Eastern Gray Squirrel Survival in a Seasonally-Flooded Hunted Bottomland Forest Ecosystem

Sarah B. Wilson, *School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Dr. Auburn University, AL 36849*

Stephen S. Ditchkoff, *School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Dr. Auburn University, AL 36849*

Robert A. Gitzen, *School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Dr. Auburn University, AL 36849*

Todd D. Steury, *School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Dr. Auburn University, AL 36849*

Abstract: Though the eastern gray squirrel (*Sciurus carolinensis*) is an important game species throughout its range in North America, little is known about environmental factors that may affect 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 annual flooding conditions from November through the following September. Our 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 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 lowest during winter (0.23; 0.11–0.50, 95% CL). We found squirrels were more likely to die during the flooded winter 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.

Key words: flooding, mortality, predation, *Sciurus*

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To understand the dynamics of wild animal populations and to manage them appropriately, various demographic rates of the population, including reproduction, recruitment, and survival, need to be known. Theory suggests that the growth rate of populations is most influenced by changes in survival (Caswell 2001). Previous studies have confirmed that population dynamics are heavily influenced by survival 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). Successful management of wildlife populations requires a thorough understanding of animal survival and the factors that influence it.

Despite the eastern gray squirrel (*Sciurus carolinensis*) 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 their survival in the southern United States or about factors that influence survival rates. Although studies of predation rates are lacking, research has examined the annual survival of this species in four states (North Carolina, Ohio, Virginia, Minnesota) and one Canadian province (Ontario), with estimates of annual survival ranging from 0.20 to 0.58 (Table 1; Longley 1963, Mosby 1969, Barkalow et al. 1970, Nixon et al. 1975, Thompson and Thompson 1980). These rates are relatively low and variable compared to other tree squirrels (fox squirrel [*Sciurus niger*], 0.69, Conner 2001 and 0.49, Prince et al. 2014; Abert's squirrel [*Sciurus aberti*], 0.78, Dodd et al. 2003). Previous work also examined a few factors that influenced survival, finding some evidence for effects of sex, whether or not the species was hunted, and variation in food supply (Mosby 1969, Barkalow et al. 1970, Nixon et al. 1975). While harvest mortality is generally assumed to be compensatory in eastern gray squirrel populations (Connelly et al. 2012), hunting mortality may be more homogeneous between sexes than predation mortality. Greater movement rates and home range sizes of males (Doebel and McGinnes 1974) may expose them more to opportunistic predators, whereas human hunters also focus their attention on less active squirrels in the canopy. However, previous eastern gray squirrel survival analyses used capture-recapture methods, failing to distinguish between dispersal and mortality and, therefore, were unable to confirm death (and its cause) for a true description of survival (Longley 1963, Mosby 1969, Barkalow et al. 1970, Nixon et al. 1975, Thompson and Thompson 1980).

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), and the cause of this variation could change depending on the climate. Eastern gray squirrels scatter hoard hard mast during the fall for nutrition needed to survive winter months, when food typically is scarce (Goodrum

Table 1. Previously recorded annual survival of the eastern gray squirrel (*Sciurus carolinensis*) from eastern North America, 1963–2018.

	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 et al. 1970	North Carolina	0.52	0.44	0.59
	Longley 1963	Minnesota	0.48	–	–
	Thompson 1978	Ontario	0.46	–	–

1940, Brown and Yeager 1945, Nixon et al. 1968, Thompson and Thompson 1980, Korschgen 1981, Spritzer 2002). Populations of this species experience greater survival rates during years of good mast production (Barkalow et al. 1970, Nixon et al. 1975). However, in southeastern bottomland hardwood types, winter flooding could reduce the amount of scatter hoarded food available during the winter and result in lower survival rates (Nixon and McClain 1969, Barkalow 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 limited information about annual survival or seasonal variation in survival in eastern gray squirrel populations inhabiting seasonally flooded areas in the Southeast.

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 lowest 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

Our 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 bottomland hardwood swamp in central Alabama. Management at LWMA focuses on improving habitat conditions for populations of game species such as white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), mourning dove (*Zenaida macroura*), and various waterfowl. Annual hunting season for gray and fox squirrels occurs mid-September through the first week of March. Annual precipitation is 135 cm with mean temperatures of 8° C in January and 27° C 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 consisted of a mix of willow oak (*Quercus phellos*), southern red oak (*Quercus falcata*), water oak (*Quercus nigra*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*) in the overstory and an understory of red maple (*Acer rubrum*) and American hornbeam (*Carpinus caroliniana*). The 2 ha of pine habitat and small portions of the hardwood habitat immediately bordering this pine habitat remained dry year round. Large portions of the core study area (86.19% or 12.93 ha) exhibited seasonal flooding each winter from the adjacent Alabama River and associated wetlands.

Methods

We trapped eastern gray squirrels using Tomahawk live traps (Collapsible Squirrel Trap Model 202; Hazelhurst, Wisconsin) baited with corn July 2015–July 2016. 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 two uniquely colored ear tags (Brodin 1994, Steele et al. 2011). Each squirrel was anesthetized with Isoflurane before being fitted with a very high frequency (VHF) radio-telemetry collar (Advanced Telemetry Systems M1640, Isanti, Minnesota). 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 occurred under Alabama Department of Conservation and Natural Resources permit 2015024640868680 before data collection began.

Each collared squirrel was located by homing on the animal using radio telemetry during daylight hours 1–3 times per week from the date 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. Squirrels were assumed to be alive if a signal was determined to be in a tree. If a squirrel was relocated to the same tree two times in a row, the next relocation of the squirrel was conducted at a different time of day in an attempt to locate the squirrel while it was active. Using this method, all squirrels (dead or alive) were found within three attempts to relocate them. If a squirrel was found dead, we attempted to identify the cause of mortality as hunter kill, predation, or unknown. Mortalities were attributed to hunters if the squirrel was returned or reported by the hunter. No previously collared 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, we made the assumption that the animal was taken by a hunter, whereas if a collar was found closed (nut still in place) with no remains, it was recorded as predation. Death was also recorded as predation if the remains were not scattered haphazardly, there were signs of mortality (collar found with blood, large amounts of squirrel fur, etc.), there was damage to the carcass, or there were signs of a predator (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). Predation was classified as mammalian if the squirrel's body was cached (under leaf litter or in a burrow), few remains were left or remains were scattered in piles ≤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, we created a flood polygon of the water level in the core study area after each major rain event November 2016–March 2017. Flood levels were highest during January 2017 and 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 our observations of conditions at the study area. We determined dry season to be September–October 2015 and September–November 2016. Duration of the flood season and flooding levels at the site were similar between the two years in this study, based on personal observations in the field.

Data Analysis

To estimate survival, we calculated Kaplan-Meier survival estimates 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). Survival calculations for a given season only included those squirrels alive at the start of that season (e.g., summer survival included only those alive on 31 May). 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. To assess differences in survival between seasons (summer, 1 June–31 August; fall, 1 September–30 November; winter, 1 December–28 February; and spring, 1 March–31 May) and sexes, we used Cox proportional hazard regression (Hosmer et al. 2008). We modeled the effect of flooding by creating a continuous time varying covariate with time partitioned 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 our study, 47 eastern gray squirrels were collared, including 27 males and 20 females. The fate of eight of these squirrels was unknown because the radio-telemetry signal was lost. Thirty-four squirrels were confirmed dead (two by avian predators, 10 by mammalian predators, 10 by unknown predators, nine by hunters, and three unknown deaths) and five 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 statistically significant ($P = 0.16$). Although we had data for seven 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 flooded winter (2.28–25.96, 95% CL) as the dry fall ($P = 0.001$). 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 ($P = 0.001$).

Discussion

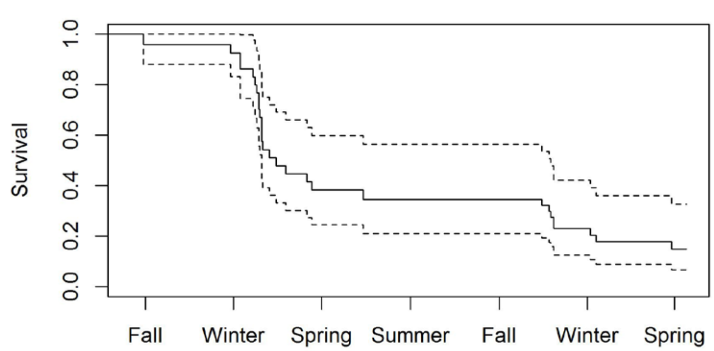

Figure 1. Survival of 35 radio-collared eastern gray squirrels (*Sciurus carolinensis*) assessed from 24 July 2015–17 April 2017 on Lowndes Wildlife Management Area, Alabama. Dashed lines indicate 95% confidence limits.

Our survival estimate of 0.25 for this hunted population of eastern gray squirrels on LWMA in Alabama was similar to other hunted populations in more northern upland habitats with higher hunting pressure than LWMA. Survival of hunted populations is more varied than unhunted populations in colder climates with two studies estimating annual survival to be less than 0.30 (0.27, Minnesota, Longley 1963; 0.20, Illinois, Nixon et al. 1975), while a third study found survival to be 0.52 (Virginia, Mosby 1969). In areas where hunting was prohibited, only four studies of eastern gray squirrel survival have been conducted, with estimated annual survival rates ranging from 0.46 to 0.58 (Minnesota, Longley 1963; Virgina, Mosby 1969; North Carolina, Barkalow et al. 1970; Ontario, 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 mortalities, at the upper end of the contribution of predation to total mortality in comparison to that of fox squirrel (*Sciurus niger*, 64.3%; Mccleery et al. 2008), western gray squirrel (*Sciurus griseus*, 63.0%; Vander Haegen et al. 2013), and Arizona gray squirrel (*Sciurus arizonensis*, 37.5%; Cudworth and Koprowski 2014). We are not aware of any other studies examining 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 two previous studies on eastern gray squirrels tested for a sex-specific difference for survival. In Illinois, Nixon et al. (1975) found no difference in a hunted population (0.20 males, 0.21 females) and in North Carolina, Barkalow 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 in Virginia 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). Similarly, at the relatively low rates of harvest we observed, hunting mortality is generally considered compensatory in harvested squirrel populations (Connelly et al. 2012).

With a winter survival rate of 0.25, our expectation that survival would be lowest during the flood season was supported. Squirrels were more likely to die during the flooded winter season, and mortality increased with the extent of flooding. In a companion study, we found that during the 2016 dry season (fall), this population scatter hoarded 72% of radio-tagged acorns in areas that would become unavailable for recovery due to flooding during the 2016–2017 flooded winter season (Wilson 2018). Other studies have found similar patterns to ours when environmental conditions reduce the size of the mast crop available to scatter hoarders. Specifically, squirrels are known to experience decreased survival rates during years of poor mast crop production (Virgina, Mosby 1969; Ohio, Nixon and McClain 1969; Ohio, Nixon et al. 1975; Kansas, 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 (Nixon and McClain 1969).

When managing a population of squirrels in a flooded forest in the southeastern United States, it is important to consider how fluctuating environmental conditions may affect survival. The presence and degree of winter flooding can affect the recovery of scatter hoarded food. Winter is typically a season with little to no food available for these animals, and since squirrels rely on scatter hoarded food to survive winter, changes in the availability of this resource can affect their survival. Managers should consider the effects of the winter conditions of the habitat when moving forward with their goals pertaining to management of the squirrel population.

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