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Factors Influencing Post-Capture Survival and Survival of Eastern Wild Turkeys in Alabama

by

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Abstract

The Alabama Department of Conservation and Natural Resources (ADCNR) has recently initiated research on the eastern wild turkey (*Meleagris gallopavo silvestris*) population due to perceived declines in abundance throughout the state. Addressing this concern has profound effects on the social, economic and legal circumstances associated with Alabama's turkey population. The Alabama Cooperative Fish and Wildlife Research Unit (ACFWRU) is developing a decision support tool to inform and support the ADCNR's future harvest regulations. The decision support tool will allow the ADCNR to access the effects of current and future harvest regulations based on empirical data, and provide a framework to address the perceived decline. Estimates of annual and seasonal survival are important in understanding the size, structure, and growth rates of wildlife populations, are a critical component of the decision support tool, and addressing the perceived decline of wild turkeys in the state of Alabama. Following a brief introduction in chapter one, I discuss the effects of the capture, handling, and marking process on wild turkey survival post-capture. The implications of this chapter could influence the methodologies with which wild turkeys are captured, handled, and marked, as well as how we analyze monitoring data to estimate survival rates. In chapter three, I provide seasonal and annual estimates of survival for each age and sex class of wild turkey, as well as identify potential factors influence survival. In the final chapter, I discuss some general thoughts on wild turkey survival rates, how we estimate them, and future areas of research.

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CHAPTER I: INTRODUCTION

The Alabama Department of Conservation and Natural Resources (ADCNR) has recently initiated research on the eastern wild turkey (*Meleagris gallopavo silvest*ris) population due to perceived declines in abundance throughout the state. Addressing this concern has profound effects on the social, economic and legal circumstances associated with Alabama's turkey population. Each year, 98,000 hunters pursue wild turkeys in Alabama, amass over 1 million days spent afield, and spend approximately 52 million dollars (Harris 2010) on recreational activities related to wild turkeys. Part of this annual spending includes license sales, which in conjunction with federal aid, are the only sources of revenue the ADCNR has to implement wildlife management projects and initiatives statewide. Furthermore, the ADCNR's role in the management and protection of wild turkeys, for a variety of stakeholder groups, is a legal responsibility established by the North American Model of Wildlife Conservation and the Public Trust Doctrine (Smith 2011).

The primary method the ADCNR uses to address population declines is changes to harvest regulations. It has been 32 years (Speake et al. 1985) since the last comprehensive study of eastern wild turkey demographics in Alabama. Due to the expanding range and population size of wild turkeys since that time (Vangilder and Kurzejeski 1995), the demographics of turkey populations have likely changed. To effectively address the perceived decline, the ADCNR needs current demographic rates and the tools to make informed decisions regarding season length, timing, and bag limits.

The Alabama Cooperative Fish and Wildlife Research Unit is developing a decision support tool to inform and support the ADCNR's future harvest regulations. The decision support tool will allow the ADCNR to assess the effects of current and future harvest regulations based on empirical data, and provide a framework to address the perceived decline. The decision support tool will utilize an adaptive harvest management approach, current estimates of wild turkey demographic rates, and intensive monitoring programs, to precisely evaluate the effects of various harvest regulation alternatives.

Before the decision support tool can be used to inform harvest regulation, the status of the turkey population must be known. The decision support tool helps inform harvest regulations by estimating the changes in population size, structure, and growth rates under each harvest regulation alternative. The population processes that influence population size, structure, and growth rates are survival and productivity (Lebreton et al. 1993). Survival and productivity influence sex and age distributions, and levels of recruitment into the population (Caughley 1977). Understanding sex and age distributions, as well as recruitment, are necessary to estimate population trends, and how harvest regulation alternatives may influence those trends. Survival and productivity rates are expected to vary spatially across landscape types (Pollentier et al. 2014) emphasizing the need to collect these rates across the range of landscapes found in Alabama. This variation could have profound effects on the harvest regulations recommended and implemented by the ADCNR in different areas of the state.

Before estimating survival rates, I examine the assumptions used in survival rate estimation. Most notably, is the assumption that capture, marking, and handling does not influence annual and seasonal survival. Researchers often assume that survival of radio-marked wild turkeys is not adversely affected by capture and marking beyond 14-days post-capture (Roberts et al. 1995, Nguyen et al. 2003, Holdstock et al. 2006, Pollentier et al. 2014). However, there is little-published information to support this assumption. Not only might demographic rates be biased by assuming there was no effect of capture on survival after 14 days, but the impact on the population of study might also become detrimental to the research objectives. Quantifying the rates and timing of capture-related mortality, as well as determining the factors that have the greatest influence on capture-related mortality can help address this information gap. Ecological, environmental, and research protocols are hypothesized to influence post-capture survival. In the following chapters, I explore how each factor influences post-capture survival. With this information, I can inform current and future turkey research protocols to eliminate potential sources of bias in survival rate estimation.

Once I have addressed the assumptions used in survival rate estimation, I estimate annual and seasonal survival rates. Given the relationship of age and sex to survival and their potential to affect the number of birds in each class (Caughley 1977), it is important to have accurate and precise estimates of seasonal survival for each age and sex class. I explore the effects of biological, environmental, and landscape level factors and identify the factors with the greatest influence on survival rates. With this information, I can help managers understand the status of turkey population in Alabama, as well as predict population dynamics and inform effective management objectives.

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CHAPTER II: POST-CAPTURE SURVIVAL OF EASTERN WILD TURKEYS.

Abstract

Researchers often assume that survival of radio-marked eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter, turkeys) is not adversely affected by capture and marking beyond 14-days post-capture. However, there is little published information to support this assumption. We captured and marked turkeys (n = 273) over two years and examined their daily survival rates for 45-days post-capture. We compared models using Akaike's Information Criterion (AIC) to determine factors with greatest influence on post-capture survival. We found that the best approximating model supported the hypothesis that survival odds increased linearly post-capture and that increasing ambient temperature at the time of capture had an adverse effect on survival. Post-hoc processing suggested that capture and marking may have adversely affected survival for approximately 33 days, 19 days longer than the traditionally used 14-day period. The 33-day post-capture survival rate was 0.71 (SE = 0.03, 95% CI = 0.64-0.76). Additionally, for each day post-capture, turkeys were 1.06 times more likely to survive (SE = 0.012, 95% CI = 1.03-1.08). Lastly, for each 5℃ increase in temperature at capture, wild turkeys were 0.83 times as likely to survive (SE = 0.08, 95% CI = 0.70-0.99). The duration of post-capture censoring periods has the potential to bias estimates of survival rates. Addressing these potential biases using empirical data and biologically defensible hypotheses is critical to improving estimates of turkey demographics.

Introduction

Capturing, handling, and marking of eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter, turkeys) are often assumed to have no effect on individuals beyond 14-days post-capture (Roberts et al. 1995, Nguyen et al. 2003, Holdstock et al. 2006, Pollentier et al. 2014). It is believed that the effects of capture, handling, and marking processes on behavior and vital rates are negligible after this time (Nenno and Healy 1979). As a result, a 14-day conditioning period is often censored from analysis. Making this assumption is necessary for many methods of data analysis, as failure to account for changes in behavior and vital rates can bias estimates (Tsai et al. 1999). However, there is little published information to support the 14-day post-capture censoring practice. Not only might demographic rates be biased by assuming there was no effect of capture on survival after 14 days, but the impact on the population of study might also become detrimental to research objectives. Quantifying rates and timing of capture-related mortality, and determining factors that have greatest influence on capture-related mortality, can help address this information gap. With a greater understanding of factors that influence capture-related mortality, we can improve capture protocols and reduce future research-related mortality. Furthermore, determining duration of time turkeys are at risk of capture-related mortality will reduce bias in survival rate estimation associated with the capture, handling, and marking process.

Capture-related mortality includes any source of mortality associated with the capture, handling and marking process. This includes mortality due to natural processes immediately during or after capture, mortality caused by injuries sustained during capture, radiotransmitter effects, or capture myopathy (Arnemo et al. 2006). Mortality related to the capture process is often minimal, due to the refinement of capture methods over time. Additionally, Nenno and Healy (1979) and Hernandez et al. (2004) reported that radiotransmitter effects are negligible. However, the risk of capture myopathy remains a primary concern during and after capture. Capture myopathy is caused by reduced blood flow to muscles while individuals are restrained (Spraker et al. 1987), which can lead to a lactic acid buildup in affected muscles and may result in cellular death (Nicholson et al. 2000). Capture myopathy has been observed in ungulates

(Herbert and Cowan 1971, Beringer et al.1996) and avian species (Windingstad et al.1983, Dabbert and Powell 1993, Nicholson et al.2000, Rogers et al. 2004). Treatment of wildlife suffering from capture myopathy has been largely unsuccessful (Businga et al. 2007). Thus, preventing capture myopathy must be the primary focus. Identifying the factors that influence capture-related mortality, and developing new procedures is essential to minimizing the adverse effects of trapping and marking procedures.

Age and sex are both potential factors influencing the risk of capture myopathy in wild turkeys. A number of physiological responses differ between adults and subadults and are potential indicators of greater risk of capture myopathy in subadults (Kock et al. 1987). Elevated internal body temperature, pulse-rate, respiration, and glucose levels have been observed in subadults, and are indicative of greater stress levels (Kock et al. 1987). Additionally, Herbert and Cohen (1971) suggest that nutritional deficiencies of dietary selenium may predispose an individual to a greater risk of capture myopathy. Dietary selenium is used by females in egg production and developing poults for growth (Cantor and Scott 1974), suggesting that females and developing poults may be predisposed to dietary selenium deficiency and subject to greater risk of capture-myopathy. Furthermore, Weinstein et al. (1995) also observed an influence of capture, marking, and handling on reproductive success, further suggesting that these processes influence behavior post-capture. Spraker et al. (1987) observed that juvenile birds made up 73% of all cases of capture myopathy, while adults made up only 17%. This observation supports the hypothesis that juveniles may be more susceptible to capture myopathy than adult birds. However, Nicholson et al. (2000) reported no significant difference in capture myopathy rates between adults and juveniles. Dabbert et al. (1993) noted that in their study of capture myopathy in mallards (*Anas platyrhynchos*), that larger openings in nets promoted greater struggle in captured birds by entangling them in unnatural positions. If smaller turkeys are more likely to become entangled they may be more susceptible to capture myopathy when compared to larger individuals.

Uncertainty remains concerning the influence of ambient temperature on post-capture survival. In Mississippi, environmental factors did not appear to influence post-capture survival (Miller et al. 1996), whereas studies in Colorado and Oklahoma observed the opposite effect (Spraker et al.1987, Nicholson et al. 2000). Nicholson et al. (2000) found that increased body and ambient temperature were positively associated with post-capture mortality rates. As ambient temperatures increase from 0℃ to 20℃, the probability of mortality was approximately 5 times greater (Nicholson et al. 2000). Contrary to the effects of ambient temperature, Nicholson et al. (2000) observed that relative humidity at the time of capture was negatively associated with post-capture mortality. Mortality at 40% relative humidity was nearly 4 times as likely when compared to 90% relative humidity. They suggested that high ambient temperatures and low relative humidity promoted quicker rates of dehydration, causing additional physiological stress during trapping procedures.

Method of release and processing time likely played a role in post-capture mortality (Nicholson et al. 2000). We used two methods of release: (1) group release upon conclusion of data collection and marking of all captured turkeys, and (2) individual release upon conclusion of data collection and marking of individual birds. Releasing the flock as a group is believed to help maintain flock integrity and reduce stress on captured turkeys immediately after capture and release. However, holding turkeys after they have been marked increased length of time that they were restrained. Nicholson et al. (2000) observed that as processing time increases, there was an increased probability of mortality. Releasing marked turkeys individually was believed to increase the time until flocks can reform, and potentially could increase the susceptibility of birds to other threats, such as predation, in the meantime. Collecting empirical data from mortality events within 14-days post-capture, and using that information in a survival analysis was imperative for understanding mortality related to capture, and identifying means to improve future trapping efforts.

Currently, information regarding capture-related mortality rates, the factors that influence them, and duration of time turkeys are at risk of capture-related mortality is limited. Gaining precise estimates of these effects will allow the development of practices that minimize the occurrence of capture-related mortality and eliminate potential biases in other forms of survival analysis.

Study Areas

Barbour County Wildlife Management Area (WMA) was approximately 28km northwest of Eufaula, Alabama and was contained in Barbour and Bullock counties. It was approximately 11,700 hectares of public land categorized as mixed hardwood forest interspersed with stands of longleaf (*Pinus palustris*) and loblolly pine (*P. taeda*). There were approximately 200 wildlife openings evenly distributed across the WMA. We defined wildlife openings as clearings in the forest lacking overstory and midstory components and dominated by grasses, forbs, or crops planted for the benefit of a variety of wildlife species. Wildlife openings were created by natural or anthropogenic disturbance. Human development was minimal across the WMA, with most development concentrated along county road 47 and 49, the only county roads contained in the WMA boundary. Spring turkey season on Barbour was shorter than the statewide season, with the first day of spring hunting season beginning 22 March, one week after the statewide start date.

James D. Martin Skyline WMA was located 40km North of Scottsboro, Alabama, and was contained in Jackson County. Skyline WMA was approximately 24,600 ha of public land classified primarily as hardwood forest with approximately 300 wildlife openings clustered where topography and access were permissible. Skyline WMA was interspersed with large tracts of privately owned forest and agriculture land. Additionally, it was the most fragmented of my study sites in terms of ownership. The turkey season followed statewide regulations set by the Alabama Department of Conservation and Natural Resources (ADCNR). Spring turkey season was open from 15 March to 30 April with the permitted harvest of one male per day, and a total combined of 5 males during the spring season.

Oakmulgee WMA was contained in the Talladega National Forest and was approximately 15km east of Moundville, Alabama. This WMA was contained in Bibb, Hale, Perry, and Tuscaloosa counties. It was approximately 18,010 ha of nearly contiguous public land, with small portions of private land and human development interspersed across the area. It was comprised of mixed hardwood forest interspersed with longleaf and loblolly pine stands. There were approximately 100 wildlife openings. There was a moderate density of human development across the study area, primarily in the form of churches and privately owned parcels of land. The spring turkey season followed statewide timing and bag limit regulations.

Methods

Data Collection

In the spring (February-March) and summer/fall (July-October) of 2015-16, we captured turkeys at all three study areas. We focused trapping efforts on baited game cameras sites, deployed over wildlife openings, using cannon nets (Dill and Thornsberry 1950) and walk-in traps. Upon capture, we removed all turkeys from the net or walk-in trap and placed them in holding boxes. We determined age by observing the molting pattern of rectrices and barring of the ninth and tenth primary wing feathers (Pelham and Dickson 1992). We determined sex by observing the shape and coloration of breast feathers, presence of metatarsal spurs, and presence/absence of a beard (Pelham and Dickson 1992). Each turkey received an appropriately sized aluminum leg band (National Band and Tag Co., Newport, KY) with a unique identification number, secured with a rivet (Diefenbach et al. 2009). Additionally, we fitted captured turkeys with a 76g back-mounted (Kurzejeski et al. 1987), encoded, very high frequency (VHF) radiotransmitter (model # A1540C, Advanced Telemetry Systems, Inc., Isanti, MN). We deployed larger radiotransmitters with additional GPS location and activity logging capabilities (96g, model # W510-Wildlink Loggers) on a subset of female turkeys. Activity was recorded as number of times the radiotransmitters' onboard accelerometer was tripped in the 15 minutes prior to location logging.

We recorded the method of capture, method of release, and total handling time (minutes) for each turkey. Cannon nets and walk-in traps were the only methods of capture used. Method of release was limited to single or group release. When we released turkeys alone, we released them immediately after marking. When we released turkeys in groups, we held them in plywood boxes until all captured birds had been processed, and we released all individuals simultaneously. We calculated total handling time as time of capture until time of release. We recorded capture time as the arrival time at a walk-in trap or time of net deployment. We used ambient temperature (°C) and relative humidity (%) at time of capture from the nearest National Oceanic and Atmospheric Administration (NOAA) weather station. Environmental data for BWMA, OWMA, and SWMA was collected from Weedon Field Airport in Eufaula, Al, Tuscaloosa Regional Airport in Tuscaloosa, Al, and Scottsboro Airport in Scottsboro, AL, respectively. The NOAA weather stations used in this study were ≤32km away from our study sites.

We monitored fate (alive or dead) of turkeys fitted with VHF radiotransmitters at least once every two weeks for 45 days. However, monitoring frequency varied among individuals dependent on perceived risk of mortality. Risk of mortality represented the perceived condition of the individual during the capture, marking, and release process. High-risk individuals included those with non-mortal injuries, extreme feather loss, heavy panting, or erratic behavior immediately following release. We monitored these individuals more frequently than others for the first 14-days post-capture. After 14-days post-capture, we determined fate of each radiomarked turkey biweekly.

We determined fate based on radiotransmitter pulse rate and coded mortality signals activated when the radiotransmitter had been stationary for at least 12 hours. For turkeys fitted with GPS loggers, we remotely downloaded data stored on loggers either bi-weekly (2 September - 28 February) or once every six weeks. We determined fate and time of mortality from logged data based on movement and activity data. We recorded year-round location and activity data at 0100 and 1500 each day. During 15 March - 30 September, we also logged location and activity data at 0700, 0900, 1100, 1300, 1700, and 1900 every other day. We assumed that mortality occurred just prior to the time when radiotransmitter became stationary, and activity ceased. Upon evidence suggesting a potential mortality, we attempted to flush or obtain other visual verification of the turkey's fate.

Statistical Analyses

We used nest survival models (Dinsmore et al. 2002) to estimate daily survival rates (DSR) for the 45-day post-capture period. Additionally, we estimated the relationship between DSR and covariates using the logit link in program Mark (White and Burnham 1999). Nest survival models require 4 parameters: (1) The day each individual was deemed at risk (AR), (2) the last day the individual was monitored and alive (LMA), (3) the day the individual was last monitored (LM), (4) and the fate of the individual at the end of the study (F). We set the start of the study for each individual to 1, corresponding to the day each individual was captured and entered into the AR category. Last monitored alive was the number of days post-capture that the bird was monitored and determined to be alive. LM was the number of days post-capture that the individual was monitored, and F corresponded to the last known fate of the individual (Hogan et al. 2013).

Encounter histories had three possible outcomes. If an individual survived the entire period then AR = 1, LAM = LM = 45, and F = 0. If an individual died during the study period, then AR = 1, LAM ≤ LM, and F = 1. If the fate of an individual could not be determined during the period (right-censored), then AR = 1, LAM = LM on the last day known alive, and F = 0. Additionally, we assumed that our inability to locate and determine the individual's fate was unrelated to the fate of the individual.

We compared models representing hypotheses that subadults would have greater rates of capture-realted mortality relative to adults, females would have greater rates of capture-realted mortality relative to males, and that subadult females would have greater rates of capture-realted mortality relative to all other age and sex classes. We also compared models representing hypotheses that turkeys captured with cannon nets would experience higher rates of capture-related mortality than those caputred with walk-in traps, and turkeys realeased in groups would have greater rates of capture-related mortality than those released indivudally. Our last set of hypotheses tested whether greater relative humidity at the time of capture, greater ambient temperature at the time of capture, and greater relative humidity and ambient temperature at the time of capture would result in greater capture-realted mortality. Models associated with each hypothesis were compared based on Akaike's Information Criterion corrected for small sample size (AICc; White and Burnham 1999, Anderson et al. 2000, MARK version 8.1). We used AICc weights and model averaging to estimate capture-related mortality rates and to determine the best approximating models and factors with the greatest influence on capture-related mortality. Where appropriate, we estimated parameters and sufficient statistics (Johnson 1999).

We addressed questions regarding how time since capture influences post-capture survival rates, and investigated the duration of time turkeys were at risk of capture-related mortality post hoc. The *a priori* top model with additional linear and quadratic time trends in the odds of survival were used to address how post-capture survival changed over time. Joint linear models corresponding to different durations of time post-capture were used to identify the duration of time turkeys were at risk of capture-related mortality. Similar to *a priori* hypotheses, post hoc models were compared using AICc to determine the best approximating models.

Results

During 2015 to 2017, we estimated daily survival rates for the 45-day post-capture period using observations from 226 wild turkeys. We captured 87 adults (30 male, 57 female), 34 juveniles (14 male, 10 female), and 115 poults (41 male, 51 female, 23 unknown). Of the captured females, 41 received radiotransmitters with additional GPS logging capabilities (36 adult, 5 juvenile). Ambient temperature at the time of capture ranged from 1.1℃ - 35.3℃. Five percent of captures were at temperature <10℃, 22% of all captures were in the 10.1℃-20.0℃

temperature range, 53% of captures were in the 20.1℃ - 30.0℃ temperature range, and 20% of captures were in the 30.1℃ – 40.0℃ temperature range. Relative humidity at the time of capture ranged from 20% relative humidity to 100% relative humidity. Seventy nine percent of all captures occurred between 30.1% relative humidity and 80.0% relative humidity. We captured 221 turkeys using cannon nets, and 5 turkeys using walk-in traps. We released 201 turkeys using the single release method, and 24 turkeys using the group release method. Lastly, handling times for captured turkeys ranged from 4 minutes to 120 minutes. Seventy four percent of captured turkeys were released in ≤40min.

The best models were those that incorporated environmental (i.e., temperature and relative humidity) and protocol driven (i.e., handling time, release method) covariates (Table 2.1). Ambient temperature at the time of capture (ATemp) was present in all of the top-ranked models. Relative humidity at the time of capture (RHumid), release method (SRel), and total handling time (HTime) also appeared in top-ranked models Table 2.2). However, small ΔAICc (<2) relative to the number of additional parameters, suggest these additional covariates may be uninformative parameters (Arnold 2010). Surprisingly, models including sex and age covariates performed the worst of all candidate models, securing less than four percent of the cumulative weight.

Of the 226 turkeys captured, we caught 221 with cannon nets and 5 with walk-in traps. We were unable to estimate the relationship between method of capture and post-capture survival because all turkeys captured in walk-in traps survived the 45-day conditioning period, and sample size was low. We released 202 turkeys using the single release method, and 24 turkeys using the group release method. Turkeys released using the single release methods were 0.95 times as likely to survive when compared to turkeys released in groups (95%CI = 0.2377-

1.4701). The relationship between handling time and post capture survival was also important. The model ATemp+HTime (ΔAICc = 1.66, ω = 0.11), indicated that for each 10-minute increase in handling time, wild turkeys were 0.68 times as likely to survive (95%CI = 0.33-1.03).

Models incorporating effects of environmental covariates performed the best of all candidate models. The top performing *a priori* model, ATemp, indicated that ambient temperature at the time of capture had the greatest influence on post-capture survival. For each 10 ℃ increase in ambient temperature at the time of capture, wild turkeys were 0.66 times as likely to survive (95%CI = 0.47-0.948). Additionally, the second ranked model, ATemp+RHumid (ΔAICc = 0.62, ω = 0.18), indicated that the relationship between relative humidity at the time of capture and post-capture survival was also important. For each 10% increase in relative humidity, turkeys were 0.92 times as likely to survive (95%CI=0.78-1.06).

We evaluated how post-capture survival changed over time by incorporating linear (LTT) and quadratic (QTT) time trend variables to the best-fit *a priori* model, ATemp. The LTT + ATemp model performed better than the QTT + ATemp (Δ AICc = 1.99; Table 2.3) model and became the basis for investigating the duration of time turkeys were at risk of capture-related mortality. Post-hoc models to assess the duration of time turkeys were at risk of capture-related mortality increased in performance as risk period increased (Table 2.4). The model incorporating a 33-day risk period (AICc = 519.01) outperformed the LTT + ATemp model (AICc = 519.10), while the model incorporating a 32-day risk period underperformed when compared to the LTT + ATemp model (AICc = 519.12).

Cumulative daily survival rates for the 45 days post-capture, using the LTT + ATemp model, were approximately 0.68 (95% CI = 0.62-0.74). The estimate of 14-day survival was 0.80 (95% CI = 0.75-0.85), and the estimate of 33-day survival was 0.71 (95% CI = 0.64-0.76).

Furthermore, for each one additional day post-capture, turkeys were 1.06 times as likely to survive (95%CI = 1.03-1.08), and for each 5℃ increase in ambient temperature, turkeys were 0.83 times as likely to survive (95% CI = 0.70-0.99).

Discussion

Studies of wild turkey demographics often incorporate survival rates to estimate population size, structure, and growth rates. For these estimates to be precise, it is important that we eliminate all foreseeable sources of bias in our estimates. One potential source of bias in vital rate estimation is the failure to meet the underlying assumptions of the models (Tsai et al.1999). An assumption often made in survival rate estimation is that marking individuals does not influence their fate (Tsai et al.1999). Conditioning periods from 7 (Kurzejeski et al. 1987, Miller et al. 1998, Vangilder 1995, Kane et al. 2007) to 30 (Collier et al. 2007) days have been used to satisfy this assumption in demographic studies of wild turkeys. However, a conditioning period of 14-days is traditionally used in estimating wild turkey survival rates (Godwin et al. 1991, Roberts et al. 1995, Nguyen et al. 2003, Holdstock et al. 2006, Pollentier et al. 2014). Nenno and Healy (1979) suggest that a 14-day conditioning period may be adequate to eliminate biases associated with radiotransmitter effects. Additionally, lethal cases of capture myopathy in avian species, appear to occur most often within the first 14-days post-capture (Nicholson et al. 2000, Hanley et al. 2005, Marco et al. 2006, Ruder et al. 2012). However, there is little evidence supporting 14 days as an appropriate conditioning period to encompass all direct and indirect radiotransmitter effects and occurrences of capture myopathy.

Models including age and sex covariates had little support in our analyses and performed worse than all other candidate models (Table 2.1). In previous studies of capture myopathy in avian species, age and sex effects have been prevalent (Spraker et al. 1987, Dabbert and Powell

1993). The physiological burden of reproduction on females could leave them more susceptible to additional physiological stressors and mortality (Williams 1966). Secondly, physiological responses in subadults, such as increased internal temperature, pulse-rate, respiration, and glucose have been observed (Kock et al. 1987), and are likely a result of higher stress. We expected these additional stressors to lead to more stress-related mortality among adult females. The poor performance of age and sex models in our analysis suggests that females and sub-adults are more resilient to capture related stress than traditionally thought.

Our results may have been affected by the timing of trapping. We were most successful trapping turkeys in the early spring, and late summer. During the early spring, poults were unavailable for capture, and juvenile birds, hatched the previous year, may have physiological responses similar to adults. Further, during the late summer, adult females may have had ample time to recover from physiological burden of nesting.

Ambient temperature at the time of capture was present in all top competing models, suggesting it had the greatest influence on post-capture survival of turkeys (Table 2.1). As the ambient temperature at the time of capture increased, we observed a decreased probability of survival (Fig. 2.1). Our results are consistent with Nicholson et al. (2000), who observed similar trends in a study of turkeys in Oklahoma, where ambient temperatures ≥ 10°C resulted in less than 70% survival post-capture. Conversely, trapping efforts at low ambient temperatures may also be detrimental (Miller et al. 1996), as the additional stress of capture in conjunction with thermoregulatory stress, could increase rates of capture-related mortality. The minimum critical temperature for adult female turkeys is 10.9°C (Haroldson et al. 1998). Below this ambient temperature, turkeys are required to increase food consumption to maintain internal body temperature (Haroldson et al. 1998). Ambient temperature at the time of capture for our study encompassed a wide range of values (1.1°C - 35.3°C), and our data suggests no detrimental effect on post-capture survival of turkeys when ambient temperatures were below 11°C. This was likely related to the absence of snow, which can limit forage availability in northern climates. Because survival increased as ambient temperatures decreased, and we observed no negative effect of trapping at temperatures below their minimum critical temperature, we recommend that researchers in southern areas, like Alabama, focus trapping efforts on periods with the lowest ambient temperatures.

Our data suggests that increased relative humidity at the time of capture had an adverse effect on post-capture survival. Nicholson et al. (2000) found that post-capture survival of turkeys was greater in high relative humidity, with relative humidity ≥ 60% resulting in >86% survival. However, their models did not account for the interaction between temperature and relative humidity. Lin et al. (2005) suggest that thermoregulatory ability of poultry is influenced by this interaction. When temperatures were <35°C, high relative humidity facilitated redistribution of heat within the body, increasing peripheral temperature and facilitating heat loss. However, at >60% relative humidity and temperatures ≥35°C, the ability to redistribute heat is compromised and can result in heat stress. Our results support that temperature and relative humidity may be important ($S_{ATemp+RHumid+ATemp*RHumid}$, Table 2.1). However, these results should be interpreted with caution. Due to the low ΔAICc relative to the number of additional parameters, the additional Rhumid and ATemp*Rhumid parameters may be uninformative (Arnold 2010).

Poor fit of the models incorporating release method effects on post-capture survival suggests that method of release may not have a significant influence on post-capture survival. Group and single release effects may have been confounded with ambient temperature and handling time effects, as release methods subject individuals to varying durations of handling, and greater durations of time exposed to the higher internal temperatures of the holding boxes. This could be addressed by improving ventilation, decreasing the internal temperature of the holding boxes, or releasing birds in smaller groups as opposed to releasing the captured flock at one time. Greater performance of the ATemp+HTime model suggests that adverse effects of the release methods are likely better predictors of post-capture survival.

Due to a low sample size of turkeys captured in walk-in traps, and their high 45-day survival, we were unable to estimate the relationship between capture methods and post-capture survival. If we had been able to capture more turkeys in walk in traps, we may have been able to estimate an effect. High 45-day survival for turkeys captured in walk-in traps (S=1.0) suggests that walk-in traps may reduce post-capture mortality rates when compared to cannon nets. Beringer et al. (1999) observed similar results in white-tailed deer (*Odocoileus virginianus*). Regardless, the low success of capture using walk-in traps forced us to-use cannon nets as the primary method of capture.

Nicholson et al. (2000) observed that greater handling times increased risk of capture-related mortality, and our data substantiate this claim. We suspect that greater handling times increased duration of elevated stress, increasing turkey susceptibility to capture myopathy (Nicholson et al. 2000). Because we suspected that greater handling time was resulting in greater rates of capture-related mortality, we made a concerted effort to maintain short handling times for all captured birds. To achieve the quickest possible processing times, we eliminated all measurements of physical characteristics, recording just age, sex, and radiotransmitter information. We believe that the tradeoff favoring reduced handling times at the expense of collecting measurements of physical characteristics was warranted. Weight, tarsus length, and ulna length may be related to post-capture survival, but effects of these physical characteristics were likely represented in age and sex covariates. Because we reduced handling times in our study, it was possible that we skewed our handling time data below the threshold to observe the influence of handling time on capture-related mortality.

Failure to use appropriate conditioning periods biases estimates of survival. Conditioning periods that do not encompass the period of higher capture-related mortality will bias survival estimates low. Alternatively, overestimating the capture-related mortality window could lead to poor estimates of survival. Furthermore, over or under estimation of the timing of capture-related mortality can influence estimates of frequency of capture-related mortality. This can have profound effects on estimates of population size, structure, and growth rates, and affect management decisions based on estimates of these population parameters.

Because we captured most turkeys during September and October, the ambient temperature and relative humidity at capture were right-skewed, resulting in estimates of capture-related mortality that were high. However, because we trapped turkeys over a range of temperatures and relative humidity, we believe that our estimates of those two covariates were unbiased. Had we been able to capture birds during times of the year with cooler ambient temperatures and reduced relative humidity, we would have had less capture-related mortality. However, trapping was limited to hotter, more humid times of the year due to high mast production during cooler times of year, which limited turkey response to baited net sites. Additionally, we were unable to interfere with hunting seasons on the study areas, forcing us to limit baiting and trapping to a limited number of locations across each study area.

Due to the reduction in time we took to process birds, total handling times for turkeys were left-skewed. Because the time turkeys were processed encompassed a wide range of times, we believe our estimates of effect of handling time on post-capture survival to be unbiased. Each age and sex class was well represented in our data, suggesting our estimates of the effects of age and sex on post-capture survival are precise. Poor representation of walk-in traps leads us to believe that estimates of the relationship between the two covariates may be biased. Increasing the sample size of birds captured using walk-in traps, would improve precision. Lastly, poor representation of the group release method may be biased estimates of release method effects. Increasing number of individuals released in groups would improve precision in estimates of those covariates.

Because the linear time trends outperformed the quadratic time trends, our data suggest that the odds of turkey survival increased by the same rate each day post-capture. Few studies in the literature have explored the timing of capture-related mortality. Our post-hoc models also indicate that the traditional 14-day censoring period may not be adequate to satisfy assumptions made in survival analysis. Our data suggest that capture-related mortality may be a factor in mortality as long as 33 days post-capture, 19 days longer than the traditional censoring period.

It could be argued that these results are confounded with age. However, our results show Age+ATemp and Age+RHumid models fit poorly suggesting that age had little effect on capture-related mortality.

Research Implications

Ambient temperature at time of capture appears to be the factor that had greatest influence on capture-related mortality. Accounting for ambient temperature can influence the time of year and day that trapping is conducted. While avoiding trapping efforts at high ambient temperatures can be prohibitive in achieving research objectives, it is critical that researches minimize the negative effects of capture, handling, and marking, on study species. Curtailing trapping efforts on days with high ambient temperatures, or developing tools to keep captured turkeys cool during the marking processes are potential ways in which researchers could mitigate the negative effects.

Monitoring and accounting for extended capture-related risk periods may provide the more accurate estimates of capture-related mortality and survival over longer periods. While extending the conditioning period may eliminate bias associated with capture, marking, and handling, there is the potential that the increase may bias estimates of annual and seasonal survival rates high by censoring natural mortality that occurs during some periods. Investigating the cause of mortality could help identify the prevalence of non-capture-related (i.e., natural) mortality during conditioning periods. Additionally, using strict monitoring schedules would allow the use of more robust models to estimate post-capture survival and improve the precision of estimates.

Together, these results, and future study design considerations can have major implications for wild turkey research in the southeastern United States. Our hope is that current and future turkey research projects will incorporate study-specific capture-related mortality rates. Addressing how vital rates and behavior changes post-capture could influence estimates of survival over longer periods of time, as well as the management actions based on those estimates.

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Table 2.1. Comparison of a priori models for estimating daily survival rates for eastern wild turkeys in Alabama 2015-2016. Values for AICc, relative differences in AICc model probability (ω), Likelihood (*L*), number of parameters in each model (*K*), and deviance are shown.

Modela	AICc	Δ AICc	ωi	*L*	*K*	Deviance
SATempb	542.78	0.00	0.253	1.00	2	538.78
SATemp+RHumidc	543.41	0.62	0.186	0.73	3	537.40
SATemp+SReld	544.03	1.25	0.136	0.54	3	538.03
SATemp+RHumid+ATempxRHumid	544.39	1.60	0.114	0.45	4	536.38
SATemp + Htimee	544.45	1.66	0.110	0.44	3	538.44
SATemp + Htime + Atemp x HTime	545.83	3.05	0.055	0.22	4	537.83
$S_{(.)}$[f]	546.40	3.62	0.042	0.16	1	544.40
SSRel	546.91	4.13	0.032	0.13	2	542.91
SHTime	547.71	4.93	0.022	0.09	2	543.71
SRHumid	548.37	5.59	0.016	0.06	2	544.37
SAge+Sex + ATemp	549.17	6.38	0.010	0.04	6	537.16
SSex	549.43	6.65	0.009	0.04	3	543.43
SAge	549.43	6.65	0.009	0.04	3	543.43
Sage+Rhumid	551.42	8.64	0.003	0.01	4	543.42
Sage + Sex	551.56	8.77	0.003	0.01	5	541.55

[a] Notation follows that of Hogan et Al. 2013, S = daily survival, 2015-2017

[b] Ambient temperature at the time of capture

[c] Relative humidity at the time of capture

[d] Single Release

[e] Total handling time

Table 2.2. Beta (β) estimates and standard errors for the most parsimonious (Δ AICc ≤ 2) a priori models of daily survival. 2015-2017

	Intercept		Atemp		Rhumid		Srel		Atemp x Rhumid		Htime	
Model	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
SATemp	5.65	0.47	-0.04	0.02*	-	-	-	-	-	-	-	-
SATemp+Rhumid	6.44	0.85	-0.05	0.02*	-0.01	0.01	-	-	-	-	-	-
SATemp+Srel	5.93	0.59	-0.04	0.18*	-	-	-0.39	0.47	-	-	-	-
SATemp+RHumid+ATempxRHumid	5.08	1.54	0.00	0.06*	0.01	0.02	-	-	0.00	0.00	-	-
SATemp+Htime	5.51	0.52	-0.04	0.02*	-	-	-	-	-	-	0.00	0.01

* Significantly different then 0

Table 2.3. Post Hoc models of daily survival with different trends in survival post capture. 2015-2017

Model	AICc	Δ AICc	ωi	*L*	K	Deviance
SATemp $_{+ LTTa}$	519.103	0.00	0.73027	1.00	3	513.099
SATemp $_{+ QTTb}$	521.095	1.9921	0.26971	0.3693	4	513.089
SATemp	542.783	23.6809	0.00001	0.00	2	538.782

[a] Linear time trend

[b] Quadratic time trend

Table 2.4. Post hoc models of daily survival rates with different risk periods. 2015-2017

Model	AICc	Δ AICc	ωi	*L*	K	Deviance
SATemp $_{+\ LTT\_33a}$	519.01	0.00	0.28	1.00	3.00	513.00
SATemp $_{+\ LTT}$	519.10	0.10	0.27	0.95	3.00	513.10
SATemp $_{+\ LTT\_32}$	519.12	0.11	0.27	0.95	3.00	513.11
SATemp $_{+\ LTT\_21}$	521.77	2.76	0.07	0.25	3.00	515.77
SATemp $_{+\ LTT\_14}$	525.07	6.06	0.01	0.05	3.00	519.06
SATemp $_{+\ LTT\_7}$	531.76	12.76	0.00	0.00	3.00	525.76
SATemp	542.78	23.78	0.00	0.00	2.00	538.78

[a] Linear time trend for 33 days post capture, followed by constant survival

Fig 2.1. Cumulative daily survival for 45 days post-capture under various ambient temperatures at the time of capture. 2015-2017.

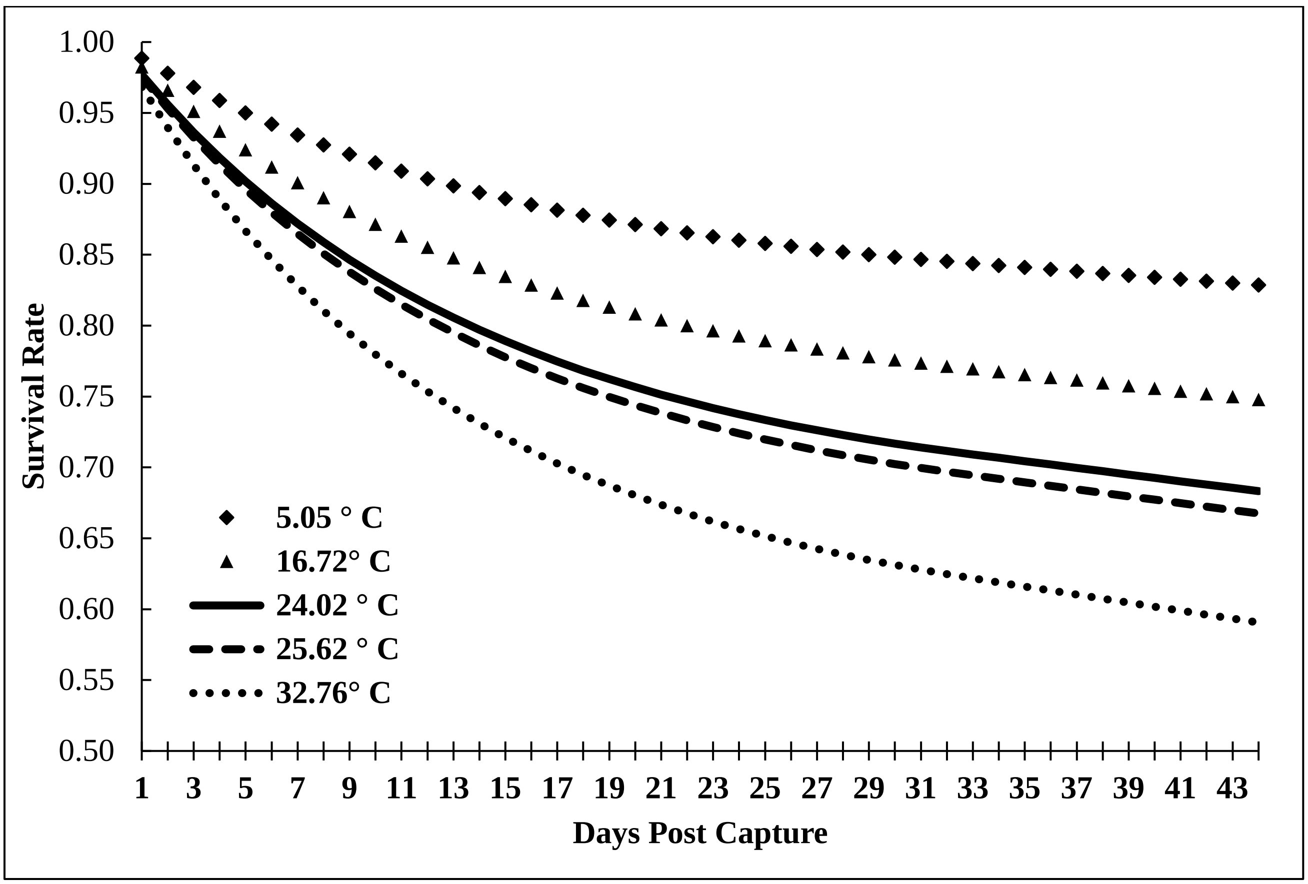


Fig. 2.2. Daily survival rates corresponding to different hypotheses about the changes and timing of capture-related mortality. 2015-2016.

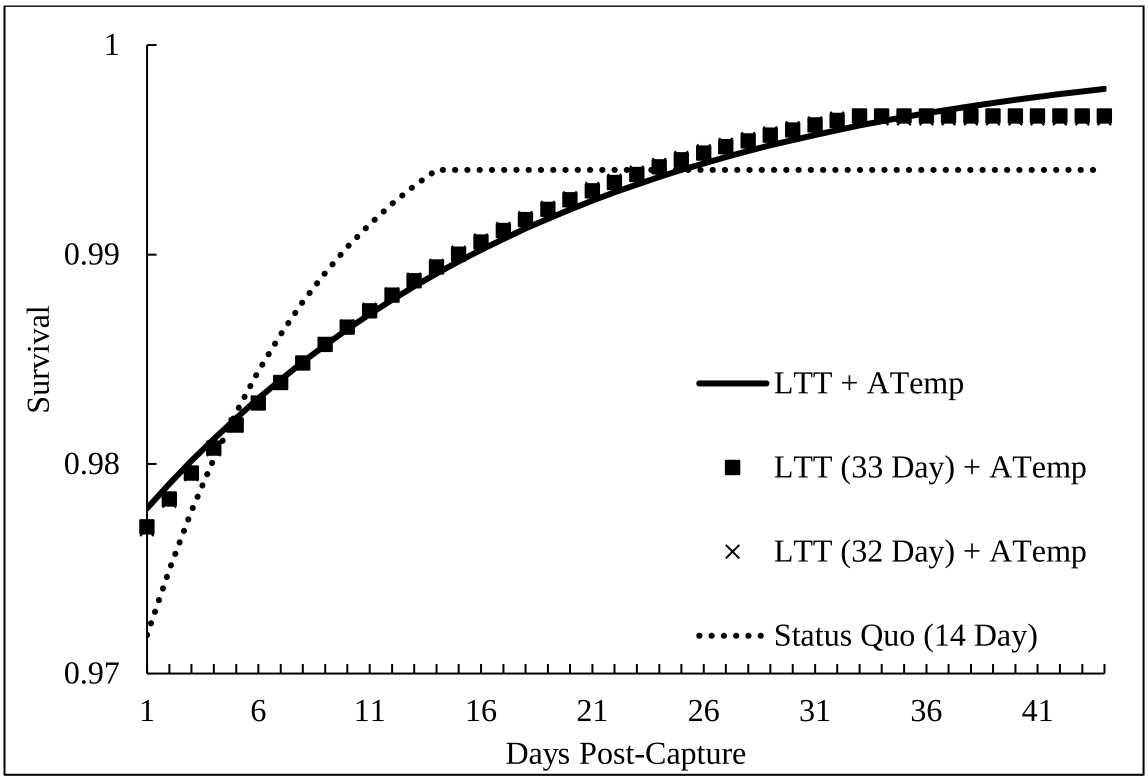
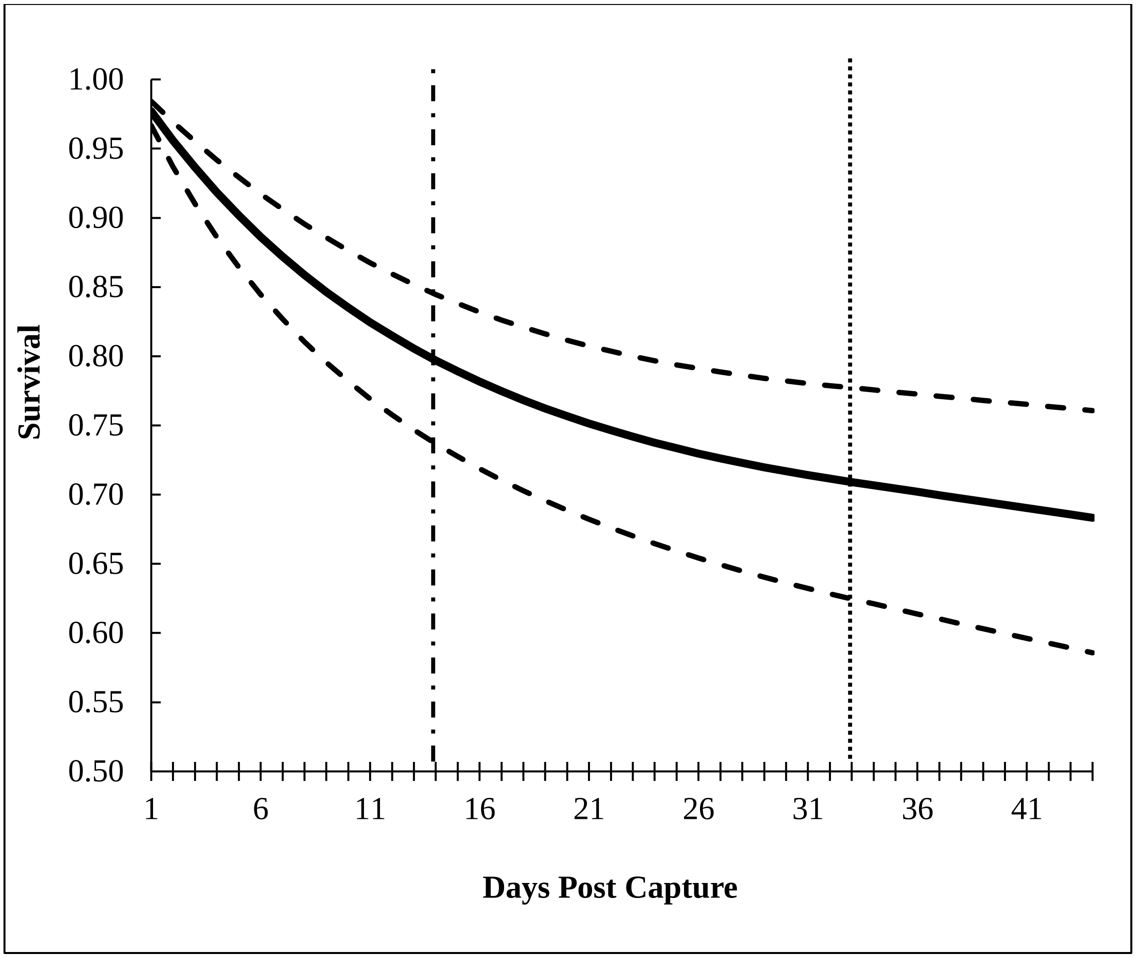


Fig 2.3 Cumulative daily survival rates for the top performing LTT + ATemp model with comparisons between 14 and 33-day survival rates. 2015-2017.



CHAPTER III: SURVIVAL RATES OF EASTERN WILD TURKEYS

Abstract

Estimates of annual and seasonal survival are important in understanding the size, structure, and growth rates of wildlife populations, and are a critical part in addressing the perceived decline of eastern wild turkeys (M. g.; hereafter, turkey) in the state of Alabama. Therefore, we captured and marked turkeys (*n* = 273) over two years and examined their annual and seasonal survival rates. We compared models using Akaike's Information Criterion (AIC) to determine factors that were most related to survival rates. We found that the best approximating model supported the hypothesis that survival rates varied with age, sex, and season. Annual survival of adult males was 0.44, and seasonal survival was greatest in the fall. Annual survival was 0.48 for adult females, 0.54 for subadult males, and 0.57 for subadult females. Seasonal survival rates of adult females and both subadult sex classes were greatest in the winter. Results suggest that the harvest of adult males during the spring hunting season, and predation or illegal harvest of subadult males during the fall, were the greatest sources of male mortality. Additionally, the greatest source of mortality for both adult and subadult females was predation in the spring and summer during nesting and brood rearing. Our results suggest that management focused on reducing the vulnerablility of turkeys to predation and harvest would have the greatest influence on survival rates.

Introduction

Understanding the dynamics of wildlife populations is necessary for effective management (Caughley 1977, Vangilder and Kurzejeski 1995, Anders and Marshall 2005) and the demographic rates most important in understanding and predicting population dynamics are survival and productivity (Lebraton et al. 1993). Influence of survival and productivity on population size, structure, and growth rates is dictated by life history of the study species (Caughley 1977, Coulson et al. 2005). Eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter, turkeys) are a polygamous, short-lived species, that produces large clutches and matures at a young age (Blankenship 1992). In avian species that have similar life history patterns, production and survival of offspring and adult female survival are the primary contributors to population growth (Saether and Bakke 2000). Past research on turkeys has substantiated these claims (Miller and Leopold 1992, Peoples et al. 1995, Roberts et al. 1995). Both nest success, a component of production, and poult and adult female survival, have been observed to affect annual fluctuations in abundance as well as long-term population growth (Roberts et al. 1995, Miller and Leopold 1992, Rolley et al. 1998, Pack et al. 1999). Addressing knowledge gaps in each of these areas will be critical to understanding the status of the turkey population in Alabama and predicting population dynamics to inform effective management objectives.

In addition to population growth, resource managers are often tasked with providing quality stakeholder experiences (Wynveen et al. 2005). Hearing, seeing, and harvesting male turkeys are the greatest contributors to quality experiences and stakeholder satisfaction (Wynveen et al. 2005). Therefore, maintaining or increasing abundance of males is an important management objective, and without accurate and precise estimates of male survival, it is difficult to understand the current or future availability of harvestable males.

Survival rates of wild turkeys are influenced by predation, harvest, and environmental factors (Paisley et al. 1995, Roberts et al. 1995, Vangilder 1995, Roberts and Porter 1998, Wright and Vangilder 2001, Hamberg et al. 2008,), and evidence suggests that these factors affect each age and sex classes differently (Vangilder 1995). Predation is one of the leading causes of mortality in male and female turkeys (Kurzejeski et al. 1987, Vander Haegen et al. 1988, Paisley et al. 1995, Vangilder 1995, Wright et al. 1996, Miller et al. 1998, Hubbard et al. 1999,Wright and Vangilder 2001, Hamberg et al. 2008), and is believed to be less common among adult males when compared with subadult males (Wright and Vangilder 2001), and less common in males when compared to females (Vangilder 1995). Predation of females occurred most frequently during nesting and brood rearing seasons (Kurzejeski et al. 1987, Wright et al. 1996), and amongst reproductively active females (Miller et al. 1998a). More adult females than subadults are reproductively active (Miller et al. 1998a), suggesting adult hens may be more susceptible to predation while nesting or rearing poults.

Harvest, both legal and illegal, is a significant source of mortality in some turkey populations (Paisley et al. 1995, Vangilder 1995, Wright and Vangilder 2001, Hamberg et al. 2008, Suchy et al. 1983, Vangilder and Kurzejeski 1995, Bailey and Rinell 1968), and is believed to be the greatest source of mortality in males (Godwin et al. 1992, Lelmini et al. 1992). Furthermore, studies conducted in Georgia, Kentucky, and Missouri reported harvest rates of adult males that were greater than subadult male harvest rates (Lelmini et al. 1992, Wright and Vangilder 2001, Hubbard and Vangilder 2005), suggesting harvest has a greater impact on survival of adult males when compared to subadults. Instances of illegal male harvest have been reported in many states across the turkey's range (Godwin et al. 1992, Lelmini et al. 1992, Paisley et al. 1995, Vangilder 1995, Wright and Vangilder 2001). However, few studies have reported significant male mortality attributed to illegal harvest (Godwin et al. 1992, Ielmini et al. 1992, Paisley et al. 1996, Wright and Vangilder 2001). Regarding females, studies have identified that illegal harvest exceeds that of legal harvest and can have a significant influence on survival (Roberts et al. 1995, Vangilder and Kurzejeski 1995). Miller et al. (1998a) reported greater incidence of illegal harvest in females that were not reproductively active, suggesting juvenile females are at greater risk of illegal harvest mortality.

Weather conditions are also a source of mortality that may affect turkey survival (Roberts and Porter 1998). Most notable are severe winter conditions (Roberts and Porter 1998), and precipitation (Rolley et al. 1988). Severe winter conditions have been reported in studies of northern turkey populations (Austin and DeGraff 1975, Wunz and Hayden 1975, Vander Haegen et al. 1988, Porter et al. 1989, Roberts et al. 1995), and may result in long periods during which turkeys are subject to thermoregulatory deficiency and low food abundance (Austin and Degraff 1975). Mortality associated with severe winter conditions likely influences subadults more than adults, and females more than males, due to the greater surface to mass ratio and greater metabolic demands (Roberts and Porter 1996). Porter et al. (1989) reported that severe winter conditions have the potential to influence subadult survival during the spring if winter conditions deplete nutritional reserves and more time must be spent foraging in favor of brooding young.

Abundance of terrestrial organisms is affected by precipitation, suggesting an influence of precipitation on survival rates (Krebs 1994). Increased precipitation during droughts can increase forage availability, decrease predator efficiency through increased vertical cover (Bowman and Harris 1980, Rolley et al. 1998), and decrease hunter effort (Rivrud et al. 2014). However, increased precipitation has been hypothesized to improve scenting conditions for predators (Roberts et al. 1996) and increase metabolic costs to maintain body temperature (Welty and Baptista 1988). Effects of precipitation are believed to have a significant effect on poult survival (Roberts and Porter 1998), but the relationship between precipitation and survival of older age classes is rarely explored.

Reported survival rates of wild turkeys have displayed variation between forest and landscape compositions (Pollentier et al. 2014). Mast is the most valuable food resource available to many wildlife species, including turkeys, during times of the year when herbaceous growth is limited (Mcshea et al. 2007). Increased species richness in forest communities has been observed to increase forest productivity (Zhang et al. 2012), indicating that diverse forest composition could support a greater abundance of turkeys. Increased proportions of specific forest types may reduce competition and increase survival (Lambert et al. 1990). Because females are more selective than males in the habitat types they occupy (Miller et al. 1999), forest composition likely affects females more than males.

Wild turkey use and interactions with roadways are complex, and information regarding effects are limited (McDougal et al. 1990). Increased road density can have positive effects on survival through increasing foraging opportunities (Oxley et al. 1973), or have negative effects through increased hunter access and predation (Holbrook and Vaughn 1985, Thogmartin and Schaeffer 2000, Francis et al. 2009). Because harvest mortality and predation likely influence adult survival more than subadult survival, increases in hunter and predator efficiency with increased road density likely influences adults more than subadults.

Given the relationships of age and sex to survival and their potential to affect number of turkeys in each class (e.g., Caughley 1977), it is important to have accurate estimates of seasonal survival for each age and sex class. The overall goal of this study is to provide a better understanding of turkey survival rates and the factors that influence them. Given this goal, our objectives are to: 1) estimate annual and seasonal survival rates of each turkey age and sex class and 2) determine the relationship of turkey survival to temperature, precipitation, forest composition, road density, and study area.

Study Areas

For a description of the study areas where turkeys were capture, marked, and monitored for survival analysis, see Chapter II of this thesis.

Methods

Data Collection

For a description of how turkeys were captured, marked, and monitored for survival analysis, see chapter II of this thesis.

We determined road density (% of study area's total area comprised of roads) of the study area using aerial imagery and available GIS layers. We assumed roads were 4.5 meters wide and calculated road density for each study area by dividing the area comprised of roads by total size of study areas. We determined forest composition percentages using National Land Cover Data (NLCD; Homer et al. 2015). The resolution for NLCD was 30m x 30m. We classified study areas by their percentage of total area comprised of hardwood, pine, mixed forest, or lack of overstory components (open). National Land Cover Data classified grids as hardwood or pine forests when they were comprised of >75% deciduous or evergreen tree species respectively. We classified grids as mixed forests when neither the hardwood or pine components were >75% of the total cover. Lastly, open forest type corresponded to grids that lacked a forest component, most notably, areas of grass or herbaceous cover, pastures, cultivated crops, or shrubland associated species. We determined percentage of the study area comprised of each forest cover type by taking total area for each forest type and dividing that by total area of each study area. Geospatial data was provided by the ADCNR and supplemented using aerial imagery (NAIP 2015, NAIP 2016) in ArcGIS (Version 10.3.1; ESRI, Redlands, CA, USA).

Both initially provided and supplemental data was verified in the field using Garmin GPS map 76x (Garmin, Canton of Schaffhausen, Switzerland). In addition to road density and forest composition, we calculated total precipitation (cm) for each survival interval using weather data collected from the nearest available National Oceanic Atmospheric Administration (NOAA) weather station. See chapter II of this thesis for location of NOAA weather stations and distance from study sites.

Statistical Analysis

We used known fate models (Pollock et al. 1989) to estimate seasonal survival rates. Additionally, we estimated the relationship between seasonal survival rates and covariates using the logit link in Program Mark (White and Burnham 1999). We located and determined status (alive or dead) of each individual for each survival interval. If we failed to detect individuals during any given interval, we censored those individuals. Conditions in which we censored individuals included radiotransmitter failure or emigration from the study area. We re-entered censored individuals into the at-risk pool once we relocated them. We assumed that censorship was not related to fate. Furthermore, we censored turkeys surviving <33 days post-capture to eliminate any potential capture-related biases (Chapter II).

We tested models representing biologically feasible hypotheses (Table 3.1) and ranked them based on Akaike's Information Criterion corrected for small sample size (AICc; Anderson et al. 2000, White & Burnham 1999) (MARK version 8.1). Age and sex were included in all models, as we believe both to always influence survival rates. We used AICc weights to determine the best approximating models, estimate survival rates, and to determine the factors with the greatest influence on survival. Where appropriate, we estimated parameters and sufficient statistics (Johnson 1999).

Results

During 2015-2017, we captured 273 turkeys. We censored 96 (35%) of these due to radiotransmitter loss, emigration from the study area, or potential capture and marking biases. The remaining individuals (177) were well-distributed among all ages and sexes. Our sample was comprised of 87 adults (33 male, 54 female), 81 subadults (39 male, 42 female), and 9 unknowns that were unable to be sexed at the time of capture. The best fit models were those that incorporated seasonal variation in survival rates. All models that included seasonal covariates performed better than the $S_{age + sex}$ model (Table 3.2.). The top-performing model ($S_{age + sex + fall + winter + age*season + sex*season}$) gathered nearly half of the cumulative weight (ω = .49), while the next best model (ΔAICc = 2.01) gathered 18% of the total weight. Models incorporating landscape or environmental covariates performed poorly, securing less than 4% of the cumulative weight.

Annual survival of adult males was 0.44 (SE=0.07). Fall survival of adult males was slightly greater than winter survival, and spring and summer survival was the lowest (Table 3.3). Annual survival of adult females was 0.48 (SE=0.06). Winter survival of adult females was greater than in any other season, followed closely by fall. Both winter and fall survival of adult females were greater than spring and summer survival (Table 3.3). Annual survival of male subadults was 0.54 (SE=0.08). Winter survival of subadult males was greater than any other season. Seasonal survival in spring and summer was the next highest, with survival being least in the fall (table 3.3). Subadult females had an annual survival of 0.57 (SE=0.07). Survival was s greater in winter when compared to fall, and fall survival was greater than spring and summer survival (table 3.3.).

Discussion

Age and sex effects were included in each model, as past research has observed variation in survival rates between age and sex classes (e.g., Vangilder 1995). In addition to age and sex effects, our top performing models also included seasonal effects. Our top model identified survival differences among fall, winter, and spring and summer, indicative of physiological and social changes in turkey populations (Ellis and Lewis 1967). Precision of survival rate estimates relative to each other was low (Table 3.3). We based our estimates of seasonal survival on the effects described by the top performing model and how they influenced overall performance of the model, not on the confidence limits of the survival rates. However, the poor performance of models including environmental and land cover factors was not expected. Precipitation, forest composition, and road density have been observed to influence survival (Oxley et al. 1973, Holbrook and Vaughn 1985, McDougal et al. 1990, Krebs 1994, Thogmartin and Schaeffer 2000, Francis et al. 2009, Pollentier et al. 2014). However, their poor performance suggests that they had little influence during our study. Poor performance of models including precipitation suggests that cumulative precipitation events had little influence on survival. Because we censored the first 33 days post-capture from analysis, and it is believed that turkeys are most susceptible to mortality attributed to precipitation with the first 2 weeks post-hatch (Roberts and Porter, 1998), it is likely that we censored any effects of precipitation on survival from our study. A potential explanation for the poor performance of the models incorporating landscape level effects may be the scale with which we collected data. Each of the variables were measured at the study area level, a scale that may not be biologically relevant to individual turkeys. Additionally, interval precipitation totals varied little across the study sites, road densities for each study site were low, and with exception to Skyline WMA, differences between forest compositions at the study sites were minimal. Lack of variability amongst the variables at the study sites could have contributed to the poor performance of these models.

Annual survival of adult males in our study was greater than rates reported in Kentucky (26%, Wright and Vangilder 2001), Kansas (36%, Holdstock et al. 2006), and Missouri (37%, Hubbard and Vangilder 2005), and was within the ranges reported in Georgia (44-64%, Lelmini et al. 1992) and Mississippi (39-54%, Godwin et al. 1991). The primary source of mortality in each of these studies was harvest during the spring hunting season. Twenty-four percent of adult males in our study were harvested, suggesting that spring hunting season may be the primary source of adult male mortality. Additionally, we expected seasonal survival during the spring to be lowest of all seasons because of spring harvest.

Annual survival of adult females in our study was greater than annual survival rates reported in Ontario (29%, Nguyen et al. 2003) and Kansas (40%, Hennen and Lutz 2001). Our rates were comparable to reported survival in Mississippi (24-77%, Miller et al. 1998), and Missouri (45-69%, Vangilder and Kurzejeski 1995), and less than reported survival in New York (50%, Roberts et al. 1996), Louisiana (67%, Wilson et al. 2005), and another study in Mississippi (68%, Palmer et al. 1993). Common sources of mortality throughout these studies were predation and severe weather conditions. Weather conditions were more important in studies of northern turkey populations (Roberts et al. 1995), which can be subjected to prolonged periods of deep snow, and in Rio Grande wild turkeys (*Meleagris gallopavo intermedia*) in Kansas (Hennon and Lutz 2001) when above-average precipitation events coincide with nesting. Because winter weather conditions are milder in Alabama when compared to New York and Ontario (National Oceanic and Atmospheric Administration 2011), extreme weather events are less common in Alabama when compared to Kansas (National Oceanic and Atmospheric

Administration 2011), and we observed our lowest seasonal survival being during the sping and summer, we believe that predation is the primary source of mortality in Alabama's adult female population. As expected, fall and winter survival were much greater than spring and summer survival. It is commonly reported that predation occurs most frequently during nesting and brood rearing, when female nesting and brood rearing behavior makes them more vulnerable to predators (Roberts et al. 1996, Hubbard et al. 1999, Kurzejeski and Vangilder 1987, Vander Haegen et al. 1988, Palmer et al. 1993).

Annual survival of subadult males in our study was comparable to rates reported in Kentucky (55%, Wright and Vangilder 2001), and slightly less than reported rates in Georgia (44-64%, Lelmini et al. 1992). Both studies reported that harvest was the primary source of mortality. Because our results contradict the findings in Kentucky and Georgia, and we observed greatest seasonal survival during spring, it is unlikely that harvest had the greatest effect on subadult male survival in our study. Spring and summer survival have been greater due to the unique behavior of subadults during this time. Nonreproductive subadult male flocks are motivated by avoiding disturbance and finding food rather than breeding (Ellis and Lewis 1967). Additionally, studies in Georgia (Lelmini 1992), western Kentucky (Wright 2001), and Missouri (Hubbard and Vangilder 2005) identified greater harvest mortality in adult males when compared to subadult males, suggesting hunters may have a preference toward harvesting older, more mature turkeys. Both the differences in behavior and the potential hunter selectivity could potentially expose subadult males to less risk of harvest. Another possible explanation for our results could be increased mortality during dispersal, as dispersal and migration have been suggested to influence subadult survival (Lehman et al. 2005).

Annual survival estimates of subadult females in our study were greater than rates reported in Merriam's wild turkeys (*Meleagris gallopavo merriami*) in South Dakota (49%, Lehman et al. 2005), and less than rates reported in Iowa (71%, Hubbard et al. 1999). Low survival in South Dakota was attributed to severe weather conditions and predation. Similar to our conclusions for adult females, we believe weather had little effect on subadults female survival, and that predation was likely the greatest source of mortality. Miller et al. (1998) observed greater rates of mortality in reproductively active females. Because subadult females are less likely to be reproductively active (Miller et al. 1998), they may be less affected by predation. Seasonal survival of subadult hens was least in spring and summer, consistent with much of the past literature (Kurzejeski and Vangilder 1987, Vander Haegen et al. 1988, Palmer et al. 1993, Roberts et al. 1996, Hubbard et al. 1999).

Annual and seasonal survival rates were expected to vary between age and sex classes (Vangilder 1995). We observed greater subadult survival for both males and females. Regarding males, we identify harvest during the spring as a primary source of mortality for adults. It appears that subadult males were not subject to the same harvest risk. This suggests that hunters may be selective in the turkeys they harvest. Lelmini et al. (1992) and Wright and Vangilder (2001) reported a similar trend. Although we had a small sample of harvested males, our results support this hypothesis. Of all reported harvests (n=11), 8 were adult males, and 3 were juvenile males, even though we captured and marked a greater number of subadults.

Similarly, subadult female survival was greater than adult female survival. Badyaev et al. (1996) suggested that greater movements and increased habitat sampling by females would improve nest-site selection and increase survival. Our results, as well as those of Hubbard et al. (1999), refute this hypothesis. Hubbard et al. (1999) observed that distance between nesting and wintering grounds increased mortality. Moreover, our observation of greater subadult survival in conjunction with the fact that adults tend to have greater home ranges (Badyaev et al. 1996) also refutes the hypothesis suggested by Badyaev et al. (1996). Perhaps a better explanation for our observed differences between adult and subadult female survival is the increased risk to adult females while they are nesting and brood rearing.

Management Implications

Our data suggests that most turkeys are susceptible to mortality during spring and summer. Improving quality and quantity of nesting and brood rearing habitat may help reduce the risk of predation and improve survival of adult and subadult females. The trends I observed in my study indicate that male mortality in the spring is likely indicative of hunters being selective in the turkeys they choose to harvest. Although likely to stimulate negative feedback from stakeholders in the short term, making harvest regulations more conservative by reducing the season length or bag limit of the spring turkey season may improve adult male survival. Hunters would experience a reduction in the time they have to hunt, and the number of turkeys they could harvest, but this would increase the number of turkeys available to be hunted. Greater subadult survival facilitated by these harvest regulations may lead to high recruitment into the adult age class and more high-quality hunting opportunities.

Long term implications of the survival rate estimates provided should be interpreted with caution. Survival rate estimates provided, in conjunction with productivity rate estimates from Alabama (Gonnerman 2017), indicate that the turkey population is declining at a rate greater than previously believed. However, survival and productivity rates have been observed to vary considerably amongst years (Miller et al. 1998a, 1998b). Thus, without data collected over longer time periods to encompass annual variability, we cannot infer that turkey population is exhibiting a short term pattern, or a long term trend of decline.

Further investigation is needed to determine the influence of landscape and environmental conditions on survival rates. Because landscape and environmental covariates were measured at the study scale, they are likely relevant to turkey populations (Glennon and Porter, 1999), but we observed little effect on the survival of individual turkeys. Future research should emphasize collecting data at scales that are biologically relevant to individual turkeys.

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Table 3.1. Hypotheses and their associated models used to identify annual and seasonal survival rates of turkey, as well as the factors with the greatest influence on survival.

Model	Hypothesis
$S_{(Age + Sex + Fall + Winter + Seasons*Age + Seasons*Sex)}$	Seasonal effects for fall and winter survival vary from spring and summer, and the effects of season vary for each age and sex class.
$S_{(Age + Sex + Fall + Winter + Seasons*Age)}$	Seasonal effects for fall and winter survival vary from spring and summer, and the effects of season vary for each age class.
$S_{(Age + Sex + Spring + Summer + Winter + Age*Seasons + Sex*Seasons)}$	Seasonal effects for each season vary, and the effects of season vary for each age and sex class
$S_{(Age + Sex + Spring + Summer + Seasons*Sex)}$	Seasonal effects of spring and summer survival vary from fall and winter, and the effects of season vary for each sex class.
$S_{(Age + Sex + Fall + Winter + Seasons*Sex)}$	Seasonal effects of Fall and winter survival vary from spring and summer, and the effects of season vary for each sex class
$S_{(Age + Sex + Fall + Winter)}$	Seasonal effects of fall and winter survival vary from spring and summer.
$S_{(Age + Sex + Spring + Summer)}$	Seasonal effects of spring and summer survival vary from fall and winter.
$S_{(Age + Sex + Spring + Summer + Winter)}$	Seasonal effects on survival vary for each season.
$S_{(Age + Sex + Spring + Summer + Seasons*Age + Seasons*Sex)}$	Seasonal effects on survival vary for each season, and the effects of season vary for each age and sex class.
$S_{(Age + Sex + Precip + Sex*Precip + Age*Precip)}$	Precipitation totals for each interval influenced survival, and the effects of precipitation on survival vary for each age and sex class.
$S_{(Age + Sex + Precip)}$	Precipitation totals for each interval influenced survival.
$S_{(Age + Sex + Spring + Summer + Seasons*Age)}$	Seasonal effects of spring and summer vary from fall and winter, and the effects of season vary for each age class.
$S_{(Age + Sex)}$	Survival is influenced by age and sex class.
$S_{(Age + Sex + Precip + Age*Precip)}$	Precipitation totals for each interval influenced survival, and the effects of precipitation on survival vary for each age class.
$S_{(Age + Sex + ForestComp(HW))}$	The percentage of the study are comprised of hardwood stands influenced survival.
$S_{(Age + Sex + ForestComp(Pine))}$	The percentage of the study are comprised of pine stands influenced survival.
$S_{(Age + Sex + RdDensity)}$	The percentage of the study area comprised of roads influenced survival.
$S_{(Age + Sex + ForestComp(Mixed))}$	The percentage of the study are comprised of mixed pine-hardwood stands influenced survival.
$S_{(Age + Sex + Precip + Sex*Precip)}$	Precipitation totals for each interval influenced survival, and the effects of precipitation on survival vary for each sex class
$S_{(Age + Sex + ForestComp(Open))}$	The percentage of the study are comprised of open landscapes influenced survival.
$S_{(Age + Sex + ForestComp(all))}$	The percentage of the study area comprised of each forest composition influenced survival.
$S_{(Age + Sex + ForestComp(HW+Mixed))}$	The percentage of the study area comprised of hardwood and mixed pine hardwood stands influenced survival.
$S_{(Age + Sex + ForestComp(Pine + Mixed))}$	The percentage of the study area comprised of pine and mixed pine hardwood stands influenced survival.
$S_{(Age + Sex + StudyArea)}$	Survival rates vary between study areas
$S_{(Age + Sex + RdDensity + Age*RdDensity)}$	The percentage of the study area comprised of roads influenced survival, and the effect of road density vary for each age class.
$S_{(Age + Sex + RdDensity + Sex*RdDensity)}$	The percentage of the study area comprised of roads influenced survival, and the effect of road density vary for each sex class.

Table 3.2. A priori models for estimating seasonal and annual survival rates of eastern wild turkeys in Alabama 2015-2016. Values for AICc, relative differences in AICc model probability (w), Likelihood (L), number of parameters in each model, and deviances are shown.

Model	AICc	Δ AICc	ωi	*L*	*K*	Deviance
S(Age + Sex + Fall +Winter + Seasons*Age + Seasons*Sex)	492.00	0.00	0.49	1.00	12	467.44
S(Age + Sex + Fall +Winter + Seasons*Age)	494.01	2.01	0.18	0.37	8	477.76
S(Age + Sex + Spring + Summer +Winter + Age*Seasons + Sex*Seasons)	496.29	4.30	0.06	0.12	16	463.32
S(Age + Sex + Spring + Summer + Seasons*Sex)	496.35	4.35	0.06	0.11	9	478.03
S(Age + Sex + Fall +Winter + Seasons*Sex)	496.39	4.39	0.05	0.11	10	476.00
S(Age + Sex + Fall +Winter)	496.59	4.60	0.05	0.10	6	484.45
S(Age + Sex + Spring + Summer)	498.16	6.16	0.02	0.05	6	486.01
S(Age + Sex + Spring + Summer +Winter)	498.44	6.44	0.02	0.04	7	484.24
S(Age + Sex + Spring + Summer + Seasons*Age + Seasons*Sex)	500.17	8.17	0.01	0.02	12	475.61
S(Age + Sex + Precip + Sex*Precip + Age*Precip)	500.60	8.60	0.01	0.01	8	484.35
S(Age + Sex + Precip)	500.68	8.68	0.01	0.01	5	490.57
S(Age + Sex + Spring + Summer + Seasons*Age)	500.70	8.70	0.01	0.01	8	484.45
S(Age + Sex)	500.76	8.76	0.01	0.01	4	492.69
S(Age + Sex + Precip + Age*Precip)	500.95	8.96	0.01	0.01	6	488.81
S(Age + Sex + ForestComp(HW))	501.07	9.07	0.01	0.01	5	490.97
S(Age + Sex + ForestComp(Pine))	501.19	9.20	0.00	0.01	5	491.09
S(Age + Sex + RdDensity)	501.71	9.71	0.00	0.01	5	491.61
S(Age + Sex + ForestComp(Mixed))	501.98	9.98	0.00	0.01	5	491.88
S(Age + Sex + Precip + Sex*Precip)	502.02	10.02	0.00	0.01	7	487.82
S(Age + Sex + ForestComp(Open))	502.38	10.38	0.00	0.01	5	492.28
S(Age + Sex + ForestComp(all))	503.11	11.12	0.00	0.00	6	490.97
S(Age + Sex + ForestComp(HW+Mixed))	503.11	11.12	0.00	0.00	6	490.97
S(Age + Sex + ForestComp(Pine + Mixed))	503.11	11.12	0.00	0.00	6	490.97
S(Age + Sex + StudyArea)	503.11	11.12	0.00	0.00	6	490.97
S(Age + Sex + RdDensity + Age*RdDensity)	503.15	11.15	0.00	0.00	6	491.00
S(Age + Sex + RdDensity + Sex*RdDensity)	503.28	11.28	0.00	0.00	6	491.13

Table 3.3. Seasonal survival rate of each age and sex class of wild turkey in Alabama. 2015-2017

	Winter		Spring		Summer		Fall	
	S	(SE)	S	(SE)	S	(SE)	S	(SE)
Male								
Adult	0.84	(0.06)	0.79	(0.05)	0.79	(0.05)	0.85	(0.05)
Sub Adult	0.98	(0.02)	0.85	(0.04)	0.85	(0.04)	0.78	(0.08)
Female								
Adult	0.92	(0.04)	0.77	(0.04)	0.77	(0.04)	0.90	(0.04)
Sub Adult	0.99	(0.01)	0.83	(0.04)	0.83	(0.04)	0.85	(0.05)

CHAPTER IV: CONCLUSIONS

Accurate and precise estimates of survival are crucial for determining the size, structure, and growth rate of Alabama's wild turkey population. Each of which is important in understanding the current population status, as well as how it will respond to different harvest regulation alternatives. I identified and addressed a potential source of bias in estimates of turkey survival, and incorporated those findings in the estimation of annual and seasonal survival rates.

I established that ambient temperature at the time of capture appears to be the factor with the greatest influence on capture-related mortality. Furthermore, I illustrated that the influence of the capture, marking, and handling processes may be affecting wild turkeys for 33 days. Censoring 33-days post-capture is more than twice as long as previously suggested in the literature. Future research efforts should take into account the environmental factors that have the greatest influence on post-capture survival so that they can minimize the loss of data. Additionally, researchers should censor more observations post-capture to minimize bias in survival rate estimation due to post-capture effects.

I also established seasonal and annual survival rates for each age and sex class of wild turkeys. Not only will this help identify the population size, structure, and growth rate of Alabama's turkey population, but it will also help identify potential ways in which survival rates can be improved. There is room for improvement in this research. Collecting environmental and landcover data at finer scales more applicable to wild turkeys may provide more insight, specifically how environmental and landscape level factors influence survival. Information regarding environmental effects can help predict survival rates used in population models, and understanding the influence of landscape level factors can help inform management initiatives targeted to increase survival rates Regardless, the estimates of annual and seasonal survival for each age and sex are up to date, state-of-the art, and useful for advancing our knowledge of turkey population size, structure and growth rate trends.

Appendix A. Beta estimates for top a priori model of survival 2015-2017.

Covariate	β	SE	LCI	UCI
Intercept	1.57532	0.305067	0.97739	2.173251
Age	-0.38821	0.33293	-1.04075	0.26433
Male	0.127645	0.326523	-0.51234	0.767629
Unknown	1.053502	1.07102	-1.0457	3.152701
Fall	0.175913	0.522149	-0.8475	1.199324
Winter	2.903836	0.96968	1.003263	4.804408
Age*Fall	0.831047	0.569224	-0.28463	1.946725
Age*Winter	-1.70672	0.922221	-3.51427	0.100834
Male*Fall	-0.60417	0.585504	-1.75176	0.543418
Male*Winter	-0.88284	0.721711	-2.29739	0.531719
Unknown*Fall	-1.5815	1.300299	-4.13009	0.967087
Unknown*Winter	-3.80015	1.388925	-6.52244	-1.07786