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Research Article

Coyote Removal, Understory Cover, and Survival of White-Tailed Deer Neonates

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ABSTRACT Predation by coyotes (*Canis latrans*) on white-tailed deer (*Odocoileus virginianus*) neonates has led to reduced recruitment in many deer populations in southeastern North America. This low recruitment combined with liberal antlerless deer harvest has resulted in declines in some deer populations, and consequently, increased interest in coyote population control. We investigated whether neonate survival increased after coyote removal, whether coyote predation on neonates was additive to other mortality sources, and whether understory vegetation density affected neonate survival. We monitored neonate survival for 4 years prior to (2006–2009) and 3 years during (2010–2012) intensive coyote removal on 3 32-km² units on the United States Department of Energy's Savannah River Site, South Carolina. We removed 474 coyotes (1.63 coyotes/km² per unit per year), reducing coyote abundance by 78% from pre-removal levels. The best model ($w_i = 0.927$) describing survival probability among 216 radio-collared neonates included a within-year quadratic time trend variable, date of birth, removal treatment, and a varying removal year effect. Under this model, survival differed between pre-treatment and removal periods and it differed among years during the removal period, being >100% greater than pre-treatment survival (0.228) during the first removal year (0.513), similar to pre-treatment survival during the second removal year (0.202), and intermediate during the third removal year (0.431). Despite an initial increase, the overall effect of coyote removal on neonate survival was modest. Mortality rate attributable to coyote predation was lowest during the first removal year (0.357) when survival was greatest, but the mortality rate from all other causes did not differ between the pre-treatment period and any year during removals, indicating that coyote predation acted as an additive source of mortality. Survival probability was not related to vegetation cover, either directly or in interaction with coyote abundance. When the objective is to increase the recruitment of white-tailed deer, we conclude that neither coyote control nor vegetation management appear effective. Reduction of the antlerless harvest may be necessary to meet this objective, but this harvest strategy warrants additional research in Southeastern deer populations. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Canis latrans*, coyote, fawn, mortality, neonate, *Odocoileus virginianus*, predation, Savannah River Site, South Carolina, survival, white-tailed deer.

White-tailed deer (*Odocoileus virginianus*) populations in portions of southeastern North America have declined during the past decade. A growing body of research indicates that coyotes (*Canis latrans*), relatively new in Southeastern ecosystems, can have significant influence on recruitment rates of white-tailed deer (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Nelson 2013, Chitwood 2014). In addition, antlerless harvest programs in many states were designed in the 1980s and 1990s to control

deer populations that were increasingly overabundant at the time. These liberal harvest limits were largely set prior to the widespread establishment of coyotes in the region and prior to the knowledge that coyotes could substantially affect recruitment. The reduced recruitment caused by coyote predation, combined with liberal antlerless harvests, likely explain most observed declines in deer populations in the region (Kilgo et al. 2012). In response, several states (e.g., Alabama, Georgia, South Carolina) have reduced or are considering reducing antlerless harvest quotas.

Although reductions in antlerless harvest could offset losses to coyotes and reverse declining population trends, considerable interest exists among the hunting public in the use of coyote control as a management tool to increase deer recruitment. Coyote control has been used for over a century in the western United States with the intent of minimizing livestock depredation and benefiting game populations.

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Temporary local reductions in coyote populations are achievable, but coyotes have expanded their range concurrent with this sometimes intensive persecution, and the species now occupies most of the continent (Gompper 2002). Coyote control programs must be intensive and extensive both temporally and spatially to be effective (Knowlton et al. 1999). Several studies have examined the effects of coyote control on ungulates. Effects of coyote control on recruitment in pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) populations have been examined in large-scale replicated studies and found to be minimal (Harrington and Conover 2007, Brown and Conover 2011, Hurley et al. 2011). In contrast, coyote control or exclusion has been shown to increase recruitment, sometimes dramatically, in white-tailed deer populations (Beasom 1974, Stout 1982, Kie and White 1985, Howze et al. 2009, VanGilder et al. 2009). However, among these latter studies, all but Stout (1982) were conducted on single, relatively small units on which both coyotes and bobcats (*Felis rufus*) were removed or excluded and all used measures of recruitment (fawns:adult F) rather than radio-telemetry to assess predation effects. Therefore, they were unable to assess patterns in cause-specific mortality or the relative importance of coyote and bobcat predation.

If various sources of mortality operating on neonates, including predation by coyotes, are compensatory, then coyote control cannot be expected to result in increased recruitment. Under compensatory mortality, when one mortality source decreases another increases (Bartmann et al. 1992, Ballard et al. 2001, Heisey and Patterson 2006); neonates not depredated by coyotes would succumb to other mortality agents (e.g., bobcat predation, malnutrition, disease). In contrast, when a mortality source is additive it fluctuates independently of others, which means that a reduction in coyote predation rate would reduce total mortality rate. Therefore, in assessing the efficacy of coyote control as a means to enhance recruitment, an understanding of whether various mortality agents are additive or compensatory is important. Kilgo et al. (2012) concluded that coyote predation on neonate deer in their study population was likely additive to other mortality sources. Evidence included the fact that recruitment at their study site in South Carolina was stable for approximately 30 years prior to the establishment of coyotes, that recruitment declined because of coyote predation on neonates after coyotes became established, and that winter mortality in the mild climate of the southeastern United States is low (i.e., compensatory mortality apparently does not occur during winter because overwinter mortality is low). However, this evidence was circumstantial, and manipulative experiments are needed to confirm the mechanisms by which various mortality agents operate in Southeastern deer populations.

In addition to better understanding the manner in which coyote predation affects deer populations, information on potential influences on predation pressure is needed. For example, predation by coyotes on neonates may be affected by habitat conditions. In particular, dense understory cover may render neonates less susceptible to predation. Coyotes

are thought to rely more heavily on visual than olfactory cues when hunting, and their hunting success is greater when visual stimuli are present (Wells and Lehner 1978, Wells and Bekoff 1982). However, dense vegetation conceivably could affect either sense to limit hunting efficiency. Several studies have reported that fawn mortality attributable to coyotes was greater where vegetative cover was low (Carroll and Brown 1977, Nelson and Woolf 1987, Piccolo et al. 2010), but none have quantitatively linked mortality risk from coyote predation on white-tailed deer neonates to vegetative cover. Further, any ameliorating effects of cover on predation risk may be influenced by coyote density. When coyotes are abundant, evading predation may be more difficult, regardless of cover conditions, simply because of the greater number of coyotes hunting an area, whereas at lower coyote abundance, neonates with good cover may face lower predation risk.

Our objectives were to determine the effect of coyote control on neonate survival and cause-specific mortality, and to assess whether coyote predation on fawns represents an additive source of mortality in a white-tailed deer population in South Carolina. In addition, we evaluated whether understory vegetation cover affected probability of predation by coyotes and whether such a relationship was affected by coyote removal treatments (i.e., by coyote abundance).

STUDY AREA

We conducted the study on the United States Department of Energy's Savannah River Site (SRS; Fig. 1), a 78,000-ha National Environmental Research Park located in the Upper Coastal Plain physiographic region of South Carolina. Loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*) forests dominated upland sites and were managed on 100- or 120-year rotations, respectively, over most of SRS, though in some areas loblolly pine was managed on 50-year rotations. 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.

The SRS deer population was maintained at a low density (4–8 deer/km²) via dog drive hunts conducted from late October to mid-December. Most units were hunted only 1 day per season, with limits per hunter per hunt ranging from 1 male and 1 female to unlimited for either sex. Coyotes were not documented at SRS until the mid-1980s, but at the beginning of our study, density was estimated at 0.8–1.5 coyotes/km² (Schrecengost 2007). Prior to removal treatments for this study, coyote harvest at SRS was limited to a few shot opportunistically during deer hunts (<25 per year), though human-induced mortality from trapping, shooting, and vehicle collisions was high when coyotes emigrated from SRS (Schrecengost et al. 2009). In response to reduced deer recruitment perceived to have been caused by coyote predation on neonates, SRS reduced deer harvest goals beginning in 2005. During this study, total annual deer harvest averaged 450 deer, compared to 1,244 from 1980 to 1999. See Johns and Kilgo (2005) and Kilgo et al. (2010) for more detail on deer and coyote management history at SRS.

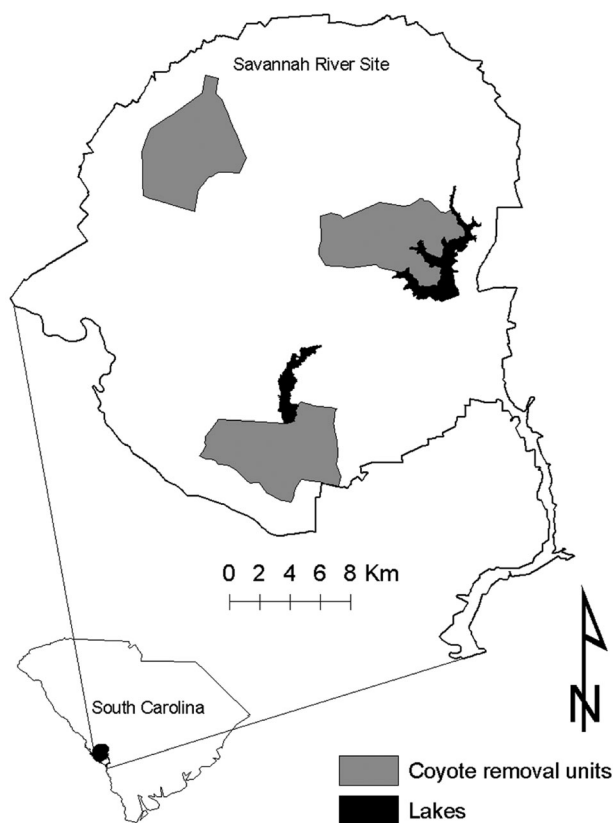


Figure 1. Map of the Savannah River Site (SRS) study area, showing location of SRS within South Carolina and locations within SRS of coyote removal treatment units. Prior to coyote removal, we captured and monitored neonates throughout SRS. During coyote removal, we captured and monitored neonates only within coyote removal units.

METHODS

To evaluate the effect of coyote removal on fawn survival and recruitment, we used a before–after design in which we compared survival and cause-specific mortality data collected from across SRS during 2006–2009 (Kilgo et al. 2012) prior to coyote removal against that collected in 3 replicate coyote removal units on SRS (Fig. 1) immediately following removal efforts that occurred each year during 2010–2012. Removal units were 32 km², which is the average home range size of coyotes, including transients, on SRS (Schrecengost et al. 2009). Units were separated by at least 6.4 km, the diameter of a circle of 32 km², in an effort to maintain independence among experimental units and ensure minimal use of multiple units by the same coyote. Prior to coyote removal (2006–2009), we did not focus deer capture efforts on any portion of the SRS so that our data would adequately reflect conditions for the entire site. During the coyote removal period, we captured deer only within the removal units, aiming for similar numbers of deer within each unit.

Coyote Removal Treatments

We selected contractors for coyote removal through an open bid process following federal and South Carolina procurement guidelines, with competent low bidders being awarded contracts. One contractor per unit removed coyotes via

trapping between 18 January and 6 April during 2010–2012. Trappers used No. 1.75 or No. 2 foot-hold traps and dispatched coyotes using a 0.22 caliber rifle. All trapped animals other than coyotes were released. Trapping was conducted under South Carolina Department of Natural Resources Research Collection Permit No. 010610-01.

We assessed treatment efficacy each year using scat deposition surveys in each removal unit during May for 1 year pre-removal (2009) and each year of removal. Scat deposition surveys have been shown to reliably index coyote abundance (Kayes et al. 2008, Gulsby 2014). We surveyed 2–5 road segments totaling 10 km in each unit. After initially clearing all scats directly in the roadway, we counted and removed scats weekly and summarized data as number of scats/km/day.

Deer Capture and Monitoring

We used vaginal implant transmitters (VIT; Model M3930, Advanced Telemetry Systems, Inc., Isanti, MN) in females ≥ 1.5 years old to facilitate capture of neonates following the procedures described by Kilgo et al. (2012). We primarily used tranquilizer guns from tree stands over bait to capture females during January–April 2006–2012, although we captured some deer with rocket nets or tranquilizer guns from vehicles with spotlights. We used Telazol (250 mg; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine hydrochloride (150 mg; ZooPharm, Fort Collins, CO) in 1-cc transmitter darts, and we reversed the xylazine hydrochloride portion with tolazoline hydrochloride (160–180 mg; ZooPharm). In addition to implanting a VIT, we radio-collared (Model 2510B, Advanced Telemetry Systems, Inc.) and ear-tagged each female. See Kilgo et al. (2012) for details of handling procedures. We conducted deer capture and handling under the authority of South Carolina Department of Natural Resources Research Collection Permit No. 120406-01.

We monitored VIT signals at 8-hour intervals (beginning at 0600, 1400, and 2200) throughout the fawning season. We allowed a period of ≥ 3 hours immediately post-partum for grooming and initial bonding between female and neonate but otherwise initiated searches with thermal imaging cameras immediately upon detecting an expelled VIT. We returned at 8–24-hour intervals over the following 3–5 days for additional searches if we did not locate a neonate on the initial search.

We weighed neonates, determined sex, and attached an expandable breakaway radio-collar (Diefenbach et al. 2003; Model M4210, Advanced Telemetry Systems, Inc.) equipped with a motion-sensitive mortality switch on a 4-hour delay. For neonates captured opportunistically from unmarked females, we estimated age using new hoof growth (Sams et al. 1996). Handling duration averaged 6 minutes (range 2–18 min).

We monitored neonates every 8 hours to ≥ 4 weeks of age, 1–3 times daily to 12 weeks of age, weekly until 16 weeks of age, and 1–4 times monthly to 12 months of age. We monitored neonates more intensively at younger ages because most mortality occurred during this period (Kilgo

et al. 2012). Frequent monitoring allowed for more rapid recovery of carcasses post-mortem and hence, more accurate identification of cause of death. To obtain points within each neonate's home range at which to characterize understory vegetation cover (below), we estimated neonate locations via triangulation every 32 hours (every fourth mortality check) from birth to approximately 3 weeks of age, which yielded 15 locations within 22 days. We used a radio receiver (Advanced Telemetry Systems, Inc.) and a hand-held 3-element yagi antenna to determine 3–4 bearings from georeferenced positions. We used the maximum likelihood estimator in program LOAS version 4.0.3.3 (Ecological Software Solutions, Sacramento, CA) to estimate locations and accepted only locations with error polygons ≤ 2 ha.

We assigned cause of death based on evidence at the carcass recovery site. We confirmed predation when killing bite wounds (as evidenced by subcutaneous trauma) were present on the head and neck, when available, or by other sign of the presence of a predator at the carcass. We identified predator species using a combination of field and genetic methods as described by Kilgo et al. (2012). Field evidence included characteristics of caching, patterns of consumption, and presence of tracks. Genetic evidence consisted of DNA in residual predator saliva recovered from the carcass or collar. Genetic analysis was performed by Wildlife Genetics International, Inc., (Nelson, British Columbia, Canada). We recognize that coyotes may have scavenged neonates that died of causes other than predation. However, we never recovered a carcass with evidence of scavenging, that is, a predator present but killing bite wounds absent. Our frequent monitoring schedule was designed to minimize the potential for a scavenger to detect a carcass before we did (Kilgo et al. 2012). Therefore, we considered carcasses with evidence of a predator to have been killed by that predator.

Understory Cover Sampling

We sampled understory structure each year at the 15 locations (birth or capture plus 14 telemetry locations) obtained for each neonate during its first 3 weeks of life. Because of telemetry error, these locations were not intended to represent precise neonate bed or activity sites but rather the general cover conditions within the neonate's area of use. For neonates that did not survive until we obtained 15 locations, we used the Hawth's Tools extension in ArcMAP 9.3 (ESRI Systems Ltd, Redlands, CA) to delineate the minimum convex polygon from the available locations. We then located sufficient random points within the polygon to meet the complement of 15 sampling locations to characterize the area. We used a 3-m tall vegetation profile board (Nudds 1977) to quantify understory cover. We placed the board at each sampling location and estimated (0–4 index) percentage cover for each 0.5-m interval from a distance of 5 m in each of the cardinal directions. We averaged the 120 readings for the 2 lowest height intervals (≤ 1 m; 15 locations \times 4 directions \times 2 heights) in each neonate's home range to obtain an index of understory cover density. We considered vegetation in this height range most

appropriate to represent cover that would provide visual or olfactory concealment against predators.

Statistical Analysis

We used an information theoretic approach (Burnham and Anderson 2002) to evaluate relative support for 6 a priori models describing coyote abundance trends, as indexed by scat deposition rate, before and during our removal treatments. Candidate general linear models used a normal distribution and included the following variables, individually or in combination: removal treatment (pre-removal [2009] versus removal [2010–2012]), individual year, and removal unit. We used PROC MIXED in SAS 9.4 (SAS Institute, Cary, NC) to fit models and estimate parameters. We treated all factors as fixed effects and tested them over the residual error term. We evaluated relative support for the models using Akaike's Information Criterion corrected for small sample size (AIC_c).

We used known-fate modeling in Program MARK (White and Burnham 1999) to compare models representing various a priori hypotheses of the effect of coyote removal treatment and vegetation cover on survival. Models estimated survival to 16 weeks, at which time we considered neonates recruited to the huntable population (Kilgo et al. 2012). We entered neonates in the sample at birth and based analysis on age in weeks rather than calendar week. We used a 2-step process to identify the best-supported models describing survival pattern relative to coyote removal treatment. We first assessed the relative support for 3 variables describing survival during the removal period by comparing 4 models: a base model, base model + treatment year, base model + treatment unit, and base model + unit-specific scat deposition index. For our base model, we used the best-supported model describing survival rate during the pre-treatment period (Kilgo et al. 2012), which included a within-year quadratic time trend (T^2) and Julian date of birth (DOB). We treated years as group variables and treatment unit and scat index as covariates. We then used variables from the best-supported models identified in this step to build candidate models for assessment of coyote removal treatment effect.

To assess the effect of coyote removal on neonate survival, our candidate set of models included our base model, the best-supported models from the previous step, and 3 a priori models related to treatment and time period. Our base model ($T^2 + \text{DOB}$) described variation within years but did not include a predictor variable related to coyote removal treatment (i.e., support for this model would indicate that survival was not affected by coyote removal). The 3 treatment-time models included the base model plus variables describing 3 different temporal responses to removal treatments: survival differed between pre-treatment and removal periods; survival differed between pre-treatment and removal periods and differed among removal years, increasing or decreasing linearly; and survival differed between pre-treatment and removal periods and differed among removal years randomly. For this analysis, we designated 2 group variables: treatment status and time

period. Treatment status groups were pre-treatment and removal periods. For time periods, we assigned neonates to 4 groups, including the pre-treatment period (2006–2009; no differences existed in survival rates among years during this period; Kilgo et al. 2012) and each of the removal years (2010, 2011, and 2012), indicated by dummy variables. We used AIC_c and Akaike weights (w_i) to evaluate the strength of evidence among competing models (Burnham and Anderson 2002). We considered those models ≤ 2.0 AIC_c units from the best approximating model to be the most plausible models (Burnham and Anderson 2002), unless they contained uninformative parameters. Arnold (2010) defined models with uninformative parameters as those models ≤ 2 AIC_c units of the best approximating model but which contained only 1 additional parameter and had essentially the same model deviance. For such models, we followed Arnold's (2010) recommendation for small sets of a priori models by reporting all models but dismissing those with uninformative parameters. We could not assess goodness-of-fit of the global model ($S(\text{yr} \times t)$) because the global model for known fates data was a saturated model.

We estimated rates of cause-specific mortality by generating the nonparametric cumulative incidence function estimator (NPCIFE; Heisey and Patterson 2006) using the *csm* function in the *wild1* package (Sargeant 2011) for R software (version 2.14.2; R Development Core Team 2012). The NPCIFE uses a competing risks framework to estimate cumulative hazard rate, accounting for the fact that mortality from 1 source precludes mortality from another source. We report cause-specific mortality rates for coyote predation, bobcat predation, emaciation, and all other causes for the pre-treatment period and for each removal year. To evaluate whether coyote predation on neonates was additive to other sources, we generated the cause-specific mortality rate for all non-coyote-predation mortalities and assessed whether 95% confidence intervals overlapped between the pre-treatment period and the removal years. In the presence of coyote-induced mortality, overall mortality (from all causes) was high (Kilgo et al. 2012). Lack of compensation (i.e., increase) in other sources of mortality after removal of coyotes would indicate that coyote-induced mortality was additive (Heisey and Patterson 2006). We recognize that compensatory mortality may have occurred after the 16-week neonatal period. However, survival of neonates at our study site was 1.0 from the ninth to sixteenth week of life (Kilgo et al. 2012), indicating that mortality among older fawns is low. Additionally, mortality from winter stress is likely low because of the mild climate of the southern United States. To confirm this, we computed Kaplan–Meier survival estimates for >16-week-old fawns during October–April using monthly intervals.

We evaluated the hypothesis that understory vegetation density affected risk of predation from coyotes by assessing degree of support among a set of 5 a priori survival models, some of which included our index of understory density for each neonate's home range, using Program MARK. We eliminated from the dataset all mortalities attributable to causes other than coyote predation. Models in this candidate

set included our base model ($T^2 + \text{DOB}$), the best-supported model from the analysis of treatment effect on overall survival, these 2 models each with the addition of the vegetation density covariate, and the best-supported model with a treatment status \times vegetation density interaction term added. The latter model allowed for different effects of vegetation density between pre-treatment and removal periods. We used AIC_c weights from the models in the candidate set to compute the model-averaged estimate of β for the vegetation density effect and its unconditional 95% confidence intervals (Burnham and Anderson 2002).

RESULTS

Coyote Removal and Coyote Abundance

Trappers removed 474 coyotes from our experimental units: 169 in 2010, 137 in 2011, and 168 in 2012. Removal rates (coyotes/km²) generally were similar among units and years, although they were somewhat lower in 2011 (see Table S1, available online at www.onlinelibrary.wiley.com). Average removal rate across units and years was 1.63 coyotes/km². Among models predicting scat deposition rate, only the removal treatment model (pre-removal versus removal) received support, with a model weight of 0.947 (Table 1). Removal treatment effect size indicated a reduction of 0.056 (95% CI: 0.030, 0.083) scats/km/day from pre-removal to removal period (Fig. 2), representing a 78% reduction from the pre-removal mean of 0.072 scats/km/day. The remaining models received negligible support ($w_i \leq 0.05$).

Effect of Coyote Removal on Neonate Survival

We captured and implanted 135 individual adult female deer during the study. We captured 115 of these only once, 12 during 2 years, and 8 during 3 years. Thus, the sample of implanted females we monitored totaled 163: 67 during the pre-treatment period, 26 in 2010, 38 in 2011, and 32 in 2012. We successfully captured ≥ 1 live neonate from 131 of the 163 monitored VITs (80%), yielding 192 neonates (74 during the pretreatment period, 30 in 2010, 51 in 2011, and 37 in 2012), including 61 twin litters and 1 triplet litter. We did not include in our sample 4 stillborn neonates found at 3 birth sites (2 of which also produced live neonates) and 1 neonate found dead at the birth site from apparent drowning. Reasons for failure to capture neonates from monitored VITs

Table 1. Model selection results, ranked by change in corrected Akaike's Information Criterion (ΔAIC_c) and Akaike weight (w_i), used to evaluate the effects of coyote removal treatment (2009 = pre-removal; 2010–2012 = removal), treatment unit, and treatment year on coyote abundance, as indexed by scat deposition rate (scats/km/day) at the Savannah River Site (SRS), South Carolina, 2009–2012.

Model	K^a	AIC_c	ΔAIC_c	w_i
Treatment	2	–46.5	0.0	0.947
Intercept only	1	–40.6	5.9	0.050
Unit + treatment	4	–34.1	12.4	0.002
Year	4	–33.1	13.4	0.001
Unit	3	–29.3	17.2	0.000
Unit + year	6	–20.6	25.9	0.000

^a No. of parameters plus an intercept term.

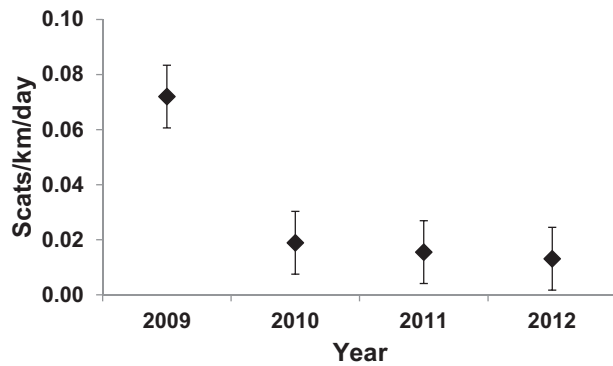


Figure 2. Least square mean (\pm SE) coyote abundance in 3 removal units at the Savannah River Site, South Carolina, during 2009 (pre-removal) and 2010–2012 (removal), as indexed by scat deposition surveys.

included transmitter failure prior to parturition ($n=9$), expulsion of the VIT prior to parturition ($n=1$), death of the female prior to parturition (from vehicle collisions, $n=4$, and unknown cause, $n=1$), loss of contact with female prior to parturition ($n=1$), stillbirth of litter ($n=1$), female not pregnant ($n=4$), and failure to locate neonate after apparently normal parturition ($n=11$). We also captured 25 neonates from unmarked females (17 during the pretreatment period, 2 in 2010, 1 in 2011, and 5 in 2012). Thus, after deleting from the sample 1 fawn whose collar dropped the first day, our total sample included 216 neonates (91 during the pretreatment period, 31 in 2010, 52 in 2011, and 42 in 2012). Because of various logistical and biological constraints, we were unable to secure an even distribution of deer across the 3 removal units during the coyote removal period, with 77 (61.6%) of the 125 monitored neonates occurring in 1 unit (see Table S2, available online at www.onlinelibrary.wiley.com).

Our only model describing survival during the removal period with $\Delta AIC_c < 2.0$ was the base model + year; models for treatment unit and scat deposition index received essentially no support (Table 2) and therefore were not carried forward to the candidate set assessing treatment effect. Our best-supported model describing neonate survival in relation to coyote removal included the additive effects of

Table 2. Model selection results, ranked by change in corrected Akaike's Information Criterion (ΔAIC_c) and Akaike weight (w_i), used to evaluate factors affecting survival probability (S) of radio-collared white-tailed deer neonates during the coyote removal period at the Savannah River Site (SRS), South Carolina, 2010–2012.

Model ^a	K^b	AIC_c	ΔAIC_c	w_i	Deviance
$S(T^2 + DOB + year)$	6	482.72	0.00	0.970	470.64
$S(T^2 + DOB)$	4	490.79	8.06	0.017	482.74
$S(T^2 + DOB + scat\ index)$	5	492.19	9.45	0.009	482.12
$S(T^2 + DOB + unit)$	6	494.36	11.64	0.003	482.28

^a T^2 , within-year quadratic time trend; DOB, date of birth; year, a parameter indicating survival varied among removal years; scat index, a parameter indicating survival varied according to coyote scat deposition index value; unit, a parameter indicating survival varied among replicate coyote removal units.

^b No. of parameters plus an intercept term.

Table 3. Model selection results, ranked by change in corrected Akaike's Information Criterion (ΔAIC_c) and Akaike weight (w_i), used to evaluate the effects of coyote removal treatment on survival probability (S) of radio-collared white-tailed deer neonates at the Savannah River Site (SRS), South Carolina, 2006–2012.

Model ^a	K^b	AIC_c	ΔAIC_c	w_i	Deviance
$S(T^2 + DOB + treatment + removal\ year)$	7	835.39	0.00	0.945	821.32
$S(T^2 + DOB + treatment)$	5	842.21	6.82	0.031	832.17
$S(T^2 + DOB + treatment + linear\ removal)$	6	844.14	8.75	0.012	832.08
$S(T^2 + DOB)$	4	844.17	8.77	0.012	836.14

^a T^2 , within-year quadratic time trend; DOB, date of birth; treatment, coyote removal treatment effect; removal year, a parameter indicating survival varied among removal years; linear removal, a parameter indicating survival varied in a linear manner during the removal period.

^b No. of parameters plus an intercept term.

the within-year quadratic time trend, date of birth, treatment, and the varying removal year effect (Tables 3 and 4). This model was our only model with $\Delta AIC_c < 2.0$ and it received an Akaike weight of 0.922, nearly 30 times more likely than the next most supported model. Under this model, survival varied between pre-treatment and removal periods and among years during the removal period (Fig. 3). During the first year of removal, survival rate (0.513) was more than twice that of the pre-treatment level (0.228). During the second year of removal, survival rate (0.202) was nearly identical to the pre-treatment level, and during the third year of removal, survival rate (0.431) was nearly twice that of the pre-treatment level, though the 95% confidence interval overlapped that of the pre-treatment level.

Among 152 mortalities, predation by coyotes was the most frequent cause of death, both before and during the coyote removal period (Table 5). Coyote predation accounted for 80% of all mortality during the pre-removal period and 73% during the removal period. Cause-specific mortality rate attributable to coyote predation was lowest during 2010

Table 4. Parameter estimates, standard errors, and 95% confidence intervals for the predictor variables in the best model describing the effect of coyote removal treatment on survival probability of radio-collared white-tailed deer neonates at the Savannah River Site (SRS), South Carolina, 2006–2012.

Variable ^a	β	SE	95% CI
Intercept	3.467	0.745	2.006 to 4.927
T	0.042	0.112	–0.178 to 0.262
T^2	0.021	0.011	0.000 to 0.042
DOB	–0.013	0.005	–0.022 to –0.004
Treatment	–0.607	0.256	–1.108 to –0.105
Period 1	0.243	0.356	–0.456 to 0.941
Period 2	–0.694	0.280	–1.242 to –0.146

^a T, within-year linear time trend; T^2 , within-year quadratic time trend; DOB, date of birth; treatment, coyote removal treatment effect; Period 1 and Period 2, dummy variables used in conjunction with treatment to indicate time period (pre-treatment, removal years 1, 2, and 3), which allows survival to vary among removal years (for pre-treatment period, treatment = 1, Period 1 = 0, and Period 2 = 0; for removal year 1, treatment = 0, Period 1 = 1, and Period 2 = 0; for removal year 2, treatment = 0, Period 1 = 0, and Period 2 = 1; and for removal year 3, treatment = 0, Period 1 = 0, and Period 2 = 0).

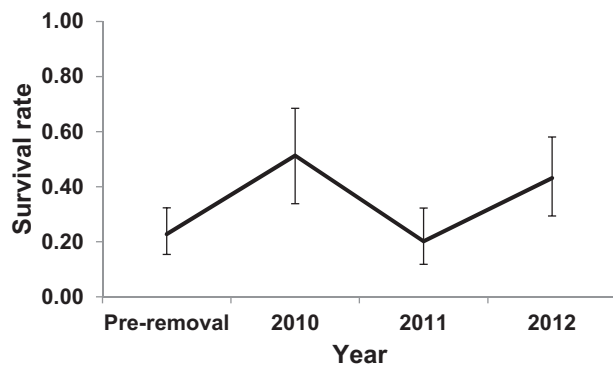


Figure 3. Survival rates (16-wk; 95% CI) of radio-collared white-tailed deer neonates during 2006–2009 (prior to coyote removal) and 2010–2012 (during removal) at the Savannah River Site, South Carolina.

when overall survival was greatest (Table 5). Mortality rates attributable to each of bobcat predation, emaciation, and all other causes of death generally were <0.100 per year, although the bobcat predation rate was 0.115 during 2011. Despite the reduction in coyote predation rate during 2010, non-coyote-predation mortality rate did not increase (95% CIs overlapped extensively) between the pre-removal period and any year during the removal period (Fig. 4). Overwinter survival rate (Oct–Apr) among all monitored fawns that survived their first 16 weeks, irrespective of treatment, was 0.886 (95% CI = 0.792–0.980), with only 5 mortalities observed among 50 fawns (2 vehicle collisions, 1 hunter kill, 1 accident, and 1 unknown).

Understory Vegetation Cover and Neonate Survival

Three of the 5 models in our candidate set assessing the effect of understory vegetation cover on survival had $\Delta AIC_c < 2.0$ and were thus competing models (Table 6). All 3 competing models included the terms from our best-supported model describing treatment effect, and 2 models included the vegetation cover index. However, we concluded that vegetation density was an uninformative parameter in these models because the models included 1–2 parameters more than the best treatment model yet their deviance was similar to that of the best treatment model. In addition, the unconditional 95% confidence interval of the model-averaged β for the effect of vegetation density overlapped zero (-0.845 – 0.370), and the sign of the β was opposite the effect we hypothesized ($\beta = -0.238$; Fig. 5). Collectively, these results indicate that vegetation density had little to no

effect on survival probability, but if any effect existed, it was counterintuitive; survival probability may have increased as understory cover decreased.

DISCUSSION

Predation by coyotes on white-tailed deer neonates appeared to represent an additive source of mortality. When coyote predation is additive to other mortality sources, coyote control should increase overall survival (Ballard et al. 2001). Consistent with this prediction, we observed a moderate increase in neonate survival during 2 of 3 years of coyote removal. However, both the magnitude of the increase and its consistency among years were less than expected because coyotes could not be completely removed. The amount of vegetative cover available within a neonate's area of use had little influence on its probability of survival, either before or during coyote removal periods.

Evidence for additivity of coyote predation as a mortality source among neonates in the SRS deer population exists in the response of non-coyote mortality sources. When the coyote predation rate declined during 2010, non-coyote-predation mortality did not increase, indicating a lack of compensation among mortality rates from different sources. A new source of mortality can be considered additive if the hazard functions from existing sources do not change with the addition or removal of the new source (Heisey and Patterson 2006). Although we did not compare hazard functions from different mortality sources across the entire first year of life, mortality was very low after the 16-week period for which we did compare hazard functions, consistent with other research indicating that overwinter survival of fawns is high in the Southeast (Morgan et al. 1995). Thus, our analyses covering the first 16 weeks of life covers most mortality to this age class. Our findings are consistent with the conclusion of Ballard et al. (2001) that when coyotes are the primary predator on white-tailed deer populations below carrying capacity, predation tends to be additive to other mortality sources.

Scat deposition indices indicated that our coyote removal treatments reduced coyote abundance in our treatment units. Our removal rates were high relative to the best available estimates of coyote abundance prior to removal. Schrecengost (2007) used elicited howl surveys to estimate that coyote density at SRS prior to removal ranged from 0.8 to 1.5 coyotes/km². We removed an average of 1.6 coyotes/km² from each of our units, greater than the maximum estimated

Table 5. Cause-specific mortality, as estimated by the nonparametric cumulative incidence function (95% CI), and number of deaths (n) among 216 radio-collared white-tailed deer neonates prior to (2006–2009) and during (2010–2012) coyote removal at the Savannah River Site, South Carolina, USA.

Cause of death	Pre-removal			2010			2011			2012		
	Rate	95% CI	n	Rate	95% CI	n	Rate	95% CI	n	Rate	95% CI	n
Coyote predation	0.615	0.521–0.710	56	0.357	0.187–0.526	11	0.577	0.449–0.705	30	0.454	0.300–0.607	19
Bobcat predation	0.066	0.056–0.158	6	0.000		0	0.115	0.015–0.216	6	0.071	0.000–0.161	3
Emaciation	0.077	0.000–0.155	7	0.065	0.000–0.151	2	0.058	0.000–0.139	3	0.024	0.000–0.102	1
Other causes ^a	0.011	0.000–0.053	1	0.032	0.000–0.094	1	0.077	0.000–0.164	4	0.024	0.000–0.070	1

^a Includes respiratory failure (1), drowning (1), accident (mired in mud, 1), vehicle collision (1), and unknown causes (3).

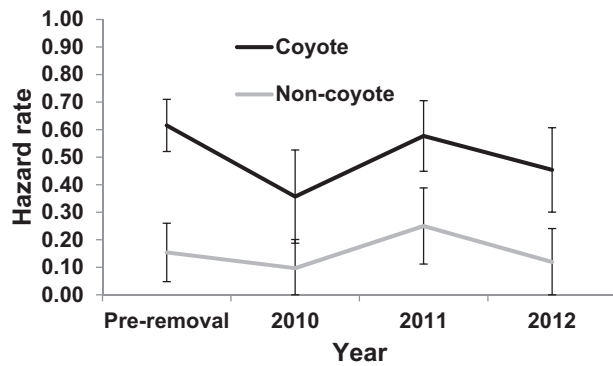


Figure 4. Cumulative hazard rates (16-wk; 95% CI) attributable to coyote predation and all other causes (non-coyote) among radio-collared white-tailed deer neonates during 2006–2009 (prior to coyote removal) and 2010–2012 (during removal) at the Savannah River Site, South Carolina.

pre-removal density, each year for 3 successive years. However, given our high rate of removal, the apparent reduction in abundance was less than anticipated. Immigration by coyotes into our units may explain lower than expected reduction. Coyotes are known to disperse long distances (Carbyn and Paquet 1986, Harrison 1992), and growing evidence suggests that such dispersal occurs regularly within the recently occupied Southeastern Coastal Plain. Hinton et al. (2012) reported dispersal distances by 3 coyotes ranged from 77 km to 393 km, and we trapped a radio-collared coyote that traveled approximately 430 km from its original capture location in Auburn, Alabama. Similar movements have been recorded in eastern North Carolina, South Carolina, and Virginia (M. Elfelt, North Carolina State University, unpublished data). Literature values for the proportion of populations that are transients or dispersers range from 0.13 to 0.58 (summarized by Pitt et al. 2003). The proportion of the coyote population in our study area that were transients or dispersers is unknown, but the high mobility and transient nature of many coyotes likely facilitated rapid recolonization of our treatment units (Harrison 1992, Knowlton et al. 1999). Thus, the size of our removal units may have been insufficient to be able to greatly reduce the coyote population size, despite the fact that they were based on local coyote home range size (Schrecengost et al. 2009).

Although we documented modest increases in survival rate during the removal period, coyote abundance in our removal

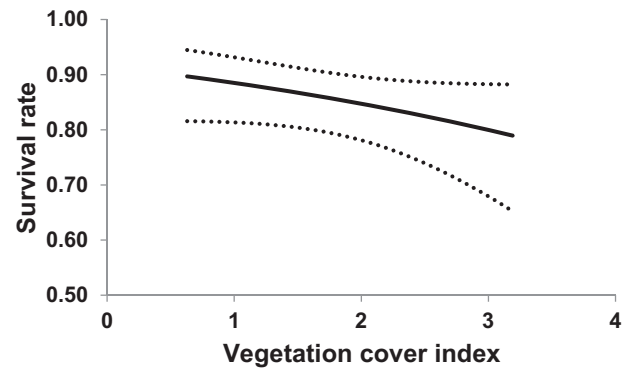


Figure 5. Effect of understory vegetation cover (0–4 index) on weekly survival rate (95% CI) of radio-collared white-tailed deer neonates during 2006–2009 (prior to coyote removal) and 2010–2012 (during removal) at the Savannah River Site, South Carolina. We estimated survival using our best-supported model describing the effect of vegetation cover index, irrespective of treatment and year, while holding time constant at the first week of life (the week of lowest survival) and date of birth constant at 17 May (median birth date for all neonates). We show estimates only for the range of values of the cover index for which we had data (0.63–3.19).

units clearly remained sufficiently high to affect survival, as predation by coyotes continued to account for $\geq 70\%$ of mortality. The increase in survival rate was significant during the first year of the removal period and approached significance during the third year, but survival during the second year of removal was essentially identical to the pre-removal rate. Moreover, even though survival during the first year was greater than twice that of the pre-removal period, it still was only 51%, low compared to many populations. Fawn survival rates $>80\%$ have been reported in white-tailed deer, even where coyotes are present (Brinkman et al. 2004, Pusateri Burroughs et al. 2006, Grovenburg et al. 2011). Although we reduced coyote abundance, coyote predation still accounted for 79%, 70%, and 79%, respectively, of total mortality during the 3 years of removal, compared with 80% prior to removal. In addition to the apparently high immigration discussed above, our trapping efforts may have been less successful at removing those individual coyotes responsible for much of the predation. Because of their age, experience, and familiarity with their home range, trapping tends to be less effective at removing alpha coyotes than transient and dispersing coyotes (Sacks et al. 1999a). Alphas account for a higher proportion of predation on large animals such as deer (*Odocoileus* spp.), elk (*Cervus elaphus*),

Table 6. Model selection results, ranked by change in corrected Akaike's Information Criterion (ΔAIC_c) and Akaike weight (w_i), used to evaluate the effects of understory vegetation cover on probability of surviving predation by coyotes (S) among radio-collared white-tailed deer neonates at the Savannah River Site (SRS), South Carolina, 2006–2012.

Model ^a	K^b	AIC_c	ΔAIC_c	w_i	Deviance
$S(T^2 + DOB + \text{treatment} + \text{removal year} + \text{vegetation})$	8	643.46	0.00	0.417	627.35
$S(T^2 + DOB + \text{treatment} + \text{removal year})$	7	643.86	0.40	0.341	629.78
$S(T^2 + DOB + \text{treatment} + \text{removal year} + \text{vegetation} + \text{treatment} \times \text{vegetation})$	9	645.01	1.55	0.192	626.88
$S(T^2 + DOB)$	4	648.73	5.27	0.030	640.70
$S(T^2 + DOB + \text{vegetation})$	5	649.59	6.13	0.019	639.55

^a T^2 , within-year quadratic time trend; DOB, date of birth; treatment, coyote removal treatment effect; removal year, a parameter indicating survival varied among removal years; vegetation, index of understory vegetation cover.

^b No. of parameters plus an intercept term.

and sheep than subdominant classes (Gese and Grothe 1995, Sacks et al. 1999b, Blejwas et al. 2006), though whether this pattern holds for neonatal deer is unclear. In addition, environmental factors we did not measure may have increased predation pressure during the second year of removal. For example, during that year, production of wild plum (*Prunus americana*) and blackberry (*Rubus* spp.) fruit was extremely low (J. C. Kilgo, United States Department of Agriculture Forest Service, personal observation), and these fruits represent the most important items in coyote diets at SRS during May and June (Schrecengost et al. 2008). Future research should address the extent to which fluctuations in other important food resources affect predation rates on neonates.

Our hypothesis that neonate survival would be related to understory vegetation density was not supported. In contrast, Carroll and Brown (1977) attributed the 90% loss of fawns during 1 year in south central Texas to the combined effects of poor nutrition and lack of hiding cover caused by drought conditions. In southern Illinois, Nelson and Woolf (1987) reported that 64% of fawns taken by canids occupied areas characterized as open terrain. Similarly, neonate survival was greater in a suburban Chicago, Illinois forest preserve with denser understory than in one with more open understory (Piccolo et al. 2010). However, none of these studies directly correlated survival with the cover available to individual fawns in the same time period or location. Our attempt to do so revealed no relationship. The above studies were conducted under conditions with extreme differences in cover conditions. Although cover indices for individual neonates in our study were moderate, averaging 1.95 (on a scale of 0–4), they ranged from 0.63 to 3.19, presumably sufficient to have detected a relationship had it existed. Further, the lack of support for our model relating survival to an interaction between coyote removal treatment and vegetation cover indicated that the relationship between survival and cover was not dependent on coyote abundance; that is, even at reduced coyote abundance, the amount of cover available to neonates within their area of use did not affect their probability of survival. Conceivably, the effect of vegetation on neonate survival is manifested at a finer scale than we examined. Further research should focus on the relationship of predation risk to fine-scale vegetation conditions, such as those at neonate bedsites. Alternatively, survival may be affected by habitat conditions at the landscape scale (Rohm et al. 2007) or only when cover is extremely dense (Piccolo et al. 2010).

In situations such as SRS where coyote removal and understory enhancement hold little promise for improving recruitment, the best option remaining to managers who wish to increase population density may be reduction of adult female harvest (Robinson et al. 2014). For example, a 75% reduction in antlerless harvest over 4 years stabilized the SRS deer population, despite high predation pressure (Kilgo et al. 2012). The amount of harvest reduction required in a local population likely depends also on factors other than recruitment level, such as non-hunting mortality of adults. In addition, adult female harvest in some populations may be so

low that little room for adjustment exists. For example, Chitwood (2014) reported that only 8% of adult females were harvested annually in a declining deer population in North Carolina. Additional information is needed on predation effects in areas with greater deer population density and different cover conditions and on mitigation of predation effects through harvest adjustment.

Strength of inference from our study is limited by the fact that year and treatment effects were confounded in our before–after design. Had we been able to randomly assign coyote removal (treatment) and non-removal (control) among many replicate units, year and treatment effects would have been more clearly discrete. Neonate survival did not vary among the 4 years prior to initiation of our removal experiment (Kilgo et al. 2012), but we cannot rule out the possibility that the higher survival rates we observed during 2010 and 2012 were attributable to annual fluctuations unrelated to our removal treatment. In addition, distribution of neonates among our removal units was unequal, with neonates from a single unit comprising 62% of our sample. Although we detected no evidence of variation among units in either coyote abundance or neonate survival, lower sample sizes in 2 units may have limited our power to detect such differences, and 1 unit may have disproportionately influenced our results. Future research on neonate survival in the southeastern United States should endeavor to employ designs that may incorporate controls for pre and post-treatment differences, but challenges will be considerable. For example, to obtain adequate sample sizes, the dense understory characteristic of the region requires the use of VITs to aid in neonate capture, particularly in low-density deer populations. The costs associated with adult female capture and additional radio transmitters dramatically increase the expense and logistics of neonate survival research. In addition, the scale of coyote movements requires large study units. Such considerations greatly limit the number of replicate units that can be adequately sampled. Nevertheless, our understanding of the complex dynamics among neonate survival, predators, and habitat conditions, as well as the potential role of environmental factors such as weather and the abundance of alternative predator food sources, will benefit from strong experimentation.

MANAGEMENT IMPLICATIONS

Based on our findings, coyote control may not be a viable tool for most land managers in the eastern United States hoping to improve recruitment or increase deer population density. That we did not realize a consistent large increase in survival despite intensive coyote removal highlights the difficulty of achieving adequate coyote control in forested areas such as the southeastern United States, where aerial gunning is not possible. The level of coyote removal necessary to increase deer recruitment to desired levels is unknown but appears difficult to achieve through ordinary trapping. Effective coyote control may be even more difficult on smaller tracts than we studied, because of the more limited number of individuals that could be removed from a small area combined with the wide-ranging movements and apparently

high immigration potential of coyotes. Additionally, coyote trapping can entail high costs because of the labor, equipment, and fuel required. Our contract cost per coyote removed ranged from \$120 to \$250 and averaged \$199, which would equate to \$123 had contractors been permitted to commercialize their catch (based on average annual commercial value of coyotes in South Carolina; Butfiloski 2011, 2012). The marginal gains in recruitment that we observed may not justify such an investment.

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