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Research Article

Predation by Coyotes on White-Tailed Deer Neonates in South Carolina

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ABSTRACT Coyotes (*Canis latrans*) are novel predators throughout the southeastern United States and their depredation of white-tailed deer (*Odocoileus virginianus*) neonates may explain observed declines in some deer populations in the region, but direct evidence for such a relationship is lacking. Our objective was to quantify neonate survival rates and causes of mortality at the United States Department of Energy's Savannah River Site (SRS), South Carolina to directly evaluate degree of predation in this deer population. From 2006 to 2009, we radio-monitored 91 neonates captured with the aid of vaginal implant transmitters in pregnant adult females and opportunistic searches. Overall Kaplan–Meier survival rate to 16 weeks of age was 0.230 (95% CI = 0.155–0.328), and it varied little among years. Our best-fitting model estimated survival at 0.220 (95% CI = 0.144–0.320). This model included a quadratic time trend variable (lowest survival rate during the first week of life and increasing to near 1.000 around week 10), and Julian date of birth (survival probability declining as date of birth increased). Predation by coyotes was the most frequent cause of death among the 70 monitored neonates that died, definitively accounting for 37% of all mortalities and potentially accounting for as much as 80% when also including probable coyote predation. Predation by bobcats (*Felis rufus*) accounted for 7% (definitive) to 9% (including probable bobcat predation) of mortalities. The level of coyote-induced mortality we observed is consistent with the low recruitment rates exhibited in the SRS deer population since establishment of coyotes at the site. If representative of recruitment rates across South Carolina, current harvest levels appear unsustainable. This understanding is consistent with the recent declining trend in the statewide deer population. The effects of coyote predation on recruitment should be considered when setting harvest goals, regardless of whether local deer population size is currently above or below desired levels, because coyotes can substantially reduce fawn recruitment.

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

Overabundance of white-tailed deer (*Odocoileus virginianus*) is a problem facing wildlife managers in the United States, particularly in urban areas (Warren 1997). Even in rural and wild land areas, attempts to limit deer population size through antlerless harvest have been a primary focus of management programs (Miller and Marchinton 1995). Yet despite the prevalence of overabundance problems, some areas of the southeastern United States recently have experienced declines in deer numbers, harvest, or recruitment. Although some of these declines may have been welcomed by wildlife managers, maintaining reduced populations at desired levels will require an understanding of the mechanisms that caused the decline.

Kilgo et al. (2010) hypothesized that depredation of neonatal fawns by coyotes (*Canis latrans*) may have been responsible for declining metrics in South Carolina deer populations and elsewhere. Coyotes are recent, non-native additions to the fauna of the eastern United States, having occupied southeastern states largely by anthropogenic means only during the past 10–40 years (Hill et al. 1987, Gompper 2002). Timelines of coyote population growth vary across the Southeast, but populations have been established in many areas <20 years (Kilgo et al. 2010). For example, coyotes were first recorded in South Carolina in 1978, but they were not established statewide until the mid-1990s (Ruth 2010). Kilgo et al. (2010) cited the following factors as suggestive of a potential effect of coyotes: the South Carolina deer population declined coincident with the establishment and increase of coyotes; deer recruitment rates at the United States

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Department of Energy's Savannah River Site (SRS) declined coincident with the establishment and increase of coyotes; population modeling demonstrated that a new mortality source began operating in the SRS deer population coincident with the establishment and increase of coyotes; and a coyote food habits study at SRS indicated a high prevalence of neonate consumption (Schrecengost et al. 2008). Furthermore, coyotes are well-known predators of neonates in the western United States (Mech 1984) and can be limiting for deer populations in northeastern North America (Patterson et al. 2002).

Despite the evidence they presented, Kilgo et al. (2010) recognized that it did not demonstrate a relationship between the establishment and increase of coyotes and the decline of deer. In fact, the level of coyote predation on deer in the southeastern United States is virtually unknown; except for 1 study from an exurban landscape (Saalfeld and Ditchkoff 2007), no direct assessment of the effect of coyotes on deer survivorship has been conducted in the region. Some research from within the historic range of coyotes has documented minimal predation by coyotes on deer (5–17%; Heugel et al. 1985, Brinkman et al. 2004, Grovenburg et al. 2011). In addition, although suppression of deer by coyotes has been observed in some areas (Ballard et al. 1999), such effects may not occur in the mild climate of the southeastern United States where alternative food sources for coyotes are abundant. For example, the ability of coyotes to affect deer in the Northeast may be facilitated by the severity of winter weather, the added stress of which may render deer more vulnerable to predation (Patterson and Messier 2000). In short, factors other than predation by coyotes (e.g., changes in habitat quality, long-term drought, competition from wild pigs [*Sus scrofa*]) may have been instrumental in the decline of South Carolina deer populations. Therefore, assessment of the effects of coyote predation on neonatal fawn survival still is needed. Our objective was to quantify neonate survival rates and identify causes of mortality to directly evaluate whether coyotes may be responsible for declining recruitment in a South Carolina deer population.

STUDY AREA

We conducted the study on the SRS, a 78,000-ha National Environmental Research Park located in the Upper Coastal Plain physiographic region of South Carolina. Elevations ranged from 20 m to 130 m, and the terrain was gently rolling to flat. The climate was humid subtropical with mean annual temperature of 18°C and mean annual rainfall of 122.5 cm (Blake et al. 2005). Uplands were dominated by loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*) forests managed on 100- or 120-year rotations, respectively (approximately two-thirds of the SRS), or on 50-year rotations (approximately one-third of the SRS). Bottomland hardwood and cypress (*Taxodium distichum*)-tupelo (*Nyssa aquatic* and *N. sylvatica* var. *biflora*) forests occurred on floodplains.

Deer population density was low (4–8 deer/km^2) and the sex ratio was approximately even (Johns and Kilgo 2005). Hunts were conducted by dog drive from late October to mid-December, with most units hunted only 1 day per season. Limits per hunter per hunt ranged from 1 male and 1 female to unlimited for either sex, depending on unit-specific harvest goals. Total annual harvest during the study averaged 385 deer, or approximately 0.5 deer/km^2, only 36% of the long-term average, 1965–1999. With the exception of hounds during the fall hunting season, domestic or feral dogs (*Canis familiaris*) were not known to occur in our study area. Coyotes were first documented at SRS in 1986. Data are unavailable on the growth trend but population size appeared to stabilize during the late 1990s–early 2000s (J. C. Kilgo, USDA Forest Service, personal observation). During February 2006, density was estimated at 0.8–1.5 coyotes/km^2 (Schrecengost 2007). Coyotes were not harvested at SRS except for a few shot opportunistically during deer hunts; however, coyotes that left SRS suffered considerable human-induced mortality, primarily from legal trapping (Schrecengost et al. 2009). See Johns and Kilgo (2005) and Kilgo et al. (2010) for more detail on the management and history of deer and coyote populations at SRS.

METHODS

Adult Female Capture and Handling

We used vaginal implant transmitters (VIT; Model M3930, Advanced Telemetry Systems, Isanti, MN) in females $\geq$1.5-year old to facilitate capture of neonates. We captured females during January–April, 2006–2009 using rocket nets on food plots baited with shelled corn and using tranquilizer guns, both from vehicles with spotlights and from tree stands over bait. We radio-collared (Model 2510B; Advanced Telemetry Systems), ear-tagged, and implanted each female with a VIT. Implantation procedures generally followed those described by Bowman and Jacobson (1998) and Carstensen et al. (2003), except that we did not trim protruding antennas. For handling deer captured via rocket net, we blind-folded and physically restrained them with nylon ties, although we sedated some deer captured prior to February 2007 with an intramuscular injection of 150 mg of xylazine hydrochloride (ZooPharm, Fort Collins, CO), which we reversed with an intravenous injection of 15 mg yohimbine hydrochloride (ZooPharm). For tranquilizer gun capture, we used Telazol (250 mg; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine hydrochloride (150 mg) in 1-cc transmitter darts. Upon locating chemically immobilized deer, we placed them on an insulated mat in a sternal position and covered them with a blanket to aid in thermoregulation during anesthesia. We applied ophthalmic ointment and a blindfold and monitored vital signs at 10-minute intervals. After removing the dart, we irrigated the wound with 10% betadine solution and applied a topical antibiotic. At 80-minutes post-injection, we reversed the xylazine hydrochloride portion with tolazoline hydrochloride (160–180 mg; ZooPharm) and continued to monitor the deer until recovery. Deer capture and handling was conducted under the authority of South Carolina

Department of Natural Resources Research Collection Permit No. 120406-01.

Neonate Capture and Handling

In addition to a thermistor that detected and signaled the change in temperature associated with expulsion of the transmitter during parturition, VITs also were equipped with a timer that indicated the number of 30-minute intervals elapsed since parturition (i.e., temperature change). We monitored VIT signals weekly from capture until mid-April, daily until the first birth, and at 8-hour intervals (beginning at 0600, 1400, and 2200 hour) thereafter until the last birth. We allowed a $\geq$3-hour period immediately post-parturition for grooming and initial bonding between female and neonate, but otherwise initiated searches immediately upon detecting an expelled VIT. Searches were aided by thermal imaging cameras at night and when ground temperature conditions permitted during daylight. We proceeded first to the female and noted her location if not at the VIT, and then to the VIT. If we did not locate a neonate by the time we reached the VIT, we searched an area of approximately 200 m between and surrounding the female and VIT locations. If we did not find a neonate on the initial search, we returned at 8- to 24-hour intervals over the following 3–5 days for additional searches, using subsequent locations of the female as focal areas.

We blindfolded neonates and handled them only with nonscented latex gloves, except when we placed them in a cotton bag to obtain weight. Because neonates were a few hours old at capture and therefore already should have nursed, we acknowledge that our measurement of weight only approximates birth mass. We estimated age of neonates captured opportunistically from unmonitored females using new hoof growth (Sams et al. 1996). We determined sex, attached an expandable breakaway radio-collar (Diefenbach et al. 2003; Model M4210, Advanced Telemetry Systems) equipped with a motion-sensitive mortality switch on a 4-hour delay, and released neonates at the capture location. Handling duration averaged 6 minutes (range 2–18 min).

Fate Determination

Cause of death based on field methods.—We monitored neonates every 8 hours to $\geq$4 weeks of age, 1 to 2 times daily to 12 weeks of age, and weekly until 16 weeks of age. We monitored neonates more intensively at younger ages because we suspected this may have been the period when most mortality occurred (Cook et al. 1971). More intensive monitoring allowed us to recover carcasses sooner after death, hopefully prior to the loss or deterioration of evidence that would aid in determining cause of death, as well as better pinpointing date and time of death. Upon detecting a mortality signal, we proceeded immediately to recover the transmitter and carcass to determine cause of death. Access afforded by the extensive road system at SRS allowed us to reach most carcasses in $\leq$1 hour. Thus, given the 4-hour delay on transmitter mortality switches, the range in time between cessation of movement at death and detection of mortality was 4–13 hours ($\leq$8 hr since last live signal + 4-hr mortality delay + $\leq$1-hr recovery time).

Despite the frequency of our monitoring, the possibility remained that a scavenger may have reached a neonate that died of other causes prior to our arrival. Therefore, we conservatively assigned predation as the cause of death only when we recovered sufficient remains to discern killing bite wounds; that is, canine puncture wounds on the head and neck accompanied by subcutaneous hemorrhaging (White 1973, Garner et al. 1976). In such cases, we identified predator species (either bobcat [*Felis rufus*] or coyote) based on cache characteristics, other evidence at the recovery site (e.g., tracks, scat), and location of the recovery site in relation to the neonate's home range. Bobcats typically feed upon carcasses at or near the kill site (Beale and Smith 1973, Labisky and Boulay 1998, Roberts 2007, S. Roberts, Idaho Department of Fish and Game, unpublished data), whereas coyotes may carry carcasses considerable distances (e.g., to a den or rendezvous site; Harrison and Gilbert 1985) prior to or after partial consumption. We assigned coyote predation when remains were buried under mineral soil, when fresh coyote tracks were <5 m from the remains, or when remains were >1 km from the nearest live location of the neonate. We assigned bobcat predation when remains were covered with litter or sticks but mineral soil was not disturbed or when fresh bobcat tracks were <5 m from the remains. When we did not recover the head and neck but the above evidence suggested the presence of a particular predator species, we classified cause of death as probable bobcat or probable coyote. Additionally, we assigned probable coyote when killing bite wounds indicated predation as the cause of death but the carcass was not cached (because bobcats usually cover carcasses and coyotes sometimes do not), and when we recovered only the radio-collar and bone fragments or blood (because consumption of the whole carcass is generally more typical of coyote than bobcat predation; Cook et al. 1971, White 1973, Garner et al. 1976, Epstein et al. 1983, Labisky and Boulay 1998).

Cause of death based on DNA identification of predator species.—To decrease uncertainty in the assignment of predator species, during 2008 and 2009 we attempted to collect residual predator saliva for DNA identification of species. We wiped a cotton swab around killing bite wounds, other remains, or radio-collars, depending on what we recovered. When we did not recover definitive evidence of predation (i.e., killing bite wounds) but did recover predator DNA from remains, we conservatively assigned cause of death as probable coyote or bobcat, because of the possibility of scavenging. Wildlife Genetics International (WGI; Nelson, Canada) conducted genetic analyses, which also entailed determination of sex and individual identity of predators when sufficient DNA was obtained.

Wildlife Genetics International used QIAGEN DNeasy Tissue kits (Valencia, CA) to extract DNA from material clipped from swabs. The species identification test was a sequence-style analysis of the 16S rRNA mitochondrial gene (Johnson and O'Brien 1997). After initial attempts at analysis were complicated by the detection of prey DNA, WGI designed Carnivora-specific primers that reduced the amplification of cervid 16S sequence (primers: TTC TCC GAG

GTC ACC CCA ACC TAA AT; AGA CGA GAA GAC CCT ATG GAG CTT TAA TTA A). They compared the sequence profiles to reference profiles from coyote, dog/wolf (*Canis familiaris/lupus/rufus*, which were indiscernible in this analysis), bobcat, and deer to determine a match, thus identifying predator species. When mtDNA testing identified samples as either coyote or dog/wolf, WGI conducted genotyping analysis using 17 microsatellite markers known to be on separate chromosomes in dogs, and with mean observed heterozygosity of 0.77 in coyotes from this study area. This genotyping allowed additional analyses to confirm whether samples identified as dog by mtDNA tests actually were dog or coyote, since introgression of dog mitochondrial DNA haplotypes is known to exist in southeastern coyote populations (Adams et al. 2003). This situation allows an animal that is predominantly coyote, both genotypically and phenotypically, to appear as dog/wolf on the mtDNA species test. Wildlife Genetics International conducted assignment tests on the multilocus data using clustering analysis in program GENETIX (Belkhir et al. 2004), comparing the ambiguous dog/wolf samples against 39 known dogs and 179 known coyotes. They also used multilocus genotypes to identify individuals, using selective re-analysis of mismatching markers (Paetkau 2003) to prevent the recognition of false individuals through genotyping error. Finally, using only samples that had already shown consistent amplification of multiple coyote microsatellite markers, WGI analyzed sex for at least 1 sample per individual using a male-specific SRY marker (Griffiths and Tiwari 1993, Taberlet et al. 1993) that does not amplify from deer (WGI, unpublished data).

When no evidence of predation was present and the carcass was emaciated, we listed cause of death as emaciation. We submitted emaciated carcasses for full necropsy to the University of Georgia College of Veterinary Medicine's Veterinary Diagnostic and Investigational Laboratory (Tifton, GA). Although many researchers have eliminated emaciated neonates from their sample on the assumption that emaciation resulted from marking-induced abandonment, other research has concluded that the risk of marking-induced abandonment in white-tailed deer is minimal and that the omission of abandoned neonates can underestimate natural mortality (Ozoga and Clute 1988, Carstensen Powell et al. 2005). Natural abandonment, or maternal rejection syndrome, is well documented among white-tailed deer and is attributable to various causes (Langenau and Lerg 1976). Therefore, to guard against underestimation of this natural mortality source we retained such neonates in our sample. However, we acknowledge that if our activities caused abandonment, we may have overestimated mortality. Therefore, we also present the survival rate excluding emaciated neonates for comparison.

Statistical Analysis

We conducted known-fate modeling in Program MARK (White and Burnham 1999) to estimate survival rate to 16 weeks and to examine the influence of factors potentially affecting survival. We chose the 16-week survival rate to focus on neonatal survival rather than autumn and winter survival. Most fawns reached 16 weeks of age during September, and as antlerless hunting season in South Carolina began 15 September, we considered them recruited to the huntable population at this time. We based the analysis on neonate age in weeks; that is, we did not use a staggered entry approach to add neonates to the sample by calendar week born, but rather began the first weekly interval of the analysis at birth (Bishop et al. 2008).

We used an information theoretic approach to draw inference regarding a priori hypotheses about potential influences on survival rates (Burnham and Anderson 2002). We first assigned neonates to 4 groups based on calendar year (2006–2009) and tested for within and among year temporal effects on survival by comparing models in which survival varied by week (t), varied by year (yr), varied differently among weeks between years (yr × t), varied linearly through time (T), or varied quadratically through time (T^2; i.e., in a nonlinear manner). We then established a set of a priori candidate models that incorporated the best time trend predictor and were based on neonate characteristics (sex, mass; Rohm et al. 2007) and Julian date of birth (Bishop et al. 2009) to test for potential effects on survival rates (Burnham and Anderson 2002). To minimize the effect of age-related weight gain, we assigned opportunistically captured neonates >1-day-old ($n = 7$) the mean mass of all neonates <1 day old of the same sex from that year. Model definitions and names followed the conventions of Lebreton et al. (1992) and White and Burnham (1999).

We used Akaike's Information Criterion adjusted for small sample size (AIC_c) for model selection. We considered our most plausible models to be those models ≤ 2.0 AIC_c units from the best approximating model (Burnham and Anderson 2002). We used Akaike weights (w_i) to evaluate the strength of evidence among competing models (Burnham and Anderson 2002). The global model ($S(\mathrm{yr} \times \mathrm{t})$) was a saturated model and assessment of the goodness-of-fit of this model was not possible.

We believe our study met the following assumptions required for Kaplan–Meier survival analysis (Winterstein et al. 2001). First, our radio-collared neonates represented a random sample of the population because our use of VITs and thermal imaging cameras allowed us to locate virtually all neonates born to our implanted females, regardless of the location or cover in which they were born, thus greatly reducing any potential bias associated with concealment of birth or bed sites. In addition, our use of multiple capture methods (rocket nets, tranquilizer guns) and locations (food plots, roadways, off-road wooded areas) helped minimize potential bias toward susceptible individuals in our sample of implanted females. Second, we believe survival was independent among individuals in the sample. Although we included both members of twin sets, potentially compromising independence, Bishop et al. (2008) concluded that treating sibling neonates as independent sample units resulted in limited overdispersion (i.e., sibling dependence) and was thus reasonable. Predation tends to act independently on sibling neonates because of the spatial separation they maintain and the limited interaction between dams and neonates

(Bishop et al. 2008). Third, censoring of neonates was independent of the fate of those neonates; that is, their death did not cause failure of the transmitter and hence censoring. We censored only 3 neonates (1 each in 2007, 2008, and 2009), 2 when their radio-collars dropped prematurely and 1 when we lost contact because of inability to access the area. Thus, censoring resulted from our inability to monitor and not from destruction of the neonates and their transmitters. Finally, we are confident that radio transmitters did not affect neonate survival. Camera surveys conducted during September revealed that the fawn:doe ratio in the unmarked component of the population was similar to that in our radio-collared sample (J.C. Kilgo, unpublished data).

RESULTS

We implanted 3 females in 2006, 21 in 2007, 20 in 2008, and 23 in 2009. We monitored 3 females during 2 years, resulting in 64 individual deer and 67 VITs monitored during the study. Fifty of the 67 VITs (75%) resulted in the successful capture of $\geq$1 neonate, yielding 74 neonates (4 in 2006, 20 in 2007, 26 in 2008, and 24 in 2009), including 24 twin sets and 26 singletons. Some single neonates that we located may have had siblings that we failed to locate. Reasons for failure to capture neonates from monitored VITs included transmitter failure prior to parturition ($n = 7$), expulsion of the VIT prior to parturition ($n = 2$), death of the female prior to parturition (from vehicle collisions, $n = 3$), loss of contact with female prior to parturition ($n = 1$), late parturition (after cessation of monitoring, $n = 2$), and failure to locate neonate after apparently normal parturition ($n = 2$). We also captured 17 neonates from unmonitored, unmarked females (1 in 2006, 2 in 2007, 8 in 2008, and 6 in 2009). Thus, our total sample included 91 neonates (5 in 2006, 22 in 2007, 34 in 2008, and 30 in 2009).

Sex ratio among radio-collared neonates was biased toward males (57 of 91, 63%) in all years: 5 of 5 (100%) in 2006; 13 of 22 (59%) in 2007; 21 of 34 (62%) in 2008; and 18 of 30 (60%) in 2009. Neonate mass averaged 2.70 ± 0.07 (SE) kg for males and 2.51 ± 0.10 kg for females, and did not vary among years ($F_{3,81} = 0.55$, $P = 0.65$). Mean date of birth was 22 May but it differed among years ($F_{3,87} = 3.42$, $P = 0.021$), being earlier in 2007 (16 May) than in 2008 (28 May). Earliest dates of birth were 30 April (2007), 17 April (2008), and 18 April (2009). Latest dates of birth were 31 May (2007), 30 June (2008), and 22 June (2009).

The cumulative Kaplan–Meier survival rate (from model *S*(t)) to 16 weeks was 0.230 (95% CI = 0.155–0.328). When we excluded emaciated neonates from the sample, survival to 16 weeks under *S*(t) increased to 0.247 (95% CI = 0.164–0.354), only 0.017 greater than when included. We observed little annual variation in survival rates. Annual survival rates ranged from 0.167 in 2009 to 0.318 in 2007, and 95% confidence intervals overlapped among all years (Table 1). In addition, both models containing the variable year had AIC$_c$ weights of 0.000 and were the 2 least supported models (Table 2). The best model describing temporal trends in survival within the fawning season was the quadratic time trend model ($S(T^2)$; Fig. 1). Survival rate was lowest during the first week of life and increased to near 1.000 around week 10. This pattern was attributable to the fact that the number of mortalities per week declined sharply after the first week of life and no mortalities occurred after week 9 (Fig. 2). To account for this pattern, we included the quadratic time trend as an additive effect in all models assessing effects of other covariates.

Table 1. Annual and overall survival rates, *S*(t), among radio-collared white-tailed deer neonates at the Savannah River Site, South Carolina, USA, 2006–2009.

Year	Survival rate	SE	95% CI
2006	0.200	0.179	0.027–0.691
2007	0.318	0.099	0.160–0.534
2008	0.232	0.073	0.119–0.403
2009	0.167	0.068	0.071–0.343
Overall	0.230	0.044	0.155–0.328

Our best-supported model estimated survival at 0.220 (95% CI = 0.144–0.320). In addition to the quadratic time trend variable, this model included date of birth, indicating that survival probability was negatively associated with a neonate's Julian date of birth (Fig. 3). This model was our only plausible model (ΔAIC$_c$ < 2.0) and it received an Akaike weight of 0.775, nearly 5 times more likely than the next most supported model (Table 2). Neonate sex and mass apparently had little effect on survival, as the best model including these variables received little support from our data and the models including either variable alone received virtually no support (Table 2).

Predation was the cause of death for 31 (definitive) to 63 (definitive plus probable) of the 70 neonates that died (Table 3). Based on field methods, we determined predator species to at least the probable level for 50 neonates. We submitted swab samples from 41 of the 43 neonates suspected of being depredated during 2008–2009 for species identification from DNA in predator saliva (22 in 2008, 19 in 2009). Mitochondrial DNA testing successfully identified predator species for samples from 37 of the 41 neonates (90%; 20 of 22 in 2008 and 17 of 19 in 2009). Among this subsample, 28

Table 2. Model selection results used to estimate survival rates (*S*) of radio-collared white-tailed deer neonates at the Savannah River Site, South Carolina, 2006–2009. We ranked candidate models using change in Akaike's Information Criterion (ΔAIC$_c$) and Akaike weight (w_i).

Model[a]	K[b]	AIC$_c$	w_i	ΔAIC$_c$
$S(T^2 + \text{JDOB})$	4	347.21	0.775	0.00
$S(T^2 + \text{sex} + \text{mass} + \text{JDOB})$	6	350.35	0.161	3.14
$S(T^2)$	3	354.09	0.025	6.88
$S(T^2 + \text{sex})$	4	354.22	0.023	7.01
$S(T^2 + \text{mass})$	4	356.08	0.009	8.87
$S(T)$	2	356.92	0.006	9.71
$S(\text{t})$	16	371.02	0.000	23.81
$S(.)$	1	411.42	0.000	64.22
$S(\text{yr})$	4	412.92	0.000	65.71
$S(\text{yr} \times \text{t})$	64	460.24	0.000	113.04

[a] T^2, quadratic time trend; JDOB, Julian date of birth; *T*, linear time trend; t, time effect allowed to vary weekly; (.), constant survival.

[b] No. of covariate terms plus an intercept.

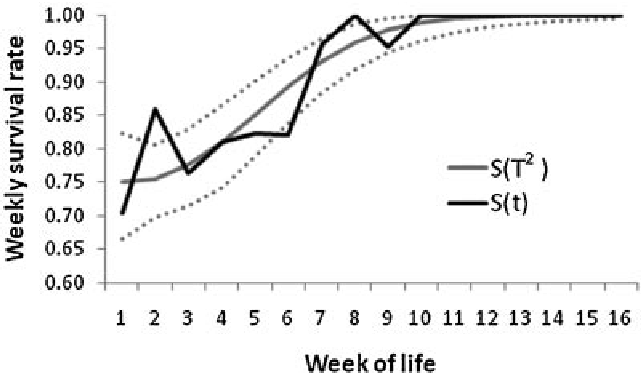

Figure 1. Observed weekly survival rates, S(t), and survival rates modeled with a quadratic time trend, $S(T^2)$, for radio-collared neonatal white-tailed deer fawns during their first 16 weeks of life at Savannah River Site, South Carolina, 2006–2009. Dashed lines represent 95% profile likelihood confidence interval for the quadratic time trend model.

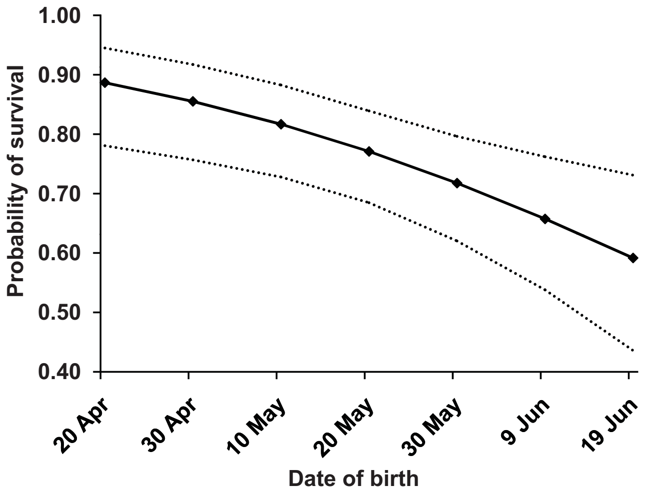

Figure 3. Effect of date of birth on weekly survival rate (±95% CI) of radio-collared white-tailed deer neonates at Savannah River Site, South Carolina, 2006–2009. We estimated survival while holding time constant at the first week of life, the week of lowest survival.

were coyote, 7 were dog/wolf, 1 was bobcat, and 1 contained both coyote and bobcat. Follow-up genotyping analysis of the 7 dog/wolf samples determined that all 7 were in fact predominantly coyote in genetic composition, yielding 35 identified as coyote. We assigned cause of death of the neonate from which we recovered both bobcat and coyote DNA as probable bobcat, considering it more likely to have been scavenged or stolen by a coyote after a bobcat kill than vice versa. Excepting this case, which we had assigned as probable coyote based on field evidence, all DNA identifications confirmed our field determination (including 19 neonates assigned as probable coyote predation). Therefore, when DNA testing failed to identify predator species, we relied on field evidence to assign predator species.

Predation by coyotes was the most frequent cause of death among the 70 monitored neonates that died (Table 3), with coyote predation accounting for 26 (37%) mortalities definitively and as many as 56 (80%) potentially, when including probable coyote predation. The oldest neonate depredated by a coyote was in its ninth week of life. Predation by bobcats accounted for 7% (definitive) to 9% (including probable bobcat predation) of mortalities. The oldest neonate depredated by a bobcat was in its sixth week of life. One neonate discovered at its birth site had slow, labored, and irregular breathing when found, and it died within 5 minutes. Necropsy determined that death was attributable to respiratory failure of unknown origin. Seven neonates died of emaciation, with 6 (84%) of these cases occurring during the latter half of the 2009 fawning season.

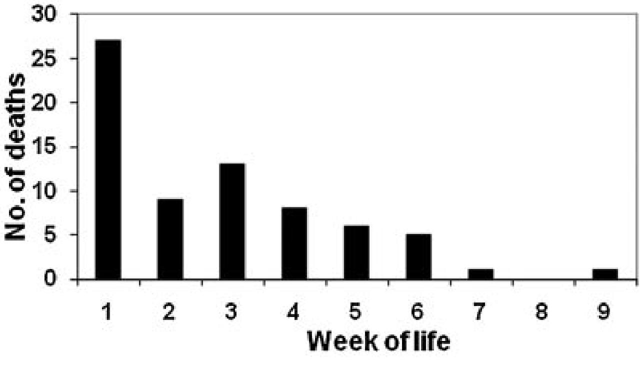

Figure 2. Number of deaths among radio-collared white-tailed deer neonates by week of life at Savannah River Site, South Carolina, 2006–2009.

Among those neonates determined through DNA analysis to have been fed upon by coyotes ($n = 35$), sufficient DNA was recovered from 24 (14 in 2008, 10 in 2009) for individual coyote identification. Most neonates were fed upon by different coyotes. Twenty-two individual coyotes were present at the 24 neonates (12 coyotes at 14 neonates in 2008, 10 coyotes at 10 neonates in 2009), but only 2 coyotes were detected from multiple neonates; during 2008, 2 of the 12 coyotes each were detected from 2 neonates. Even when both members of a twin pair were fed upon by coyotes, the same coyote was never detected from both neonates. Among the 22 individual coyotes, 8 were male and 14 were female (5 male, 7 female in 2008; 3 male, 7 female in 2009).

DISCUSSION

Predation by coyotes was the greatest source of mortality among neonates at SRS, ranging from at least 37% (including only definitive cases) to 80% (including probable cases) of all mortalities. Most cases we classified as probable coyote predation had clear evidence of coyote involvement (e.g., DNA, buried remains, tracks) and only lacked sufficient remains (i.e., the head and neck with killing bite wounds) to confirm that predation was the cause of death. We acknowledge the impossibility, lacking kill wounds, of distinguishing between predation and scavenging of neonates that died of other causes; hence our conservative assignment of probable rather than definitive coyote predation. However, we believe that our frequent monitoring and consequent rapid recovery of mortalities following death (4–13 hr for 67 of 70 mortalities, 4–17 hr for the remaining 3 mortalities) greatly minimized the possibility that a scavenging coyote

Table 3. Causes of mortality among radio-collared white-tailed deer neonates at the Savannah River Site, South Carolina, USA, 2006–2009.

Cause of death	2006 *n*	2006 %	2007 *n*	2007 %	2008 *n*	2008 %	2009 *n*	2009 %	Total *n*	Total %
Coyote predation	2	50.0	3	20.0	11	42.3	10	40.0	26	37.1
Probable coyote[a]										
From DNA					8	30.8	9	36.0	17	24.3
From field evidence	2	50.0	8	53.3	3	11.5			13	18.6
Emaciation					1	3.8	6	24.0	7	10.0
Bobcat predation			4	26.7	1	3.8			5	7.1
Probable bobcat					1	3.8			1	1.4
Natural causes[b]					1	3.8			1	1.4

[a] Neonates with coyote DNA or field evidence but from which the head and neck with killing bite wounds were not recovered. Neonates from which coyote DNA was recovered are listed only on that line, though field evidence was usually present also.

[b] Respiratory failure due to unknown causes.

discovered a carcass before we did. In addition, except for the 7 emaciated neonates (none of which had been scavenged), 100% of the 31 neonates for which we recovered the head and neck did have killing bite wounds; that is, when sufficient remains were available to assess the possibility of scavenging, predation was always the cause of death. Thus, we believe that most or all of the cases we classified as probable coyote predation were in fact coyote predation.

Mortality attribution in wildlife studies can be uncertain even when employing the most scrupulous and thorough methodologies. Our procedures for determining cause of death, particularly our use of DNA to identify predator species and our requirement that killing bite wounds be recovered to definitively assign predation as cause of death, were more rigorous than any study with which we are familiar, yet our probable assignments remain only probable and not definitive. However, even acknowledging less certainty in some points of our argument, our conclusion that coyote predation has affected recruitment does not change. The argument is as follows. We consider our most reliable finding, supported by a robust sample and consistent results among years, to be that recruitment was very low in the SRS population. Second, we recovered irrefutable evidence of the presence of predators from most mortalities, demonstrating that predators either killed or scavenged most neonates that died. Finally, somewhat less certain are our conclusions that predation was the dominant cause of death and that coyotes were the dominant predator that caused the majority of mortality. Most conservatively, coyotes were directly responsible for 37% of the mortalities. Therefore, given that recruitment is low, that predation appears to be the cause of the low recruitment, and that much of the predation is definitively attributable to coyotes, unless we assume that coyote predation is entirely compensatory, we must conclude that this exotic predator has significantly reduced recruitment.

The survival rate of 22% among neonates at SRS was extremely low. Studies from the western and northeastern United States have reported comparably low survival rates (<30%) when predation by coyotes was the primary source of mortality (Cook et al. 1971: 28%; Garner et al. 1976: 12%; Bartush and Lewis 1981: 10%; Long et al. 1998: 26%). Conversely, other studies have found much higher survival rates (>80%) when coyote predation was present (Brinkman et al. 2004: 84%; Pusateri Burroughs et al. 2006: 91%; Grovenburg et al. 2011: 87%). Many factors have been suggested as potentially influencing the magnitude of the effect coyotes have on neonate survival at different times and locations, including local coyote density, local deer density, abundance of alternative food sources for coyotes, and amount and density of vegetative hiding cover (Kilgo et al. 2010). The relatively low density of deer (4–8 deer/km^2; Johns and Kilgo 2005) combined with the relatively high density of coyotes (0.8–1.5 coyotes/km^2; Schrecengost 2007) at SRS may explain the low rate of neonate survival we observed. The SRS coyote population may attain a higher density than in other areas of the species' range due in part to a potentially greater abundance and diversity of alternative food resources, including soft mast (abundant from May through Nov) and wild pigs in addition to the small animals and other items that typically comprise coyote diets range-wide. Further, the availability of alternative food resources may explain the high mortality to very young neonates in that as neonates become more mobile, coyotes simply shift to more easily obtainable food items. Similarly, predation pressure by bears (*Ursus americanus*, *U. arctos*), also generalist omnivores, on elk (*Cervus elaphus*) calves in Yellowstone National Park is greatest on very young neonates and accounts for more predation events than all other predators combined (Barber-Meyer et al. 2008). Regardless of the factors involved, our finding from a forested landscape of South Carolina corroborates that of Saalfeld and Ditchkoff (2007) from an exurban landscape in Alabama, suggesting that significant predation by coyotes on white-tailed deer neonates may be widespread in the southeastern United States.

Whatever the mechanism that allowed such a high level of predation at SRS during our study, survival rates this low are consistent with, and indeed are necessary to explain, the depressed recruitment observed since establishment of coyotes at the site (Kilgo et al. 2010). Adult females (≥1.5-yr old at conception) at SRS each produce an average of 1.84 fetuses per year (Dapson et al. 1979). In 1999, the SRS fawn recruitment index declined below 0.56 fawns:adult female for the first time on record (dating to 1965) and remained below 0.56 through 2007 (Kilgo et al. 2010). From 1999–2007, an average of 0.41 fawns was recruited per adult female at SRS (Kilgo et al. 2010). Comparing these figures yields a crude apparent survival estimate of 22.2% ([0.41 fawns recruited/1.84 fetuses produced] × 100), nearly identical to and corroborating our estimate. Furthermore, the high level of predation we observed at SRS, if occurring more generally throughout South Carolina, together with existing harvest levels may be sufficient to explain the declining size of the state's deer population (Kilgo et al. 2010), as such low annual recruitment may be insufficient to replace the estimated 32% of the population that is harvested by hunters each year (Ruth 2010). For example, assuming an average productivity of 1.39 neonates per doe (including 0.5-yr-old females; Dapson et al. 1979) and an average sex ratio of 1 male:2.1 females (Ruth 2010), the estimated statewide population of 725,000 (Ruth 2010) would produce approximately 682,669 neonates per year. With a survival rate of 22%, the 150,187 survivors would not replace the 231,703 deer harvested by hunters in 2009, not to mention those lost to other sources of mortality.

Taken together with the historical pattern of the fawn recruitment index at SRS, our determination that the recent depression in that index is attributable to a high level of coyote-induced mortality suggests that predation by coyotes represents an additive source of mortality in the SRS deer population. The recruitment index exhibited 3 general phases between 1965 and 2007 (Kilgo et al. 2010): a period of relative stability from 1965 through the late 1980s, during which it remained above 0.80 fawns:adult female; a period of steady decline during the 1990s; and a second period of stability at a lower level from the late 1990s through 2007, during which it never surpassed 0.60 fawns:adult female and averaged 0.41 fawns:adult female (1999–2007). These 3 phases approximately correspond to the pre-coyote period at SRS, the period of coyote population establishment and growth, and the post-establishment period, respectively, thus providing a post-hoc before-after comparison of the effect of coyote predation. During the pre-coyote period, predation by bobcats, disease, malnutrition, and doubtless many other mortality factors operated in the SRS population without excessively depressing recruitment. Dapson et al. (1979) estimated annual non-hunting mortality in the SRS population (among all age classes, including neonates) from 1965–1971 to be 38–39% and Novak et al. (1991) estimated it to be only 26% from 1965 to 1986. Only since the establishment of coyotes did mortality increase and recruitment decline. Although other factors conceivably may have suppressed recruitment coincident with the establishment of coyotes, the addition of a mortality source that results in a survival rate of 22% is sufficient to explain the observed reduction without invoking alternative explanations. Conversely, evidence from studies of mule deer (*O. hemionus*) in Colorado has shown that coyote predation on neonates is compensatory to mortality from winter stress and malnutrition (Bartmann et al. 1992, Bishop et al. 2009). The SRS recruitment index is measured during autumn. Thus, although winters are mild in South Carolina, we cannot definitively conclude that coyote-induced mortality is additive until controlled, manipulative experiments are conducted.

Probability of survival was greatest for neonates born early in the season and declined progressively for neonates with later birth dates (Fig. 3). A similar pattern was reported for red deer (*Cervus elaphus*) calves (Clutton-Brock et al. 1987) and mule deer neonates (Lomas and Bender 2007), but in those cases, mortality was attributable not to predation on neonates but to stress, malnutrition, and disease impacts on smaller, later-born offspring during winter. Only Bishop et al. (2009), working on mule deer neonates, found a predation-induced pattern similar to the one we observed. Many studies conducted where predation was a significant source of mortality on neonatal ungulates have reported no effect of birth date on survival (Fairbanks 1993, Smith and Anderson 1998, Vreeland et al. 2004, Saalfeld and Ditchkoff 2007), although Gregg et al. (2001) found that pronghorn (*Antilocapra americana*) neonates born during the peak period of fawn drop had higher survival than those born during the non-peak period. In contrast to our findings, Whittaker and Lindzey (1999) reported that among sympatric mule and white-tailed deer neonates in Colorado, late born neonates survived better than early born, which they attributed to the swamping effect of the greater density of neonates available during and after the peak drop than before it. We suspect that at SRS the number of neonates available at any time during the fawning season is insufficient to satiate the coyote population, because of the low density of the deer population combined with the heavy mortality suffered even by early born neonates. Rather, aspects of the coyote life cycle apparently result in greater pressure on neonates as the fawning season progresses. For example, the nutritional demands of pup-rearing increase through the fawning season. Pups are born during April (J. C. Kilgo, unpublished data), resulting in lactation demands on females during the early portion of the fawning season, and are weaned during June, resulting in high protein requirements by growing pups during the latter portion of the fawning season. In addition, the hunting skills of 1-year-old coyotes, which comprise 59% of the SRS population (J. C. Kilgo, unpublished data) and are in their first fawning season independent of their parents, may increase as the season progresses.

The effect of date of birth on survival, combined with our use of VITs to locate neonates, may have contributed to our apparently low survival rate relative to other studies of neonate survival (e.g., Heugel et al. 1985, Nelson and Woolf 1987, Ballard et al. 1999). A considerable portion of the total mortality suffered by neonates occurred when neonates were very young, with 39% occurring during the first week of life. Our use of VITs to locate neonates shortly after parturition permitted us to detect these mortalities, many of which would have been overlooked in studies conducted prior to the advent of VITs, wherein neonates were captured at older ages, in some cases up to 2 weeks of age (Bishop et al. 2007). In addition, VITs precluded the bias against late born neonates that may accompany studies employing more traditional search techniques, as such searches may terminate when a target sample is reached or when the number of new neonates detected declines to a point of diminishing returns (Bishop et al. 2007). Without very young neonates and late-born neonates in the sample, our survival rates would have been biased upward.

Emaciation potentially resulting from abandonment by the female was a minor source of mortality that decreased survival by <2%. Our rate of 8% (7 of 91 neonates monitored) mortality from emaciation was intermediate to that reported by Ballard et al. (1999; 0%), Vreeland et al. (2004; 10%), Saalfeld and Ditchkoff (2007; 17%), and Grovenburg et al. (2011; 4%). Two factors suggest this mortality was not induced by capture. First, 6 of 7 neonates had twins that were captured and handled in the same manner and did not die of emaciation. Second, 6 of the 7 mortalities occurred during a single 4-week period (the latter half of the 2009 fawning season), with 6 of the 11 neonates captured during that time succumbing to emaciation. Nevertheless, whether caused by an environmental stressor peculiar to that period, by our capture and handling process, or by some other factor, the effect of emaciation-related mortality on survival probability was negligible. Conceivably, some mortalities we attributed to predation may have represented neonates that had been abandoned and were thus more susceptible to predation. If so, our data may underestimate the effect of abandonment and overestimate the effect of predation. However, among the carcasses we attributed to predation, none were emaciated, so we suspect that any such bias was minimal.

The degree to which coyotes are capable of affecting deer populations on a broad scale in the Southeast may depend on whether their effect is related to local deer population density. Neonate survival may be greater in higher density deer populations in the region because of the swamping effect (Whittaker and Lindzey 1999). Populations managed with heavy female harvest to achieve an even sex ratio and hence a fawning season that is concentrated during a short period (Hamilton et al. 1995) may further benefit from such an effect. If the ability of coyote predation to affect deer populations is density dependent, then such effects would have been evident at SRS with its low density population before many other areas of the Southeast. However, recruitment indices (fawns:adult female) from camera surveys conducted at SRS and in areas with 3- to 4-fold greater densities were nearly identical (J. C. Kilgo, unpublished data), suggesting similarly low survival rates in the higher density populations. Furthermore, despite having a sex ratio that has approached parity for more than 40 years at SRS (Johns and Kilgo 2005), parturition among our monitored females was protracted over nearly 2.5 months in 2008, suggesting that an even sex ratio may not always result in a concentrated fawning season. The decline in the size of the statewide deer population in South Carolina suggests that higher density populations are not immune to predation effects, but more research is needed to understand whether and in what conditions coyotes might affect high-density deer populations in the region.

MANAGEMENT IMPLICATIONS

Our data demonstrate that coyote predation on neonates can be substantial in the Southeast. Although additional research is needed to better understand the dynamics of the relationship between coyotes and deer in the region, deer managers should consider mortality from coyote predation when setting harvest goals, regardless of whether local deer population densities are at, above, or below desired levels. In populations well above desired densities, predation by coyotes may facilitate population reduction on a more rapid time scale. Conversely, in populations below desired levels, harvest reductions, particularly among females, may be necessary to offset losses to predation. For example, female harvest at SRS averaged 636 deer per year from 1990–2004 (the period of coyote population establishment and growth). During 2005–2008, harvest was intentionally reduced to an average of 161 females per year. This 75% reduction in annual harvest, apparently necessary to offset the 77% mortality we observed among neonates, halted the decline and resulted in a more stable population trend (Kilgo et al. 2010). Such adjustments in deer harvest management may be necessary in many areas across the region.

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