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Adult white-tailed deer survival in hunted populations on public and private lands

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Abstract

Estimates of sex- and age-specific survival are important for guiding population management decisions for white-tailed deer (*Odocoileus virginianus*). However, differences in deer survival between public and private lands can exist and, if unaccounted for, may affect wildlife agencies' ability to effectively manage statewide and local deer populations. From 2014 to 2016, we radiocollared and monitored survival of 79 adult white-tailed deer (141 deer-years; 62 male, 79 female) on 2 public and 2 private properties in Alabama, USA. We assessed the effects of sex, age, and landownership type (i.e., public or private) on adult white-tailed deer harvest and survival patterns using an information-theoretic approach. Hunter harvest accounted for 77% of observed mortalities ($n = 23/30$), but harvest and survival rates varied by sex and age. Harvest and survival were similar between public and private property despite more restrictive hunting regulations for antlered deer on public areas. Similar harvest rates were likely due to self-imposed, quality deer management (QDM) harvest strategies on private land that emulated the effects of a state-mandated antler point restriction (APR) on public land. Our findings indicate survival rates of adult white-tailed deer may be applicable across landownership types where state-mandated harvest regulations with respect to males are more restrictive on public than private property, due to the popularity of QDM by private-land

deer hunters. However, where regulations are similar across landownership types (e.g., no state-mandated APR), differences in harvest and survival rates may exist.

KEYWORDS

Alabama, antler point restriction, *Odocoileus virginianus*, private land, public land, quality deer management, radiotelemetry, selective harvest criteria, survival, white-tailed deer

White-tailed deer (*Odocoileus virginianus*; hereafter deer) are one of North America's most important wildlife species, with considerable value among the general public (Conover 2011), as well as being the continent's most sought-after game species, supporting hundreds of thousands of jobs and supplying billions of dollars in economic stimulation on an annual basis through recreational hunting (Adams et al. 2009). As such, abundant deer populations are desirable to many; however, overabundant deer can negatively impact ecosystems and human societies (Conover et al. 1995). Wildlife agencies, charged with the responsibility of managing wildlife for the public trust, strive to maintain deer populations at biologically and socially acceptable levels to maximize positive attributes and minimize negative impacts of the species (Demarais et al. 2000).

Estimates of sex- and age-specific survival are key pieces of information used to make effective deer management decisions. Adult female survival is among the most important vital rates impacting deer population dynamics (Chitwood et al. 2015) and age-specific male survival directly influences male age structure, which can impact hunter satisfaction and participation (Gigliotti 2000, Siemer et al. 2015). While numerous studies have examined deer survival across the species' range, direct survival comparisons between public and private lands are lacking. Wiskirchen et al. (2017) observed greater harvest rates among visibly marked female deer on public compared to private land in Alabama and South Carolina, USA. Similarly, Haus et al. (2019) observed greater mortality among yearling males on public compared to private land in Delaware, USA, providing evidence that survival differences between landownership types occur. Given that hunter harvest is often the primary force driving deer population dynamics (Hansen and Beringer 2003, Webb et al. 2007, Magle et al. 2012), differences in hunter attitudes (Stedman et al. 2008, Harper et al. 2012), selective preferences (Wiskirchen et al. 2017), and deer management styles and philosophies that may exist between public and private lands create the potential for survival rates to vary dramatically between landownership types.

Quality deer management (QDM) is an approach commonly employed on private property, whereby landowners seek to improve the quality (i.e., body condition and average antler size) of the deer herd by harvesting a sufficient number of female deer to maintain the population below biological carrying capacity and limiting harvest of young males, often through establishment of selective harvest criteria (SHC), to increase male age structure (Hamilton et al. 1995). While similar deer management goals are frequently set for public hunting areas, managers must consider that public land deer hunters may be less willing to harvest antlerless deer or view themselves as deer managers compared to private land deer hunters, which can impact harvest decisions and limit hunter investment in achieving long-term management goals on public areas (Stedman et al. 2008). Hunter density on public land also tends to be greater than on most private properties (Root et al. 1988, Small et al. 1991, Haus et al. 2019). Thus, harvest regulations may need to be modified on public lands to account for differing hunter preferences and harvest intensities compared to private property to maintain desirable deer numbers, herd demographics, and to provide a quality hunting experience.

The differences in deer harvest and survival rates between public and private land within a state are not well understood, which may be problematic for wildlife managers making deer management decisions across different landownership types. Further examination of the relationship between landownership type and deer survival would lead to a more complete understanding of deer population dynamics at broad and localized spatial scales. Furthermore, to our knowledge survival of adult male white-tailed deer has not been quantified within the southeastern United States using data collected more recently than 2008 (Thayer et al. 2009). Given that QDM application is at or near an all-time high within the region, our study aimed to provide updated estimates of survival for male and female deer under the QDM management paradigm. Our specific objectives were to 1) determine sex- and age-specific survival rates of adult deer across monitored populations on public and private lands in Alabama, USA, 2) determine the contribution of cause-specific mortality sources toward seasonal and annual survival, and 3) assess the relative importance of various factors, including landownership type, in explaining deer survival and harvest patterns.

STUDY AREA

We conducted our study across 4 areas in Alabama, USA (Figure 1): 2 public-use wildlife management areas (Barbour WMA and Oakmulgee WMA) managed by the Alabama Department of Conservation and Natural Resources (ADCNR), and 2 privately-owned tracts (Marengo and Pickens). Marengo included private property owned as well as adjacent property leased from a private timber company. Pickens was owned by a private timber company and leased in approximately 400-ha tracts to private hunting clubs. Combined land area across all locations was 374 km^2 (Barbour WMA = 114 km^2, Marengo = 31 km^2, Oakmulgee WMA = 180 km^2, Pickens = 49 km^2). Barbour WMA and Marengo were situated in the northern portion of Alabama's lower coastal plain (Gray et al. 2002) and were characterized by gently rolling terrain, while Oakmulgee WMA and Pickens were situated in

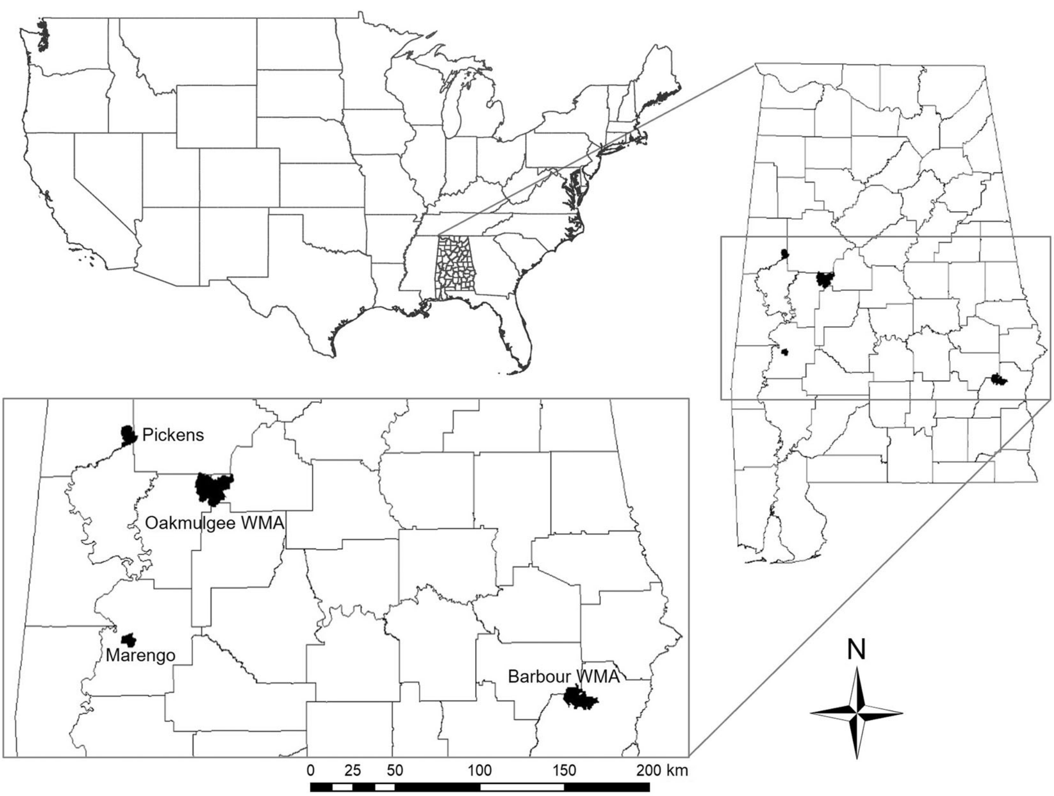

FIGURE 1 Location of study areas in Alabama, USA, used to evaluate white-tailed deer (*Odocoileus virginianus*) survival in hunted populations on public and private lands during 2014–2016.

the southern foothills of the Appalachian Mountains and consisted of more rugged terrain of steep to moderate slope. Habitat on public-use areas was predominantly mixed pine-hardwood stands consisting of loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*), oaks (*Quercus* spp.), maples (*Acer* spp.), sweetgum (*Liquidambar styraciflua*), sycamore (*Platanus occidentalis*), and yellow poplar (*Liriodendron tulipifera*) managed on a 3–5-year prescribed burn rotation. Portions of upland areas also contained mature or regenerating stands of longleaf pine (*P. palustris*) that were more frequently burned. Private-land areas were primarily managed for timber production and existed in various regenerative stages of loblolly and shortleaf pine, with hardwoods restricted to streamside management zones. Across study areas, mean annual precipitation was 147 cm. Winter (Jan–Mar) temperatures fluctuated from −1 to 20°C and summer (Jul–Sep) temperatures fluctuated from 18 to 34°C, with only minor variation across study areas (www.prism.oregonstate.edu).

Each study area had a 109-day deer hunting season, but season dates varied to correspond with the timing of deer breeding in that portion of Alabama. On Oakmulgee WMA and Pickens, deer season occurred during 15 October–31 January. On Barbour WMA and Marengo, deer breeding peaked slightly later and deer season occurred during 25 October–10 February. Statewide hunting regulations permitted the harvest of one antlerless and one antlered deer/hunter/day, with a maximum harvest of 3 antlered deer/hunter throughout the season. On private property, a state-mandated antler point restriction (APR) applied to 1 of the season limit of 3 antlered deer, requiring ≥4 antler points (≥2.54 cm) on at least one side. However, no legal restrictions applied to the harvest of the other 2 antlered deer taken on private property. Statewide, Alabama deer hunters averaged 1.4 and 1.5 deer per hunter during the 2014–15 and 2015–16 deer seasons, respectively. Of those, ≤40% of harvested deer were males (C. W. Cook, ADCNR, unpublished data), indicating the APR had a negligible impact on male harvest composition on private property. However, private landowners and hunting clubs which comprised Marengo and Pickens self-imposed restrictions in excess of those mandated by the state, requiring all antlered deer to be at least 3.5 years old as estimated using live body characteristics (Demarais et al. 1999) prior to harvest. Youth hunters were typically not held to the self-imposed restrictions. Failing to abide by harvest rules could result in fines or revocation of future hunting privileges (R. G. Basinger, Westervelt Wildlife Services, personal communication). On Barbour WMA, each harvested, antlered deer was required to have ≥3 antler points (≥2.54 cm) on at least one side. On Oakmulgee WMA, state-mandated harvest regulations were the same as on private property during the 2014–2015 deer hunting season. During the 2015–2016 deer hunting season, Oakmulgee WMA was split into 2 management zones of approximately equal size, with one zone requiring each harvested antlered deer to have ≥3 points (≥2.54 cm) on at least one side and the other zone having the same harvest regulations as on private property. Hunting effort on public and private study areas varied by day of the week, but on Saturdays when activity was the greatest, mean hunting effort was 0.72 (SE = 0.19) hunters/km^2/day and 0.013 (SE = 0.002) hunter hours/ha/day on public and private areas, respectively (Wiskirchen et al. 2022). Assuming public-land deer hunters spent an average of 3 hours afield each day, hunting effort on public areas was 1.7 times that on private areas.

METHODS

Capture and monitoring

From October 2013 to March 2014, and during May–September of 2014 and 2015, we immobilized adult (≥1-yr-old) male and female deer with an intramuscular injection of Telazol (100 mg/mL at an approximate rate of 4.0 mg/kg, Fort Dodge Animal Health, Fort Dodge, IA, USA) and xylazine-hydrochloride (100 mg/mL at an approximate rate of 2.0 mg/kg; Lloyd Laboratories, Shenandoah, IA, USA) using a transmitter dart delivery system (Pneu-Dart, Inc., Williamsport, PA, USA). We fitted deer with a very high frequency (VHF) radiocollar equipped with an 8-hour mortality sensor (Mod M2510B; Advanced Telemetry Systems), and attached a small, metal ear tag (Style No. 681; Hasco Tag Company, Dayton, KY, USA) with a unique ID number to one ear. We lined collars fitted to ≤2.5-year-old females, and to males of all ages, with a pliable foam material to allow for neck growth and swelling (Ditchkoff 2011). We estimated deer age at the time of capture in half-year increments (i.e., 1.5, 2.5, 3.5, etc.) for animals captured during October–March and whole-year increments (i.e., 1.0, 2.0, 3.0, etc.) for animals captured during May–September using a combination of tooth replacement and wear (Severinghaus 1949) and live body characteristics (Demarais et al. 1999) to maximize aging accuracy (Bowman et al. 2007). We administered an intramuscular hand-injection of tolazoline (100 mg/mL at an approximate rate of 2.0 mg/kg; Lloyd Laboratories) as an antagonist for xylazine-hydrochloride when handling was complete.

Telemetry studies involving radio-collared white-tailed deer have been shown to yield unbiased survival estimates (Buderman et al. 2014); however, steps were taken to inform the public about our study to reduce biases within our study (Wiskirchen 2017). We asked hunters to treat collared deer the same as an uncollared deer with respect to harvest decisions, and to report their harvest by calling the telephone number printed on each collar. We monitored deer for mortality events on a weekly basis over a continuous, 2-year period beginning on 15 February 2014 and ending on 14 February 2016. Upon detection of a mortality, we immediately located the carcass and performed a field investigation to determine cause of death and we classified mortalities as harvest (e.g., legal harvest, illegal harvest, unknown harvest), natural (e.g., suspected hemorrhagic disease, post-rut exhaustion, unknown natural), or unknown (Bowman et al. 2007).

Data analysis

We estimated annual and seasonal survival rates, and cause-specific mortality rates (i.e., harvest, natural, and unknown), of deer in Program MARK (White and Burnham 1999) using the known fate model modified for staggered entry (Pollock et al. 1989). For estimating annual survival, the year began on 15 February and ended on 14 February the following year. Seasonal survival estimates were based on 3 biologically relevant periods: post-breeding (15 Feb–14 Jun), parturition (15 Jun–Oct 14), and breeding (15 Oct–14 Feb). The breeding season encompassed the period of peak breeding activity as well as the entirety of the deer hunting season across study areas, and parturition typically peaked in late July or early August (C. W. Cook, ADCNR, unpublished data). In some deer populations, male dispersal rate is greatest just prior to parturition, possibly due to social pressure from the dam as she prepares to give birth (DeYoung and Miller 2011). Dispersal is energetically expensive and involves leaving the natal home range and entering unfamiliar areas. Thus, it is reasonable to assume that dispersal events are associated with a greater risk of mortality (Roseberry and Klimstra 1974, Nixon et al. 1991, Hölzenbein and Marchinton 1992), and increased mortality among dispersing white-tailed deer relative to non-dispersers has been documented in some cases (Nixon et al. 2001, McCoy et al. 2005), but not in others (Haus et al. 2019, Long et al. 2021). We grouped deer of each sex as <3.5-year-olds (hereafter immature) and ≥3.5-year-olds (hereafter mature) for age-specific survival estimates and individuals progressed from one age class to the next on 15 October, at the start of the breeding season. For sample size reporting, we considered each deer a separate individual during each annual cycle or when they transitioned from one age class to the next (Bowman et al. 2007, Wiskirchen et al. 2017). Immature males typically lack substantial antler development relative to mature males (Ditchkoff et al. 2000) and may be selected differently by hunters compared to older individuals. Given the enforcement of an APR across most of our public-land study areas, a portion of males were unavailable for harvest, with a disproportionate number of protected males in our younger age cohort (Strickland et al. 2001, Hansen and Beringer 2003). Likewise, QDM harvest practices on private-land study areas discouraged the harvest of males <3.5 years old. Immature male and female deer may also exhibit a high rate of dispersal, with a lower likelihood of dispersal among older deer (Hawkins et al. 1971, Nixon et al. 1991).

We estimated cause-specific mortality rates using a 2-step process. We calculated harvest mortality by censoring all non-harvest mortalities to derive an estimate of survival ($\hat{S}$) influenced only by harvest. We then used $1 - \hat{S}$ as the harvest mortality rate (Thayer et al. 2009). We calculated confidence intervals for estimates of cause-specific mortality in a similar manner, using 1 – *[UCL of $\hat{S}$]* for the lower confidence limit and 1 – *[LCL of $\hat{S}$]* for the upper confidence limit. We left-censored individuals from estimates of survival and cause-specific mortality until the first full season following capture and right-censored animals that disappeared from the study and were never relocated (Keller et al. 2013). We did not include individuals in survival calculations for the season in which they were captured to avoid biasing estimates of survival upward (Pac and White 2007).

We developed 2 model sets in Program MARK to assess the relative importance of covariates in explaining deer survival and probability of hunter harvest. We built the first model set (hereafter survival model set) using the complete survival dataset, including all observed mortalities. The survival model set included main effects models for sex, age (immature and mature), and landownership (public and private), as well as models with an interaction term between landownership and other main effects to explicitly examine the importance of landownership toward overall survival patterns. We also included a constant model, providing a single survival estimate for the study. We built a second model set (hereafter harvest model set) using a dataset that excluded non-harvest mortalities so that the impact of various factors on the probability of hunter harvest could be examined. The harvest model set included main effects models for sex, age, and landownership, interaction terms between landownership and other main effects, and a constant model. Since we expected season to explain most of the variation in survival and harvest rates (Thayer et al. 2009), we excluded season from both model sets so as not to mask the effects of other potentially important factors. We did not include year in either model set because we did not feel we could adequately evaluate the effect of year with only 2 years of survival data. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to select the most parsimonious model among those considered in each model set, and competitive models were those with $\Delta AIC_c \le 2.0$ (Burnham and Anderson 2002).

RESULTS

We captured and monitored the fate of 79 radio-collared deer (33 M, 46 F). Accounting for age transitions and animals that contributed survival information over multiple years, our total sample size was 141 deer-years (Table 1). Mean age at the point of entry into the study was 3.3 years (min–max = 1.0–6.5 yr), and mean age at death was 4.0 years (min–max = 2.5–6.5 yr). We documented 30 mortalities throughout the study: 23 (77%) harvest-related, 5 (17%) from natural causes, and 2 (6%) from unknown causes (Table 2).

The top-ranked model within the survival model set included the interacting effects of sex and age, accounting for 97% of the model weight among those considered, and there were no other competitive models identified (Table 3). Mortality of mature males was 6.8 (2.1–22.4, 95% CI; $P = 0.002$) times as likely as that of immature males, but there was no difference in the likelihood of mortality among female age classes ($P = 0.619$, Table 4). Notably, each model containing landownership was ranked below the constant model, indicating that no amount of variation in survival was explained by landownership type. The top-ranked model within the harvest model set also included the interacting effects of sex and age (Table 5). The second-ranked harvest model, accounting for 24% of the model

TABLE 1 Sample[a] of adult (≥1.0-yr-old) white-tailed deer (*Odocoileus virginianus*), by landownership type (Public or Private), sex (male [M] or female [F]), and age (years), monitored using radiotelemetry during 2014–2016 in Alabama, USA.

	Public		Private		
Age	M	F	M	F	Total
<3.5	15	13	20	9	57
≥3.5	11	31	16	26	84
Total	26	44	36	35	141

[a]Seventy-nine unique animals that were considered a separate individual each new annual cycle or as they transitioned from one age class to the next.

TABLE 2 Number of observed cause-specific mortalities among 79 adult (≥1.0-yr-old) white-tailed deer (*Odocoileus virginianus*) on public and private lands, by season and sex (male [M] or female [F]), during 2014–2016 in Alabama, USA.

		Cause of death			
Land-ownership	**Season**[a]	**Harvest**[b]	**Natural**[c]	**Unknown**	**Total**
Public	Post-breeding	0	1 (1 M, 0 F)	0	1 (1 M, 0 F)
	Parturition	0	1 (1 M, 0 F)	0	1 (1 M, 0 F)
	Breeding	12 (5 M, 7 F)	0	1 (1 M, 0 F)	13 (6 M, 7 F)
Private	Post-breeding	1 (0 M, 1 F)	0	0	1 (0 M, 1 F)
	Parturition	0	2 (1 M, 1 F)	0	2 (1 M, 1 F)
	Breeding	10 (7 M, 3 F)	1 (1 M, 0 F)	1 (1 M, 0 F)	12 (9 M, 3 F)
Total		23 (12 M, 11 F)	5 (4 M, 1 F)	2 (2 M, 0 F)	30 (18 M, 12 F)

[a]Post-breeding = 15 Feb–14 Jun, Parturition = 15 Jun–14 Oct, and Breeding = 15 Oct–14 Feb.

[b]Harvest = legal harvest, illegal harvest, and unknown harvest.

[c]Natural = suspected hemorrhagic disease, post-rut exhaustion, and unknown natural.

TABLE 3 Summary of a model set explaining survival of 79 adult (≥1.0-yr-old) white-tailed deer (*Odocoileus virginianus*) during 2014–2016 in Alabama, USA.

Model	***K***[a]	**AIC$_c$**[b]	**ΔAIC$_c$**	**Weight**
Sex × Age	4	176.6	0.0	0.97
Sex	2	185.0	8.4	0.01
Age	2	187.4	10.8	0.00
Constant[c]	1	187.7	11.2	0.00
Sex × LO[d]	4	188.6	12.0	0.00
LO	2	189.8	13.2	0.00
Age × LO	4	190.2	13.6	0.00

[a]Number of estimated model parameters.

[b]Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 2002).

[c]Constant model; one estimate for the entire study.

[d]Model variable LO = landownership (i.e., public or private land).

weight among those considered, was the constant model which predicted no variation in harvest rates. Similar to overall survival, harvest of mature males was 3.9 (1.1–14.1, 95% CI; $P = 0.036$) times as likely as harvest of immature males; however, there was no difference in the likelihood of harvest between female age classes ($P = 0.471$). Once again, landownership was not included in competing harvest models and did not explain variation in harvest rates between public and private land.

DISCUSSION

Hunter harvest, accounting for 77% of all observed mortalities, was the primary factor driving patterns in adult deer survival in our study. In the absence of other apex predators, humans are frequently the leading selective pressure on adult white-tailed deer (Hawkins et al. 1970, Ditchkoff et al. 2001, Thayer et al. 2009, Webb et al. 2010,

TABLE 4 Survival and cause-specific mortality rates of adult (≥1.0-yr-old) white-tailed deer (*Odocoileus virginianus*), by sex, age (years), and interval, during 2014–2016 in Alabama, USA.

			Survival			Cause-specific mortality					
						Harvest[a]		Natural[b]		Unknown	
Sex[c]	Age	Interval[d]	*n*[e]	Rate	95% CI	Rate	95% CI	Rate	95% CI	Rate	95% CI
M	<3.5	Post-breeding	16	1.000	1.000–1.000	0.000	0.000–0.000	0.000	0.000–0.000	0.000	0.000–0.000
		Parturition	28	1.000	1.000–1.000	0.000	0.000–0.000	0.000	0.000–0.000	0.000	0.000–0.000
		Breeding	19	0.789	0.554–0.919	0.211	0.081–0.446	0.000	0.000–0.000	0.000	0.000–0.000
		Annual	35	0.789	0.554–0.919	0.211	0.081–0.446	0.000	0.000–0.000	0.000	0.000–0.000
	≥3.5	Post-breeding	10	0.900	0.533–0.986	0.000	0.000–0.000	0.100	0.014–0.467	0.000	0.000–0.000
		Parturition	10	0.800	0.459–0.950	0.000	0.000–0.000	0.200	0.050–0.541	0.000	0.000–0.000
		Breeding	24	0.542	0.346–0.725	0.381	0.203–0.598	0.071	0.010–0.370	0.133	0.034–0.405
		Annual	27	0.390	0.213–0.601	0.381	0.203–0.598	0.331	0.129–0.624	0.133	0.034–0.405
F	<3.5	Post-breeding	10	1.000	1.000–1.000	0.000	0.000–0.000	0.000	0.000–0.000	0.000	0.000–0.000
		Parturition	14	1.000	1.000–1.000	0.000	0.000–0.000	0.000	0.000–0.000	0.000	0.000–0.000
		Breeding	15	0.733	0.467–0.896	0.267	0.104–0.533	0.000	0.000–0.000	0.000	0.000–0.000
		Annual	22	0.733	0.467–0.896	0.267	0.104–0.533	0.000	0.000–0.000	0.000	0.000–0.000
	≥3.5	Post-breeding	27	0.963	0.779–0.995	0.037	0.005–0.221	0.000	0.000–0.000	0.000	0.000–0.000
		Parturition	31	0.968	0.804–0.995	0.000	0.000–0.000	0.032	0.005–0.196	0.000	0.000–0.000
		Breeding	55	0.891	0.778–0.950	0.109	0.050–0.222	0.000	0.000–0.000	0.000	0.000–0.000
		Annual	57	0.830	0.689–0.915	0.142	0.067–0.276	0.032	0.005–0.196	0.000	0.000–0.000

[a]Harvest = legal harvest, illegal harvest, and unknown harvest.

[b]Natural = suspected hemorrhagic disease, post-rut exhaustion, and unknown natural.

[c]M = male, F = female.

[d]Post-breeding = 15 Feb–14 Jun, Parturition = 15 Jun–14 Oct, Breeding = 15 Oct–14 Feb, and Annual = 15 Feb–14 Feb.

[e]Effective sample sizes. Animals which contributed survival information during multiple seasons or years were counted as separate individuals.

Kilgo et al. 2016), demonstrating the important role that recreational hunters play in deer population management (Hewitt 2015) and underscoring the continued need to monitor effects of hunting and associated regulatory frameworks on populations across deer management units and landownership types to ensure that management goals are being met.

We observed similar harvest and survival rates between public and private land despite differences in state-mandated harvest regulations between landownership types and potentially greater hunting effort on public compared to private sites. Our findings differ from previous reports of variation in deer harvest and survival by landownership type (Wiskirchen et al. 2017, Haus et al. 2019). In the case of Haus et al. (2019), researchers observed lower survival of yearling males on public land (20%) compared to private land (69%), despite similar harvest regulations across landownership types. The authors postulated that the difference in survival may have been due, in part, to a concerted effort by private landowners to increase male age structure through selective harvest. In our study, a state-mandated APR applied to all harvested males on at least a portion of public study areas, but there were no harvest regulations on individual antlered males on private property (unless harvesting >2 antlered males). Given that APRs are effective at reducing harvest rates of young males relative to older males (Strickland et al. 2001, Demarais et al. 2005, Hansen et al. 2017, Wallingford et al. 2017), this regulatory difference

TABLE 5 Summary of a model set explaining the likelihood of harvest mortality among 79 adult (≥1.0-yr-old) white-tailed deer (*Odocoileus virginianus*) during 2014–2016 in Alabama, USA.

Model	K[a]	AIC_c[b]	ΔAIC_c	Weight
Sex × Age	4	155.2	0.0	0.34
Constant[c]	1	156.0	0.7	0.24
Sex	2	156.5	1.3	0.18
Age	2	157.7	2.4	0.10
LO[d]	2	157.9	2.7	0.09
Sex × LO	4	160.3	5.0	0.03
Age × LO	4	160.7	5.4	0.02

[a]Number of estimated model parameters.

[b]Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 2002).

[c]Constant model; one estimate for the entire study.

[d]Model variable LO = landownership (i.e., public or private land).

alone might have yielded lower harvest rates of immature males on public land compared to private land. However, QDM harvest strategies were in place on private study areas, whereby hunters self-restricted removal of young males beyond what was legally required, which may have had the same effect on private-land male harvest rates as the APR had on male harvest rates on public land.

In the absence of SHC, immature male deer experience greater harvest rates than mature males due to greater susceptibility to unbiased harvest (Dasmann and Taber 1956, Van Etten et al. 1965). We observed the opposite relationship across landownership types, indicating both management strategies in place on our study areas (i.e., APRs on public land and QDM on private land) were effective at limiting harvest of young males. Furthermore, we observed low natural and other non-harvest mortality among immature males, suggesting that most of these individuals, if not removed by hunters, will advance in age and be available for harvest during subsequent hunting seasons. The same conclusion was reached by Bowman et al. (2007), who monitored survival and harvest rates of male deer across private properties in Mississippi, USA, and reported young age classes (<3.5 yr old) had greater annual survival compared to older males, attributable largely to QDM practices that directed harvest away from young males and toward older males.

Similar harvest and survival rates of female deer on public and private land in our study were surprising given potentially greater hunting effort on public study areas. However, this is supported by Stedman et al. (2008), who documented a decreased willingness among public-land deer hunters in Pennsylvania, USA, to harvest antlerless deer and lower overall harvest success compared to private-land deer hunters. Greater collective effort on public areas in our study may have been offset by lower per-capita harvest, resulting in similar female harvest and survival rates across landownership types. The difference in selective preferences between public- and private-land deer hunters may be amplified in areas where QDM is practiced on private land, as in our study, where hunters are making a concerted effort to harvest sufficient antlerless deer to meet specific management goals.

Our annual survival estimate for mature female deer falls within the range previously reported in other studies from across the southeastern United States, and immature female survival was only slightly lower than previous estimates. Research within the region spanning 3 decades has documented a fairly narrow range (77–89%) of adult female survival rates (Land et al. 1993, Storm et al. 2007, Webb et al. 2010, Haymes et al. 2018, Peters et al. 2020). Adult male survival within the Southeast has been more variable, ranging from 22 to 91% (DeYoung 1989, Heffelfinger et al. 1990, Campbell et al. 2005, Bowman et al. 2007, Webb et al. 2010). Our estimates of adult male annual survival fall within the previously reported range, though our annual survival estimate for mature males is among the lowest recorded at 39%. Low observed annual survival for mature males is reflective of intense hunter selection driven by SHC across study areas that shifted harvest pressure toward that segment of the population, combined with higher natural mortality within the age cohort compared with immature males. Our models also indicated a strong interacting effect of sex and age within survival patterns. Whereas mature males had lower survival than immature males, there was no difference in survival between female age classes. While lower harvest rates among immature males compared with mature individuals is the goal and anticipated outcome of SHC, similar means of selective harvest are not available for female deer, resulting in comparable female harvest rates among immature and mature individuals.

Our study encompassed only 2 private tracts of land, and we acknowledge that QDM harvest practices in place on our private study areas did not necessarily represent deer harvest strategies implemented on other private property. However, available data demonstrate that QDM is a common deer management practice on private land across the southeastern United States that has grown in popularity through time. As of 2000, 60% of private land hunting clubs in Arkansas, USA, self-implemented male harvest restrictions in excess of state-mandated regulations, largely as a result of widespread involvement by private-land hunters in QDM programs (Collier and Krementz 2006). Since then, QDM has been referred to as a common management paradigm in Mississippi, USA (Bowman et al. 2007), and 91% of private-land hunting club members in Tennessee, USA, reported a preference for hunting under QDM restrictions (Harper et al. 2012). Although updated information is needed to quantify the current level of QDM implementation on private property, available evidence suggests that QDM is a widespread practice across the Southeast, and that our findings extend beyond the properties included in this study.

One of our public land study areas (Oakmulgee WMA) had similar harvest regulations to our private land study areas during the first year of our study, and half of the area had similar harvest regulations to private land during the second year of the study, which could have been a confounding factor in our public and private land comparison. However, while efforts were made to achieve an evenly distributed sample across all study areas, only 23% (3/13) of male deer on public land included in our study were on Oakmulgee WMA, with the majority being on Barbour WMA where the APR applied to all male deer. Thus, observed patterns in male harvest rates on public land were primarily driven by what occurred on Barbour WMA. Furthermore, other factors besides harvest regulations were likely involved in driving patterns of deer survival and harvest on public areas, including hunting effort and hunter goals and motivations that may differ between public- and private-land deer hunters (Stedman et al. 2008, Wiskirchen et al. 2017, Haus et al. 2019).

MANAGEMENT IMPLICATIONS

Wildlife managers will benefit from updated survival and cause-specific mortality estimates for adult white-tailed deer within a portion of the species' geographic distribution where information was previously lacking. Low harvest and high survival of male deer <3.5 years old indicated that both QDM and APRs may result in an older male age structure through time. Furthermore, a lack of observed variation in deer survival and harvest rates between public and private lands suggests that survival information can be used for informing management decisions across landownership types in some cases. This is especially true where regulations on public land restrict harvest of young male deer (e.g., APR or other selective harvest criteria), which appeared to have a similar effect on male and female harvest as QDM strategies on private land. However, where regulations are similar across landownership types (e.g., no state-mandated APR), differences in harvest and survival rates may exist (Haus et al. 2019).

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Animal capture and handling methods used in this study were approved by the Auburn University Institutional Animal Care and Use Committee (PRN No. 2013-2323) and followed the guidelines of the American Society of Mammalogists (Sikes 2016).

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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