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Research Article

White-Tailed Deer Population Dynamics Following Louisiana Black Bear Recovery

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ABSTRACT Changing predator communities have been implicated in reduced survival of white-tailed deer (*Odocoileus virginianus*) fawns. Few studies, however, have used field-based age-specific estimates for survival and fecundity to assess the relative importance of low fawn survival on population growth and harvest potential. We studied white-tailed deer population dynamics on Tensas River National Wildlife Refuge (TRNWR) in Louisiana, USA, where the predator community included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and a restored population of Louisiana black bear (*Ursus americanus luteolus*). During 2013–2015, we radio-collared and monitored 70 adult (≥2.5 yrs) and 21 yearling (1.5-yr-old) female deer. Annual survival averaged 0.815 (95% CI = 0.734–0.904) for adults and 0.857 (95% CI = 0.720–1.00) for yearlings. We combined these estimates with concurrently collected fawn survival estimates (0.27; 95% CI = 0.185–0.398) to model population trajectories and elasticities. We used estimates of nonhunting survival (annual survival estimated excluding harvest mortality) to project population growth (λ) relative to 4 levels of harvest (0, 10%, 20%, 30%). Finally, we investigated effects of reduced fawn survival on population growth under current management and with elimination of female harvest. Despite substantial fawn predation, the deer population on TRNWR was increasing ($\lambda = 1.06$) and could sustain additional female harvest; however, the population was expected to decline at 20% ($\lambda = 0.98$) and 30% ($\lambda = 0.94$) female harvest. With no female harvest, the population was projected to increase with observed ($\lambda = 1.15$) and reduced fawn survival ($\lambda = 1.02$), but the population could not sustain current female harvest (10%) if fawn survival declined ($\lambda = 0.90$). For all scenarios, adult female survival was the most elastic parameter. Given the importance of adult female survival, the relative predictability in response of adult survival to harvest management, and the difficulty in altering fawn survival, reducing female harvest is likely the most efficient approach to compensate for low fawn survival. On highly productive sites such as ours, reduction, but not necessarily elimination, of harvest can mitigate effects of low fawn survival on population growth. © 2020 The Wildlife Society.

KEY WORDS harvest, Louisiana black bear, mortality, *Odocoileus virginianus*, population growth, recruitment, survival, white-tailed deer.

Population dynamics of ungulates are complex and the direct and interactive effects of predation and resource availability on population growth has been debated and appears context-dependent (Peek 1980, Gaillard et al. 2000, Sinclair and Krebs 2002). Recognizing influences of selected vital rates (e.g., age-specific survival and fecundity) on population dynamics is important to predict population trends and inform management decisions. Ungulate populations are typically characterized by high and stable survival rates of adult females, moderately variable fecundity rates, and widely variable neonate survival rates (Gaillard et al. 1998, 2000). In addition, population growth is affected by variability and elasticity of vital rates (Gaillard et al. 1998). Demographic analyses can provide insight into which vital rates have the greatest influence on population growth and should be targeted by managers (Wisdom et al. 2000, Reed et al. 2002, Mills 2007, Chitwood et al. 2015*a*).

Recent declines in white-tailed deer (*Odocoileus virginianus*) fawn survival have been documented in many parts of southeastern United States (Kilgo et al. 2010), and researchers in some areas have reported fawn survival to be low (14–33%; Epstein et al. 1985, Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Chitwood et al. 2015*b*, Nelson et al. 2015). Robinson et al. (2014) concluded that reduced female harvest might be sufficient to offset projected deer population declines due to increased predation on fawns; however, they acknowledged that in areas with low recruitment (e.g., 25%),

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reduced female harvest might not be sufficient to stabilize populations. In a recent study on an area with low fawn survival (14%), Chitwood et al. (2015*a*) confirmed this hypothesis, concluding that protection of adult females from harvest may not completely offset projected population declines. Unfortunately, site-specific population models or sensitivity analyses are rare, particularly following predator restoration efforts primarily because site-specific information on adult female survival is lacking (Robinson et al. 2014).

We studied population dynamics of white-tailed deer on a study area in northeastern Louisiana, USA, where the fawn predator guild included coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and a restored population of Louisiana black bear (*Ursus americanus luteolus*). Louisiana black bear was listed as threatened under the Endangered Species Act in 1992; however, translocation efforts during 2001–2008 resulted in positive population growth, a high likelihood of long-term persistence, and delisting in 2016 (Benson and Chamberlain 2010, Laufenberg et al. 2016, U.S. Fish and Wildlife Service [USFWS] 2016). A concurrent study conducted during 2013–2015 reported survival of white-tailed deer fawns to 12 weeks was 27%, predation accounted for 88% of fawn mortalities, and Louisiana black bear was the primary predator (Shuman et al. 2017). The influence of low fawn survival on deer population growth and harvest potential remains an open and important question.

Our goal was to project white-tailed deer population growth under demographic scenarios reflecting observed field-based estimates, and hypothetical changes in female harvest and fawn survival. Our specific objectives were to estimate yearling and adult female observed and nonhunting annual survival rates, parameterize stage-based population models with field-based estimates of vital rates to project population growth and assess the relative importance of age-specific vital rates to population growth, and evaluate population growth under scenarios that reflect variable (i.e., 0, 10%, 20%, and 30%) female harvest and fawn mortality. We tested the hypothesis that reduction or elimination of female harvest would increase population growth, despite observed low fawn survival (Shuman et al. 2017) or scenarios of decreased fawn survival.

STUDY AREA

We conducted research on the Tensas River National Wildlife Refuge and adjacent private lands (TRNWR) located in northeastern Louisiana in 2013–2015 in the upper Tensas River Basin (Fig. 1). The 30,750-ha refuge was established in 1980 and was once extensively logged hardwoods and agricultural lands. Since acquisition by the USFWS, forests on the refuge have been allowed to mature into bottomland hardwoods and swamps, and abandoned agricultural fields have been replanted in native hardwoods.

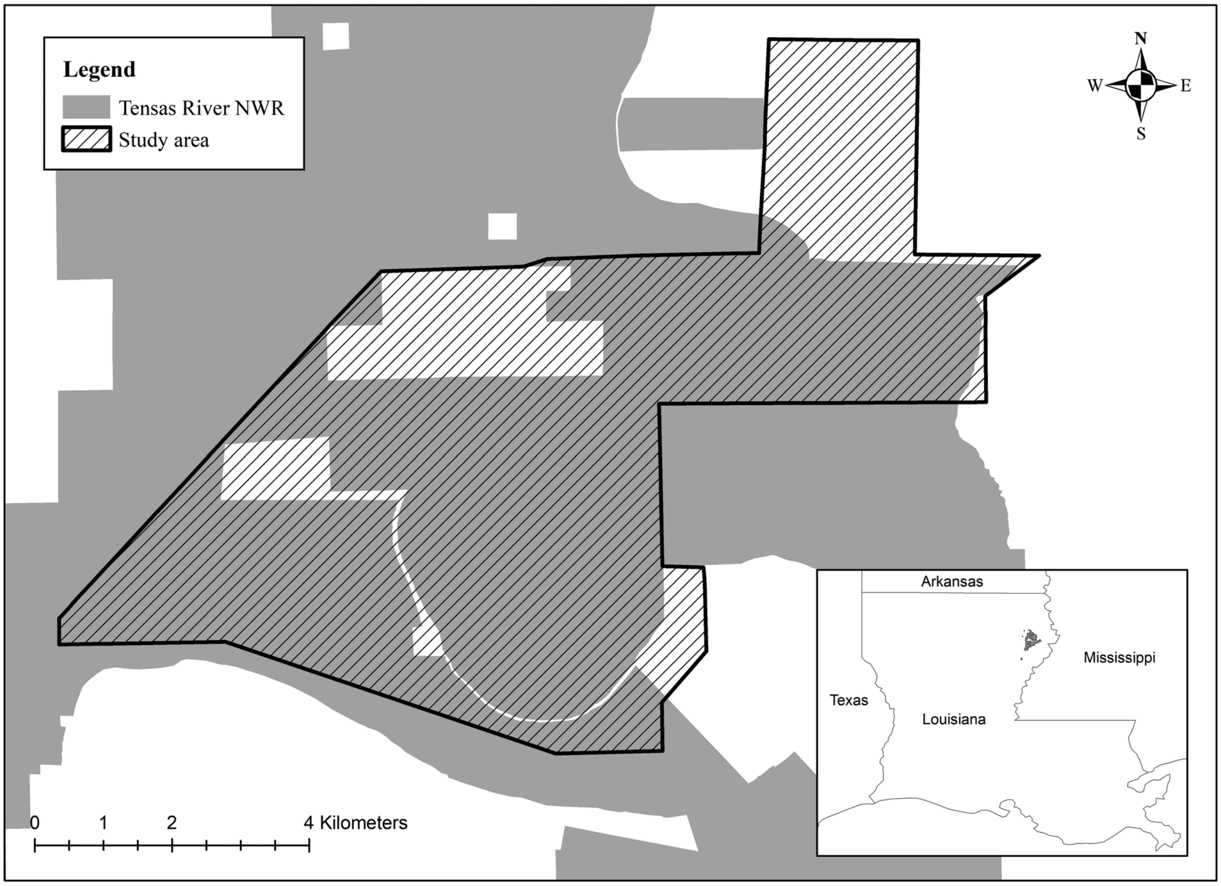

Figure 1. Study area including the Tensas River National Wildlife Refuge (NWR) boundary and adjacent private lands. Map inset indicates the study area location within Louisiana, USA.

The TRNWR was bordered almost entirely by agriculture on all sides, making it an island of habitat for many species including deer and the Louisiana black bear.

The Tensas River and surrounding areas were once the location of the main channel of the Mississippi River, and are in the western Mississippi River floodplain. Topography on TRNWR is flat to slightly undulating with 0–8% slopes and elevations ranging from 17–23 m above mean sea level (U.S. Geological Survey [USGS] 1995). Typical of a Mississippi River floodplain, ridge-swale, oxbow lakes, and backwater swamps are present. Soils are alluvial, poorly drained but highly fertile, and are composed mostly of the Tensas-, Sharkey-, or Alligator-series (USDA 1968).

The climate of TRNWR was humid subtropical. Mean annual temperature was 19°C with mean high and low temperatures of 25°C and 12°C, respectively, and annual precipitation averaged 130 cm (National Oceanic and Atmospheric Administration 2015). Weather during our study was similar to these long-term trends. During our study the composition of vegetation cover types on TRNWR included mature bottomland hardwoods (77%), early to mid-successional hardwood plantings (20%), wetlands-open water (2%), moist-soil management areas (<1%), cropland (<1%), and administrative sites (<1%). Overstory vegetation consisted of water oak (*Quercus nigra*), willow oak (*Q. phellos*), hickory (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), and sugarberry (*Celtis laevigata*), with interspersed bald cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) swamps. The understory consisted of dwarf palmetto (*Sabal minor*), poison ivy (*Toxicodendron radicans*), blackberry (*Rubus* spp.), trumpet creeper (*Campsis radicans*), and greenbrier (*Smilax* spp.). Several mast-producing species such as blackberry and pokeweed (*Phytolacca americana*) were abundant along roads and edges and where forest management practices have maintained a more open canopy. Early to mid-successional hardwood plantings initiated between 1985 and 2009 were distributed throughout TRNWR. Agricultural crops grown on TRNWR included corn, cotton, soybeans, and rice. Dominate fauna included Louisiana black bear, coyote, bobcat, gray fox (*Urocyon cinereoargenteus*), northern raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), cotton rat (*Sigmodon hispidus*), deer mice (*Peromyscus* spp.), and bottomland hardwood associated avian communities.

Deer densities on TRNWR during our study were approximately 17–22 deer/km^2 (S. Durham, Louisiana Department of Wildlife and Fisheries, personal communication). Annual harvest during the study averaged 903 ± 55 (SE) deer/year, an approximately 25% decline from the average of 1,197 ± 49 deer/year in the 1990s (J. Dickson, USFWS, unpublished data). Deer hunting season on adjoining private land began with archery hunting on 1 October and lasted until 31 January with 20 days of primitive weapon hunting and 65 days of modern firearms hunting. On TRNWR, archery hunting began in early November and lasted until the end of January. Deer hunting season on TRNWR also included 7 days of modern firearms hunting (2 days of youth only, 1 day antlerless only, 4 days of lottery hunts) and 2 days of primitive weapons hunting.

METHODS

Female Capture and Survival

During January–April 2013–2015, we captured yearling (1.5 yrs) and adult (≥2.5 yrs) females using a combination of drop nets, rocket nets, and darting with a pneumatic dart rifle (Dan-Inject, Børkop, Denmark) from a tree stand over bait. We anesthetized deer caught under nets with an intramuscular injection of ketamine hydrochloride (3.5 mg/kg; Congaree Veterinary Pharmacy, Cayce, SC, USA) and xylazine hydrochloride (2.5 mg/kg; Congaree Veterinary Pharmacy). When darting, we used Telazol (250 mg; Fort Dodge Animal Health, Fort Dodge, IA, USA) and xylazine hydrochloride (225 mg) in 1-ml Pneu-Dart transmitter darts (Pneu-Dart, Williamsport, PA, USA). We estimated age using tooth wear and replacement (Severinghaus 1949) and the presence of staining on the third premolar. We radio-collared (model 2510B, Advanced Telemetry Systems, Isanti, MN, USA), ear-tagged, and implanted each female with a vaginal implant transmitter (VIT; model M3930 or M3930L, Advanced Telemetry Systems). Radio-collars were equipped with an 8-hour mortality switch. Following instrumentation, we reversed the xylazine hydrochloride with tolazoline hydrochloride (150 mg intravenous and 150 mg intramuscular; Congaree Veterinary Pharmacy) and monitored deer until ambulatory. Capture and handling protocol was approved by the University of Georgia Institutional Animal Care and Use Committee (permit A2012 06-006-Y3-A2).

We monitored females via radio-telemetry weekly from capture until 1 June, ≥7 times weekly June through August, and ≥1 time monthly September through January. When we detected a mortality signal, we located radio-collars as soon as possible (i.e., <2 hr) and assigned cause of death as natural (predation, disease) or hunting-related. We used Kaplan-Meier models in the survival package in R (version 3.2, R Core Team, Vienna, Austria) to estimate annual survival based on cause of death (i.e., natural or hunting) for yearling and adult females over monthly intervals from capture until 14 January to create observed and nonhunting survival estimates. We estimated observed survival rates including all mortality observed during the study. To create nonhunting survival estimates, we fit Kaplan-Meier models and right censored deer at harvest. This approach provided baseline survival estimates given other mortality sources that we used to assess various levels of harvest mortality, assuming harvest was an additive mortality source. We used a staggered-entry approach (Pollock et al. 1989) and categorized deer into groups based on 1-month capture periods with 15 January as the annual starting date.

Model Structure and Development

To examine current population growth and effects of different scenarios on deer population dynamics, we used a female-based Lefkovitch matrix model (Lefkovitch 1965) with a 1-year time step where fawns and yearlings automatically transition to the next class:

$$\mathbf{A} = \begin{bmatrix} 0 & F\,(\text{yearling}) & F\,(\text{adult}) \\ S\,(\text{fawn}) & 0 & 0 \\ 0 & S\,(\text{yearling}) & S\,(\text{adult}) \end{bmatrix}$$

Our model was composed of 3 stages, which corresponded to fawns (0–1 yr old), yearlings (1–2 yrs old), and adults (≥2 yrs old) and included elements of fecundity (F) and survival (S) for each stage. Using the population matrix (**A**), we calculated the change in population using the equation:

$$\mathbf{n}(t+1) = \mathbf{A} \times \mathbf{n}(t)$$

where $\mathbf{n}(t)$ was a vector giving abundances of each stage in the population at time t. The left eigenvector of $\mathbf{A}$ gave expected relative contribution of a female in a given stage to future population growth. For comparison to previous works, we made 5 simplifying assumptions for our model: density independence, geographic closure, no male limitation, homogeneity of parameters for each stage, and no reproductive senescence (Chitwood et al. 2015*a*).

We parameterized our population matrix using vital rates derived from radio-telemetry data collected on our study site. To calculate adult and yearling fecundity, we used the number of fawns produced per female from births documented via vaginal implant transmitters (Shuman et al. 2017). Because our matrix was female-based, we included only the female portion of the fecundity rate. We assumed a 1:1 male-to-female fawn ratio, and therefore divided fecundity rates by 2. For adult females, we documented 28 births yielding 51 fawns during 2013–2015; thus, the adult fecundity rate was 1.82. For females bred as yearlings, we documented 5 births, yielding 6 neonates during 2013–2015, so the yearling fecundity rate was 1.20. Although the fecundity sample sizes were low, these data were consistent with rates documented in northeastern Louisiana (R. S. Durham, unpublished data). Given limited data, we did not investigate variation in fecundity and used these site-specific values in all models. We assumed that the fawn class had negligible fecundity and set fawn fecundity at zero (Dye 2007, Chitwood et al. 2015*a*). We based fawn survival rates on estimates of fawn survival to 12 weeks during 2013–2015 (Shuman et al. 2017; $n = 70$). In 2013 and 2014, Shuman et al. (2017) monitored radio-collared fawns weekly from 12 weeks old until collar failure (~6–9 months of age) and did not document any natural mortality. Furthermore, 94% of all mortalities occurred during the first month of life and all observed fawn mortalities occurred during the first 7 weeks of life. Although it is possible that fawns died after our monitoring period, we think that the 12-week survival rate adequately estimated annual survival, while acknowledging it may be overestimated. We used field-based adult and yearling survival rates described above for age-specific survival rates. We estimated initial population size ($n = 8{,}252$) for female fawns ($n = 3{,}541$), yearlings ($n = 1{,}170$), and adults ($n = 3{,}541$) using density and sex ratio estimates derived from harvest and survey data on TRNWR (S. Durham, unpublished data) and published estimates of female age structure in white-tailed deer populations (Dapson et al. 1979, Dusek et al. 1989). We parametrized stage-based population models to assess λ, sensitivities and elasticities of vital rates, and population size after 10 years to represent 7 scenarios:

1. observed adult, yearling, and fawn survival,
2. no adult and yearling harvest (nonhunting survival) and observed fawn survival,
3. 10% adult and yearling harvest (nonhunting survival minus 10% harvest mortality) and observed fawn survival,
4. 20% adult and yearling harvest (nonhunting survival minus 20% harvest mortality) and observed fawn survival,
5. 30% adult and yearling harvest (nonhunting survival minus 30% harvest mortality) and observed fawn survival,
6. observed adult and yearling survival and reduced fawn survival, and
7. no adult and yearling harvest (nonhunting survival) and reduced fawn survival.

To assess the observed population trajectory, we used field-based age-specific estimates of survival and fecundity collected during 2013–2015. We assigned female-based fecundity values of 0.91, 0.60, and zero for adults, yearlings, and fawns, respectively. Adult, yearling, and fawn survival estimates did not differ annually; therefore, we used the estimates combining years (Table 1). This approach limited potential error by incorporating annual estimates from years with small sample sizes for a given age class. To investigate all possible combinations of realistic vital rates, we parameterized 3 × 3 stage-based matrices drawing values from random uniform distributions generated within the 95% confidence interval of age-specific survival estimates for adults, yearlings, and fawns (Table 1). We parameterized

Table 1. Values for parameters used in the population matrix based on observed vital rates and hypothetical reduced fawn survival of white-tailed deer on Tensas River National Wildlife Refuge, Louisiana, USA, 2013–2015. Fecundity parameters were fixed values, whereas we sampled survival from a random uniform distribution within the range provided. The range represents the 95% confidence interval for the age-specific parameters estimated from known-fate models derived from radio-collared deer.

	Stage	Beta	Model parameter
Fecundity	Fawn (F_f)		0
	Yearling (F_y)		0.600
	Adult (F_a)		0.910
Observed survival	Yearling (S_y)	0.857	0.720–1.00
	Adult (S_a)	0.815	0.734–0.90
Nonhunting survival	Yearling (S_y)	0.952	0.866–1.00
	Adult (S_a)	0.914	0.873–1.00
Observed fawn survival[a]	Fawn (S_f)	0.270	0.185–0.398
Reduced fawn survival[b]	Fawn (S_f)	0.141	0.075–0.249

[a] Concurrent study reported in Shuman et al. (2017).

[b] Reported in Chitwood et al. (2015*b*).

1,000 matrices drawing samples from these distributions to fully cross all possible vital rates and to generate means and distributions of probable λ, sensitivities, and elasticities values. We used the popbio package in R to determine the stable stage distribution (SSD) and run the matrix at SSD to determine λ, sensitivities, elasticities, and to project population size for 10 years.

We then modified this model to represent the 6 management scenarios. Elimination of female harvest has been suggested as a strategy to offset population declines in systems with low fawn survival (Robinson et al. 2014, Chitwood et al. 2015*a*). Therefore, we parameterized a scenario using nonhunting survival rates for adults and yearlings, and observed fawn survival estimates. We then created 3 additional scenarios representing common harvest management objectives in the region by reducing the adult and yearling nonhunting survival rate by 10%, 20%, and 30% to represent increasing harvest intensity. We followed the procedure described above but instead sampled from the 95% confidence intervals for adult and yearling nonhunting survival estimates and subtracted the appropriate level of harvest mortality (0, 10%, 20%, 30%) for each scenario.

Next, we explored scenarios with reduced fawn survival. For comparison to extant literature, we used fawn survival estimates reported in Chitwood et al. (2015*b*), which were used in Chitwood et al. (2015*a*) to parametrize matrix models. This fawn survival rate (14%) was among the lowest reported in the literature and was sufficiently low to result in population decline in the absence of female harvest on a low-productivity site in North Carolina, USA. We generated a random uniform distribution within the 95% confidence interval for overall fawn survival reported in Chitwood et al. (2015*b*; 95% CI = 0.08–0.25). We parameterized 2 scenarios using this distribution representing reduced fawn survival. We parameterized the first scenario with the observed adult and yearling survival estimates, to evaluate the effect of reduced fawn survival under current management on population growth. We parameterized the second scenario with nonhunting adult and yearling survival estimates to represent no harvest in response to reduced fawn survival. For each scenario, we assigned fecundity values of 0.91, 0.60, and 0 for adults, yearlings, and fawns respectively. We then repeated the procedure detailed above to determine the SSD, and ran the matrix at SSD to determine λ, sensitivities, and elasticities, and to project population size for 10 years.

RESULTS

We captured and radio-collared female deer on 91 occasions, including 70 adult captures (21, 21, and 28 in 2013–2015, respectively) and 21 yearling captures (8, 9, and 4 in 2013–2015, respectively). We recaptured 11 females following their initial capture (3 in 2014, 8 in 2015), resulting in 81 adults used in our analysis. Mean annual survival of adults was 0.815 (95% CI = 0.734–0.904) and of yearlings was 0.857 (95% CI = 0.720–1.00; Table 2). Accounting for only nonhunting mortality, mean annual nonhunting survival of adults was 0.914 (95% CI = 0.854–0.977) and of yearlings was 0.952 (95% CI = 0.866–1.00).

The observed scenario, using field-based age-specific survival and fecundity rates, projected a growth rate of λ = 1.06 (interquartile range [IQR] = 1.02–1.09), with 85% of projections reporting a positive growth rate (Fig. 2). The scenario of no female harvest projected λ = 1.15 (IQR = 1.11–1.15), with 100% of projections predicting positive population growth (Fig. 3). The scenario of 10% harvest was similar to the observed scenario λ = 1.06 (IQR = 1.03–1.10), and projected positive population growth. The 20% and 30% harvest scenarios both predicted negative population growth: λ = 0.98 (IQR = 0.94–1.01) and λ = 0.90 (IQR = 0.87–0.94), respectively. If fawn survival declined to the lower limits reported in the literature (Chitwood et al. 2015), under current management (i.e., observed adult and yearling survival), the population was projected to decline with a growth rate of λ = 0.97 (IQR = 0.93–1.00). But the elimination of female harvest was sufficient to mitigate effects of reduced fawn survival. The scenario of no female harvest and reduced fawn survival projected a growth rate of λ = 1.02 (IQR = 0.99–1.06; Fig. 4).

Table 2. Annual survival of yearling (1.5 yrs) and adult (≥2.5 yrs) female white-tailed deer at Tensas River National Wildlife Refuge, Louisiana, USA, 2013–2015.

Cause of mortality	Stage	Year	*n*	Survival rate	SE	95% CI
Nonhunting	Yearling	2013	8	0.875	0.117	0.673–1.000
		2014	9	1.000		
		2015	4	1.000		
		Overall	21	0.952	0.047	0.866–1.000
	Adult	2013	21	0.905	0.641	0.788–1.000
		2014	24	0.875	0.068	0.752–1.000
		2015	36	0.944	0.038	0.873–1.000
		Overall	81	0.914	0.031	0.854–0.977
Observed	Yearling	2013	8	0.750	0.153	0.503–1.000
		2014	9	0.889	0.105	0.706–1.000
		2015	4	1.000		
		Overall	21	0.857	0.076	0.720–1.000
	Adult	2013	21	0.714	0.099	0.545–0.936
		2014	24	0.875	0.068	0.752–1.000
		2015	36	0.833	0.062	0.720–0.964
		Overall	81	0.815	0.043	0.734–0.904

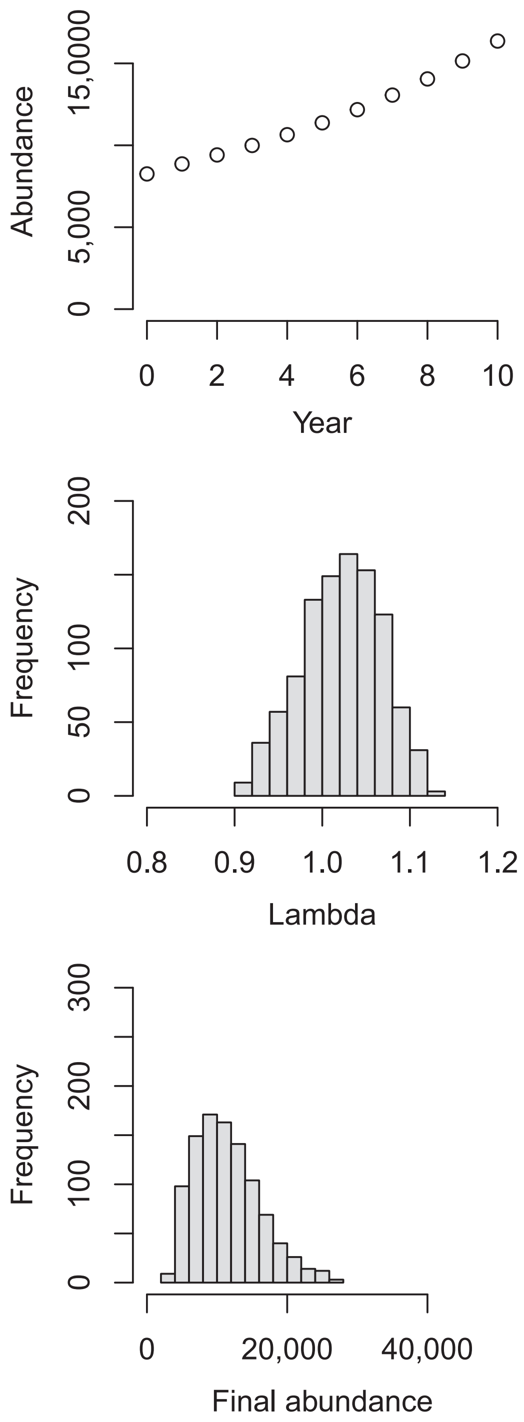

Figure 2. White-tailed deer projected population trajectory, distributions of predicted population growth (lambda) values, and final abundances after 10 years using observed estimates of adult, yearling, and fawn survival and fecundity on Tensas River National Wildlife Refuge, Louisiana, USA, 2013–2015.

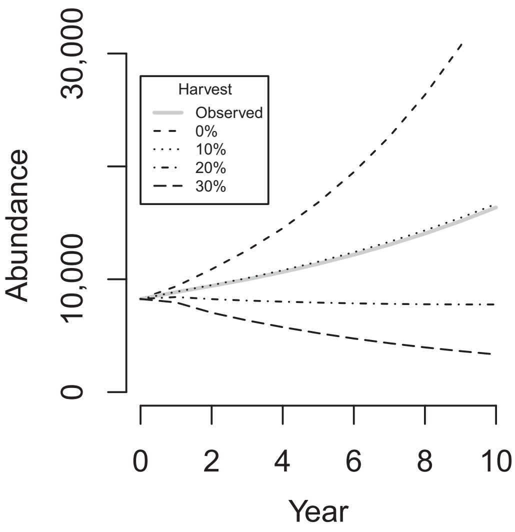

Figure 3. Predicted population trajectory of white-tailed deer population for 10 years with 0, 10%, 20%, and 30% hunting female mortality at Tensas River National Wildlife Refuge, Louisiana, USA, 2013–2015.

For current, 0%, and 10% hunting mortality, and reduced fawn survival with no hunting mortality scenarios, the most sensitive vital rate was adult female survival. In the reduced fawn survival with observed adult and yearling survival scenario, and the observed adult and yearling survival with 20% and 30% hunting mortality scenarios, the most sensitive vital rate was fawn survival (Table 3). The most elastic vital rate in all scenarios was survival of adult females (Table 3).

DISCUSSION

We provide field-based estimates of an increasing deer population trajectory following the restoration of the Louisiana black bear, an important fawn predator, and demonstrate tradeoffs between low fawn survival and harvest potential. Despite substantial fawn predation (Shuman et al. 2017) the deer population on TRNWR could sustain additional female harvest. We observed approximately 10% harvest and projected approximately 6% annual population growth; however, with 20% and 30% harvest mortality, the population was projected to decline. Additionally, effects of further declines in fawn survival on population growth could be mitigated by reduced female harvest. In the absence of female harvest, the population was projected to increase

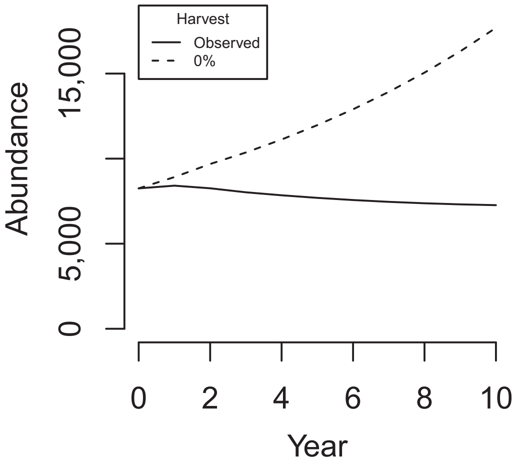

Figure 4. Predicted white-tailed deer population projections for 10 years with hypothetical reduced fawn survival (14%; 95% CI = 0.075–0.246) under observed management and no female hunting mortality at Tensas River National Wildlife Refuge, Louisiana, USA, 2013–2015.

Table 3. Sensitivities and elasticities for vital rates in all scenarios of white-tailed deer population trends at Tensas River National Wildlife Refuge, Louisiana, USA, 2013–2015.

Scenario	Parameter	Sensitivity	Elasticity
Observed	Fawn survival	0.641	0.173
	Yearling survival	0.180	0.146
	Adult survival	0.653	0.507
	Yearling fecundity	0.048	0.027
	Adult fecundity	0.169	0.146
0% hunting	Fawn survival	0.594	0.151
	Yearling survival	0.161	0.130
	Adult survival	0.699	0.568
	Yearling fecundity	0.039	0.020
	Adult fecundity	0.165	0.130
10% hunting	Fawn survival	0.619	0.167
	Yearling survival	0.181	0.142
	Adult survival	0.664	0.522
	Yearling fecundity	0.047	0.026
	Adult fecundity	0.166	0.142
20% hunting	Fawn survival	0.645	0.187
	Yearling survival	0.206	0.153
	Adult survival	0.624	0.471
	Yearling fecundity	0.056	0.034
	Adult fecundity	0.166	0.154
30% hunting	Fawn survival	0.664	0.213
	Yearling survival	0.231	0.167
	Adult survival	0.574	0.407
	Yearling fecundity	0.067	0.046
	Adult fecundity	0.165	0.167
Reduced fawn survival	Fawn survival	0.778	0.127
	Yearling survival	0.129	0.114
	Adult survival	0.744	0.630
	Yearling fecundity	0.023	0.014
	Adult fecundity	0.121	0.114
Reduced fawn survival and 0% hunting	Fawn survival	0.706	0.105
	Yearling survival	0.110	0.095
	Adult survival	0.790	0.695
	Yearling fecundity	0.017	0.009
	Adult fecundity	0.112	0.095

rapidly with observed fawn survival rates, and be stable to slightly increasing with reduced fawn survival rates. But if fawn survival rates declined, the population could not sustain current harvest pressure (10%).

Although Chitwood et al. (2015*a*) documented similar survival rates for adult females in North Carolina, they projected a declining deer population under current conditions. Robinson et al. (2014) projected declines in deer populations when fawn survival was low (23%) and adult female mortality was 10% above estimates of natural mortality rates but reported increasing populations when female mortality was reduced to 5% above natural mortality. Our findings suggest that the TRNWR population is increasing despite a 10% hunting mortality rate. When we modeled populations on TRNWR using observed adult and yearling vital rates, and fawn survival rates reported in Chitwood et al. (2015*a*), we also documented a declining population trend. In our study the elimination of female harvest offset the reduction of fawn survival, whereas Chitwood et al. (2015*a*) concluded that elimination of female harvest would not completely offset population declines. Although our vital rates for adult female survival were similar to Chitwood et al. (2015*a*) and Robinson et al. (2014), the difference in population projections was due to higher fecundity rates and deer densities (17–22 deer/km^2) in our study. Robinson et al. (2014) based their population projections on densities reported throughout the eastern United States (range = 5.4–9.2 deer/km^2), and Chitwood et al. (2015*a*) reported a density of 6 deer/km^2.

Knowledge of age-specific survival rates of female deer is important for sustainably managing deer herds, but few studies have evaluated age-specific survival in the southeastern United States. We provide estimates of yearling and adult female survival, and deconstruct mortality into nonhunting and hunting mortality. Our nonhunting and total mortality rates for yearling (5% and 14%, respectively) and adult (9% and 18%, respectively) females were similar to those throughout white-tailed deer range (DeYoung 2011) and to adult female mortality in North Carolina (20%; Chitwood et al. 2015*a*) and South Carolina, USA (13%; Kilgo et al. 2016). Previous studies in the southeastern United States assumed adult female mortality rates of 25% (South Carolina; Comer et al. 2005) and 30% (Mississippi, USA; Gruver et al. 1984) or a nonhunting mortality rate of 10% (Georgia, USA; Keyser et al. 2006). Although we reported similar nonhunting mortality rates, we observed lower hunting mortality rates. Because mortality rates vary spatially, use of empirically derived mortality rates instead of assumed rates will provide better data for local management decisions.

Survival of adult females was the most elastic vital rate, consistent with other studies of large herbivores (Gaillard et al. 1998, Eberhardt 2002, Chitwood et al. 2015*a*). Elasticity is valuable analytically but has limitations. Elasticities cannot always predict how population growth will change as vital rates change, and although it can be a good indicator of growth-rate changes, management actions rarely change vital rates by the same proportionate amount determined by the sensitivity analysis (Mills et al. 1999). Vital rates with low elasticities typically have higher variance than rates with higher elasticities (Pfister 1998), and rates with low elasticities changing over wide ranges could affect growth rate as much as the vital rate ranked as most important based on elasticities alone (Gaillard et al. 1998). This underscores the importance of accounting for all vital rates when making management decisions, and suggests management actions that have potential to affect fecundity and survival, such as habitat management, should be favored. But given the universal importance of adult female survival, management aimed at altering adult female survival, such as harvest management, are likely to be more influential on population growth than management actions that enhance fawn survival, such as predator removal.

We acknowledge several limitations to our approach that should be considered when interpreting our results. First, we projected population growth assuming density independence. Density dependence should be considered for all populations, but effects increase as populations approach high or low densities relative to carrying capacity. On our highly productive site, fecundity rates were already sufficiently high to be unlikely to respond substantially to projected reductions in density. Our scenario with the greatest potential population growth (no harvest) was the most likely scenario to be overestimated based on the lack of inclusion of a density-dependent effect. But from a management perspective, the conclusion that the population was likely to grow substantially in the absence of harvest remains sound even if the effect size was overestimated because of the assumption of density independence.

Second, we assumed fawn survival to 12 weeks represented annual fawn survival and fawn fecundity was zero. It is likely some animals died following our monitoring period, which would inflate estimates of fawn survival and population growth. On highly productive sites or sites with asynchronous breeding seasons, fawns can reach sexual maturity during their first breeding season (Ditchkoff 2011); hence, our assumption of no reproduction for the fawn class would underestimate the potential contribution of female fawns to population growth. We suggest these conflicting biases and their combined effects were negligible.

Third, when estimating nonhunting survival, we assumed harvest was an additive mortality source and marking (collars and ear tags) did not influence hunter selectivity. Given relatively high nonhunting survival, there is limited opportunity for high rates of compensatory mortality; however, we acknowledge harvest likely was at least partially compensatory, which would result in an overestimation of the negative effect of harvest on population growth potential. Hunter bias against harvesting marked deer is typically minimal (Buderman et al. 2014), but to further minimize hunter bias in harvest of marked deer, we coordinated with management agencies to encourage hunters to not let the presence of markings influence their harvest decision. Although understanding the scenario-specific directionality and likelihood of biases is important, we suggest their effects were minimal, the assumptions that led to these limitations facilitated comparisons with previous work (Chitwood et al. 2015*a*), and our results are useful for considering tradeoffs between fawn survival and female harvest potential.

Habitat and landscape associations can influence fawn survival (Gulsby et al. 2017, Hasapes and Comer 2017, Shuman et al. 2017, Gingery et al. 2018) and deer select habitat at multiple scales during fawning, in part to minimize fawn predation risk (Lashley et al. 2015, Cherry et al. 2017, Shuman et al. 2018). Deer in multi-predator landscapes face the challenge of variation in species-specific predator hunting strategies, habitat associations (Sih et al. 2012), and the temporal efficacy of predation (Vreeland et al. 2004), potentially leading to lower survival than deer in landscapes with few predator species. But some evidence is beginning to emerge that suggests predator richness may not dictate white-tailed deer population growth trends or survival (Kautz et al. 2019). We report positive population growth in a 3-predator system, whereas Chitwood et al. (2015*a*) reported lower fawn survival and population decline in a 2-predator system. Furthermore, fawn survival in our 3-predator system (27%) was similar to other studies conducted in the region at similar latitudes, on sites with only 2 predators (Kilgo et al. 2012 [23%]; Nelson et al. 2015 [29%]). Clearly, more work is needed to understand how predator richness influences fawn survival given how complex and dynamic predation can be across landscapes. We offer that addressing this question has important implications for predicting deer population responses to expanding predator communities, and to predator control in systems where not all predators can be targeted for removal.

Our approach investigated how harvest management could mitigate effects of low (i.e., <20%) fawn survival. This approach should be part of a broader management plan including other strategies to influence vital rates such as habitat improvement to increase fawn survival and adult fecundity rates. Predator control also may improve fawn survival rates, although results can be inconsistent (Kilgo et al. 2014, Conner and Morris 2015, Gulsby et al. 2015). Furthermore, predator control when some members of the predator community cannot be targeted based on their conservation status may not benefit fawn survival if compensatory mortality from the remaining predators occurs. Our lack of understanding of the effects of predator richness on fawn survival limits our ability to predict results of predator control under these conditions. Nonetheless, given the importance of adult female survival to population growth and the predictable response of adult female survival to harvest management, manipulation of female harvest is the most viable option for mitigating effects of low fawn survival. Because deer density, demography and predator communities vary spatially, research should address regional and site-specific population responses to fawn predation, how other demographic parameters such as fecundity and adult female survival influence population resiliency to low fawn survival, and how predation affects harvest potential.

MANAGEMENT IMPLICATIONS

Our results suggest managers could continue to maintain stable deer populations with further reductions of female harvest, even if fawn survival declined further. Although our results are useful to assist management at this specific intersection of rare-species conservation (Louisiana black bear) and game management (white-tailed deer), they may also generalize to other high productivity sites with low fawn survival. For white-tailed deer populations with high fecundity rates, low fawn survival can be mitigated through reduction of female harvest. Given the importance of adult survival to population growth, the predictable response of adult female survival to harvest prescription, the relatively lower importance of fawn survival to population growth, and the unpredictable responses of fawn survival to management actions (i.e., predator control), management of adult female harvest remains the most viable tool for addressing low fawn survival.

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