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RESEARCH ARTICLE

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Survival and cause-specific mortality of male wild turkeys across the southeastern United States

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Abstract

Estimating survival and cause-specific mortality of male eastern wild turkeys (*Meleagris gallopavo silvestris*) is important for understanding population dynamics and implementing appropriate harvest management. To better understand age-specific estimates of annual survival and harvest rates, we captured and marked male wild turkeys with leg bands (*n* = 311) or bands and transmitters (*n* = 549) in Georgia, Louisiana, North Carolina, and South Carolina, USA, during 2014–2022. We fitted time to event models to data from radio-marked birds to estimate cause-specific mortality and annual survival. We used band recovery models incorporating both band recovery and telemetry data to further investigate harvest rates and survival. Annual survival from known-fate models in hunted populations was 0.54 (95% CI = 0.49–0.59) for adults and 0.86 (95% CI = 0.81–0.92) for juveniles. Cause-specific mortality analysis produced an annual harvest estimate of 0.29 (95% CI = 0.24–0.33) for adults and 0.02 (95% CI = 0.01–0.03) for juveniles, whereas predation was 0.15 (95% CI = 0.10–0.20) and 0.12 (95% CI = 0.08–0.17), respectively. Annual survival for adult males in a non-hunted

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population was 0.83 (95% CI = 0.72–0.97). Survival rate was negatively correlated with harvest rate, indicating harvest was an additive mortality source. Annual survival from band recovery models was 0.40 (95% CI = 0.37–0.44) for adults and 0.88 (95% CI = 0.81– 0.93) for juveniles, whereas annual harvest estimates were 0.24 (95% CI = 0.23–0.25) for adults and 0.04 (95% CI = 0.03–0.05) for juveniles. Both models suggested no differences in annual survival across years or among study areas, which included privately owned and public properties. Harvest was an additive mortality source for male wild turkeys, suggesting that managers interested in increasing annual survival of adult males could consider ways of reducing harvest rates.

KEYWORDS
Barker recovery model, harvest, known-fate, *Meleagris gallopavo*, predation

Estimates of survival and cause-specific mortality and assessments of harvest rates are necessary for sustainable management of game species (Arnold et al. 2016, Prieto et al. 2019, Israelsen et al. 2020). A primary objective of harvest management is to achieve a sustainable yield, where a harvestable surplus is permitted by compensatory mortality (Larkin 1977, Robinson et al. 2014). To achieve this objective, harvest rate must not surpass effects of natural mortality by decreasing natural mortality after hunting (Bartmann et al. 1992, Boyce et al. 1999, Sandercock et al. 2011) or harvest and natural mortality must be less than the number of individuals being recruited into the population via reproduction (Swenson 1985, Bro et al. 2003) or immigration (Smith and Willebrand 1999, Martin et al. 2000). Determining the threshold wherein harvest mortality becomes additive to non-harvest mortality generally requires estimating survival while experimentally varying harvest rates (Nichols et al. 1984, Sandercock et al. 2011, Woodard et al. 2022) or studies of marked populations subjected to no and varying levels of harvest (Burnham and Anderson 1984, Sedinger et al. 2010, Pearse et al. 2020).

Marked individuals in hunted populations offer researchers the ability to collect data for estimating survival and mortality from harvest and non-harvest causes (Smith and Willebrand 1999, Israelsen et al. 2020, Norman et al. 2022). These data can be collected by marking individuals and determining status via reencounters, locational data, band-recovery data reported by hunters, or some combination (Buderman et al. 2014, Wann et al. 2020). Monitoring individuals using telemetry provides information on fate and cause-specific mortality, which can be used for direct estimates of harvest and survival (Robinson et al. 2014, Millsap et al. 2022). Monitoring with telemetry can be expensive for a sufficient number of individuals because of costs associated with transmitters and tracking (Millspaugh 2001, Rogers and White 2007). Conversely, monitoring banded individuals can lower costs, allowing more animals to be marked but restricting information on individuals harvested and reported by hunters (Brownie et al. 1985, Schwarz et al. 1993). Approaches combining data from radio-marked and banded individuals can provide robust inferences about survival and harvest rates by increasing the number of estimable parameters, while also increasing the accuracy and precision of the estimates by reducing bias (Nasution et al. 2001, Buderman et al. 2014, Buckley et al. 2022).

Eastern wild turkey (*Meleagris gallopavo silvestris*; wild turkey) is the most abundant wild turkey subspecies in North America and is a game bird of cultural and economic significance (Chapagain et al. 2020, Chamberlain et al. 2022). Over the last 2 decades, managers observed decreases in abundance, recruitment, and spring harvest throughout broad areas of the subspecies' range (Byrne et al. 2015, Casalena et al. 2015, Chamberlain et al. 2022). Population declines resulted in concern by state wildlife agencies as to the status of wild turkey populations and concomitant increases in research throughout the species' range. The relationship between harvest mortality and survival of wild turkeys has been studied, but survival rates of hunted wild turkey populations need to be continually assessed to develop appropriate harvest limits, and studies investigating annual survival and harvest in the last decade are lacking (Vangilder and Kurzejeski 1995; Chamberlain et al. 2012, 2022). Extant literature supports the assumption that spring-only hunting constitutes an additive mortality source for males (Vangilder and Kurzejeski 1995, Wright and Vangilder 2001, Moore et al. 2008, Chamberlain et al. 2012). This assumption has only been verified in a single study area subjected to varying levels of harvest (Moore et al. 2008).

To better understand wild turkey demography, we used telemetry and banding data collected from research projects across 4 states in the southeastern United States to estimate annual survival, harvest, and rates of cause-specific mortality for male wild turkeys. Our primary objective was to produce age-specific estimates of annual survival and harvest rates for male wild turkeys. Second, we evaluated potential differences in these vital rates across study sites and years, and estimated rates of cause-specific mortality from harvest and non-harvest sources. Lastly, we evaluated the assumption that spring harvest represents an additive mortality source for male wild turkeys by comparing data across various hunted sites to a non-hunted site.

STUDY AREA

We conducted research on 8 study areas across Georgia, Louisiana, North Carolina, and South Carolina, USA (Figure 1). The climate across our study region was subtropical, with annual temperatures ranging from 5.9°C to 26.5°C and annual precipitation ranged from 92.5 cm to 256.5 cm (www.prism.oregonstate.edu, accessed 5 May

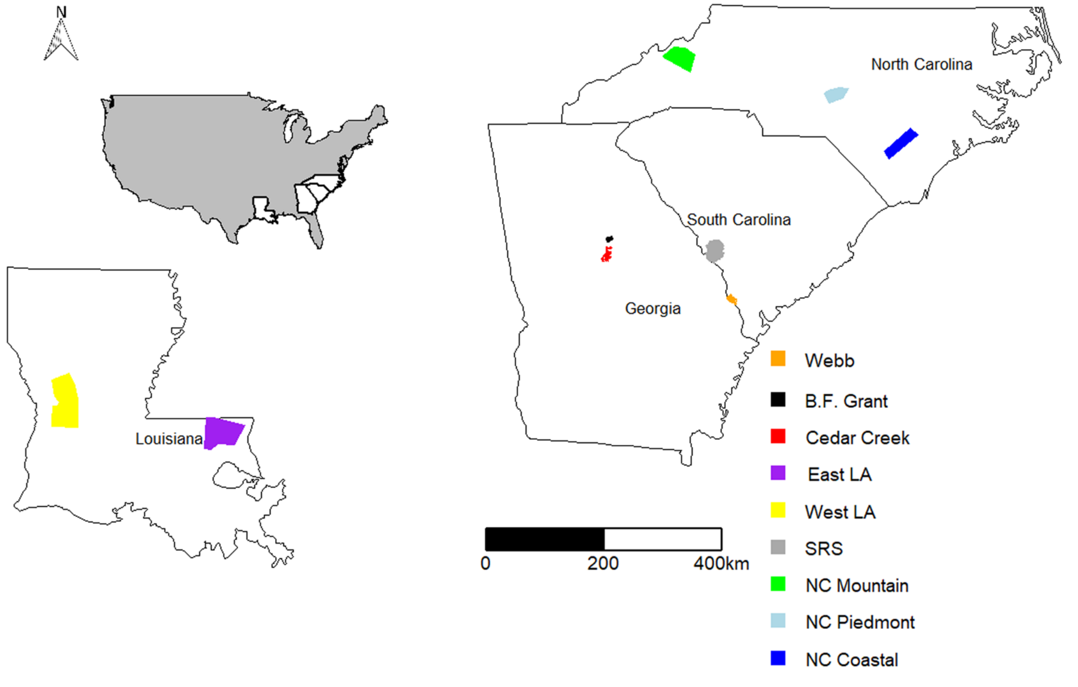

FIGURE 1 Distribution of 8 study sites across the southeastern United States where we studied survival of male eastern wild turkeys during 2014–2022.

2023). Common fauna across all study areas known to predate male wild turkeys included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and great horned owls (*Bubo virginianus*). The study period varied across study areas, as data collection occurred for multiple research projects with varying funding and objectives. Furthermore, land-management approaches varied across study areas depending on ownership, goals, and objectives. Lastly, season dates and bag limits for male wild turkey varied across study areas, as they occurred across multiple states and ownerships with different regulatory frameworks. We conducted research on B. F. Grant Wildlife Management Area (WMA), Cedar Creek WMA, and surrounding private property in Georgia during 2017–2022. The B. F. Grant WMA, a 4,613-ha area located in Putnam County, Georgia, was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia and managed cooperatively with the Georgia Department of Natural Resources Wildlife Resources Division. The property consisted of managed forest, predominately loblolly pine (*Pinus taeda*) and mixed hardwood-pine (*Pinus* spp.) forests, and experimental agricultural grazing land for livestock. The understory was dominated by eastern redbud (*Cercis canadensis*), sweetgum (*Liquidambar styraciflua*), muscadine (*Vitis rotundifolia*), and briars (*Rubus* spp.). Wild turkey hunting season on B. F. Grant WMA was spring only and split into 3 segments, the first an 8-day youth-only hunt that began the fourth Saturday in March and was followed by an 80-person quota that lasted 7 days. The final hunt began after the quota hunt, was open to the general public, and lasted until 15 May. In 2022 the youth hunt did not start until the second Saturday in April, the duration was the same for the first and second hunt from previous years, whereas the final hunt followed the second hunt and closed on 15 May. Cedar Creek WMA was 16,187 ha located in Jasper, Jones, and Putnam counties, Georgia. Cedar Creek WMA was owned by the United States Forest Service and managed in partnership with the Georgia Department of Natural Resources. The site was composed of loblolly pine forests and mixed hardwood pine forests with similar understory composition to B. F. Grant WMA. In 2017 and 2018, the spring only wild turkey hunting season was open to the public from the fourth Saturday in March to 15 May, whereas in 2019–2022 the season ran from the first Saturday in April to 15 May. During 2017–2021 wild turkey hunters in the state of Georgia could harvest up to 3 male wild turkeys; this changed to 2 in 2022. Both study sites also included adjacent private properties. Forest management on both sites was primarily through patch cuts, thinning, and prescribed fire applied on an approximately 3–5-year rotation. Areas surrounding B. F. Grant and Cedar Creek WMAs were predominately pine forests and agricultural fields for livestock, and average elevation was 520 m. The climate for B. F. Grant and Cedar Creek WMAs was characterized by hot, dry summers and cool, wet winters.

We also conducted research on the Kisatchie National Forest (KNF), Fort Polk WMA, Peason Ridge WMA, and surrounding private properties in west-central Louisiana during 2013–2022. The KNF was divided into 5 districts encompassing over 244,000 ha in Rapides, Vernon, Grant, Winn, Natchitoches, Webster, and Claiborne parishes, and was owned and managed by the United States Department of Agriculture-Forest Service. Fort Polk and Peason Ridge WMAs were in Vernon, Sabine, and Natchitiches parishes and jointly owned by the United States Forest Service (39,710 ha within KNF) and the United States Army (managed 70,100 ha of land). Both sites and surrounding private properties were composed of pine-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility rights-of-way, and forest roads distributed throughout. Average elevation was 60 m for KNF and Fort Polk and Peason Ridge WMAs. The understory was dominated by little bluestem (*Schizachyrium scoparium*), sweetgum and other hardwood regeneration, yaupon (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), blackberry, greenbrier (*Smilax* spp.), wild grape (*Vitis* spp.), and woodoats (*Chasmanthium* spp.). In 2013–2017, the spring only wild turkey hunting season opened the fourth Saturday in March and lasted 23 days on public lands and 30 days on private property, whereas in 2018–2022 the season started the first Saturday in April and lasted 23 days on public lands and 30 days on private property. From 2013–2022, there was a youth season the Saturday and Sunday prior to the regular season opening date. During all years of the study, wild turkey hunters in the Louisiana could harvest up to 2 male wild turkeys. Prescribed fire was applied on an approximately 3- to 5-year return interval on both sites. The KNF and Fort Polk and Peason Ridge WMAs were characterized by subtropical climates, with hot, wet summers and cool, wet winters. Yeldell et al. (2017) provides a detailed description of site conditions on KNF and Fort Polk WMA.

During 2020–2022, we conducted research across a broad suite of private and public lands, including the Sandy Hollow WMA, in Tangipahoa and Washington parishes in southeastern Louisiana. The region was composed of rolling hills with hardwood riparian zones interspersed with loblolly pine plantations and agricultural production (grazing) as the dominant private land uses. The understory was dominated by yaupon, sweetgum and other hardwood regeneration, American beautyberry, blackberry, greenbrier, wild grape, and woodoats on most private tracts. The Sandy Hollow WMA consists of 1,888 ha of rolling hills with intensively managed longleaf pine (*Pinus palustris*) forest and hardwood riparian zones. It was managed using prescribed burning on a 1–2-year return interval to benefit northern bobwhite quail (*Colinus virginianus*) and other grassland birds. The understory on Sandy Hollow WMA was dominated by little bluestem, goat's rue (*Galega officinalis*), partridge pea (*Chamaecrista fasciculate*), numerous other native grasses and forbs, and scattered American beautyberry, blackberry, sweetgum, and other hardwood regeneration. The spring only wild turkey season opened on the first Saturday in April and lasted 16 days on public lands and 30 days on private property. There was a youth hunt on the Saturday and Sunday prior to the regular season opener on private land only. Mean elevation was 66 m and climate was characterized by hot, humid summers and mild to cool winters.

During 2014–2018, we conducted research on 3 contiguous WMAs in South Carolina known as the Webb WMA Complex, which was 10,483 ha in Hampton and Jasper counties, owned and managed by the South Carolina Department of Natural Resources. Webb WMA Complex consisted of 45% (4,674 ha) bottomland hardwoods with upland hardwood stands along drainages typical of southeastern river floodplains. Planted and managed upland pines comprised 32% (3,346 ha), consisting primarily of loblolly and longleaf pine. The remaining 23% (2,464 ha) was composed of mixed-pine hardwoods, wildlife openings, and wetlands. Management activities on the Webb WMA Complex included prescribed fire, active timber management, fallow field management, and agricultural food plots used to promote and enhance wildlife habitat and populations. Prescribed fire was conducted during growing and dormant seasons on return intervals of 2–3 years. The spring only wild turkey-hunting season opened annually on 1 April with a youth hunt on the Saturday prior, and ended in the first week of May, with hunting permitted from Monday–Saturday. During 2014–2015 wild turkey hunters in South Carolina could harvest up to 5 male wild turkeys; this changed to 3 in 2016. Elevation on the Webb WMA complex ranged from 8 m to 85 m and the climate was characterized by hot, humid summers and mild to cool winters. Wightman et al. (2019) provides a detailed description of the Webb WMA complex.

During 2020–2022, we conducted research on the Savannah River Site (SRS), a 78,000-ha tract in Aiken and Barnwell counties owned by the United States Department of Energy. More than 90% of the SRS was forested and consisted of upland and bottomland hardwoods, mixed-pine hardwoods, and planted stands of longleaf pine, loblolly pine, and slash pine (*P. elliottii*). Depending on site-specific management objectives, pine forests were managed on 50- to 120-year rotations and primarily for wood fiber production. Non-forested areas were primarily marshes, grassland open areas, and utility rights-of-way. Approximately 30% of SRS was managed for red-cockaded woodpeckers (*Leuconotopicus borealis*), with prescribed fire applied on a 3- to 5-year burn rotation. Wild turkey hunting did not occur on SRS during 2020 and 2021, and in 2022 hunting occurred during a 2-day event for 25 mobility-impaired hunters. These hunts took place on portions of SRS that did not include marked birds. Elevation on SRS ranged from 25 m to 85 m and the climate was characterized by hot, humid summers and mild to cool winters. Wightman et al. (2019) provides a detailed description of site condition.

During 2020–2022, we conducted research on 3 disjunct study areas in North Carolina, 1 each in the mountain region in the northwestern portion of the state (Madison, McDowell, Mitchel, Yancey counties), the Piedmont region in the central portion of the state (Moore County), and the coastal region in the southeastern portion of the state (Bladen, Duplin, Sampson counties). All properties where wild turkeys were trapped were privately owned, but some properties bordered publicly owned lands. The combined areas of the properties where access was granted were 3,041 ha, 3,074 ha, and 2,843 ha in the mountain, Piedmont, and coastal regions, respectively. The properties in the mountain region were in heterogeneous topography, ranging from 500 m to 1,800 m in elevation. The climate was characterized by mild winters and cool summers, and annual precipitation was 130–250 cm/year, primarily as rain. Mountain region properties were a mix of forest and agricultural (i.e., pasture and cropland) land cover, and land uses included livestock grazing, haying, and periodic timber harvesting. Forest cover was mixed hardwoods with scattered pine species, often with a dense ericaceous understory of mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron* spp.). The Piedmont region properties were mostly forested, with scattered pastures, and elevation ranged from 75 m to 180 m. The climate was characterized by mild winters and warm-temperate, humid summers, and annual precipitation averaged 120 cm/year. Upland forest cover was dominated by loblolly pine overstory, and lowlands were mixed hardwoods. Land use was mostly wood fiber production and livestock grazing, and some properties periodically received prescribed fires. Elevation of the coastal region properties ranged from 0–30 m. The climate was characterized by mild winters and warm, humid summers, and annual precipitation averaged 160 cm/year. The properties most commonly were commercial swine and poultry farms, embedded in a mix of unmanaged pine and mixed pine-hardwood forest. The farms typically included row-crop and pasture, which often were used as spray fields for lagoon wastewater. From 2020 to 2022, the general spring only statewide wild turkey hunting season in North Carolina opened the second Saturday in April and lasted 29 days. The week-long statewide youth hunting season opened the Saturday before the general season. During all years of the study, wild turkey hunters in North Carolina could harvest up to 2 male wild turkeys.

METHODS

Capture and monitoring

We captured male wild turkeys using rocket nets baited with corn during January–March. We aged captured individuals based on presence of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). We banded each individual with a uniquely identifiable aluminum rivet leg band (National Band and Tag Company, Newport, KY) and tagged a subset of individuals with a backpack-style global positioning system (GPS)-very high frequency (VHF) transmitter (Guthrie et al. 2011) or a VHF-only transmitter produced by Biotrack (Wareham, Dorset, United Kingdom). We immediately released all wild turkeys at the capture location after processing.

Both GPS and VHF transmitters were equipped with a mortality sensor, so a mortality signal was activated whenever the wild turkey was not in motion for 12–24 hours. We monitored live-dead status ≥3 times a week from capture through summer (31 Jul) and monthly for the remainder of the year (1 Aug–31 Dec). We censored mortalities that occurred within the first 14 days after capture to reduce bias in survival estimates from capture-related mortality. We investigated mortality signals as soon as possible upon initial detection. We located individuals and attempted to determine cause of death based on evidence at or around the mortality site, such as hair, tracks, bite marks, and cache characteristics (Moore et al. 2008, Norman et al. 2022). We assigned hunting mortalities to those recovered and reported directly by hunters or when we determined the cause of death resulted from crippling loss under the following 3 circumstances: a transmittered bird that was with another harvested transmittered bird and was found dead within 48 hours of the harvest and the carcass was indicative of crippling; a transmittered bird was known to be shot at by a hunter and visually wounded based on a conversation with the hunter, which likely resulted in mortality; and a transmitter bird was recovered dead during the wild turkey season with no apparent signs of predation and during necropsy we found evidence of gunshot pellets throughout the bird's carcass. We considered instances where the transmitter harness had been cut and discarded to be illegal kills and we included such mortalities as harvest. We recorded whether harvested birds were shot on private or public property, as game species on public property can experience higher harvest and lower survival (Small et al. 1991, Lebel et al. 2012, Haus et al. 2019). We classified remaining causes of deaths as non-harvest and specific causes included predation, vehicle strikes, or disease. We classified cause of death as unknown when we could not determine clear evidence of cause.

Known-fate analysis

We conducted all known-fate analysis in Program R version 4.0.2 (R Development Core Team 2023). We fit time-to-event models using a Kaplan-Meier estimator with staggered entry (Pollock et al. 1989) to data from radio-marked birds to estimate annual survival and cause-specific hazard rates. We assessed age-specific differences in survival across years and sites using Cox proportional hazards models and the Wald Z-test. We determined cause-specific mortality rates via the competing-risks nonparametric cumulative incidence function estimator described by Heisey and Patterson (2006) using the wild1 R package (Sargeant 2011). We placed mortality events into 5 competing risks, and then estimated cumulative mortality by predation, harvest, vehicle strikes, disease, and unknown causes. We tested differences in cause-specific mortality rates between juveniles and adults, and across sites and years, by fitting Cox proportional hazards models and using the Wald Z-test to assess statistical significance. To quantify how survival and cause-specific hazard rates changed throughout the annual cycle, we modeled the 7-day smoothed instantaneous hazard functions using the gss package (Gu 2014) via smoothing splines of the hazard rates (Sandercock et al. 2011). We used the uniquely identifiable band number for each wild turkey in each model as a random effect to account for lack of independence. We conducted the known-fate survival analyses using the survival package (Therneau and Lumley 2015).

We used cause-specific mortality rates to evaluate the assumption that spring harvest served as an additive mortality source using 2 approaches. First, we compared the cumulative incidence function (CIF) from the nonparametric cumulative incidence function estimator for hunting and all other mortality sources. If hunting mortality was additive, we would expect an increase in the CIF for hunting mortality, whereas the CIF for non-hunting mortality would be constant (i.e., no compensatory decrease in other mortality sources in the presence of hunting). Conversely, if hunting mortality was compensatory, we would expect an increase in the hunting CIF with a concurrent reduction in the CIF for non-hunting mortality (Pepe and Mori 1993, Pintilie 2006). We then regressed survival of adult males against harvest rate (Robinson et al. 2014). If hunting were compensatory, we would expect survival to remain constant as harvest increased, whereas if harvest were additive, we would expect a decrease in survival with an increase in harvest (Williams et al. 2002, Robinson et al. 2014). We acknowledge that this approach does not model potential density-dependent effects and does not consider the possible effects of environmental factors on variations in annual survival and harvest (Riecke et al. 2022).

Joint live-dead analysis

We used the Barker multi-state joint live and dead encounters and resighting model (Barker 1997, 1999; Barker and White 2004; Kendall et al. 2013) to estimate annual survival and harvest rate of radio-marked and banded birds. The model consisted of 7 parameters: survival (S_i; probability an individual alive at time i survived to $i + 1$), capture probability (p_i; the probability an individual at risk of capture at trapping occasion i was captured), reporting rate (r_i; the probability that an individual died between i and $i + 1$ and was found dead and reported), resight (R_i; the probability a marked individual survived from i to $i + 1$ and was resighted during this time frame and reported), resighted before death (R'_i; the probability a marked individual was alive at time i but died before $i + 1$ and was resighted alive and reported during that time frame), site fidelity (F_i; the probability that an individual at risk of capture at time i was again at risk of capture at $i + 1$), and temporary emigrants (F'; the probability an individual not at risk of capture at time i was at risk of capture at $i + 1$). The model allowed us to incorporate resighting data (i.e., live or dead) from radio-telemetry tracking to increase precision in survival estimates (Barker 1997, Buckley et al. 2022). Estimates of interest were survival (S_i) and reporting rate (r_i); therefore, we treated R, R'_i, F_i, and F'_i as nuisance parameters, meaning these variables were needed to ensure model validity but were not directly linked to the parameters of interest (Buckley et al. 2022). Because we had recapture and resighting data for banded and radio-marked wild turkeys, we modeled detection probability (p_i) and R_i using a covariate for mark type

(Buckley et al. 2022). We were interested in assessing harvest effects on survival, so we held R'_i fixed at zero because we censored natural mortalities (i.e., predation) observed for males fitted with telemetry units (Buckley et al. 2022). We had no evidence of true dispersal or permanent emigration from study sites, so we fixed $F_i = F'_i = 1$ to indicate no emigration (Barker and White 2001). We used the Seber reporting rate ($f = r(1–S)$) from the Barker model as an index for harvest rate (Sedinger et al. 2010).

We categorized all wild turkeys as either adult or juvenile in the year of capture, and all juveniles that survived into the following spring were transitioned into the adult age class before harvest could occur (Laake 2013). Because male survival and harvest can vary by age (Vangilder and Kurzejeski 1995, Diefenbach et al. 2012), we incorporated age in the survival and recovery parameter for all models. We created temporal models to examine survival and recovery rate by year and spatial models to investigate differences across study sites. We estimated overdispersion for the most parsimonious model and generated a variance inflation factor ($\hat{c}$) using the median $\hat{c}$ estimation capability within Program MARK (White and Burnham 1999). For $\hat{c} > 1$, we used the quasi-likelihood modified Akaike's Information Criterion adjusted for small sample size ($QAIC_c$) and model weight (w_i) for model selection (Burnham and Anderson 2002). We used program R version 4.0.2 (R Development Core Team 2023) with package RMark (Laake 2013) to run MARK (White and Burnham 1999) on the candidate model sets. We conducted a separate Barker model with a subset of the data that only included individuals that were captured as juveniles. Our juvenile-specific analysis allowed us to estimate annual survival and harvest rates for known age classes because both can vary by age class, which is important for managers when estimating demographic parameters (Stevens et al. 2013).

RESULTS

We captured and fitted 549 (162 juveniles, 387 adults) males with radio-transmitters and banded an additional 311 (156 juveniles, 155 adults) males (Table 1). During the study, 365 males (40 juveniles, 325 adults) died. The sources of mortality for adults were harvest ($n = 240$) followed by predation ($n = 67$), vehicle strikes ($n = 3$), and the disease avian pox ($n = 1$), whereas the remaining mortalities ($n = 14$) were caused by unknown sources (Table 1). Of the males that we considered harvested, we recovered only the transmitter with a cut cord for 8 individuals, which included 4 that were poached in March before hunting season opened and 4 in April during the legal hunting season. We recovered 3 males whose mortality was from crippling loss that we considered harvested. The primary source of mortality for juveniles was predation ($n = 21$) followed by harvest ($n = 15$) and unknown causes ($n = 4$; Table 1). Of 318 males we captured as juveniles, 84 (26%) were harvested and reported during the study, 15 (18%) were harvested as juveniles, 43 (51%) as 2-year-olds, 16 (19%) as 3-year-olds, 9 (10%) as 4-year-olds, and 1 (1%) as a 5-year-old. Of the 542 males captured as adults, 240 (44%) were harvested and reported during the study. Of males harvested in Georgia, 44% were taken on private lands, whereas 22%, 59%, 28%, and 100% of males were harvested on private lands in west-central Louisiana, southeastern Louisiana, South Carolina, and North Carolina, respectively (Table 1).

Known-fate analysis

Annual survival for adults and juveniles in hunted study sites was 0.54 (95% CI = 0.49–0.59) and 0.86 (95% CI = 0.81–0.92), respectively. Score tests from Cox proportional hazards models indicated the hazard rate of adults was higher than juveniles (age hazard ratio [HR] = 4.107; 95% CI = 2.642–6.384; $Z = 6.276$; $P \leq 0.01$), demonstrating strong evidence that annual survival was lower for adults than juveniles (Figure 2). The assumption of proportional hazards was met ($\chi^2 = 1.57$; $P = 0.21$). Wald Z-tests indicated little or no evidence for differences in hazard rate or survival among hunted sites or years (all $P > 0.1$) and the assumption of proportional hazards was met for year

TABLE 1 Summary of the number of juvenile (J) and adult (A) male eastern wild turkeys captured and banded (band) or fitted with a radio-transmitter (transmitter), harvested, percent harvested on private property (private), and all other sources of mortality for each study site in the southeastern United States, 2014–2022.

Study site	Age	Captured	Transmitter	Band	Harvested	Private (%)	Predated (*n*)	Disease (*n*)	Vehicle (*n*)	Unknown (*n*)
GA	J	63	29	34	5	20	1	0	0	0
	A	56	52	4	36	47	14	0	1	0
West LA	J	86	19	67	7	29	1	0	0	1
	A	191	59	132	90	20	4	0	0	7
East LA	J	52	34	18	0	0	4	0	0	3
	A	46	39	7	27	59	4	0	0	3
Webb SC	J	38	22	16	2	100	3	0	0	0
	A	54	48	6	34	29	9	0	0	0
SRS SC	J	1	1	0	0	0	0	0	0	0
	A	43	43	0	0	0	6	1	2	0
Coastal NC	J	22	19	3	1	100	4	0	0	0
	A	46	46	0	14	100	11	0	0	0
Mountain NC	J	30	18	12	0	100	1	0	0	0
	A	56	54	2	18	100	14	0	0	2
Piedmont NC	J	26	20	6	0	100	7	0	0	0
	A	50	46	4	21	100	5	0	0	2

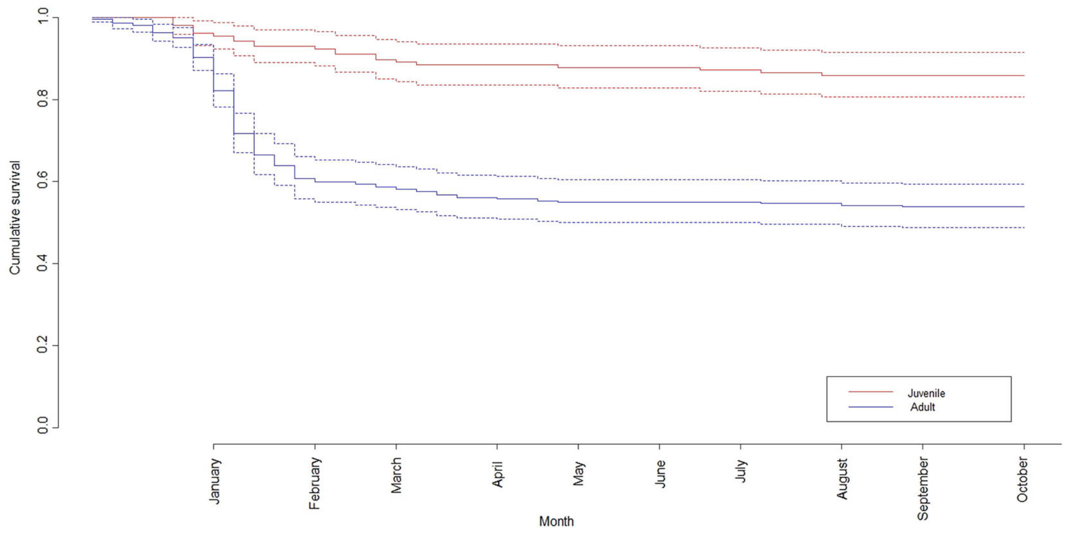

FIGURE 2 Cumulative survival and confidence intervals for juvenile and adult radio-marked male eastern wild turkeys studied across the southeastern United States, 2014–2022, calculated using time to event Kaplan-Meier known-fate models.

(χ^2 = 15; P = 0.06) but not for site (χ^2 = 10.7; P = 0.01). While there was little or no evidence of differences in survival among hunted sites (Table 2), the assumption of proportional hazards was not met because there were differences in the timing of mortality on hunted sites owing to different season date frameworks across sites. Annual survival for adult males in the non-hunted study site was 0.83 (95% CI = 0.72–0.97), which based on Wald Z-tests suggested strong evidence for greater survival than in hunted study sites (hunt HR = 3.43; 95% CI = 1.50–7.84; Z = 2.93; $P \leq 0.01$; χ^2 = 0.49; P = 0.49). We did not calculate annual survival for juveniles in the non-hunted study site because we only radio-marked a single individual.

The annual harvest estimate across hunted sites was 0.29 (95% CI = 0.24–0.33) and 0.02 (95% CI = 0.01–0.03) for adults and juveniles, respectively, whereas predation rates were 0.15 (95% CI = 0.10–0.20) for adults and 0.12 (95% CI = 0.08–0.17) for juveniles. The annual predation rate estimate for adults in the non-hunted study site was 0.11 (95% CI = 0.02–0.21). Across all sites the probability of other sources of mortality accounted for <0.03 for adults and 0.01 for juveniles. Wald Z-tests suggested strong evidence that harvest and predation rates were greater in adults (age harvest HR = 2.701; 95% CI = 1.779–4.101; Z = 4.664; $P \leq 0.01$; χ^2 = 6.5; P = 0.06, age predation HR = 1.834; 95% CI = 1.092–3.082; Z = 2.29; P = 0.02; χ^2 = 2.23; P = 0.14) but indicated little or no evidence for differences in predation or harvest rates for both age classes among sites and years (all $P > 0.01$). The assumption of proportional hazards was met for harvest by year (χ^2 = 9.94; P = 0.27), predation by site (χ^2 = 5.81; P = 0.12), and predation by year (χ^2 = 9.94; P = 0.27), but not for harvest by site (χ^2 = 10.9; P = 0.01).

Smoothed instantaneous hazard rates indicated the risk of mortality from all sources peaked in spring coinciding with the approach and opening of hunting seasons, but that the risk of harvest for juveniles peaked in late April towards the end of hunting seasons. The steepest and largest instantaneous hazard occurred for adults from harvest (Figure 3). Overall differences between the maximum hazard for harvest mortality and non-harvest mortality indicated that mortality risk from harvest was roughly 4 times greater than for non-harvest causes (Figure 3). The lack of difference in CIF of non-harvest mortality and increased estimates of annual predation in hunted versus the non-hunted population suggests harvest was additive. Furthermore, regression analysis of harvest rate and mean annual survival of adults across sites and years resulted in a negative slope of

TABLE 2 Estimated survival, harvest rate, and predation rate (95% CIs) for juvenile (J) and adult (A) male eastern wild turkeys in the southeastern United States, 2014–2022, calculated using time to event Kaplan-Meier known-fate models and joint live-dead Barker models.

Study site	Age	Known fate survival	Known fate harvest	Known fate predation	Barker model survival	Barker model harvest
GA	J	0.96 (0.9–0.99)	0.01 (0.01–0.03)	0.03 (0.01–0.09)	0.87 (0.85–0.87)	0.07 (0.07–0.8)
	A	0.55 (0.44–0.7)	0.23 (0.13–0.34)	0.22 (0.09–0.34)	0.39 (0.35–0.42)	0.23 (0.21–0.24)
West LA	J	0.95 (0.85–0.99)	0.05 (0.01–0.13)	0.01 (0.01–0.03)	0.92 (0.84–0.96)	0.05 (0.02–0.09)
	A	0.60 (0.49–0.74)	0.30 (0.20–0.40)	0.10 (0.01–0.19)	0.41 (0.36–0.45)	0.22 (0.20–0.24)
East LA	J	0.90 (0.79–0.99)	0	0.10 (0.01–0.20)	0.99 (0.97–1.00)	0.10 (0.00–0.20)
	A	0.55 (0.41–0.74)	0.36 (0.22–0.49)	0.09 (0.01–0.17)	0.48 (0.42–0.54)	0.19 (0.17–0.22)
Webb SC	J	0.82 (0.67–0.99)	0.05 (0.01–0.10)	0.13 (0.02–0.26)	0.86 (0.65–0.95)	0.08 (0.03–0.20)
	A	0.53 (0.41–0.70)	0.30 (0.18–0.41)	0.17 (0.07–0.27)	0.38 (0.32–0.45)	0.23 (0.20–0.25)
SRS SC	J					
	A	0.83 (0.72–0.97)		0.11 (0.02–0.21)		
Coastal NC	J	0.74 (0.56–0.96)	0.05 (0.01–0.14)	0.21 (0.06–0.36)	0.82 (0.60–0.94)	0.10 (0.03–0.22)
	A	0.52 (0.40–0.69)	0.26 (0.13–0.39)	0.22 (0.09–0.35)	0.37 (0.29–0.44)	0.24 (0.21–0.26)
Mountain NC	J	0.94 (0.84–0.99)	0	0.06 (0.01–0.14)	1	0
	A	0.46 (0.35–0.62)	0.28 (0.17–0.39)	0.26 (0.15–0.37)	0.46 (0.40–0.50)	0.20 (0.19–0.22)
Piedmont NC	J	0.65 (0.47–0.90)	0	0.35 (0.18–0.52)	0.87 (0.61–0.96)	0.08 (0.02–0.26)
	A	0.54 (0.42–0.71)	0.30 (0.18–0.42)	0.16 (0.08–0.29)	0.38 (0.31–0.46)	0.23 (0.20–0.26)

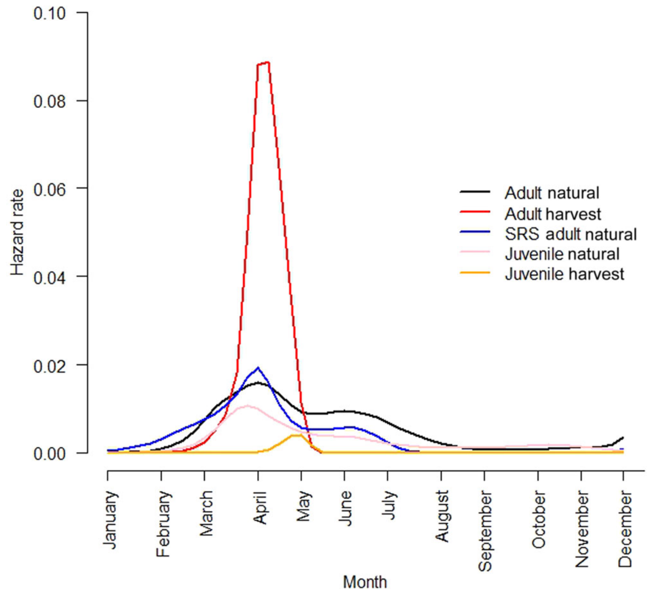

FIGURE 3 Smoothed instantaneous hazard rates for harvest and natural causes of mortality for juvenile and adult radio-marked male eastern wild turkeys studied across the southeastern United States, 2014–2022, in hunted sites and a site with no hunting (Savannah River Site [SRS]).

−0.78 ($F_{1,18}$ = 35.06, $P \leq 0.01$), showing strong evidence that the assumption of harvest mortality being additive is valid (Figure 4).

Joint live-dead analysis

The top model indicated survival and harvest rate was age-specific but did not vary by site or year ($\Delta QAIC_c > 2.0$; Table 3). Overdispersion for the top model was moderate (median $\hat{c} = 7.18$). Annual survival was 0.40 (95% CI = 0.37–0.44) and 0.88 (95% CI = 0.81–0.93) for adults and juveniles, respectively. The harvest rate estimate for adults was 0.24 (95% CI = 0.23–0.25) and for juveniles was 0.04 (95% CI = 0.03–0.05). The recapture probability for banded individuals was 0.02 (95% CI = 0.0.01–0.04), whereas the detection probability for individuals with transmitters based on recapture and resighting was 0.05 (95% CI = 0.03–0.09) and 0.86 (95% CI = 0.81–0.91), respectively. From the model containing only known-age birds, survival was estimated to be 0.90 (95% CI = 0.84–0.94) for juveniles, 0.22 (95% CI = 0.16–0.29) for 2-year-olds, 0.41 (95% CI = 0.25–0.59) for 3-year-olds, and 0.18 (95% CI = 0.05–0.51) for 4-year-olds. Likewise, harvest rate of known-aged birds was 0.03 (95% CI = 0.02–0.05) for juveniles, 0.26 (95% CI = 0.23–0.28) for 2-year-olds, 0.18 (95% CI = 0.14–0.25) for 3-year-olds, and 0.27 (95% CI = 0.16–0.31) for 4-year-olds.

DISCUSSION

Wild turkeys are one of the most popular game species in North America, and spring hunting is an activity of significant cultural and economic value (Chapagain et al. 2020). During the past 2 decades, wild turkey abundance, recruitment, and spring harvest have decreased over much of the species' range (Byrne et al. 2015, Casalena et al. 2015, Chamberlain et al. 2022). Among Galliformes and other gamebirds, wild turkey is unique because the

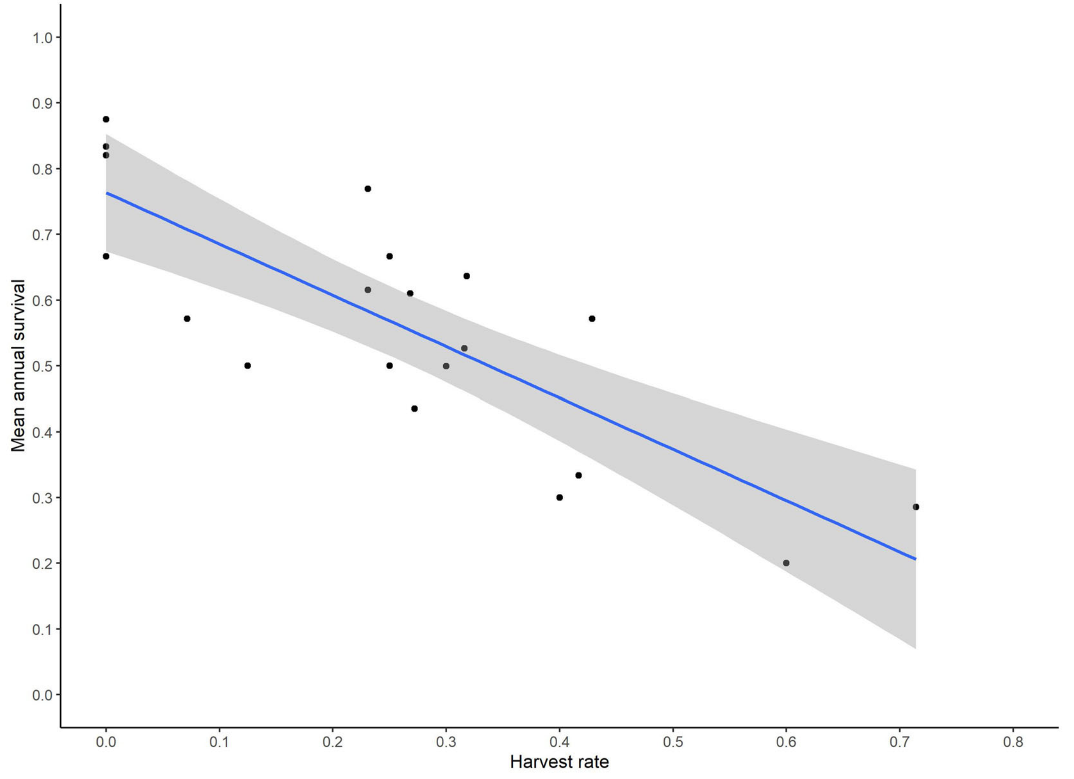

FIGURE 4 Regression of the relationship (and 95% CI) between estimated hunting mortality and annual survival of adult male radio-marked male eastern wild turkeys at each study site for each year studied (dots) across the southeastern United States, 2014–2022, calculated using Kaplan-Meier known-fate models.

species is hunted primarily during their reproductive season, which challenges managers to implement regulations that promote sustainable harvest, reproductive success, and hunter satisfaction (Chamberlain et al. 2018, Isabelle et al. 2018). We evaluated survival and harvest rates for adult and juvenile males across a suite of sites subjected to harvest, along with a site where harvest was absent. Spring harvest was the primary source of mortality for adults, resulting in a 29% harvest rate and 54% annual survival rate across hunted populations. Conversely, in the absence of hunting, annual survival of adults was 83%. Results demonstrated strong evidence that spring harvest represents an additive source of mortality for males. These findings offer managers relevant and timely information as they react to ongoing declines in male wild turkeys across the United States.

Our large-scale and nearly decade-long analysis of male wild turkey survival provided a robust basis to assess long-term changes in male harvest and survival. Survival rates of juvenile males were greater than rates reported previously, whereas harvest rates were lower (Norman et al. 2004, Eriksen et al. 2011, Chamberlain et al. 2012, Diefenbach et al. 2012). One potential explanation could be that hunters may have altered their behaviors to refrain from harvesting juvenile males (Backs and McCallen 2022, Norman et al. 2022). We observed annual survival rates for adults comparable to those reported during the 1990s (Godwin et al. 1991, Ielmini et al. 1992) but greater than those found in the 2000s (Wright and Vangilder 2001, Hubbard and Vangilder 2005, Eriksen et al. 2011, Chamberlain et al. 2012, Diefenbach et al. 2012), whereas harvest rates were comparable to published works since 2011 (Eriksen et al. 2011, Norman et al. 2022) but lower than in the late 1990s and early 2000s (Ielmini et al. 1992, Wright and Vangilder 2001, Norman et al. 2004, Hubbard and Vangilder 2005). Holistically, these findings indicate that harvest rate of adults has decreased since the early 2000s, resulting in increased annual survival. Abundance,

TABLE 3 Model selection results for Barker joint live-capture, live-resight, and band recovery models for male eastern wild turkeys, 2014–2022, in the southeastern United States with parameters survival (*S*), recapture (*p*), recovery (*r*), resighting (*R*), resighting before death (*R*'), site fidelity (*F*), and temporary emigration (*F*'). We present the number of parameters (*K*), Akaike's Information Criterion for small sample sizes ($QAIC_c$), the difference between ranked models ($\Delta QAIC_c$), and model weight (w_i).

Model[a]	*K*	$QAIC_c$	$\Delta QAIC_c$	w_i
S(age), *p*(tel), *r*(age), *R*(tel), *R*'(0), *F*(1), *F*'(1)	8	1,234.10	0.00	0.94
S(site + age), *p*(tel), *r*(age), *R*(tel), *R*'(0), *F*(1), *F*'(1)	14	1,240.16	6.05	0.04
S(age), *p*(tel), *r*(age + site), *R*(tel), *R*'(0), *F*(1), *F*'(1)	14	1,244.19	10.0	0.01
S(age), *p*(tel), *r*(age + time + site), *R*(tel), *R*'(0), *F*(1), *F*'(1)	23	1,244.87	10.76	0.01
S(age + time + site), *p*(tel), *r*(age), *R*(tel), *R*'(0), *F*(1), *F*'(1)	23	1,248.41	14.30	0.00
S(site + age), *p*(tel), *r*(age + site), *R*(tel), *R*'(0), *F*(1), *F*'(1)	20	1,249.65	15.54	0.00
S(site + age), *p*(tel), *r*(age + time + site), *R*(tel), *R*'(0), *F*(1), *F*'(1)	29	1,250.45	16.34	0.00
S(age + time + site), *p*(tel), *r*(age + site), *R*(tel), *R*'(0), *F*(1), *F*'(1)	29	1,260.36	26.25	0.00
S(age + time + site), *p*(tel), *r*(age + time + site), *R*(tel), *R*'(0), *F*(1), *F*'(1)	38	1,276.33	42.22	0.00
S(.), *p*(.), *r*(.), *R*(.), *R*'(0), *F*(1), *F*'(1)	7	1,468.47	234.36	0.00

[a]Age = adult or juvenile, tel = radio-transmitter or band only, site = study site location, time = year of study, (.) = constant, (0) = fixed at zero, (1) = fixed at 1.

reproduction, and harvest, however, have concomitantly declined throughout portions of the species' range (Byrne et al. 2015, Casalena et al. 2015, Chamberlain et al. 2022), which prompts us to question whether our observations of adult male survival are high enough to mitigate for ongoing declines in productivity. Wild turkey population trajectories are influenced primarily by productivity and adult female survival (Roberts and Porter 1996, Londe et al. 2023, Tyl et al. 2023), and it is unclear how fluctuating rates of male survival influence population trajectories (Healy and Powell 1999). We also point to the significant variation in data collection and analysis present across past studies, which could be responsible for discrepancies in published vital rates and trends. For example, we observed higher levels of harvest and survival for radio-marked birds than for banded birds, but we consider the former rates derived from known-fate analyses to be more rigorous and representative of actual harvest and survival because of less uncertainty in the outcomes (Alpizar-Jara et al. 2001, Norman et al. 2022). The inability to determine crippling loss, rates of poaching, non-reported harvest mortality, and rates of predation from band-only data likely resulted in lower harvest estimates and less certainty in survival estimates derived from banding data versus transmitter data.

We observed substantive differences in survival and harvest rates of adult versus juvenile males, wherein adults had lower survival and greater harvest rates than juveniles, consistent with many previous studies (Ielmini et al. 1992, Wright and Vangilder 2001, Eriksen et al. 2011, Chamberlain et al. 2012, Norman et al. 2022). In fact, we observed that harvest rates for juveniles were negligible, and likely biologically irrelevant from a management planning standpoint. We offer that information on survival and harvest vulnerability for known-aged wild turkeys could be important for population modeling and harvest management (Stevens et al. 2017), but few studies have attempted to estimate survival beyond the juvenile and adult age classes. Accurately estimating age for male wild turkeys at capture is not reliable beyond determining whether the individual is an adult or juvenile (Pelham and Dickson 1992), so estimating survival and harvest rates of known-aged birds relies on marking juveniles and them being harvested in the future (Norman et al. 2022). Norman et al. (2022) hypothesized that 3-year-old males would have greater survival and lower harvest rates than 2-year-olds because of age, experience, and dominance, but their findings failed to support this hypothesis. Conversely, our findings do support this hypothesis, as our survival estimate for 2-year-olds (0.22) was nearly half the estimate for 3-year-olds (0.41). We acknowledge that there was overlap in the confidence intervals of these estimates, potentially due to relatively small sample sizes of known-age individuals.

We observed no differences in annual survival and harvest rates among years or the variable study areas, which included privately and publicly owned properties. Although significant annual variation in wild turkey survival and harvest rates has been reported in some studies (Buderman et al. 2014, Norman et al. 2022), others have failed to detect variation among years (Eriksen et al. 2011, Diefenbach et al. 2012, Buckley et al. 2022) or study areas (Diefenbach et al. 2012, Norman et al. 2022). Our study sites were represented by public and private lands, but public properties were surrounded by private lands and often had private in-holdings used by marked males. Previous studies comparing survival of game species between public and private lands reported higher harvest and lower survival on public lands (Small et al. 1991, Lebel et al. 2012, Haus et al. 2019). Conversely, our findings did not indicate differences in survival and harvest rates between public and private lands, which is comparable to recent work published on white-tailed deer (*Odocoileus virginianus*) in Alabama (Wiskirchen et al. 2023). Although hunting pressure could be greater on some public properties than on most private lands, it is plausible that increased pressure on public lands could be offset by lower *per capita* harvest success.

We observed that spring harvest and predation were the most relevant sources of mortality for males, but notably, risk of harvest was 4 times greater than predation. Other sources of mortality were negligible and likely biologically irrelevant. Mortalities linked to harvest and predation in the hunted and non-hunted populations peaked in the spring around times leading up to and after the early stages of hunting season, which has been reported previously (Vangilder and Kurzejeski 1995, Wright and Vangilder 2001, Hubbard and Vangilder 2005, Norman et al. 2022). Presumably, increased risk of mortality from predation in spring is influenced by the pronounced auditory and courtship behaviors males use to secure breeding opportunities (Godwin et al. 1991, Thogmartin and Schaeffer 2000).

Survival rates were significantly greater for adult males on the non-hunted site in our study, and survival decreased as harvest mortality increased on the hunted properties. Conceptually, compensatory harvest would reduce the probability of individuals suffering from other sources of mortality after harvest, which allows survival rates to remain constant (Boyce et al. 1999, Sandercock et al. 2011). In our study predation on hunted sites was similar to the non-hunted site, and predation risk decreased later in the spring after hunting on both non-hunted and hunted sites. Collectively, our results offer evidence that spring harvest represents an additive source of mortality for adult males, consistent with earlier works that have sought to evaluate the potential for additivity relative to spring harvest in male wild turkeys (Moore et al. 2008, Chamberlain et al. 2012). We acknowledge that our survival estimates for males in the absence of hunting were derived from only a single study population. Therefore, there are potential biases in extracting these survival rates for non-hunted males across other non-hunted populations.

Few studies on wild turkeys have reported low levels of harvest (e.g., 10–15%), highlighting the need to study male survival and the potential for compensation at lower harvest rates, whether real or experimental (Devers et al. 2007, Robinson et al. 2009, Sandercock et al. 2011, Woodard et al. 2022). Likewise, compensation may exist if recruitment is greater than harvest, and earlier works on wild turkeys concluded that harvest rates of ≤30% would retain enough adult males in the population and ensure hunter satisfaction (Vangilder and Kurzejeski 1995, Healy and Powell 1999). The model developed by Vangilder and Kurzejeski (1995) assumed recruitment was approximately 3 poults/female, which is >60% greater than what has been observed across broad areas of the species' range for the past several decades (Byrne et al. 2015). The harvest rates (29% averaged across study areas) from this study, coupled with observations of reduced recruitment and ongoing declines in many wild turkey populations (Byrne et al. 2015, Casalena et al. 2015, Chamberlain et al. 2022), indicate a clear need to revisit and improve the models managers have used for decades to project appropriate harvest rates of male wild turkeys; these revised models ideally would use contemporary estimates of vital rates that influence projections of sustainable harvest.

We encourage future studies estimating survival and harvest of wild turkeys to understand the biases in band-only data and to include known fate data from transmittered birds. Our results provide evidence that age of adults may influence survival; we believe that future research investigating potential differences in known-age survival is warranted for male wild turkeys. We found little to no evidence of differences in survival and harvest between landownership types; however, we did not quantify *per capita* harvest success for public and private lands. We encourage future studies to further investigate differences in survival and harvest between landownership types, while also quantifying *per capita* harvest success. Lastly, given that our survival estimates in the absence of hunting were derived from only a single study population, we recommend that future work seek to monitor adult male survival on other non-hunted populations.

MANAGEMENT IMPLICATIONS

Our results are relevant to those tasked with managing sustainable wild turkey populations and offer insight into current levels of spring harvest on private and public lands across a large portion of the southeastern United States. Observed rates of harvest (i.e., 29% on average for adult males) may not be congruent with continued hunter satisfaction and population sustainability given relatively low estimates of recruitment. We recommend researchers and managers consider focusing efforts on use of survival and harvest rates of known-aged males in future works that model population dynamics and simulate appropriate harvest rates, and that such efforts rely primarily on known-fate data. This study provided robust evidence that harvest represents an additive mortality source for male wild turkeys and provides ample justification for reducing harvest rates as a mechanism for increasing male survival. Managers may want to consider increasing male survival to potentially mitigate ongoing male population declines and ensure hunter satisfaction. The lack of variation we observed in survival and harvest rates among study areas across the Southeast that varied widely in the relative proportion of public and private properties suggests that management actions can be consistent across a broad range of landownership types across the Southeast. Furthermore, the lack of variation observed in harvest rates across hunted populations with different hunting regulations suggests that managers may need to test alternative season length configurations, bag limits, and hunting equipment regulations to determine the most effective regulations for reducing harvest rates. Lastly, we encourage efforts to model population trajectories of male wild turkeys across broad spatial scales using contemporary estimates of survival, harvest rates, and recruitment to enhance harvest management.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All turkey capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committees at the University of Georgia (protocols A2011 07-003-R1, A3437-01, A2014 06-008-Y1-A0, A2016 04-001-Y2-A0, A2019 01-025-R2, and A2021 11-024-A1), North Carolina State University (protocols 19-739-01, 19-739-02, and 19-739-04 as amended), and Louisiana State University Agricultural Center (protocol A2014-013, A2015-07, A2018-13 and A2021-14).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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