Original Article

Factors Affecting Survival of Adult Female White-Tailed Deer After Coyote Establishment in South Carolina

JOHN C. KILGO,[1] *United States Department of Agriculture Forest Service, Southern Research Station, P.O. Box 700, New Ellenton, SC 29809, USA*

MARK VUKOVICH, *United States Department of Agriculture Forest Service, Southern Research Station, P.O. Box 700, New Ellenton, SC 29809, USA*

MICHAEL J. CONROY, *Daniel B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA*

H. SCOTT RAY, *United States Department of Agriculture Forest Service, Savannah River, P.O. Box 700, New Ellenton, SC 20809, USA*

CHARLES RUTH, *South Carolina Department of Natural Resources, 1000 Assembly Street, Columbia, SC 29201, USA*

ABSTRACT Recent evidence from the southeastern United States of high predation rates by coyotes (*Canis latrans*) on white-tailed deer (*Odocoileus virginianus*) fawns combined with reports of predation on adult female deer have prompted concern among wildlife managers and hunters regarding the effects on deer populations. We examined survival rates and causes of mortality among 138 radiocollared adult female deer over 7 years at the Savannah River Site (SRS) in South Carolina, USA, 2006–2013. Our model-averaged prediction of annual survival was 0.871 (95% CI = 0.839–0.902) and did not vary among years. The best model describing survival patterns included only month, with survival being lowest during November–December, which coincided with hunting season. Models assessing the effects of harvest and distance from a primary road also received support ($\Delta AIC_c < 2.0$), but effects of these variables were weak. Although harvest rates were low, harvest was the most frequent cause of mortality (13 of 30; 43%), followed by deer–vehicle collision (8 of 30; 27%). We did not detect predation as a cause of death among our sample; although cause of death for 7 (23%) mortalities was unknown. Even if all unknown mortalities were caused by predation, the overall effect of these mortalities on annual survival was low. Therefore, we conclude that predation by coyotes on adult females was not important in the SRS deer population demography. Managers of southern deer populations wishing to increase population growth by limiting antlerless harvest should be aware that adult female survival may already be high, so limited increases in survival may be expected, particularly if antlerless harvest already is limited. Published 2016. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Canis latrans*, coyote, deer–vehicle collision, hunter harvest, mortality, *Odocoileus virginianus*, predation, survival, white-tailed deer.

The recent expansion of coyotes (*Canis latrans*) into the southeastern United States and the subsequent growth of their populations have generated considerable concern among managers and hunters of white-tailed deer (*Odocoileus virginianus*) regarding the effects coyotes may have on deer populations (Kilgo et al. 2010). This concern has been exacerbated by recent research indicating high levels of predation by coyotes on deer fawns in the region (Saalfeld and Ditchkoff 2007; Kilgo et al. 2012, 2014; Jackson and

Ditchkoff 2013; Chitwood et al. 2015b; Nelson et al. 2015). Among these studies, fawn survival was consistently below 0.35 and ranged to a low of 0.14 (Chitwood et al. 2015b), with some populations experiencing declines in harvest or abundance at statewide levels (Kilgo et al. 2010). Additional research has also begun to consider potential nonconsumptive effects of predation through increased vigilance and associated energetic costs (Lashley et al. 2014, Cherry et al. 2015).

Despite these high predation levels by coyotes, effects of low recruitment on population size can likely be offset by reducing antlerless deer harvest levels (Kilgo et al. 2012, 2014; Robinson et al. 2014). However, this premise assumes that 1) sufficient flexibility exists for harvest reduction and 2) harvest reduction translates into increased survival among adult females. In some populations, there may be a limit to the capability of harvest reduction to offset low fawn survival (Robinson et al. 2014). In a declining North Carolina, USA,

deer population with extremely low fawn survival, antlerless harvest had already been reduced to the point that completely eliminating it was only sufficient, at best, to stabilize the population trend ($\lambda = 1.002$; Chitwood et al. 2015a). Nevertheless, survival of adult females is generally the vital rate with the greatest elasticity for ungulate populations (i.e., this vital rate has the greatest potential to influence overall changes in population size; Gaillard et al. 1998, Chitwood et al. 2015a).

Knowledge of adult female survival rates, and factors influencing them, is essential to understanding the population dynamics of deer, especially if predation levels could be substantial. However, with the exception of recent work (Chitwood et al. 2015a), published research on adult female survival is generally lacking from the southeastern United States. Research from other regions indicates that annual survival of adult females can vary considerably. For example, an annual survival rate of 0.57 was reported for a declining population of white-tailed deer in South Dakota, USA (DePerno et al. 2000); whereas, a rate of 0.88 was reported in West Virginia, USA (Campbell et al. 2005). Moreover, such variation can occur within a region and over short time spans. Annual survival was 0.48 in southern New Brunswick, Canada, during 1994–1995 but was 0.92 in northern New Brunswick during 1995–1996 as a result of variation in winter weather (Whitlaw et al. 1998). The relative influences of harvest and other forms of mortality, including predation by coyotes, varied considerably among these and other studies. Predation by coyotes on adult deer is generally low, except during severe northern winters or periods of deep snowfall (Whitlaw et al. 1998, Patterson and Messier 2000). However, predation by coyotes on adult females in a North Carolina study accounted for greater mortality rates than both hunter harvest and deer–vehicle collisions (Chitwood et al. 2014), suggesting the possibility that predation on adult females may be more important in the region than was previously believed. In the southeastern United States, mortality sources other than harvest and predation to which adult white-tailed deer commonly succumb include disease and parasites, deer–vehicle collisions, and miscellaneous other accidents (Matschke et al. 1984).

Our objectives were to quantify annual survival and causes of mortality of adult female white-tailed deer in the presence of an abundant coyote population in South Carolina where predation of fawns is high (Kilgo et al. 2012). Existing information suggests that harvest and deer–vehicle collisions could affect the study population (Novak et al. 1991, Johns and Kilgo 2005), so we also evaluated the effects of hunting and the distance of deer from a road on survival. We hypothesized that hunting would negatively influence survival rates, and distance from a road would positively influence survival rates because deer living closer to roads would be at greater risk of mortality from deer–vehicle collisions.

STUDY AREA

We conducted the study on the Savannah River Site (SRS), a 78,000-ha U.S. Department of Energy National Environ-mental Research Park in the Upper Coastal Plain of South Carolina, USA. Loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), and slash pine (*P. elliottii*) forests dominated most of the SRS landscape, accounting for 35, 23, and 11% of the area, respectively (Blake and Bonar 2005). Pine forests were managed on 100–120-year rotations, though in some areas loblolly pine was managed on 50-year rotations. Common shrub and understory species included poison oak (*Toxicodendron pubescens*), blackberry (*Rubus* spp.), sparkleberry (*Vaccinium arboreum*), wax myrtle (*Morella cerifera*), and saplings of various hardwood trees, particularly sweetgum (*Liquidambar styraciflua*) and oaks (*Quercus spp.*). Prescribed fire was used on 3–10-year intervals, depending on stand-specific management objectives and constraints. Bottomland hardwood and cypress (*Taxodium distichum*)—tupelo (*Nyssa aquatic* and *N. sylvatica* var. *biflora*) forests occurred on floodplains of the Savannah River and major tributaries, which comprise 23% of the SRS (Blake and Bonar 2005).

Since 1965, the SRS deer population has been maintained at a low density (4–8 deer/km^2) to minimize risk of deer–vehicle collisions (Novak et al. 1991, Johns and Kilgo 2005, Kilgo et al. 2010). Estimated density from spatially explicit capture–recapture analysis of camera-trap data during 2009–2012 averaged 7.1 ± 0.5 (95% CI) deer/km^2 (J. Kilgo, U.S. Department of Agriculture Forest Service, unpublished data). Dog-drive hunts were conducted during November–December, with most units hunted only 1 day/season. Hunt units averaged 1,842 ha in size and total area of SRS hunted was approximately 65,960 ha. An average of 52 dog packs (5 dogs/pack) and 171 hunters hunted each unit during 2007–2012. Dog-drive hunting has been effective at achieving desired harvest levels (Novak et al. 1991, Johns and Kilgo 2005). Bag limits per hunter per hunt range from unlimited male only to 1 male and 1 female to unlimited for either sex. Annual harvest averaged 1,244 deer from 1980 to 1999, but reduced recruitment attributable to coyote predation on fawns (Kilgo et al. 2012) led SRS to reduce annual harvest in 2005, so that it averaged 450 deer/year during this study, or 1.5 deer/km^2.

Coyotes first colonized the study area during the 1980s and increased in abundance until the early 2000s, when the population trend apparently stabilized (Kilgo et al. 2010; J. C. Kilgo, unpublished data). Density in 2006 at the beginning of our study was estimated at 0.8–1.5 coyotes/km^2 (Schrecengost 2007). During winters of 2010–2012, coyotes were intensively trapped and removed for other research on a portion of our study area, resulting in temporary (<1 yr) local reductions in density of about 78% each year (Kilgo et al. 2014). More detail on deer and coyote management history at SRS has been previously described (Johns and Kilgo 2005, Kilgo et al. 2010).

METHODS

We captured deer using tranquilizer guns from tree stands over bait or from vehicles and using rocket nets during January–April 2006–2012. We used Telazol (250 mg; Fort Dodge Animal Health, Fort Dodge, IA, USA) and xylazine

hydrochloride (150 mg; ZooPharm, Fort Collins, CO, USA) in 1-cc transmitter darts, and reversed the xylazine hydrochloride portion with tolazoline hydrochloride (160–180 mg; ZooPharm). We radiocollared (Model 2510B; 8-hr mortality delay; Advanced Telemetry Systems, Isanti, MN, USA) and ear-tagged each female ≥1.5 years old and implanted each with vaginal implant transmitters (Model M3930; Advanced Telemetry Systems) to facilitate capture of fawns for an associated study (Kilgo et al. 2014). We attempted to assign deer to yearling or adult age classes based on tooth replacement patterns (Severinghaus 1949). However, distinction between 1.5- and 2.5-year age classes during January–April is unclear, because the third milk premolar is shed just prior to or during this period (Severinghaus 1949). Therefore, we estimated age class using a combination of dentition and approximate body weight and conformation, but we did not include age class as a factor in analysis because of this uncertainty. Our sample also included females captured as fawns that we considered recruited into the yearling age class on 1 June of the following year (Kilgo et al. 2014). We conducted deer capture and handling under the authority of South Carolina Department of Natural Resources Research Collection Permit No.120406-01, and we followed taxon-specific guidelines for the use of wild vertebrates in research to ensure animals were treated ethically and humanely (Sikes et al. 2011).

We monitored deer 1–3 times daily during parturition season (Apr–Jul) and 1–4 times monthly the rest of the year. We assigned mortalities to 1 of 3 causes: hunter harvest, deer–vehicle collision, or other (including unknown). We checked deer within 1 week prior to and following hunts to detect crippling loss. We obtained dates of death for harvested deer from check-station records and from the SRS contractor that responds to and monitors deer–vehicle collisions for mortalities from vehicle collisions (P.E. Johns, Carolina Wildlife, LLC, personal communication). For other mortalities, we attempted to determine cause of death from evidence at the carcass recovery site, but the long intervals between monitoring events at some times of the year precluded cause determination when only a collar or skeletal remains were recovered.

Because some hunt units either were not hunted each year or antlerless harvest was not permitted because of unit-specific management goals, individual radiocollared deer were subjected to hunting in some years and not in others. Accordingly, we classified each deer as hunted or not in each year to evaluate the effect of hunting on survival. Thus, we treated hunting as a time-varying covariate in our models. We lacked spatial data for deer movements, so as a relative index of the distance each deer lived from a paved road, we used the distance of each deer's capture location to the nearest road. We recognize that capture location only approximated home range location but all deer were captured within their home ranges, as confirmed during subsequent mortality checks, and none dispersed to a new home range during the period of monitoring. Deer at SRS are nonmigratory and seasonal home-range size of females averages 188 ha (D'Angelo et al. 2004). We assigned a distance of 0 m for deer captured on road rights-of-way, and we determined distance of off-road capture locations to the nearest paved road using ArcMap 10.2.2 (ESRI, Redlands, CA, USA).

We used an information theoretic approach in the RMark package (Laake 2013) in Program R (R Core Team 2014) to evaluate relative support among 20 a priori known-fate models describing survival patterns of our deer. We used a staggered entry design to allow for addition to (via capture) and removal from (via mortality or censoring) the data over 84 monthly encounter periods during the 7-year period, June 2006–May 2013. Known-fate data were structured in live (L)—dead (D) encounter format for each animal during all monitoring intervals. For example, deer captured during January 2008 were left-truncated and entered the data on the twentieth interval of the 84-month capture history. We defined years as June–May because June was the first month following the mean date of birth (range = 16–28 May) for the SRS population during 2006–2009 (Kilgo et al. 2012). Our candidate model set included nine models assessing a priori hypotheses related to temporal trends (within and among years) and effects of our variables of interest (hunting and distance from a road at capture), both alone and in combination with temporal trends (Table 1). We used RMark to compute Akaike's Information Criterion adjusted

Table 1. Model definitions used to estimate survival probability of radiocollared adult female white-tailed deer at the Savannah River Site, South Carolina, USA, 2006–2013. Base terms were retained in models with interaction terms.

Model structure	Hypothesized variation in survival
$S(.)$	None (constant)
$S(\text{Month})$	Among months, constant among years
$S(\text{Month} + \text{Year})$	Among months and among years
$S(\text{Month} \times \text{Year})$	Monthly effect differed among years
$S(\text{Month} + \text{Hunt})$	Among months and lower for hunted than unhunted deer
$S(\text{Month} + \text{Dist\_road})$	Among months and increasing with distance from a road
$S(\text{Month} + \text{Hunt} + \text{Dist\_road})$	Among months, lower for hunted than unhunted deer, and increasing with distance from a road
$S(\text{Month} + \text{Year} + \text{Hunt})$	Among months, years, and lower for hunted than unhunted deer
$S(\text{Month} + \text{Year} + \text{Dist\_road})$	Among months, years, and increasing with distance from a road
$S(\text{Month} \times \text{Hunt})$	Among months, lower for hunted than unhunted deer, and hunt effect differed among months
$S(\text{Month} \times \text{Dist\_road})$	Among months, distance from road effect differed among months

for small sample size (AIC_c) for each model in the candidate set using its model likelihood (derived from its deviance from the global model [Month × Year]) and the number of parameters in the model. We used AIC_c and Akaike weights (w_i) to evaluate strength of evidence among competing models (Burnham and Anderson 2002). Initially, we also included in our candidate set models with combined and interactive effects of hunting and distance from road with year, but do not report these models because of negligible AIC_c support. We could not assess goodness-of-fit of the global model (Month × Year) because the global model for known-fate data is a saturated model. We evaluated the unsaturated Month + Year model (global model excluding the interaction term) for overdispersion and found the variance inflation factor ($\hat{c}$) < 1, indicating good fit and close adherence to binomial assumptions. We used AIC_c weights from models in the candidate set to derive model-averaged estimates of monthly and annual survival rates. For comparison with previous research, we also report annual product-limit Kaplan–Meier survival rates (Pollock et al. 1989), computed as the products of the monthly survival estimates across each calendar year from the Month × Year model, with variances computed using the delta approximation implemented in RMark (Laake 2013).

To quantify the direct effect of distance from a road on probability of mortality specifically from deer–vehicle collision, we used binomial regression (0 = survived or died from other causes, 1 = mortality from deer–vehicle collision) implemented with the glm procedure in R, with events defined over monthly periods and taking into account the number of exposure months. We assessed relative support for this model by comparing its AIC_c to that of the intercept-only model, and we assessed whether the slope of the distance effect differed from zero using a Z-test.

RESULTS

We captured and radiocollared 134 adult females, including 9 estimated to be yearlings (18–23 months), from January 2006 to June 2013. In addition, four females radiocollared as neonates were recruited into the yearling age class. Thus, our monitored sample of yearling and adult females totaled 138

deer. The median number of deer at risk per month in our sample was 32.5 (range = 3–60; total 2,735 deer-months). Mean number of deer subjected to hunting each year was 14.6 (range = 2–50), with 77 deer subjected to hunting for 1–3 years each (total 102 deer-years). The mean distance of capture location from a road was 1,685 m (SE = 139 m, range = 0–5,343 m).

Annual product-limit survival rates ranged from 0.807 to 1.000 and averaged 0.895. Model-averaged annual survival rates ranged from 0.866 to 0.880 and averaged 0.871 (95% CI = 0.839–0.904). The Year model received essentially no support (Akaike wt <0.001), indicating survival did not vary among years. Three models had a combined Akaike weight of 0.827 and included the variables Month, Dist_road, and Hunt (Table 2). Month appeared in each of the nine best-supported models and the model with Month alone received 0.461 Akaike weight (Table 2), indicating that survival varied among months in a consistent manner over the 7 years of study. Monthly survival ranged from a low of 0.953 in December to a high of 1.000 during September–October and January (Fig. 1). The Month + Dist_road and the Month + Hunt models also received some support, being within 2 AIC_c points of the best-supported model and having 0.196 and 0.170 Akaike weights, respectively (Table 2). However, effects of these variables were weak; 95% confidence intervals for coefficients for both variables overlapped zero ($\beta_{Dist\_road} = 6.69^{-5}$, 95% CL = -1.73^{-4}–3.07^{-4}; $\beta_{Hunt} = -0.06$, 95% CL = -0.80–0.68). The difference in survival of hunted (0.880) and unhunted (0.883) deer, as derived from model-averaged predictions of monthly hunted versus unhunted survival rates, was only 0.003.

The binary regression model predicting probability of mortality from deer–vehicle collision as a function of distance to a road was 8.73 Akaike points less than the intercept-only model. Probability of mortality from deer–vehicle collision decreased the further deer were from roads ($\beta = -0.001$, SE = 0.788^{-4}, $Z = -1.86$, $P = 0.06$; Fig. 2).

Thirty deer died during the study. Thirteen mortalities were attributable to legal hunting, including 2 that were unrecovered by the hunter (wounding loss); 8 were attributable to deer–vehicle collision; and 9 were attributable

Table 2. Model selection results, ranked by change in corrected Akaike's Information Criterion (ΔAIC_c) and Akaike weights (w_i), used to evaluate influences on survival probability (S) of 138 radiocollared adult female white-tailed deer at the Savannah River Site, South Carolina, USA, 2006–2013. Base terms were retained in models with interaction terms.

Model[a]	K[b]	AIC_c	ΔAIC_c	w_i	Deviance
S(Month)	12	321.05	0.00	0.461	48.25
S(Month + Dist_road)	13	322.76	1.72	0.196	296.62
S(Month + Hunt)	13	323.04	1.99	0.170	296.90
S(Month + Dist_road + Hunt)	14	324.77	3.72	0.072	296.61
S(Month + Year)	18	325.99	4.95	0.039	41.06
S(Month × Dist_road)	24	326.85	5.80	0.025	278.40
S(Month + Year + hunt)	19	327.58	6.54	0.018	289.30
S(Month + Year + Dist_road)	19	327.80	6.75	0.016	289.57
S(.)	1	332.43	11.39	0.002	81.75
S(Month × Hunt)	24	333.50	12.46	0.001	285.06
S(Month × Year)	84	422.07	101.03	0.000	0.00

[a] Dist_road, a parameter indicating survival varied according to distance of deer from a primary road; Hunt, a parameter indicating survival differed between hunted and unhunted deer.
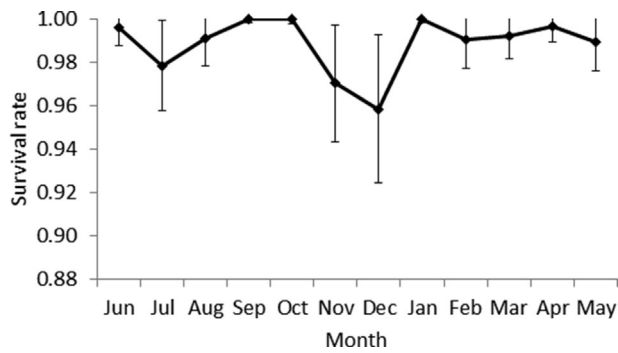[b] No. of parameters plus an intercept term.

Figure 1. Model-averaged estimates (95% CI) of monthly survival rates among radiocollared adult female white-tailed deer on the Savannah River Site, South Carolina, USA, 2006–2013.

to other causes (Fig. 3). Within the other category, one was killed by a train, one was an illegal hunter-kill, and 7 died of unknown causes. Most deer–vehicle collisions occurred from early spring–early summer (Feb–May) and most unknown mortalities occurred during summer (Jun–Aug; Fig. 3).

DISCUSSION

Annual survival of adult female white-tailed deer at SRS was high, averaging 0.871. Although annual survival rates as low as 0.57 have been observed, survival of adult females most often ranges from 0.75 to 0.88 (DeYoung 2011). In southeastern South Carolina, Rudisail (2005) reported a survival rate of 0.82. Thus, survival of adult females at SRS approached the upper end of the range of reported values for the species range-wide.

Despite the presence of an abundant coyote population that preyed heavily on fawns (Kilgo et al. 2012), we did not detect predation on adult females. The last 3 years of our study occurred during a coyote control experiment, which may have reduced the probability of predation, but predation pressure on fawns remained high (Kilgo et al. 2014) and
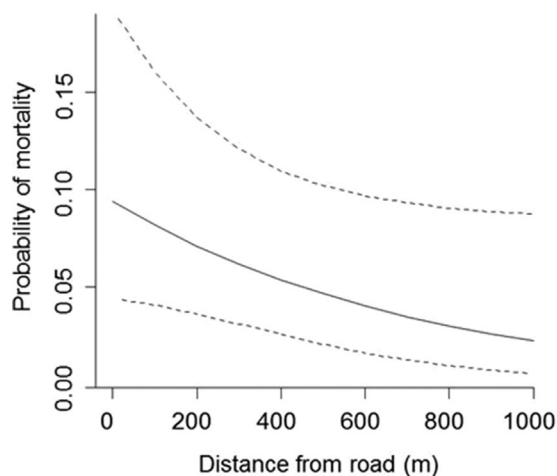

Figure 2. Effect of distance from a primary road on estimated probability of mortality from deer–vehicle collision (95% CI) among radiocollared adult female white-tailed deer on the Savannah River Site, South Carolina, USA, 2006–2013.
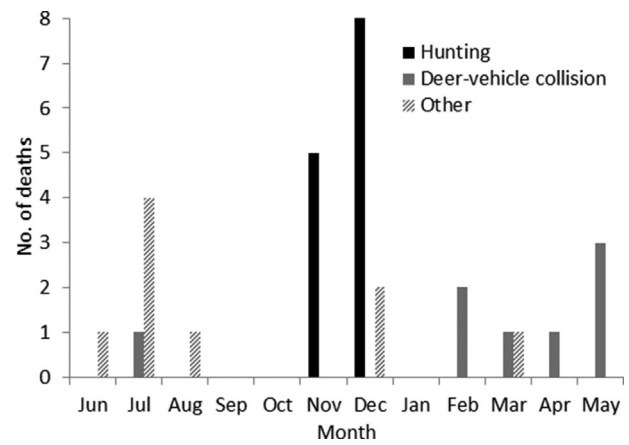

Figure 3. Causes of 30 deaths, by month, detected among 138 radiocollared adult female white-tailed deer on the Savannah River Site, South Carolina, USA, 2006–2013. Hunting includes both recovered (11) and unrecovered deer (2); other includes illegal kill (1), hit by train (1), and unknown cause (7).

adult female mortality did not decrease during this period. Therefore, coyote control apparently did not benefit adult female survival. Our infrequent monitoring during portions of the year may have precluded us from identifying predation as the cause of death among the 7 mortalities with unknown cause, so coyote predation on adults remains possible at SRS. Six of the 7 unknown causes occurred during summer (mid Jun–Aug). All coyote predation on adult females in North Carolina occurred during the fawning period (Chitwood et al. 2014). At SRS, fawning peaks during middle to late May and is largely completed by middle to late June, although a few births occur during July (Kilgo et al. 2012; J. Kilgo, United States Forest Service, unpublished data). Thus, some overlap existed between fawning season and the timing of our mortalities with unknown cause. However, these mortalities may also have been attributable to disease or other causes. For example, hemorrhagic disease is most prevalent during late summer and autumn (Davidson et al. 1981). Regardless of the cause, overall survival was sufficiently high that even if all unknown mortalities were attributable to coyotes, the predation rate would have been low enough to be unimportant (5% of our monitored sample). Coyotes are capable predators of adult deer, but previous research has shown that predation rates tend to be low in areas that do not receive heavy snowfall (DeYoung 1989, Ditchkoff et al. 2001, Campbell et al. 2005). Our results are consistent with these findings. However, the loss of 4 of 28 (14%) radiocollared adult females to coyote predation in North Carolina (Chitwood et al. 2014) suggests that, in some southern populations, coyote predation on adult deer may occur more frequently than we observed. Nevertheless, we conclude that predation by coyotes on adult females does not appear to be a limiting factor in the dynamics of the SRS deer population.

We recorded 8 mortalities from deer–vehicle collision, 7 of which occurred during the late winter to spring green-up period (Feb–May) when deer forage heavily on right-of-way vegetation (J.C. Kilgo, personal observation). Probability of

mortality from deer–vehicle collision was negatively associated with distance from a road. However, we found little evidence for an effect of distance of deer from roads on overall survival. Although, the distance from road survival model received some support in our data, the distance effect was not significant, presumably because mortality from other sources that occurred distant from roads (e.g., hunting) overwhelmed the relationship between deer–vehicle collisions and distance; deer–vehicle collisions accounted for only 27% of recorded mortalities.

Our analysis indicated minimal support for the effect of hunting on survival of adult females. Harvest is generally the most important source of mortality in most white-tailed deer populations (Patterson et al. 2002, Riley et al. 2003). This characteristic allows managers to more effectively regulate population size by adjusting harvest limits of adult females up or down in response to fluctuations in recruitment (Robinson et al. 2014). The lack of a strong effect of hunting on overall survival in our sample was likely due to the fact that, although harvest was the leading cause of mortality, harvest rates still were low because SRS managers had intentionally reduced hunting effort in response to low recruitment (Kilgo et al. 2012). For example, the numbers of hunters and dog packs per day, respectively, were 47% and 45% lower during the study than during 1995–1999 (T. Mims, U.S. Forest Service —Savannah River, unpublished data). In combination with harvest limits imposed during the study period, reduced effort resulted in a 69% reduction in female harvest between the periods. Only 13 radiocollared deer died as a result of harvest among the 77 that were subjected to hunting ≥ 1 year. Slight bias may exist in our estimates of harvest effect because of hunter reluctance to harvest radiocollared deer. However, hunter bias against harvesting radiocollared deer, especially adult females, was shown to be insignificant in Pennsylvania, USA (Buderman et al. 2014), and all hunters at SRS were informed that harvest of radiocollared deer was permissible.

If antlerless harvest is already limited, low harvest combined with high survival indicate that little flexibility may be available to managers wishing to increase population size by increasing adult female survival via limiting antlerless harvest. Population growth may be slower than expected because of the limited increase in survival of adult females that may result from further limiting antlerless harvest. Conversely, if harvest mortality is in fact additive to other sources in southern deer populations, as most evidence suggests, then most females that were harvested would have survived to produce fawns the following spring. At SRS, the net increase in recruitment provided by those females would likely be minimal because of low fawn survival in the population (0.22; Kilgo et al. 2012), but would contribute somewhat to population growth, albeit slowly. However, in populations with greater rates of antlerless harvest, limiting antlerless harvest should have greater effect because of increased flexibility to adjust hunting related mortality. Additional work is needed to clarify the ability of antlerless harvest reduction to increase adult female survival in southern deer populations with characteristics and harvest strategies different from those we studied.

LITERATURE CITED

Blake, J. I., and R. T. Bonar. 2005. Commercial forest products. Pages 329–338 *in* J. C. Kilgo and J. I. Blake, editors. Ecology and management of a forest landscape: fifty years on the Savannah River Site. Island Press, Washington, D.C., USA.

Buderman, F. E., D. R. Diefenbach, C. S. Rosenberry, B. D. Wallingford, and E. S. Long. 2014. Effect of hunter selectivity on harvest rates of radio-collared white-tailed deer in Pennsylvania. Journal of Wildlife Management 78:1456–1465.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information—theoretic approach. Second edition. Springer–Verlag, New York, New York, USA.

Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2005. Population characteristics of a central Appalachian white-tailed deer herd. Wildlife Society Bulletin 33:212–221.

Cherry, M. J., L. Mike Conner, and R. J. Warren. 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. Behavioral Ecology 26:1091–1099.

Chitwood M. C., M. A. Lashley, J. C. Kilgo, C. E. Moorman, and C. S. DePerno. 2015a. White-tailed deer population dynamics and adult female survival in the presence of a novel predator. Journal of Wildlife Management 79:211–219.

Chitwood, M. C., M. A. Lashley, J. C. Kilgo, K. H. Pollock, C. E. Moorman, and C. S. DePerno. 2015b. Do biological and bedsite characteristics influence survival of neonatal white-tailed deer? PLoS ONE 10:e0119070.

Chitwood, M. C., M. A. Lashley, C. E. Moorman, and C. S. DePerno. 2014. Confirmation of coyote predation on adult female white-tailed deer in the southeastern United States. Southeastern Naturalist 13:N30–N32.

D'Angelo, G. J., C. E. Comer, J. C. Kilgo, C. D. Drennan, D. A. Osborn, and K. V. Miller. 2004. Daily movements of female white-tailed deer relative to parturition and breeding. Proceeding of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 58:292–301.

Davidson, W. R., F. A. Hayes, V. F. Nettles, and F. E. Kellogg. 1981. Diseases and parasites of white-tailed deer. Tall Timbers Research Station, Miscellaneous Publication No. 7, Tallahassee, Florida, USA.

DePerno, C. S., J. A. Jenks, S. L. Griffin, and L. A. Rice. 2000. Female survival rates in a declining white-tailed deer population. Wildlife Society Bulletin 28:1030–1037.

DeYoung, C. A. 1989. Mortality of adult male white-tailed deer in south Texas. Journal of Wildlife Management 53:513–518.

DeYoung, C. A. 2011. Population dynamics. Pages 147–180 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Ditchkoff, S. S., E. R. Welch Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes of mortality among male white-tailed

deer support mate-competition theory. Journal of Wildlife Management 65:552–559.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Jackson, A. M., and S. S. Ditchkoff. 2013. Survival estimates of white-tailed deer fawns at Fort Rucker, Alabama. American Midland Naturalist 170:184–190.

Johns, P. E., and J. C. Kilgo. 2005. White-tailed deer. Pages 380–389 in J. C. Kilgo and J. I. Blake, editors. Ecology and management of a forest landscape: fifty years on the Savannah River Site. Island Press, Washington, D.C., USA.

Kilgo, J. C., H. S. Ray, C. Ruth, and K. V. Miller. 2010. Can coyotes affect deer populations in southeastern North America? Journal of Wildlife Management 74:929–933.

Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management 76:1420–1430.

Kilgo, J. C., M. Vukovich, H. S. Ray, C. E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. Journal of Wildlife Management 78:1261–1271.

Laake, J. L. 2013. RMark: an R interface for analysis of capture–recapture data with MARK. Alaska Fish Science Center, Processed Report 2013-01. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Seattle, Washington, USA.

Lashley, M. A., M. C. Chitwood, M. T. Biggerstaff, D. L. Morina, C. E. Moorman, and C. S. DePerno. 2014. White-tailed deer vigilance: the influence of social and environmental factors. PLoS ONE 9:e90652.

Matschke, G. H., K. A. Fagerstone, F. A. Hayes, W. Parker, D. O. Trainer, R. F. Harlow, and V. F. Nettles. 1984. Population influences. Pages 169–188 in L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole, Harrisburg, Pennsylvania, USA.

Nelson, M. A., M. J. Cherry, M. B. Howze, R. J. Warren, and L. Mike Conner. 2015. Coyote and bobcat predation on white-tailed deer fawns in a longleaf pine ecosystem in southwestern Georgia. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:208–213.

Novak, J. M., K. T. Scribner, W. D. DuPont, and M. H. Smith. 1991. Catch-effort estimation of white-tailed deer population size. Journal of Wildlife Management 55:31–38.

Patterson, B. R., B. A. MacDonald, B. E. Lock, D. G. Anderson, and L. K. Benjamin. 2002. Factors limiting population growth of white-tailed deer in Nova Scotia. Journal of Wildlife Management 66:511–521.

Patterson, B. R., and F. Messier. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. Journal of Wildlife Management 64:721–732.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riley, S. J., D. J. Decker, J. W. Enck, P. D. Curtis, and T. B. Lauber. 2003. Deer populations up, hunter populations down: implications of interdependence of deer and hunter population dynamics on management. Ecoscience 10:455–461.

Robinson, K. F., D. R. Diefenbach, A. K. Fuller, J. E. Hurst, and C. S. Rosenberry. 2014. Can managers compensate for coyote predation of white-tailed deer? Journal of Wildlife Management 78:571–579.

Rudisail, D. 2005. Mortality, emigration, and home range characteristics of a white-tailed deer population in the Coastal Plain of South Carolina. Thesis, Clemson University, Clemson, South Carolina, USA.

Saalfeld, S. T., and S. S. Ditchkoff. 2007. Survival of neonatal white-tailed deer in an exurban population. Journal of Wildlife Management 71:940–944.

Schrecengost, J. D. 2007. Home range and food habits of the coyote (Canis latrans) at the Savannah River Site, South Carolina. Thesis, University of Georgia, Athens, USA.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Whitlaw, H. A., W. B. Ballard, D. L. Sabine, S. J. Young, R. A. Jenkins, and G. T. Forbes. 1998. Survival and cause-specific mortality of adult white-tailed deer in New Brunswick. Journal of Wildlife Management 62:1335–1341.

Associate Editor: Haukos.