Survival and cause-specific mortality of female eastern wild turkeys in two frequently-burned longleaf pine savannas

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Survival and cause-specific mortality of female eastern wild turkeys in two frequently-burned longleaf pine savannas

Andrew R. Little, John F. Benson, Michael J. Chamberlain, L. Mike Conner and Robert J. Warren

Longleaf pine savannas have declined throughout the southeastern United States due to land-use change. Fortunately, natural resource professionals are currently restoring these ecologically and economically important savannas. Although efforts are underway to restore longleaf pine savannas, little information exists on female eastern wild turkey population dynamics in these systems. Therefore, we evaluated survival and cause-specific mortality of female eastern wild turkeys in two longleaf pine savannas in southwestern Georgia. We radio-marked 126 female wild turkeys during 2010–2013 and monitored their survival; 66 (52.4%) radio-marked females died during the study. We estimated causes of death for 37 mortality events with predation serving as the leading known cause of mortality, with 35.1% of mortalities attributed to mesocarnivore predation (e.g., bobcat, coyote, and gray fox). Survival of incubating females was 0.82 (95% CI: 0.71–0.93) and survival of non-incubating females was 0.67 (95% CI: 0.52–0.87). Annual survival was 0.55 (95% CI: 0.44–0.67). To ensure sustainable wild turkey populations in longleaf pine savannas, we suggest managers monitor relationships between survival and population productivity.

Longleaf pine Pinus palustris savannas are one of the most biologically diverse systems found in North America containing numerous species of flora and fauna (Alavalapati et al. 2002). Historically, longleaf pine savannas occupied over 30 million ha in the southeastern United States (Brockway et al. 2005, Van Lear et al. 2005), and were maintained by fire ignited by lightning or humans. These fires created a grassland-forb system and prevented hardwood encroachment (Komarek 1964, Pyne 1982, Kennamer et al. 1992, Robbins and Myers 1992). However, land-use changes (e.g. conversion from slower growing longleaf pine to faster growing loblolly pine Pinus taeda and slash pine Pinus elliottii; increase in agricultural practices and urban development) throughout the southeastern United States led to a decline in longleaf pine savannas (Frost 1993, Alavalapati et al. 2002, Van Lear et al. 2005). Fire suppression beginning in the late 1890s also led to changes in forest conditions (Alavalapati et al. 2002, Fowler and Konopik 2007).

Fortunately, natural resource professionals have recognized the importance of restoring longleaf pine savannas, which will potentially benefit a variety of species in the southeastern United States. Wild turkeys Meleagris gallopavo have historically been an important species present in longleaf pine savannas, and are adapted to the early-successional understory conditions created by periodic fire that also promotes insect abundance (Hurst 1981, McGlincy 1985, Landers and Mueller 1986, Exum 1988, Provancher et al. 1998). Prescribed fire is the primary tool used to reduce undesirable competing vegetation in longleaf pine savannas while stimulating growth and development of a diverse plant community in the understory (Waldrop et al. 1992, Cain et al. 1998, Barnett 1999, Steen et al. 2013). Various wildlife species found in longleaf pine savannas, such as the endangered red-cockaded woodpecker Picoides borealis and gopher tortoises Gopherus polyphemus are dependent on the use of fire to maintain open, park-like conditions for their survival (Alavalapati et al. 2002). Therefore, land managers commonly apply prescribed fire every 1–3 years to reduce hardwood encroachment and enhance grass and forb development in longleaf pine savannas (Glitzenstein et al. 2012). Wild turkeys have been an economically important upland game bird since reintroduction and restoration efforts (Baumann et al. 1990). Current efforts to restore longleaf pine savannas, coupled with the substantial economic importance of this upland game bird, justify research to address
population dynamics of wild turkeys in this ecosystem to help guide management decisions.

Wild turkey population growth is influenced by nest success, brood survival, and adult survival (Roberts et al. 1995, Vangilder and Kurzejeski 1995, Godfrey and Norman 1999). Low survival of females and broods may limit population productivity (Miller and Leopold 1992, Palmer et al. 1993, Peoples et al. 1995, Miller et al. 1998). Therefore, to effectively manage wild turkey populations, biologists and land managers need information on nest success, brood survival and adult survival in longleaf pine savannas. Little et al. (2014) reported a greater initial nest success but similar renest rates and success in longleaf pine savannas relative to other published studies in the southeastern United States (Palmer et al. 1993, Miller et al. 1998, Thogmartin and Johnson 1999, Wilson et al. 2005, Byrne and Chamberlain 2013). Survival of female wild turkeys in longleaf pine savannas has not been previously studied, yet is critical to manage turkey populations effectively and sustainably.

Predation is a primary source of wild turkey mortality (Speake 1980, Miller and Leopold 1992, Lovell et al. 1995, Moore et al. 2010). Potential predators of wild turkeys include bobcats Lynx rufus, coyotes Canis latrans, great-horned owls Bubo virginianus, gray fox Urocyon cinereoargenteus and red fox Vulpes vulpes, domestic dogs, and raccoons Procyon lotor, Miller and Leopold 1992. No information currently exists on wild turkey cause-specific mortality in longleaf pine savannas. Additionally, previous research has reported lower survival for female wild turkeys during reproductive seasons suggesting nesting females are increasingly vulnerable to predation (Palmer et al. 1993, Roberts et al. 1995, Vangilder and Kurzejeski 1995, Wright et al. 1996, Moore et al. 2010). However, none of these studies have evaluated the influence of reproduction (incubating compared to non-incubating females) on survival. Miller et al. (1998) is the only study that has evaluated the cost of reproduction (or lack thereof) on survival rates of females during the nesting season. They found reproductively active and inactive females had similar survival rates during the nesting season; however, nesting females were more susceptible to predation while non-nesting females were more susceptible to illegal harvest. Information is needed to fill this knowledge gap in our understanding of wild turkey cause-specific mortality and potential influences of reproduction on mortality in longleaf pine savannas to direct our future management decisions.

Our primary objectives were to 1) estimate annual and seasonal survival rates of female wild turkeys, and 2) document cause-specific mortality. We hypothesized that annual and seasonal survival estimates would be comparable to previous studies in forest-dominated landscapes. We hypothesized that survival would be lowest during the nesting season because incubating females remain on or close to the nest, which could make them more vulnerable to predation. We hypothesized that mesocarnivore predation would be the primary source of mortality. Our secondary objective was to evaluate the effect of nesting status on survival. Specifically, we hypothesized that reproductive activity would negatively influence survival during the nesting season (i.e. incubating females would experience lower survival than non-incubating females).

Study area
Our study was conducted on the 11735-ha Joseph W. Jones Ecological Research Center at Ichauway (hereafter, Jones Center) located in Baker County, Georgia and the 3900-ha Silver Lake Wildlife Management Area owned by the Georgia Dept of Natural Resources located in Decatur County, Georgia (hereafter, Silver Lake WMA; 42 km from Jones Center). The Jones Center was composed of approximately 39% mature pine (>20 years), 24% mixed pine/ hardwood, 11% agriculture/food plot, 8% young pine (≤20 years), 7% hardwoods, 4% scrub-shrub, 3% wetland, 3% open water, and 1% residential/barren. Wiregrass and old-field grasses (e.g. Andropogon spp.) were the dominant understory conditions in the pine and mixed pine/hardwood stands (Goebel et al. 1997). However, >1000 vascular plant species occur on the site (Drew et al. 1998). Silver Lake WMA was composed of approximately 56% mature pine (>20 years), 22% young pine (≤20 years), 10% open water, 9% mixed pine/hardwood, 1% scrub/shrub, 1% hardwood, 1% residential/barren, and <1% wetlands and agriculture/food plots. Paved, gravel and dirt road densities were 5.48 km km–2 and 6.59 km km–2 on the Jones Center and Silver Lake WMA, respectively. Total accumulated rainfall from 14 December to the following 13 December varied at the Jones Center for 2011 (89.15 cm), 2012 (96.42 cm), and 2013 (156.79 cm) (Newton; Georgia Automated Environmental Monitoring Network; <http://georgiaweather.net>), and at Silver Lake WMA for 2011 (73.13 cm) and 2012 (118.57 cm) (Lake Seminole; Georgia Automated Environmental Monitoring Network; <http://georgiaweather.net>). Additionally, the Jones Center was not hunted while Silver Lake WMA was hunted from late March until mid-May for male turkeys only.

To successfully restore and maintain longleaf pine savannas on our study sites, land managers used prescribed fire and mechanical hardwood removal. Fire was applied to mature pine, young pine, mixed pine/hardwood, and shrub/scrub stands. Prescribed fire was conducted throughout the year with >95% of burns conducted during January–June. Prescribed fire application occurred in a mosaic fashion, which promoted landscape diversity. Average patch size burned at the Jones Center was 21.41 ha (SE = 0.83; range = 0.02–240.57 ha), whereas average patch size burned at Silver Lake WMA was 14.41 ha (SE = 0.58; range = 0.66–88.27 ha). Fire return interval typically ranged from 1–3 years, but most (≥95%) fires applied to our study sites were ≤2 years (38.4%, 0-year; 34.9%, 1-year; 21.7%, 2-year; 4.9% of stands with 3-year time-since-fire). Land managers often used mechanical removal to remove large off-site hardwoods (e.g. water oak Quercus nigra) from within mature pine stands.

Methods
Turkey capture and monitoring
We captured female wild turkeys using rocket nets baited with corn during December–March of 2010–2013 and June–August of 2011–2012. We fitted all captured females
with serially numbered, butt-end (left leg) and riveted (right leg) aluminum leg bands. We also affixed a backpack-style VHF radio-transmitter, weighing approximately 60-g (Sirtrack, Havelock North, New Zealand; and Telenax, Playa del Carmen, México) to all females. All birds were released at the capture site immediately after processing. The Institutional Animal Care and Use Committee at the University of Georgia approved all turkey capture, handling, and marking procedures (protocol no. A2013 05-034-Y1-A0).

We used a hand-held, three-element Yagi antenna and Wildlife Materials TRX 2000S receiver (Wildlife Materials, Murphysboro, Illinois) to locate radio-marked females ≥ 2 times per week from mid-July to mid-March and ≥ 1 time per day from mid-March to mid-July. We triangulated each female and recorded locations using a mobile phone containing Location Of A Signal-SD software (LOAS[2010] Ecological Software Solutions LLC. Hegymagas, Hungary, ver. 4.0.3,8,) and a bluetooth-global positioning system unit.

We considered a female to be incubating if she did not move for three consecutive days during the nesting season. Once a female was determined to be incubating, we approached to within 25 m of the nest and recorded compass bearings toward the nest. After termination of incubation, we approached nest sites to determine nest fate.

We investigated mortality events immediately following detection of a mortality signal, except during the nesting season when inactive incubating females often triggered the mortality sensor. During the nesting season, we delayed investigation of mortality signals until 28 days from the estimated incubation start date so as not to disturb females that may have been nesting. We classified mortality events into four categories: 1) mesocarnivore (bobcat, coyote and gray fox); 2) great-horned owl); 3) unknown cause of death; and 4) other (e.g. vehicle collision). We based classification on evidence recovered at the site of the carcass (i.e. presence or absence of head and neck, chew characteristics on carcass and radio transmitter, detection of hair or feathers, and evidence of caching; Thogmartin and Schaeffer 2000).

Survival estimation

To evaluate annual and seasonal survival rates of female wild turkeys, we calculated annual and seasonal survival probability estimates using the Kaplan–Meier estimator (Kaplan and Meier 1958) generalized for the staggered entry case (Pollock et al. 1989). Prior to analysis, we censored all mortalities occurring within seven days of capture to mitigate the influence of capture mortality on survival estimates (Vangilder and Sheriff 1990). We censored turkeys whose radio transmitters failed or those that went missing on the last day that we recorded an active signal. We did not suspect that any mortalities occurring during the study were caused by illegal harvest. We structured the data with an annual recurrent time of origin to estimate annual survival, which allowed for re-entry of individuals that survived the previous year (Fieberg and DelGiudice 2009). Specifically, our annually recurrent biological years began on 10 May and ended on 9 May the following year. All individuals that remained alive at the end of each biological year were censored and re-entered on the first day of the next year. Prior to data analysis, we evaluated whether annual survival differed between study sites. We found similar annual survival estimates for each site (Jones Center: 0.562 [0.434–0.728]; Silver Lake WMA: 0.552 [0.407–0.749]). Therefore, we pooled survival data across both study sites. To determine seasonal survival, we delineated biologically meaningful seasons based on the reproductive chronology of turkeys on our study areas (Little et al. 2014) and previous research (Miller et al. 1999, Miller and Conner 2005, 2007). We defined winter as 1 January – 31 March, spring as 1 April – 30 June, summer as 1 July – 30 September, and fall as 1 October – 31 December. We estimated survival within these seasons using a seasonally recurrent time of origin such that all individuals that remained alive on the last day of the season were censored and, if still alive, were re-entered on the first day of the same season the following year. All survival analyses were completed in program R using package ‘survival’ (<www.r-project.org>, Therneau 2014).

Mortality risk

To determine if incubation influenced survival, we estimated survival for incubating and non-incubating females during spring (see also Little et al. 2014). Prior to data analysis, we built a data set that contained only females where apparent nestling status was determined. For example, if radio contact with an individual was lost during the nesting season and the individual reappeared later in the season, we excluded them from the analysis as we could not determine if they initiated a nest. We intended to use a Cox proportional hazards (CPH) model to determine whether incubation status (incubating vs. non-incubating) influenced the risk of mortality (Cox 1972). An important assumption of the CPH model is proportionality, which assumes the hazard function remains constant over time. We tested the proportional hazards assumption using the formal test recommended by Therneau and Grambsch (2000) using the cox.zph function in the ‘survival’ package. Our CPH model did not meet the required proportionality assumption (p = 0.013) indicating that the hazard functions were not constant over time. Given that we were unable to formally test for a difference in survival between incubating and non-incubating females using CPH, we evaluated survival separately for incubating and non-incubating females. We also provide survival curves for both groups to allow for visual evaluation.

Results

We captured and radio-marked 126 female wild turkeys and 66 (52.4%) died during the study (Table 1). We estimated known causes of death for 37 of the 66 (56.1%) mortality events (Table 2), with most deaths attributable to unknown causes (43.2%). Predation was the leading known cause of mortality, with 35.1% attributed to mesocarnivore predation and 18.9% to great-horned owl predation. One female (2.7%) was hit by a vehicle.

Annual survival was 0.55 (n = 37 mortalities; 95% CI: 0.44–0.67; Fig. 1), and survival varied seasonally with lowest survival during spring (Ŝ = 0.76; 95% CI: 0.68–0.87; n = 18 mortalities) followed by summer (Ŝ = 0.87; 95%
Table 1. Number of radio-marked female eastern wild turkeys *Meleagris gallopavo silvestris* monitored and number of individuals that died seasonally at the Joseph W. Jones Ecological Research Center (JC) and Silver Lake Wildlife Management Area (SL), southwestern Georgia, USA, 2011–2013.

| Season | Site  | n   | Mortality (n) |
|--------|-------|-----|---------------|
| Winter | JC    | 49  | 3             |
|        | SL    | 32  | 7             |
| Spring | JC    | 43  | 14            |
|        | SL    | 26  | 4             |
| Summer | JC    | 31  | 2             |
|        | SL    | 22  | 4             |
| Fall   | JC    | 23  | 3             |
|        | SL    | 15  | 0             |

\(a\) Season: winter (1 January–31 March), spring (1 April–30 June), summer (1 July–30 September), and fall (1 October–31 December).

\(b\) n: no. of radio-marked female turkeys.

\(c\) Mortality (n): no. of radio-marked female turkeys that died during the study.

Table 2. Number of radio-marked female eastern wild turkeys *Meleagris gallopavo silvestris* where known cause of death could be determined at the Joseph W. Jones Ecological Research Center (JC) and Silver Lake Wildlife Management Area (SL), southwestern Georgia, USA, 2011–2013.

| Site | Season | Cause of death | n   |
|------|--------|----------------|-----|
| JC   | fall   | avian          | 0   |
|      |        | mesocarnivore  | 0   |
|      |        | unknown predator | 3   |
|      |        | vehicle         | 0   |
|      | winter  | avian          | 1   |
|      |        | mesocarnivore  | 0   |
|      |        | unknown predator | 2   |
|      |        | vehicle         | 0   |
|      | spring  | avian          | 3   |
|      |        | mesocarnivore  | 4   |
|      |        | unknown predator | 6   |
|      |        | vehicle         | 1   |
|      | summer  | avian          | 0   |
|      |        | mesocarnivore  | 2   |
|      |        | unknown predator | 0   |
|      |        | vehicle         | 0   |
| SL   | fall   | avian          | 0   |
|      |        | mesocarnivore  | 0   |
|      |        | unknown predator | 0   |
|      |        | vehicle         | 0   |
|      | winter  | avian          | 1   |
|      |        | mesocarnivore  | 5   |
|      |        | unknown predator | 1   |
|      |        | vehicle         | 0   |
|      | spring  | avian          | 2   |
|      |        | mesocarnivore  | 1   |
|      |        | unknown predator | 1   |
|      |        | vehicle         | 0   |
|      | summer  | avian          | 0   |
|      |        | mesocarnivore  | 1   |
|      |        | unknown predator | 3   |
|      |        | vehicle         | 0   |
| Total|        |                | 37  |

\(a\) Season: winter (1 January–31 March), spring (1 April–30 June), summer (1 July–30 September), and fall (1 October–31 December).

\(b\) n: no. of radio-marked female turkeys where known cause of death could be determined.

As hypothesized, survival was greatest during the fall/winter and lowest during the spring. Our findings also indicate that mesocarnivore predation was the greatest known source of mortality. We were unable to test for a difference in survival for incubating and non-incubating females. However, we suggest future research explore whether incubation status may affect survival of female turkeys.

Annual survival was comparable to other forest-dominated landscapes in the southeastern United States (Palmer et al. 1993, Miller et al. 1998, Wilson et al. 2005). Miller et al. (1998) reported a mean annual survival of 0.51 with variation among years ranging from 0.22 to 0.77. However, compared to studies in non-forest dominated landscapes, our findings suggest that our annual survival estimate was low (Hubbard et al. 1999, Humberg et al. 2009). For example, Humberg et al. (2009) found annual survival of female turkeys was 0.80 in a northern Indiana wild turkey population. However, Hubbard et al. (1999) and Humberg et al. (2009) conducted their studies in highly agricultural landscapes, which may have influenced turkey survival. We suggest that lower annual female survival observed on our study sites may be offset by high nest and renest success (Little et al. 2014), in part due to the availability of nesting and brood-rearing cover created by fire (Dickson 1981, Hurst 1981, Landers 1981). For example, Little et al. (2014) observed greater initial nest success relative to other forested-dominated landscapes in the southeastern United States region (Palmer et al. 1993, Miller et al. 1998, Thogmartin and Johnson 1999, Wilson et al. 2005, Byrne and Chamberlain 2013). However, we acknowledge that future research should evaluate the influence of habitat types on annual survival estimates to improve our understanding of potential factors that may influence survival across different ecosystems.

Our seasonal survival estimates were comparable to previous studies (Palmer et al. 1993, Roberts et al. 1995, Hubbard et al. 1999, Wilson et al. 2005, Humberg et al. 2009). Survival was highest during the fall (flock re-establishment) followed by winter (large flocks on wintering areas), summer (brood-rearing), and spring (nesting). Previous studies have documented high survival rates during the fall (Palmer et al. 1993, Roberts et al. 1995, Hubbard et al. 1999, Wilson et al. 2005, Humberg et al. 2009). Increased fall survival is likely attributable to stable foraging resources and a lack of illegal and legal harvest (Wilson et al. 2005). Additionally, survival would be expected to be higher during the fall relative to the spring because females are not nesting (e.g. stationary).
Lower survival during spring is commonly attributed to females remaining on or near a nest site, which may lead to greater risk of predation (Little et al. 1990). Predation was the leading known cause of mortality for female turkeys in our study, which is consistent with many previous studies (Miller and Leopold 1992, Palmer et al. 1993, Wright et al. 1996, Miller et al. 1998, Humberg et al. 2009). However, we could not determine cause-specific mortality for 43.2% of mortality events. Similarly, previous studies have attributed high percentages of mortalities to unknown causes (Miller et al. 1998, Humberg et al. 2009). This finding is likely a result of scavenging activities by various predators, which may delay onset of mortality signals observed similar survival estimates for winter and summer. This finding is partially attributed to a greater risk of predation because 43% (10 mortalities during winter; six mortalities during summer) of 37 mortalities where cause of death could be assigned occurred during winter and summer. Mesocarnivores and great-horned owls were the primary causes of death for female turkeys during these seasons. Summer survival on our study areas was similar to previous studies (Palmer et al. 1993, Roberts et al. 1995, Hubbard et al. 1999, Wilson et al. 2005, Humberg et al. 2009). Survival commonly increases during summer, which is likely due to the end of nesting season and increased mobility of broods. Our estimate of spring survival was within the range of survival estimates previously reported (0.75, Wilson et al. 2005; 0.91, Humberg et al. 2009). Lower survival during spring is commonly attributed to females remaining on or near a nest site, which may lead to greater risk of predation (Little et al. 1990).

Predation was the leading known cause of mortality for female turkeys in our study, which is consistent with many previous studies (Miller and Leopold 1992, Palmer et al. 1993, Wright et al. 1996, Miller et al. 1998, Humberg et al. 2009). However, we could not determine cause-specific mortality for 43.2% of mortality events. Similarly, previous studies have attributed high percentages of mortalities to unknown causes (Miller et al. 1998, Humberg et al. 2009). This finding is likely a result of scavenging activities by various predators, which may delay onset of mortality signals

Table 3. Number of incubating or non-incubating female eastern wild turkeys *Meleagris gallopavo silvestris* that were monitored during the spring nesting season (1 April–30 June) and number of individuals that died at the Joseph W. Jones Ecological Research Center (JC) and Silver Lake Wildlife Management Area (SL), southwestern Georgia, USA, 2011–2013.

| Status        | Year | Site | n | Mortality (n) |
|---------------|------|------|---|---------------|
| Incubating    | 2011 | JC   | 6 | 2             |
|               |      | SL   | 5 | 1             |
|               | 2012 | JC   | 13| 3             |
|               |      | SL   | 13| 1             |
|               | 2013 | JC   | 15| 2             |
|               |      | SL   | 0 |              |
|               | 2011–2013 pooled among years | JC | 34 | 7 |
|               |      | SL   | 18| 2             |
| Non-incubating| 2011 | JC   | 3 | 2             |
|               |      | SL   | 4 | 0             |
|               | 2012 | JC   | 10| 3             |
|               |      | SL   | 7 | 2             |
|               | 2013 | JC   | 8 | 2             |
|               |      | SL   | 0 |              |
|               | 2011–2013 pooled among years | JC | 21 | 7 |
|               |      | SL   | 11| 2             |
| Pooled across years and sites | JC + SL | 52 | 9 |
| Pooled across years and sites | JC + SL | 32 | 9 |

* n: no. of radio-marked female turkeys including individuals that survived across years.

*Mortality* (n): no. of radio-marked female turkeys that died during the study.

*No females were monitored during 2013.*
In summary, our results are consistent with previous research in that predation was the leading known cause of mortality for female wild turkeys, especially during the spring. However, females may be able to compensate for lower annual survival by increased nest and renest success, as was observed previously on our study areas (Little et al. 2014). Provision of adequate nesting cover in longleaf pine savannas may be important to decrease predation rates during the spring. Our data also indicated that survival of non-incubating females during spring was lower than for incubating females. Although, we were unable to test for a difference due to the lack of proportional hazard over time for the two groups but note that the confidence intervals for the survival rates overlapped substantially. We suggest further research is needed to evaluate predator – wild turkey dynamics in longleaf pine savannas. Specifically, we suggest future research investigate state-space behaviors on female survival during the nesting season. For example, previous research on our study area documented multiple nesting attempts during the nesting season (Little et al. 2014); therefore, females are changing states during multiple nesting attempts from stationary to mobile to stationary. These behaviors may influence the probability of survival, specifically for individuals that are mobile and are easier to be detected by predators (Lima and Dill 1990). Given that we observed lower annual survival than some studies, we recommend that biologists monitor relationships between survival and productivity of turkeys in longleaf pine savannas to ensure the sustainability of turkey populations. This could be accomplished through mark–capture–resight methods (Weinstein et al. 1995) and line-transect-based distance sampling (Butler et al. 2007). However, we suggest future research also examine improved population monitoring techniques for wild turkeys.

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