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Research Article

White-Tailed Deer Population Dynamics and Adult Female Survival in the Presence of a Novel Predator

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ABSTRACT Recent localized declines in white-tailed deer (*Odocoileus virginianus*) populations in the southeastern United States have been linked to increasing predation pressure from coyotes (*Canis latrans*), a novel predator to the region. Studies have documented coyotes as the leading cause of mortality for neonates, and 1 study documented coyotes as a mortality factor for adult females. However, no study has used field-based vital rates to conduct sensitivity analyses or model deer population trajectories under potential harvest or predator removal strategies. We used low, medium, and high values of fawn survival, adult female survival, and fecundity data collected from Fort Bragg Military Installation, North Carolina to demonstrate the current declining population trajectory for deer ($\lambda = 0.905$; low $\lambda = 0.788$, high $\lambda = 1.003$). Consistent with other studies of ungulates, we determined adult female survival was the most sensitive and elastic vital rate. Further, for 3 potential management ("what if") scenarios, we projected the population for 10 years using estimated vital rates. Reducing adult female harvest ($\lambda = 0.935$; low $\lambda = 0.875$, high $\lambda = 1.002$) and coyote removal ($\lambda = 0.995$; low $\lambda = 0.898$, high $\lambda = 1.081$) reduced the current population decline, whereas combining both approaches ($\lambda = 1.024$; low $\lambda = 0.898$, high $\lambda = 1.141$) resulted in population increases. Our data indicate that for low-density deer populations with heavy predation pressure on neonates, protecting adult females from harvest may not completely offset population declines. Coyote removal might be a necessary strategy because it could possibly increase very low fawn survival, which appears to be the most important vital rate influencing λ in our study. However, managers may have to start with reductions in adult female harvest because coyote removal would have to be continuous and consistently effective, making it an impractical management approach by itself. © 2015 The Wildlife Society.

KEY WORDS coyote, elasticity, neonate, population dynamics, sensitivity, survival, white-tailed deer.

White-tailed deer (*Odocoileus virginianus*; hereafter, deer) are common across much of the United States, and in many areas managers struggle to control overabundant populations (Warren 1997). However, recent localized declines in fawn recruitment contrast with trends of overabundance and have been linked to the introduction and establishment of coyotes (*Canis latrans*) in the southeastern United States (Kilgo et al. 2010). Although they were originally from the western United States, coyotes now occupy most of North and Central America (Nowak 1978, Gompper 2002). Thus, deer of the southeastern United States are subject to predation by a large canid, a pressure that has not occurred since the extirpation of red wolves (*Canis rufus*).

Coyote predation on white-tailed deer, particularly neonatal fawns, can be high (e.g., Cook et al. 1971, Bartush and Lewis 1981, Whittaker and Lindzey 1999, Vreeland et al. 2004). Ballard et al. (2001) concluded that coyotes can be a significant source of mortality for deer, and Ballard et al. (1999) suggested coyotes could replace wolves as deer predators in parts of northeastern North America, where they depredate adults in winter and neonatal fawns. Coyote predation on neonates may be compensatory to other mortality factors (Bartmann et al. 1992, Bishop et al. 2009), or additive (and therefore limiting; Messier et al. 1986, Patterson et al. 2002), but most research related to coyote impacts on deer has been conducted either in the historical western range or in northeastern North America where

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winter severity contributes to predation susceptibility (Gompper 2002). Only recently have direct assessments of coyote impacts been conducted in the forested landscapes and milder climate of the southeastern United States. Though effects of coyote predation on deer may vary across the southeastern United States, evidence is mounting that neonate survival is severely affected in some areas (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood 2014). In addition, recent evidence indicates that coyotes could become an important source of mortality for adult deer, particularly females (Chitwood et al. 2014*a*). Thus, deer population dynamics could be changing and alternative management strategies might warrant consideration (Kilgo et al. 2010).

Despite establishment of coyotes in the southeastern United States and evidence from other regions that coyotes can affect deer populations, wildlife professionals have remained relatively unconcerned about potential effects (Kilgo et al. 2010). Though interest in the topic has increased notably in recent years, as evidenced by the growing number of completed or ongoing neonatal deer survival studies, Kilgo et al. (2010) surmised the lack of concern could stem from the belief that coyotes are not significant predators of deer in the southeastern United States or from the perception that deer are too abundant to worry about impacts. Because of a mild climate and low mortality from winter nutritional stress, hunter harvest is believed to drive the dynamics of most deer populations in the southeastern United States (Kilgo et al. 2010). However, Kilgo et al. (2010) presented data from South Carolina that indicated declining deer recruitment was commensurate with the increasing population of coyotes. Thus, the potential for coyote predation to affect deer populations in the region warrants consideration of adaptive changes in management where impacts are significant. However, better estimates of vital rates are needed to construct a framework for deciding which management strategies are most likely to influence population growth positively.

Understanding the influences of select vital rates (e.g., neonate survival, adult female survival, fecundity) on population dynamics is crucial for maximizing success of conservation efforts, particularly with sensitive or declining species. Demographic analyses, including sensitivity analyses of matrix population models, provide valuable insight into which vital rates have the greatest influence on population growth, are most variable, and should be targeted by managers (Wisdom et al. 2000, Reed et al. 2002, Mills 2007). Analytical sensitivity uses reproductive value and stable age distributions (or stable stage distributions, SSD) to quantify how a small, equal change in any stage-specific vital rate will change asymptotic population growth rate (i.e., the λ provided by a matrix at SSD; Mills and Johnson 2013). Analytical elasticity rescales sensitivity to account for proportional change in λ, given an incremental proportional change in a vital rate (Mills and Johnson 2013). These analyses have informed management of numerous species with economic value or conservation concern, including sea turtles (Crouse et al. 1987), tortoises (Reed et al. 2009), amphibians (Biek et al. 2002), waterfowl (Hoekman et al. 2002, Coluccy et al. 2008), big game (Raithel et al. 2007, Johnson et al. 2010), upland game birds (Clark et al. 2008, Sandercock et al. 2008, Devers et al. 2009, Taylor et al. 2012), and migratory waterbirds (Grear et al. 2009). Although white-tailed deer are not of conservation concern, their wide distribution and popularity among big game hunters make them a valuable commodity.

A recent commentary used a wide range of deer vital rates in modeling scenarios to conclude that reduced antlerless harvest was enough to offset deer population declines exacerbated by coyotes (Robinson et al. 2014). Robinson et al. (2014) contended that sources of mortality that occur prior to recruitment are not important for managing hunted populations as long as management objectives can be met (Rosenberry et al. 2011), but they acknowledged that very low neonate survival rates (e.g., Kilgo et al. 2012) may constitute an exception to this rule. Further, Robinson et al. (2014) suggested that relevant survival estimates for adult female deer in the southeastern United States are lacking and may be important for making better management decisions in the region. In the context of coyote predation impacts on white-tailed deer vital rates in the southeastern United States, we are aware of no comprehensive, site-specific population models or sensitivity analyses, both of which are necessary to identify key vital rates and improve management decisions. Thus, our objectives were to 1) provide a survival estimate for adult female deer from the region; 2) assess the relative importance of stage-specific vital rates in a declining deer population with heavy predation pressure from coyotes; and 3) present several management options (i.e., "what if" scenarios that include harvest and predator removal strategies) and demonstrate their potential to affect deer population estimates via underlying changes in vital rates.

STUDY AREA

We conducted our study at Fort Bragg Military Installation (hereafter, Fort Bragg; 40,500 ha), which was owned by the United States Department of Defense and located in the Sandhills physiographic region of central North Carolina. Open longleaf pine (*Pinus palustris*) forests dominated the uplands and were managed with growing-season prescribed fire on a 3-year fire-return interval (Lashley et al. 2014). The understory of longleaf forests was comprised of turkey oak (*Quercus laevis*) and wiregrass (*Aristida* spp.). Densely vegetated drainages were interspersed throughout the landscape and were burned infrequently.

Deer population density was relatively low (approx. 6 deer/km^2) at Fort Bragg. Hunting occurred from the first Saturday in September through 1 January in the accessible areas. Deer density decline was apparent beginning in 1989, with harvest records standardized by hunter effort showing a 30–60% reduction in deer at Fort Bragg by 2010. Although deer density estimates should be interpreted with caution, Imperio et al. (2010) demonstrated hunter harvest success was positively correlated to density of ungulates. At Fort Bragg, total hunter harvest fell from a high of 1,261 in 1989 to a low of 163 in 2003; currently, hunter harvest is around

250–300 deer per year. Though hunter effort has changed over the years, deer hunters currently harvest deer in 1 out of 33 hunts, compared to 1 out of 15 hunts in the 1980s (J. Jones, Fort Bragg Wildlife Branch, personal communication). The apparent decline in deer density was commensurate with the initiation and establishment of coyotes at Fort Bragg, which were first documented in 1989. Coyotes were considered well-established by the mid-1990s (J. Jones, personal communication), now represent the leading cause of neonatal deer mortality (Chitwood 2014), and have been confirmed as a source of mortality for adult female deer (Chitwood et al. 2014*a*). Bobcats (*Lynx rufus*) were the only other documented predator of neonates at Fort Bragg (Chitwood 2014).

METHODS

Adult Female Survival

We captured and radiocollared adult and yearling female deer from January to May in 2011 and 2012 as part of a neonate survival study (see Chitwood 2014 for capture and handling methods). Via global positioning system (GPS) technology and telemetry, we monitored females intensely during the fawning seasons of 2011 and 2012 (see Chitwood 2014 for details); we monitored them at least monthly throughout the rest of the study period (Jan 2011–Dec 2013). We determined annual survival using known-fate modeling in Program MARK (White and Burnham 1999) with a staggered entry approach (Pollock et al. 1989). Thus, radiocollared deer entered the study beginning January 2011 until capture efforts ended in May 2012. Thereafter, we monitored deer through December 2013, which allowed us to calculate cumulative survival for 36 months and annual survival from January to December each year. We used the pre-defined model set in Program MARK and did not include covariates. The pre-defined models were *S*(.), which represents constant survival, and *S*(t), which allows survival to vary by time interval. We used Akaike's Information Criterion (adjusted for small sample size; AIC$_c$) for model selection and considered plausible models to be those $\leq$2.0 AIC$_c$ units from the top model (Burnham and Anderson 2002). We used Akaike weights (w_i) to evaluate strength of evidence among competing models (Burnham and Anderson 2002). Deer capture and handling was approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (10–143-O).

Model Structure

We examined the effects of several management strategies on the dynamics of a declining white-tailed deer population using a female-based matrix model:

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

where $\mathbf{n}(t)$ was a vector of abundances for each stage in the population at time t and $\mathbf{A}$ was the population projection matrix. Our model consisted of 3 stages (Fig. 1), corresponding to fawns (0–1 years old), yearlings (1–2 years old), and adults ($\geq$2 years old). The projection interval (from t to $t+1$) was 1 year, and the model was specified using fecundity (*F*) and survival (*S*) for each stage, with the following structure:

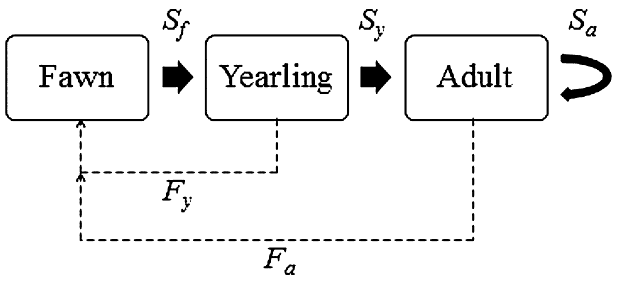

Figure 1. Life-stage model for white-tailed deer showing 3 stages: fawn (*f*), yearling (*y*), and adult (*a*). Survival between stages is represented by *S* and fecundity for yearlings and adults is represented by *F*.

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

Fecundity for yearlings and adults was calculated as follows:

$$F_i = B_i \cdot S_i$$

where for each stage *i*, *B* was birth rate and *S* was survival. We assumed the fawn class had negligible fecundity (Ditchkoff 2011), so we did not include a fecundity value for that stage.

Assumptions

Our model made several simplifying assumptions. First, we assumed density-independence; although density-dependence is a necessary consideration for all populations, the Fort Bragg deer population has been in decline for over 20 years and currently shows no signs of negative impacts on the understory structure (as evidenced by vegetation exclusion cages paired with random sites; Lashley 2014). Thus, density feedbacks on survival or fecundity in our population were likely to be small. Second, we assumed geographic closure, which is reasonable because females demonstrate high site fidelity (Lashley 2014). Third, we assumed the population was not male-limited, which allowed us to accurately assess dynamics from only females (Merrill et al. 2003). Fourth, we assumed homogeneity for each stage (i.e., all individuals in each stage had the same parameters; Merrill et al. 2003) and that individuals had constant survival and fecundity parameters over time. Finally, we assumed adult females had the same parameters at all adult ages and therefore did not include prime-aged or senescent stages, though some ungulate studies have (e.g., Raithel et al. 2007). Masters and Mathews (1990) reported white-tailed deer females >9 years of age exhibited little sign of reproductive senescence. Similarly, DelGiudice et al. (2007) reported no measurable reduction in number of offspring produced per white-tailed deer female through 15 years of age. Moreover, because our primary purpose was to demonstrate a range of possible effects for several management strategies, examining population dynamics under simple conditions was instructive (Merrill et al. 2003).

Model Development and Parameterization

To determine λ and analytical sensitivities and elasticities, we parameterized our 3×3 population matrix using vital rates derived from radiocollar-based field studies at Fort Bragg (see Chitwood 2014). We parameterized the base model (i.e., the Current Scenario) using current vital rates at Fort Bragg. However, to incorporate variability and uncertainty into our projections, we followed an approach used by Merrill et al. (2003) where we used low, medium, and high values for all parameters (Table 1) to represent the range of possible population trajectories. Medium parameter values represented our mean predictions, unless otherwise noted. Thus, our Current Scenario model with medium parameter values was:

$$\mathbf{A} = \begin{bmatrix} 0 & 0.581 & 0.701 \\ 0.141 & 0 & 0 \\ 0 & 0.775 & 0.801 \end{bmatrix}$$

For all matrices, values associated with fawn survival and adult survival and fecundity were based solely on data collected at Fort Bragg. Chitwood (2014) reported neonate survival ($n = 65$) through 16 weeks of age, and all neonates that survived that study survived the entire year (hence, the neonate survival estimate is also the fawn survival estimate). We determined adult survival as described above. To calculate adult female fecundity, we determined birth rate using the number of neonates produced per female from documented births (via vaginal implant transmitters [VIT]). Because our matrix was female-based, we included only the female portion of the birth rate. Thus, for simplicity, we assumed a 1:1 male-to-female neonate ratio, which meant birth rates determined from our VITs were divided by 2 before being included in the fecundity calculation. We documented 13 and 17 births with known litter size, yielding 21 and 32 neonates in 2011 and 2012, respectively. Thus, the adult female birth rates were 1.62 and 1.88 in 2011 and 2012, respectively. Dividing each birth rate by 2 yielded the proportion of female fawns born each year (i.e., 0.81 and 0.94), and we used the mean of the 2 years (i.e., 0.875) to inform the calculation of fecundity for adult females (Table 1).

Because of small annual sample sizes of yearlings (2011: $n = 2$; 2012: $n = 2$), we incorporated variation in yearling vital rates by using values reported in the literature (Table 1). We estimated starting population size for female fawns, yearlings, and adults using density and sex ratio estimates from Fort Bragg's trail camera survey data (C. Brown, Fort Bragg Wildlife Branch, unpublished data) following the methods of Jacobson et al. (1997). We executed the matrix in R 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria) using the popbio package to determine the stable stage distribution (SSD) and then run the matrix at SSD to determine λ, sensitivities, elasticities, and to project population sizes for 10 years.

Manipulating Vital Rates Under "What If" Scenarios

We manipulated our base model vital rates according to predicted responses under several management scenarios (i.e., "what if" scenarios [Mills and Johnson 2013]). The "what if" scenarios represent management options that could mitigate coyote impacts on deer populations (e.g., reduce female harvest, coyote removal) and were designed to illustrate a range of possible population trajectories. We constructed new matrices for each, which included adjusted vital rates (Table 2) based on data from our own study site or from other studies in the region. As described in the construction of the base model, we used low, medium, and high values to represent the potential range of variation (Table 2). We kept birth rates constant, so fecundity values changed as their stage-specific survival rates changed. We acknowledge that our approach cannot fully encompass the entire range of effects caused by various management actions, but "what if" scenarios can be useful for examining the potential effects of mitigation strategies (Mills and Johnson 2013).

Scenario 1: Reduce female harvest.—Reduction in female harvest quotas has been suggested as a potential management strategy to mitigate impacts of coyotes (Kilgo et al. 2012, Robinson et al. 2014). In fact, Fort Bragg reduced female harvest quotas beginning in 2010 in an effort to stem the decline of the deer population. Harvest records since 2010 indicated hunters killed approximately 8% of the adult females annually, so we recalculated adult female survival to reflect protection of approximately 8% of the females and used that value as the high estimate (Table 2). We changed yearling survival proportionately to adult survival. Fawn parameters would be unaffected by reductions in female harvest, so they are the same as the Current Scenario.

Scenario 2: Coyote removal.—Intensive predator removal has been evaluated as a potential management strategy to mitigate impacts of coyotes, particularly on neonates (e.g., VanGilder et al. 2009, Kilgo et al. 2014). Recent evidence

Table 1. Female parameter values used in the population matrix based on current vital rates of white-tailed deer (i.e., Current Scenario). Unless otherwise noted, we used medium values as mean predictions. Birth rates are half of actual output because the matrix is defined with females (i.e., we assumed 1:1 sex ratio in neonates). Because of low sample sizes of yearlings in our study, we assigned low and high yearling birth rates using values reported in other studies from the southeastern United States (see Ditchkoff 2011). Similarly, we assigned all survival rates for yearlings based on values reported in other studies (see DeYoung 2011). All other parameter estimates were obtained from field data collected at Fort Bragg Military Installation (Chitwood 2014), North Carolina, USA, 2011–2013.

	Stage (parameter)	Low	Medium	High
Birth rates	Yearling (B_y)	0.70	0.75	0.78
	Adult (B_a)	0.81	0.875	0.94
Survival rates	Fawn (S_f)	0.105	0.141	0.185
	Yearling (S_y)	0.630	0.775	0.880
	Adult (S_a)	0.721	0.801	0.854

Table 2. Female survival parameters used in "what if" scenario population matrices of white-tailed deer at Fort Bragg Military Installation, North Carolina, USA. Unless otherwise noted, we used medium values as mean predictions. Birth rates are not included in this table because we used the Current Scenario birth rates. All other parameter estimates were manipulated from Current Scenario survival values.

Scenario	Stage (parameter)	Low	Medium	High
Reduce female harvest	Fawn (S_f)	0.105	0.141	0.185
	Yearling (S_y)	0.775	0.804	0.833
	Adult (S_a)	0.801	0.831	0.861
Coyote removal	Fawn (S_f)	0.141	0.237	0.317
	Yearling (S_y)	0.775	0.804	0.832
	Adult (S_a)	0.801	0.831	0.860
Combined	Fawn (S_f)	0.141	0.237	0.317
	Yearling (S_y)	0.775	0.831	0.887
	Adult (S_a)	0.801	0.859	0.917

from South Carolina indicated that effects of coyote removal on neonate survival were highly variable over a 3-year removal period (−11–125% increase), with a mean response of 68% increase (Kilgo et al. 2014). Thus, for the Coyote Removal Scenario, we assigned low fawn survival to be the same as the Current Scenario, used a 68% proportional increase (from low) as the medium fawn survival, and used 125% proportional increase (from low) as the high fawn survival (Table 2). Additionally, because of documented coyote depredations on 4 adult females at Fort Bragg (Chitwood et al. 2014*a*), we recalculated adult female survival to reflect protection of approximately 7% (4 of 58) of the females on the high end. We changed yearling survival proportionately to adult survival.

Scenario 3: Combined.—This scenario combined vital rate changes from the previous 2 scenarios. Assuming additive effects of coyotes and hunter harvest, this scenario represented the most extreme potential for changing λ. We used the same fawn survival parameters from the Coyote Removal Scenario (Table 2). We recalculated adult female survival to reflect protection of approximately 15% of the females on the high end. We changed yearling survival proportionately to adult survival.

RESULTS

We captured and radiocollared 33 and 25 adult female deer in 2011 and 2012, respectively. Using all 58 females, the best model describing temporal trends in adult female survival was the S(t) model ($\mathrm{AIC}_c = 184.153$; $w_i = 0.980$); the S(.) model was not competitive ($\mathrm{AIC}_c = 191.971$; $\Delta\mathrm{AIC}_c = 7.818$; $w_i = 0.020$). The 36-month cumulative survival rate corresponding to the S(t) model was 0.509 (SE = 0.081; 95% CI: 0.355–0.662). Annual survival averaged 0.801 (SE = 0.04), and the 3 yearly survival rates were 0.721 (SE = 0.084; 95% CI: 0.534–0.584; $n = 33$), 0.854 (SE = 0.055; 95% CI: 0.710–0.933; $n = 46$), and 0.827 (SE = 0.072; 95% CI: 0.640–0.928; $n = 38$) for 2011, 2012, and 2013, respectively.

Using medium values for all parameters (Table 1), the Current Scenario projected a growth rate of λ = 0.905 (with low vital rates λ = 0.788; with high vital rates λ = 1.003), meaning the deer population was declining annually by approximately 9–10% (Fig. 2A). The Reduce Female Harvest Scenario (Fig. 2B) and Coyote Removal Scenario (Fig. 2C) predicted declining populations as well, with medium vital rates projecting λ = 0.935 (low λ = 0.875; high λ = 1.002) and λ = 0.995 (low λ = 0.898; high λ = 1.081), respectively. The Combined Scenario (Fig. 2D) predicted an increasing population, with λ = 1.024 (low λ = 0.898; high λ = 1.141). For all scenarios, the most sensitive and elastic vital rate was adult female survival (Table 3). Population projections for 10 years under all scenarios indicated a wide range of outcomes, from nearly 10% decline under current vital rates to over 2% growth under the Combined Scenario (Fig. 2).

DISCUSSION

Under current observed vital rates at Fort Bragg, where coyotes have been implicated as important predators of neonates (Chitwood 2014) and adults (Chitwood et al. 2014*a*), the white-tailed deer population is declining. Our estimate of λ is consistent with anecdotal evidence (e.g., spotlight counts, harvest records, camera surveys) collected at Fort Bragg over the last couple of decades as coyotes have become established in the region. Moreover, our data provide the first empirical, vital-rate-based examination of white-tailed deer population trajectory in the southeastern United States, which is characterized by novel predation pressure from coyotes.

Our data provide a much-needed estimate of adult female survival from the southeastern United States. As suggested by Robinson et al. (2014), adult female survival estimates are important for informing potential management actions, and little has been reported from the region. Though research shows that adult female survival in large herbivores shows low variability across space and time (Dusek et al. 1992; Gaillard et al. 1998, 2000; Patterson et al. 2002), the extent to which predation can affect adult female deer survival in the region is unknown. Our survival rate is similar to those reported across the range of deer (see DeYoung 2011), but hunter-harvest at Fort Bragg has been reduced to the point that adult female survival should approach its maximum (i.e., Fort Bragg deer are almost solely subjected to nonhunting mortality). In the absence of hunting mortality, adult female deer at Fort Bragg normally would be subjected to minor risk of vehicle collision and other non-predatory sources of mortality. However, based on data from our site, coyote predation can represent a greater percentage of mortalities

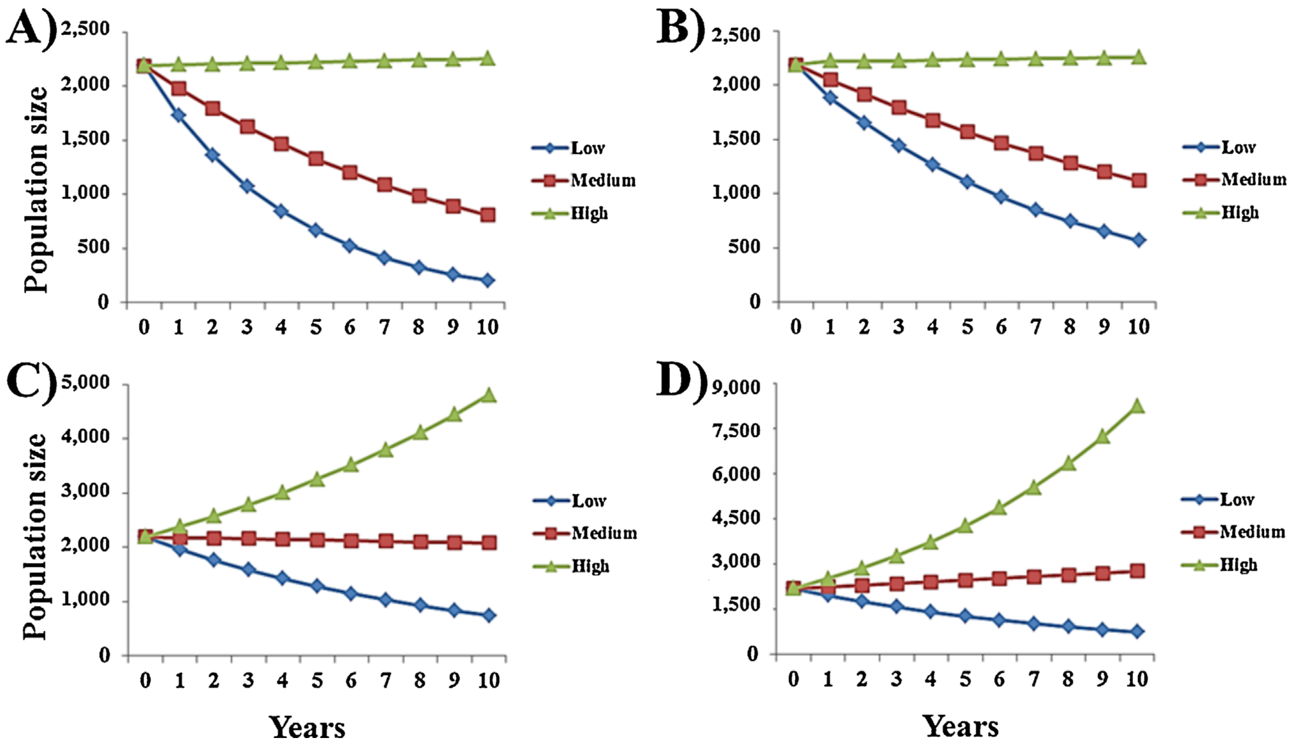

Figure 2. Predicted white-tailed deer population sizes after 10 years of A) current vital rates, B) reduced female harvest, C) coyote removal, and D) reduced female harvest combined with coyote removal at Fort Bragg Military Installation, North Carolina, USA. Predicted population sizes are based on low, medium, and high vital rates, where medium values represent mean predictions.

than either hunter-harvest or vehicle collisions (Chitwood et al. 2014*a*). The extent to which this occurs across the southeastern United States is unknown, but it warrants further research and management consideration.

Our modeling results should be interpreted with caution and extrapolated to other deer populations carefully because they are conditional on the assumptions we used to parameterize our matrices. Three important points should be considered: 1) we assumed density-independence, 2) we assumed our Combined Scenario was additive, and 3) we included no environmental uncertainty. The Fort Bragg deer population was clearly low-density, so our assumption of density-independence was defensible. However, many deer populations exist at or near nutritional carrying capacity, which could provide opportunities for density-dependent feedbacks to occur. In those situations, estimates of λ would

Table 3. Medium vital rates, sensitivities, and elasticities for all scenarios of the white-tailed deer population at Fort Bragg Military Installation, North Carolina, USA, 2011–2013.

Scenario	Parameter	Vital rate	Sensitivity	Elasticity
Current	Fawn survival	0.141	0.653	0.102
	Yearling survival	0.775	0.107	0.092
	Yearling fecundity	0.581	0.016	0.010
	Adult survival	0.801	0.797	0.705
	Adult fecundity	0.701	0.118	0.092
Reduce female harvest	Fawn survival	0.141	0.657	0.099
	Yearling survival	0.804	0.104	0.089
	Yearling fecundity	0.603	0.015	0.010
	Adult survival	0.831	0.802	0.712
	Adult fecundity	0.727	0.115	0.089
Coyote removal	Fawn survival	0.237	0.583	0.139
	Yearling survival	0.804	0.147	0.119
	Yearling fecundity	0.603	0.033	0.020
	Adult survival	0.831	0.722	0.603
	Adult fecundity	0.727	0.163	0.119
Combined	Fawn survival	0.237	0.588	0.136
	Yearling survival	0.831	0.144	0.117
	Yearling fecundity	0.623	0.032	0.019
	Adult survival	0.859	0.728	0.611
	Adult fecundity	0.752	0.159	0.117

be affected and misleading elasticity values could result (Grant and Benton 2000). Similarly, the assumption of additive effects in our Combined Scenario is simplistic and illustrative but could overlook more complicated feedbacks. However, based on the only southeastern United States study to have examined it, coyote predation appears to be an additive source of mortality for neonates (Kilgo et al. 2014). Moreover, in South Carolina, neonate mortality from coyotes remained high (Kilgo et al. 2012) even as female harvest was reduced to a point that appeared to offset those losses (Kilgo et al. 2010). Future research will need to examine potential additive effects of coyote predation on adult deer. Finally, we did not include environmental uncertainty in our models. Many factors (e.g., rainfall, drought, food abundance) could influence vital rates, but elasticity values for our mean projections should be accurate in the presence of stochastic environmental fluctuations (Grant and Benton 2000). Thus, our analysis should be robust to the potential impacts of environmental uncertainty without sacrificing our interpretation of mean population dynamics (Merrill et al. 2003).

Our data indicated adult survival was the most sensitive and elastic vital rate, which is consistent with other studies of large mammals (e.g., Gaillard et al. 2000, Eberhardt 2002). Though sensitivity and elasticity are valuable analytically, they have 2 serious limitations: 1) they do not address how much the vital rates can be changed; and 2) they rely on asymptotic dynamics (Mills and Johnson 2013). In the former, managers must consider that real world management actions rarely change vital rates by the same absolute or proportionate amount determined by sensitivity analysis (Mills et al. 1999). In the latter, asymptotic dynamics require a population be at SSD, so when populations are not at SSD (e.g., 1 age class is depredated disproportionately), the sensitivities and elasticities are invalid (Mills and Johnson 2013). For white-tailed deer at Fort Bragg, both of these limitations are relevant and could be important across the region. With regard to ability to change vital rates, recent evidence suggests the effects of predator removal on neonate survival vary considerably across years (Kilgo et al. 2014). Further, the extent to which predator removal will affect adult female survival across the region is unknown because coyote depredation of adult females has been documented only at Fort Bragg (Chitwood et al. 2014*a*). Thus, management approaches may vary in how much they can actually change the vital rate the sensitivity analysis indicates is most important. With regard to populations being at SSD, low-density deer populations suffering from high neonatal predation rates may be out of SSD, which could mean analytical sensitivities and elasticities are invalid. However, the true risk of invalidity is probably low for deer populations because most ungulate studies consistently identify female survival as the most sensitive and elastic vital rate.

Based on elasticity, the logical extension of our results is to reduce harvest of adult females. Protecting adult females is a simple, low-cost strategy for mitigating impacts of coyotes, assuming the deer population responds according to the analytical elasticities. However, variability in harvest rates and deer densities across the region will cause variation in the population response to reduced female harvest. For example, our study was conducted on a low-density deer population where female harvest quotas were low already (approx. 8% per year) because managers previously had reduced harvest quotas in response to evidence of population decline. Thus, our ability to manipulate adult female survival rates in our scenarios was limited. For example, protecting all females from harvest in our Reduce Female Harvest Scenario resulted in an annual survival increase of roughly 5–6% (from 0.801 currently to a predicted 0.861). Thus, at Fort Bragg, complete protection of females from harvest is not projected to stabilize the decline in the deer population, assuming fawn survival remains unchanged. Perhaps in areas with greater deer density and greater proportional female harvest quotas, it is more likely that reduction in female harvest could have a proportionally larger impact on adult female survival rate and subsequent population growth.

One possible drawback to focusing solely on protecting adult females is that adult survival in large herbivores tends to be high and stable, whereas juvenile survival is highly variable (Galliard et al. 1998). Moreover, temporal variation may be more important than estimated sensitivities and elasticities regarding relative demographic impact of various vital rates (Gaillard et al. 2000). In fact, the immature or juvenile stage (with high temporal variability but low elasticity) may be the most critical component of large herbivore population dynamics, despite the fact it tends to have a low relative impact on population growth rate compared to the adult stage (which has high elasticity but low variability; Gaillard et al. 2000). Our results are consistent with this premise, given the greater positive impact to λ in the Coyote Removal Scenario compared to the Reduce Female Harvest Scenario. Thus, coyote removal, which has the greatest potential to positively affect very low rates of fawn survival, should have the greatest potential to positively affect λ. Historically, predator control was a primary tool for managers focused on increasing the population sizes of game species, but those managers did not completely understand predator-prey relationships (Boal and Ballard 2013). Though studies have documented changes to deer vital rates (or surrogates thereof) after predator removals (VanGilder et al. 2009, Kilgo et al. 2014), variability in the effects of removals can be great (e.g., Kilgo et al. 2014). Our projected population under the Coyote Removal Scenario exemplifies the difficulties inherent in predator control (see Ballard 2011). Our projection assumes an immediate and constant effect of coyote removal, particularly on fawn survival. Kilgo et al. (2014) determined that coyote predation on neonates was additive, but the extent to which coyote predation is additive across the region in unknown. In fact, Chitwood et al. (2014*b*) suggested that high rates of starvation among neonates at Fort Bragg and the propensity for starving neonates to vocalize could predispose them to predation, perhaps indicating compensatory mortality. Regardless, wide annual variation in neonate survival post-coyote removal is already documented (Kilgo et al. 2014), which introduces uncertainty for return-on-investment of an expensive, timeconsuming management strategy. Also, our Coyote Removal Scenario included an increase in adult female survival because 4 adult female depredations were documented at the study site (Chitwood et al. 2014*a*). Thus, in areas where coyotes are not depredating adult females, managers should not expect increases in adult or yearling survival rates simply due to coyote removal.

As a final consideration, when vital rates are at their extremes, predictions of future growth rate based on elasticities of a mean matrix can be misleading and should be interpreted with care (Mills et al. 1999). Mills et al. (1999) suggested that studies using analytical elasticity analysis should explicitly consider the range of variation possible for different vital rates and that simulation methods are a useful approach. Our study attempted to include a wide range of observed variation, albeit a combination of true process variance and estimation error (see Gould and Nichols 1998). Perhaps as additional studies of deer in the region estimate vital rates across diverse temporal and spatial scales, future research can pursue a simulation-based approach (e.g., Life-Stage Simulation Analysis; Wisdom et al. 2000), which can include numerous vital rate estimates and correct for sampling variability. If mitigating coyote impacts on deer populations at a large scale becomes necessary, managers will need strategies based on vital rate data from deer populations of varying densities and coyote impacts.

Our data demonstrate the exception acknowledged by Robinson et al. (2014) to their conclusion that reducing adult female harvest could stabilize declining deer populations. Site-specific data (including very low hunter-harvest of adult female deer, coyote predation as a source of adult female deer mortality, and the lowest fawn survival reported from the region (Chitwood 2014)) created the perfect counter-example to modeling scenarios that draw on data sources from across the range of deer. Though we agree with Robinson et al. (2014) that reducing adult female harvest is a first and necessary management action in areas affected by high rates of coyote predation, we believe our data highlight the importance of continued research into the predator-prey dynamic in the eastern United States. In fact, if results from our Combined Scenario (i.e., 2% population growth following female harvest reduction and coyote removal) are applicable to other areas in the southeastern United States, the obvious conclusion is that some deer populations are now quite sensitive to hunter harvest, even if significant resources are devoted to coyote removal. Likewise, we agree with Robinson et al. (2014) that public perception is a significant driver of this issue and stakeholders will continue to perceive coyotes as a threat to hunting opportunity, which will likely pressure management agencies to take action against coyotes (Rosenberry et al. 2011).

MANAGEMENT IMPLICATIONS

Our results indicate that for low-density deer populations with heavy predation pressure on neonates, protecting adult females from harvest may not be a magic bullet. Coyote removal may need to be implemented in conjunction with the protection of adult females because of the possibility of increasing fawn survival, which appears to be the most important vital rate in the Fort Bragg deer population. Because of the trade-off between cost and effectiveness of coyote trapping, reducing female harvest is the most cost-efficient and logical strategy for managers to implement. However, our results indicate that managers will need to consider the possibility that some deer populations might be so sensitive to hunter harvest that antlerless seasons should be suspended, which could have important implications on hunter satisfaction, retention, and recruitment.

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