout the floodplains during the flooded season to recover and eat scatterhoarded hard mast. However, in concurrent research at LWMA, Eastern Gray Squirrels scatterhoarded 72% of radio-tagged acorns in areas that would later flood and none of the acorns were cached in trees, indicating food hoarders in the study area do not select for higher, dry locations when scatterhoarding (Wilson 2018). As a result, Eastern Gray Squirrels in our study area only had access to about 30% of their scatterhoarded mast during the flood season (Wilson 2018). If the large portions of walnut and oak we found in the diet were indeed hard mast, Eastern Gray Squirrels may have had difficulty acquiring hard mast during the flood season, likely resulting in an increase in foraging activity and predation risk. Estimated winter survival for LWMA during 2015 and 2016 was 23%, with 65% of mortalities due to predation (Wilson et al. 2019). The diversity of food items that supplemented the diet also supports the idea that Eastern Gray Squirrels were not able to find enough hard mast to eat.

Our study shows that Eastern Gray Squirrels may cope with flooding by having a more varied winter diet, including a larger number of non-hard-mast foods in their diet than previously described. Walnut was the most important food for the fall diet, while the winter diet contained more oak supplemented with other plants. Our findings suggest Eastern Gray Squirrels in warm climates may cope with environmental changes affecting their winter food by supplementing their scatterhoarded food with herbaceous plants. To confirm the widespread applicability of such a conclusion, there is a need for larger-scale research across the Southeast to assess changes in fall and winter reliance on mast as a function of gradients in temperature (e.g., latitude and large-scale elevation) and variation in mast availability.

Acknowledgments

This research was in part made possible through funding from the Alabama Department of Conservation and Natural Resources – Division of Wildlife and freshwater Fisheries with Federal Aid funds from the Wildlife and Sport Fish Restoration Program. We also thank the local hunters for graciously donating Eastern Gray Squirrels for this project.

Literature Cited

Alabama Department of Conservation and Natural Resources [ADCNR]. 2020. Squirrel season. Available online at https://www.outdooralabama.com/seasons-and-bag-limits/squirrel-season. Accessed 24 September 2020.

Brown, L.G., and L.E. Yeager. 1945. Fox Squirrels and Gray Squirrels in Illinois. Natural History Survey Division 23:454–460.

Dell'Agnello, F., C. Natali, S. Bertolino, L. Fattorini, E. Fedele, B. Foggi, M. Martini, C. Pisani, F. Riga, A. Sgarlata, C. Ciofi, and M. Zaccaroni. 2019. Assessment of seasonal variation of diet composition in rodents using DNA barcoding and real-time PCR. Scientific Reports 14124:1-11.

Edgar, R.C. 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26:2460–2461.

Feldhamer, G.A., B.C. Thompson, and J.A. Chapman. 2003. Wild Mammals of North America. John Hopkins University Press, Baltimore, MD. 1232 pp.

Goodrum, P.D. 1940. A population study of the Gray Squirrel, *Sciurus carolinensis*, in eastern Texas. Special technical report. Texas Agricultural Experiement Station, College Station, TX. 34 pp.

Griffith, G.E., J.M. Omernik, J.A. Comstock, S. Lawrence, G. Martin, A. Goddard, V.J. Hulcher, and T. Foster. 2001. Ecoregions of Alabama and Georgia. [Color poster with map, descriptive text, summary tables, and photographs; map scale 1:1,700,000.] US Geological Survey, Reston, VA.

Korschgen, L.J. 1981. Foods of Fox and Gray Squirrels in Missouri. Journal of Wildlife Management 45:260–266.

Martin, A.C., R.H. Gensch, and C.P. Brown. 1946. Alternative methods in upland gamebird food analysis. Journal of Wildlife Management 10: 8-12.

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

National Centers for Environmental Information (NCEI). 2020. Global summary of the month for Selma, Alabama. Available online at https://www.ncdc.noaa.gov/cdo-web/search. Accessed 08 Jan 2020.

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

Spritzer, M.D. 2002. Diet, microhabitat use, and seasonal activity patterns of Gray Squirrels (*Sciurus carolinensis*) in hammock and upland pine forest. American Midland Naturalist 148:271–281.

Taberlet P, E. Coissac, F. Pompanon, L. Gielly, C. Miquel, A. Valentini, T. Vermat, G. Corthier , C. Brochmann, and E. Willerslev. 2007. Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. Nucleic Acids Research 35:e14.

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

United States Geological Service (USGS). 2019. USGS 02421351 Alabama River BL Robert F Henry L&D near Benton, AL. Available online at https://nwis.waterdata.usgs.gov/nwis/uv?format=gif_default&period=&begin_date=2015-06-01&end_date=2019-02-23&cb_00065=on&site_no=02421351. Accessed 09 Sept 2020.

Vander Wall, S.B. 1990. Food Hoarding in Animals. University of Chicago Press, Chicago, IL. 453 pp.

Wilson, S.B. 2018. The ecology of scatterhoarding in a flooded ecosystem. M.Sc. Thesis. Auburn University, Auburn, AL. 90 pp.

Wilson, S.B., S.S. Ditchkoff, R.A. Gitzen, T.D. Steury. 2019. Eastern Gray Squirrel survival in a seasonally flooded hunted bottomland forest ecosystem. Journal of Southeastern Association of Fish and Wildlife Agencies. 6:161–165.