ABSTRACT

CHITWOOD, MICHAEL COLTER. White-tailed Deer Population Dynamics in the Presence of a Novel Predator. (Under the direction of Christopher E. Moorman and Christopher S. DePerno).

Coyotes (*Canis latrans*) recently expanded into the eastern U.S. and potentially have caused localized white-tailed deer (*Odocoileus virginianus*) population declines. As novel predators, coyotes are exerting a pressure on deer that has been absent for nearly 100 years in many areas of the southeastern United States. Recent research indicated neonatal fawns may be particularly vulnerable to coyotes, so understanding survival rates is crucial for managing deer populations in the presence of coyotes. In 2011 and 2012, we radiocollared 65 neonates at Fort Bragg Military Installation in North Carolina, monitored them intensively for 16 weeks, and assigned mortality causes. We determined survival and evaluated the impact of covariates on survival (Chapter 1). Additionally, we relocated neonates to quantify space use and movement, particularly in the context of avoiding predation risk. We used movement and bedsite cover data to evaluate the possibility that coyotes and cover conditions at Fort Bragg were creating an evolutionary trap for neonates (Chapter 2). We used locally derived vital rates to build a population model and perform sensitivity analysis and manipulated vital rates to explore potential effects of management actions under "what if" scenarios (Chapter 3). Results indicated that neonate survival was low and coyote predation was the leading source of mortality. Selection analysis provided support for an evolutionary trap because neonates with greater movement rates and bedsites in less dense cover were more likely to escape predation by coyotes. These results are counter to the expected hider strategy common among ungulate neonates. Population modeling revealed a declining deer population, and proposed management scenarios resulted in various population trajectories (subject to model uncertainty). We concluded that reducing adult female harvest was the least expensive, most effective strategy to mitigate negative effects of coyotes on deer populations. Overall, results indicated that coyotes can have profound impacts on white-tailed deer population dynamics in the southeastern U.S.

White-tailed Deer Population Dynamics in the Presence of a Novel Predator

by
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DEDICATION

I dedicate my dissertation to my grandparents, W. B. “Mooney” and Mary Jane “Sug” Chitwood, and the late Albert and Mary Rose “Rosie” Rollins. G-daddies and Memamas are special, so this is for them.

BIOGRAPHY

Michael Colter Chitwood was born in Dalton, Georgia, on February 6, 1983. From an early age he fished, hunted, and explored the woods and waters of north Georgia. Along the way, he developed an appreciation for wildlife and science. After graduating from Dalton High School in 2001, he pursued his Bachelor of Science degree in Environmental Sciences at the University of North Carolina at Chapel Hill, where he graduated in 2005. He returned to Georgia to work in an unrelated field, but over the next two years, his passion for higher education and continued pursuit of the sciences led him back to school. In August 2007, he entered the Fisheries and Wildlife Sciences Program at North Carolina State University and graduated with a Master of Science degree in May 2010. With his professional direction set on academic research and teaching, he transitioned into a doctoral position in the same program. Upon graduating with his Ph.D. in Fisheries, Wildlife, and Conservation Biology, he will begin work at North Carolina State University as a postdoctoral researcher.

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CHAPTER 1

Do Biological and Bedsite Characteristics Influence Survival of Neonatal White-tailed Deer?

Abstract

Coyotes (*Canis latrans*) recently expanded into the eastern U.S. and potentially have caused localized white-tailed deer (*Odocoileus virginianus*) population declines. Research has focused on quantifying coyote predation on neonates, but little research has addressed the potential influence of bedsite characteristics on survival. In 2011 and 2012, we radiocollared 65 neonates, monitored them intensively for 16 weeks, and assigned mortality causes. We used Program MARK to estimate survival to 16 weeks and included biological covariates (i.e., sex, sibling status [whether or not it had a sibling], birth weight, and Julian date of birth). Survival to 16 weeks was 0.141 (95% CI = 0.075-0.249) and the top model included only sibling status, which indicated survival was lower for neonates that had a sibling. Predation was the leading cause of mortality (35 of 55; 64%) and coyotes were responsible for the majority of depredations (30 of 35; 86%). Additionally, we relocated neonates for the first 10 days of life and measured distance to firebreak, visual obstruction, and plant diversity at bedsites. Survival of predation to 10 days (0.726; 95% CI = 0.586-0.833) was positively associated with plant diversity at bedsites. Our results indicate that neonate survival was low and coyote predation was an important source of mortality, which corroborates several recent studies from the region. Additionally, we detected only weak support for bedsite cover as a

covariate to neonate survival, which indicates that mitigating effects of coyote predation on neonates may be more complicated than simply managing for increased hiding cover.

Introduction

Recent declines in white-tailed deer (*Odocoileus virginianus*) numbers, harvest, or recruitment in some areas of the southeastern U.S. (e.g., Kilgo et al. 2010) run counter to the commonly reported trend of overabundance (e.g., Warren 1997). Though some landscapes will benefit from reduced deer numbers, the mechanisms causing the declines and the long-term trajectory of the deer populations are of interest to wildlife managers. Additionally, given the prevalence of overabundance problems, managers have attempted to limit deer population size through antlerless harvest (Miller and Marchinton 1995), so understanding how some areas are experiencing deer population decline is paramount to adaptive management programs.

Coyotes (*Canis latrans*) recently expanded into the eastern U.S. (Parker 1995) and have been implicated as a potential cause of localized deer population decline (Kilgo et al. 2012). Coyotes are non-native additions to the southeastern U.S. landscape, having occupied the region primarily by anthropogenic means during the past 10-40 years (Hill et al. 1987, Gompper 2002), with most populations established for <20 years (Kilgo et al. 2010). The absence of red wolves (*Canis rufus*), modification of the landscape by humans, and merging of local coyote populations via dispersal contributed to the expansion and increased success of coyotes (Nowak 1979, Hill et al. 1987).

Kilgo et al. (2010) hypothesized that coyote depredation of neonatal fawns could be responsible for declining deer population metrics in South Carolina and across the region.

Subsequently, Kilgo et al. (2012) documented low neonatal fawn survival at their South Carolina study site and determined coyotes were the leading cause of mortality. Though studies have documented minimal predation effects of coyotes on deer in historic coyote ranges (5-17%; Heugel et al. 1985, Brinkman et al. 2004, Grovenburg et al. 2011), the few studies conducted in the southeastern U.S. have documented considerably greater rates of coyote predation on neonates (42%, Saalfeld and Ditchkoff 2007; 37-80%, Kilgo et al. 2012; 65%, Jackson and Ditchkoff 2013). Thus, the need for additional studies is great, especially those focused on the factors that contribute to or reduce predation risk for neonatal fawns. Kilgo et al. (2010) posed several questions that had potential bearing on how researchers could better understand the deer-coyote dynamic in the Southeast, including how vegetation structure or other landscape variables would affect predation level. Thus, our objectives were two-fold: 1) quantify neonate survival and identify causes of mortality to determine whether coyotes were responsible for declining recruitment in a North Carolina deer population; and 2) evaluate the effects of vegetative cover on neonate survival. We hypothesized that neonate survival would be low and coyote predation would be the leading cause of mortality. Additionally, because neonates rely on crypsis as the primary means of predator avoidance at young ages (DeYoung and Miller 2011), we hypothesized that bedsites with greater vegetative cover would provide more protection from coyote predation and therefore be positively associated with survival.

Study Area

We conducted our study at Fort Bragg Military Installation (hereafter, Fort Bragg), a 40,500-ha property owned by the U.S. Department of Defense and located in the Sandhills physiographic region of central North Carolina. Uplands were dominated by longleaf pine (*Pinus palustris*) forests and managed with growing-season prescribed fire on a 3-yr fire-return interval. Densely vegetated drainages were interspersed throughout the landscape. An extensive, drivable firebreak network facilitated the implementation of the large-scale fire regime, while providing access for military vehicles (Lashley et al. 2014a).

Deer population density was low (2-4 deer/km2), and hunting occurred from the first Saturday in September through 1 January in most areas of Fort Bragg. Harvest records, track counts, spotlight counts, and biologists' observations indicated a decline in deer density from 1989 to present, commensurate with the initiation and establishment of coyotes at Fort Bragg (J. Jones, Fort Bragg Wildlife Branch, personal communication). Total hunter harvest fell from a high of 1261 in 1989 to a low of 163 in 2003 and currently averages 250-300 deer per year. Though hunter effort has changed over the years, deer hunters currently harvest deer in 1 out of 33 hunts, compared to 1 out of 15 hunts in the 1980s (J. Jones, Fort Bragg Wildlife Branch, personal communication). The first coyote at Fort Bragg was documented in 1989, and by the mid-1990s, coyotes were common. Coyote hunting is legal at Fort Bragg, but hunter effort and reported kill rates are low (i.e., a few coyotes per year); the few coyotes killed each year generally are shot opportunistically by deer hunters (J. Jones, Fort Bragg Wildlife Branch, personal communication). Coyote trapping is not allowed at Fort Bragg but is common on adjacent private land.

Methods

Adult Female Capture and Handling

During January-May, 2011-2012, we captured females ≥ 1.5-year old using tranquilizer guns from tree stands over food plots baited with shelled corn and from vehicles. We radiocollared (Wildcell, Lotek Wireless Inc., Newmarket, Ontario, Canada; Model 2510B, Advanced Telemetry Systems, Isanti, MN), ear-tagged, and implanted each female with a vaginal implant transmitter (VIT; Model M3930, Advanced Telemetry Systems) to facilitate capture of neonates. Implantation procedures generally followed Bowman and Jacobson (1998) and Carstensen et al. (2003), except that we did not trim protruding antennas (Kilgo et al. 2012). We used Telazol (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN), xylazine hydrochloride (2.5 mg/kg; Congaree Veterinary Pharmacy, Cayce, SC), and ketamine hydrochloride (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN) in 2-cc transmitter darts. At 80-minutes post-injection, we antagonized the xylazine hydrochloride with tolazoline hydrochloride (10 mg/kg; Midwest Veterinary Supply, Burnsville, MN) and monitored the deer until recovery. Deer capture and handling was approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (10-143-O).

Neonate Capture and Handling

We monitored VIT signals weekly from capture until 1 May, daily until the first birth, and at 8-hour intervals (beginning at 0600, 1400, and 2200 hours) thereafter. The VITs were equipped with a thermistor that detected and signaled the change in temperature associated with expulsion of the transmitter during parturition. Additionally, VITs included a timer that indicated the number of 30-minute intervals elapsed since parturition (i.e., temperature change). We allowed ≥ 2 hours after the parturition time derived from the VIT timer before initiating a search, which provided time for grooming and initial bonding between female and neonates.

When we located neonates, we used latex gloves to blindfold and weigh them in a cotton bag. We estimated age of opportunistically captured neonates using new hoof growth (Sams et al. 1996) and behavior. We determined sex, deployed an expandable breakaway radiocollar (Diefenbach et al. 2003; Model M4210, Advanced Telemetry Systems), and released neonates at the capture location. Radiocollars were equipped with a motion-sensitive mortality switch on a 4-hour delay.

Fate Determination

We monitored neonates ≤ every 8 hours to 4 weeks of age, 1 to 2 times daily to 12 weeks of age, and once every 3 days until 16 weeks of age. We monitored neonates more intensively at younger ages because it has been suggested this period is when most mortality occurs (Cook et al. 1971). Intensive monitoring allowed us to better detect mortalities, to more precisely pinpoint time of mortality, and to recover carcasses as soon as possible to reduce chance of scavenging and preserve the most evidence to be used in determining the cause of mortality (Kilgo et al. 2012). When we detected a mortality signal, we proceeded immediately to recover the transmitter and remains. We efficiently accessed all of our collared neonates due to the extensive firebreak network at Fort Bragg and reached carcasses in < 30 minutes after detections, which meant the time lag between cessation of collar movement and our recovery was between 4.5 and 12.5 hours (given that a live signal could have been detected 8 hours earlier, the collar was then motionless for 4 hours prompting the mortality signal, and it took 30 minutes to reach the collar).

Following the methods of Kilgo et al. (2012), we assigned initial, field-based cause of mortality based on evidence at or near the collar or remains. When sufficient remains were present to locate a killing bite wound (i.e., canine puncture wounds on the head or neck that included subcutaneous hemorrhaging [White 1973, Garner et al. 1976]), we assigned cause of death as predation. In these cases, we identified the predator responsible (either bobcat [*Lynx rufus*] or coyote) based on cache characteristics, tracks or scat at the recovery site, amount of remains left, parts of carcass where feeding had occurred, and location of the recovery site in relation to the neonate's home range. Bobcats typically feed at or near the kill site (Beale and Smith 1973, Labisky and Boulay 1998, Roberts 2007), while coyotes may carry kills considerable distances (e.g., to a den or rendezvous site; Harrison and Gilbert 1985). Bobcats tend to cache remains under sticks, leaf litter, or debris without digging into mineral soil, while coyotes dig into mineral soil, if they cache at all (O'Gara 1978). Bobcats tend to focus feeding on the shoulders, while coyotes feed first on the viscera and hindquarters (O'Gara 1978). Additionally, coyotes are more likely to consume the entire carcass than bobcats (Cook et al. 1971, White 1973, Garner et al. 1976, Epstein et al. 1983, Labisky and Boulay 1998). If we were unable to recover a head or neck with killing bite wounds, but the evidence suggested the presence of a particular predator as described above, we assigned the cause of mortality as predation by that particular species (e.g., a drop of blood on vegetation adjacent to a collar with a coyote track beside it would be assigned as a coyote predation).

When no evidence of predation or emaciation was present, but the carcass was otherwise intact, we assigned the cause of death as unknown. When no evidence of predation was present but the carcass was intact and emaciated, we assigned cause of mortality as starvation. We conducted field necropsies (after training with a veterinarian at the North Carolina State University College of Veterinary Medicine) to confirm starvation as the cause of death (i.e., no milk in the digestive tract). Some researchers have removed starved neonates from their samples because of potential marking-induced abandonment. However, other research has suggested that doing so is unnecessary because the risk of marking-induced abandonment in white-tailed deer is low and omitting starved neonates can underestimate natural mortality (Ozoga and Clute 1988, Carstensen Powell et al. 2005). Natural abandonment (resulting in neonate starvation) is commonly reported in white-tailed deer and attributable to various causes (Langenau and Lerg 1976).

To confirm our field-based assessments of predation-related mortalities, we collected residual predator saliva for DNA identification of predator species. Following the methods of Kilgo et al. (2012), we wiped cotton swabs around killing bite wounds, near feeding sites on carcasses, on the head of the neonate, and on the radiocollar strap and housing. Unlike Kilgo et al. (2012), when we determined by DNA that a predator was present at a radiocollar recovery site, even in the absence of killing bite wounds, we confidently assigned cause of mortality to that predator species. Though our monitoring schedule was intense, we acknowledge that it is possible that scavenging could have occurred before our recovery. However, in our study, we were unable to document a single scavenging event on 24 neonate carcasses that died of causes other than predation. Additionally, a 6-yr neonate survival study in South Carolina failed to document a single scavenging event on 21 carcasses that died of non-predatory causes (J. Kilgo, USDA Forest Service, unpublished data). Thus, the likelihood that scavenging could potentially bias our DNA-based predator identifications is low.

Wildlife Genetics International (WGI; Nelson, Canada) conducted the genetic analyses by extracting DNA from swab material using QIAGEN DNeasy Tissue kits (Valencia, CA). They determined the predator species present using a sequence-style species identification test focused on the 16S rRNA mitochondrial gene (Johnson and O'Brien 1997). Additionally, when sufficient, quality coyote DNA was obtained, WGI conducted genotyping for individual identification using 17 microsatellite markers (as described in Kilgo et al. 2012). Both analyses were designed and developed previously for this type of application (for detailed molecular methods, see Kilgo et al. 2012).

Measuring Vegetative Cover Covariates

We measured landscape covariates at neonate bedsites to determine their potential effects on neonate survival in the first 10 days of life. We focused on the first 10 days because neonates are less mobile during that period and tend to rely on crypsis to mitigate predation risk (DeYoung and Miller 2011). Once a neonate was radiocollared, we relocated them systematically via homing once every 24-hr period, making sure they were relocated at various times of day or night within the constraints of the monitoring schedule used to check VITs and neonate survival (described above). We checked the location of the dam and did not approach if she was in close proximity to the neonate. We approached neonates quietly to minimize disturbance and attempted to get close enough for a visual relocation (with ambient light or with the aid of a forward looking infrared radiometer [FLIR]). Once the bedsite was located, we took a GPS point and wrote a detailed description of the bedsite location and adjacent vegetation. If vegetation was too dense for a visual or FLIR relocation, we approached as close as possible and triangulated into the cover to determine the bedsite location. To minimize disturbance and reduce the risk of biasing neonate survival, we waited until all neonates were ≥2 weeks old to begin vegetation measurements (~first week of July for both years).

To quantify the vegetative structure at bedsites, we used a modified vegetation profile board (Nudds 1977). We estimated percent horizontal cover from 0 – 2 m in 4 50-cm height categories by assigning visual obstruction on a 0 – 5 scale in each height category (where 0 – 5 represented 0%, 1 – 20%, 21 – 40%, 41 – 60%, 61 – 80%, or 81 – 100% coverage, respectively). We averaged the scores from all 4 height categories to derive a single cover value. We placed the board at plot center (i.e., in the bedsite) and viewed it from 1-m height, from 10 m away, along bearings of 0°, 120°, and 240°. Additionally, along each bearing, we recorded the number of plant species contributing to the horizontal cover. We determined final Nudds board scores and final plant diversity scores by taking the average of the 3 profile bearings at each bedsite and then averaging across all bedsites, producing a single value per metric per neonate. Also, we created a weighted index of visual obstruction by multiplying the final Nudds board score with the final plant diversity score for each neonate (e.g., 4.5 Nudds × 10 plants = 45). We created this metric because we thought it might provide a more accurate representation of structural complexity (e.g., some bedsites with low horizontal cover were associated with high plant diversity, while some areas with high cover values had low plant diversity). We determined distance to nearest firebreak using ArcMap 10 (Environmental Systems Research Institute, Inc., Redlands, CA) by calculating the average distance from bedsites to firebreak for each neonate.

Statistical Analysis

We estimated survival rate to 16 weeks using known-fate modeling in Program MARK (White and Burnham 1999) and based the analysis on the known age of each neonate in weeks (i.e., we did not use a staggered entry approach; Bishop et al. 2008). We used an information theoretic approach to draw inferences regarding *a priori* hypotheses about potential influences on neonate survival (Burnham and Anderson 2002). Following the methods of Kilgo et al. (2012), we first assigned neonates to 2 groups based on calendar year (2011-2012) to test for within and among year temporal effects. We compared models in which survival varied by week (t), year (yr), differently among weeks between years (yr*t), linearly through time (T), or quadratically through time (T2). Next, we established a set of *a priori* candidate models that incorporated the best time trend predictor and included neonate biological characteristics (i.e., sex and birth weight [Rohm et al. 2007] and Julian date of birth [Bishop et al. 2009]) to test for potential effects on survival rate (Burnham and Anderson 2002). We imputed birth weight data for opportunistically captured neonates by randomly drawing from our distribution of values measured in that sex from that year. Additionally, we included sibling status (i.e., neonate twins were assigned a 1, while neonate singletons were assigned a 0) to model the potential effect of siblings on neonate survival rate. We imputed sibling status for opportunistically captured neonates (because we did not know their sibling status empirically) by randomly assigning a 1 or 0 based on the proportion of documented twin-sets in that year.

To evaluate the potential impacts of vegetative cover at bedsites on neonate mortality due to predation, we performed a second analysis in Program MARK. Following the procedures outlined above, we used known-fate modeling in Program MARK to estimate survival of predation to 10 days (i.e., the same time period for which we measured vegetation at bedsites). Therefore, we censored neonates that died of causes other than predation. We established a set of *a priori* candidate models based on our best time trend predictor from the first analysis and included vegetative covariates (i.e., Nudds board score, plant diversity score, weighted index of visual obstruction, and distance to firebreak).

For both analyses, we used Akaike's Information Criterion (adjusted for small sample size; AICc) for model selection and considered our plausible models to be those ≤ 2.0 AICc units from the top model (Burnham and Anderson 2002). We used Akaike weights (w_i) to evaluate the strength of evidence among competing models (Burnham and Anderson 2002).

Results

We monitored 28 VITs in 2011 and 25 in 2012; 3 individuals were monitored in both years. Thus, we monitored 53 VITs in 50 individuals during the study. We captured ≥ 1 neonate from 35 of the 53 VITs (66%), and the total VIT-based sample included 59 neonates (23 in 2011 and 36 in 2012). For the 35 known births, we documented 23 twin sets, 10 singletons, 1 set of triplets, and 1 unknown litter size. For the unknown litter, we recovered 1 fawn ~20 hrs after the VIT was expelled; thus, we do not know if it had a sibling. Additionally, 1 fawn from a twin set in 2012 was removed from the study because it had a foreleg caught in its radiocollar and starved. We captured 6 neonates opportunistically from unmarked females (4 in 2011 and 2 in 2012), resulting in a total sample of 65 neonates (27 in 2011 and 38 in 2012). Mean date of birth was 28 May in 2011 and 1 June in 2012. The earliest dates of birth were 12 May in 2011 and 15 May in 2012; the latest dates of birth were 23 June in 2011 and 15 June in 2012.

Survival rates were similar across years (i.e., confidence intervals overlapped; 2011 = 0.185, 95% CI = 0.039-0.332; 2012 = 0.105, 95% CI = 0.008-0.203), so we pooled all neonates for subsequent analyses. The best model describing temporal trends in neonate survival was the *S*(t) model, and the 16-week cumulative Kaplan-Meier survival rate was 0.141 (95% CI = 0.075-0.249). Neonate survival rate was lowest during the first week of life and increased to near 1.000 around week 8 (Figure 1).

Adding covariates to the *S*(t) model, our top model estimated survival at 0.136 (95% CI = 0.071-0.245) and included sibling status (β = -0.628, SE = 0.430, 95% CI: -1.471-0.215), indicating that survival probability was negatively associated with having a sibling. However, the top model did not carry much Akaike weight (w_i = 0.18), so consideration of competing models within 2 AICc was warranted (Table 1). Because no model clearly outperformed the rest, we summed Akaike weight by covariate to present the relative impact of each variable on survival (Table 2). Sibling status appeared the most in competing models, followed by Julian date of birth and sex (Table 2).

For the second analysis, using only the first 10 days of life to evaluate the importance of vegetative covariates on survival of predation, the *S*(t) model was again the best; it estimated survival at 0.726 (95% CI = 0.586-0.833). Adding covariates to the *S*(t) model, our top model estimated survival at 0.746 (95% CI = 0.600-0.853) and included plant diversity (β = 0.175, SE = 0.124, 95% CI = -0.069-0.419), indicating that survival probability was positively associated with bedsites with greater floral diversity. Again, the top model did not carry much Akaike weight (w_i = 0.18), so consideration of competing models within 2 AICc was warranted (Table 3). We summed Akaike weight by covariate to present the relative impact of each variable on survival (Table 4). Species diversity appeared the most in competing models, followed by distance to firebreak and the weighted index (Table 4).

Predation was the cause of death for 35 of the 55 neonates that died (Table 5). Based on field methods, we assigned a predator species to 35 cases and submitted swabs from all 35 (15 in 2011, 20 in 2012). Mitochondrial DNA testing successfully identified predator species for swabs from 32 of the 35 neonates (91%; 14 of 15 in 2011 and 18 of 20 in 2012). In all 3 cases in which predator DNA was not detected, field evidence was consistent with other depredations, allowing us to confidently assign predator species without DNA confirmation.

Predation by coyotes was the most frequent cause of mortality, accounting for 30 of the 55 deaths (55%; Table 5). Bobcats accounted for 5 of 55 deaths (9%; Table 5). Overall, neonate mortality was greatest during the first week of life (Figure 2), with the latest coyote and bobcat depredations occurring in the tenth and seventh weeks of life, respectively. Starvation was the second-leading cause of mortality and accounted for 16 of 55 deaths (29%; Table 5). All neonates that died of starvation were within the first week of life (Figure 2).

Among coyote depredations linked to coyotes by mtDNA (n = 28), sufficient DNA was obtained from 12 cases (5 in 2011, 7 in 2012) for individual coyote genotyping. Most neonates were killed or consumed by different coyotes, and we obtained 9 unique genotypes across the 12 cases. Two coyotes were detected at 2 neonates each in 2012, and 1 coyote was detected on 1 neonate in both years.

Discussion

The neonate survival rate of 14% at Fort Bragg was low relative to other studies of neonate survival in the presence of coyotes. In the western and northeastern regions of the U.S., coyotes have been implicated as the primary source of mortality, and many of those studies reported comparably low survival rates (28%, Cook et al. 1971; 12%, Garner et al. 1976; 10%, Bartush and Lewis 1981; 26%, Long et al. 1998). Interestingly, other studies conducted in the presence of coyotes have documented much greater survival rates (84%, Brinkman et al. 2004; 91%, Pusateri Burroughs et al. 2006; 87%, Grovenburg et al. 2011). Nevertheless, the few studies conducted in the southeastern U.S. where coyotes are novel predators reported low survival (33%, Saalfeld and Ditchkoff 2007; 22%, Kilgo et al. 2012; 26%, Jackson and Ditchkoff 2013), with coyotes as the leading cause of mortality.

Neonate independence is a topic of interest in survival studies due to the potential bias associated with including both individuals from a set of twins. Interestingly, we detected a small effect of sibling status on neonate survival. Our results indicated there was a slight reduction in survival for neonates having a sibling. Ecologically, this indicates that twin sets may attract more attention from predators like coyotes even if they are spatially separated. We speculate that coyotes could use behavioral cues from the dam to increase searching efficiency and perhaps benefit from twins bedded in relatively close proximity. Our results may lend support to the statistical argument that individuals from twin sets are dependent on one another and cannot both be included. However, leaving a twin uncollared or removing it randomly from later analyses does not address the dependency that exists on the landscape. The twins are still reliant upon the dam for milk, and though they are most often spatially separated, they are still dependent on the dam's attention. Our approach allows us to include the potential twin-effect in survival studies, while maintaining sample size (i.e., knowing the fate of entire litters). To determine neonate survival and recruitment into the population, collaring the greatest number of neonates possible provides the most biological information.

Kilgo et al. (2010) suggested many factors could be responsible for the magnitude of effect coyotes have on neonate survival, including coyote density, deer density, alternative coyote food sources, and vegetative hiding cover. Similar to Kilgo et al. (2012), the relatively low deer density (2-4 deer/km^2) and apparently high coyote density at Fort Bragg may explain the low rate of neonate survival in our study. Currently, reasons for high coyote density are unknown but may relate to the availability of other foods. At Fort Bragg, neonates were most susceptible to coyotes at young ages, which might indicate that coyotes switch to other food items as neonates age and become harder to catch (Kilgo et al. 2012). Additionally, we did not detect a strong effect of date of birth on neonate survival. Numerous studies with high rates of predation 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). Thus, we suspect coyotes are not satiated by the number of neonates available during the fawning season at Fort Bragg, which was consistent with the conclusions of Kilgo et al. (2012) in South Carolina. Other than density related interactions, vegetative cover seems to be a likely factor for explaining neonate survival. Unfortunately, with such a high rate of mortality as we report, it is difficult to conclude that vegetation has much effect on survival at Fort Bragg. Our best model explaining survival to 10 days included plant diversity, but the support for the model was weak. Though managers may wish to promote improvements in cover as a strategy to mitigate coyote effects on fawn recruitment, the relative ratio of coyote to deer may be more important and overwhelm any impact of improved vegetative cover. Based on our data, the diversity of flora at neonate bedsites is more important than horizontal cover. However, lack of support for cover in explaining neonate survival is not surprising, as Kilgo et al. (in press) failed to detect home range-scale effects of vegetative cover on neonate survival.

Starvation potentially resulting from abandonment by the dam was our second-leading cause of mortality (29%) and was greater than rates reported in other studies (0%, Ballard et al. 1999; 10%, Vreeland et al. 2004; 25%, Saalfeld and Ditchkoff 2007; 4%, Grovenburg et al. 2011; 8%, Kilgo et al. 2012). Though it is possible that capture and handling caused abandonment, we documented 6 sets of twins in which only 1 starved. Because we handled all neonates similarly, we do not believe capture-induced abandonment was an issue. More likely, predation risk could have indirect consequences for adult females. For example, studies with other ungulates have demonstrated that predation risk can negatively impact reproductive rate (Creel et al. 2007). Further, Lashley et al. (2014b) demonstrated that white-tailed deer females with young decreased feeding rates at baited camera sites by almost 50%, which could suppress lactation potential via reduced foraging efficiency. Aside from indirect effects of predation, heat stress may exacerbate rates of abandonment. In 2011, the starvations (n = 5) we documented occurred during a week-long period associated with a heat wave. We speculate that heat stress in the dam could have contributed to reduced milk production, which has been demonstrated in other ruminants (e.g., cattle; Rhoads et al. 2009).

Our study was not designed to determine whether or not coyote predation was compensatory or additive. Kilgo et al. (in press) documented little evidence for compensatory effects in South Carolina neonates, but we documented 5 cases where neonates were vocalizing as we approached to check survival or relocate the neonate and all 5 neonates subsequently starved (Chitwood et al. in press). As discussed by Chitwood et al. (in press), it is possible that increased vocalization due to abandonment could predispose a neonate to coyote predation, thereby inflating the role of coyote depredation and potentially masking a compensatory effect. However, similar to Kilgo et al. (2012), we failed to document a case in which a depredated neonate was emaciated. Regardless, studies of mule deer (*O. hemionus*) have documented that coyote predation on neonates can be compensatory to mortality from winter stress and malnutrition (Bartmann et al. 1992, Bishop et al. 2009). Though winters in the southeastern U.S. are mild by comparison, other nutritional stressors (e.g., drought, low nutritional plane) could explain the level of abandonment in our study; if females are nutritionally constrained and cannot meet lactation demands, some neonates may starve. Future research should explore the extent to which coyote predation may be compensatory to other sources of mortality.

Some areas may be immune to the direct predation effects of coyotes due to high deer density and the swamping effect (Whittaker and Lindzey 1999), regardless of landscape conditions. The swamping effect is based on birth phenology and synchrony, which are traits that could be derived from predation pressure. Birth phenology is likely linked to peak nutritional conditions during spring (DeYoung and Miller 2011) because females with young need highly nutritious diets to meet lactation demands; thus, lactating while spring foods are available has evolutionary advantage (DeYoung and Miller 2011). However, some studies suggest that birth synchrony is driven by predation pressure, and in theory, reducing the time span of births for a prey species makes the predator less likely to find all the vulnerable young (for review, see Ims 1990). Interestingly, in complex environments with generalist predators (e.g., coyotes), selection should favor asynchronous births (Ims 1990, Testa 2002). Commonly, the functional response of generalist predators is prey switching, so asynchronous births become advantageous. The scant current evidence from the southeastern U.S. supports this premise and indicates swamping effects are unlikely in some areas.

Evidence is mounting that coyotes are capable of affecting deer populations across the southeastern U.S., at least in local areas with high coyote density. Our low neonate survival helps explain the apparent drop in recruitment documented by Fort Bragg during the establishment of the coyote population. However, the possible range of effects that coyote predation can have on deer vital rates and behaviors is unknown, so future studies need to document how coyotes impact deer in areas with greater deer density or lower coyote density.

Management Implications

Our data confirm that coyote predation on neonates is substantial in some areas of the southeastern U.S., so managers need to consider this source of mortality in setting harvest goals. Although additional research is needed to better understand the deer-coyote dynamic, in areas where deer density reduction is needed, coyotes will be an asset for managers. Conversely, harvest reductions on the female segment of the deer population may be required to offset impacts of coyote predation, particularly in areas with deer densities below target or with unsustainably low fawn recruitment. Further, managers should focus on density issues first because vegetative cover at neonate bedsites may not provide a buffer against the impacts of coyote predation.

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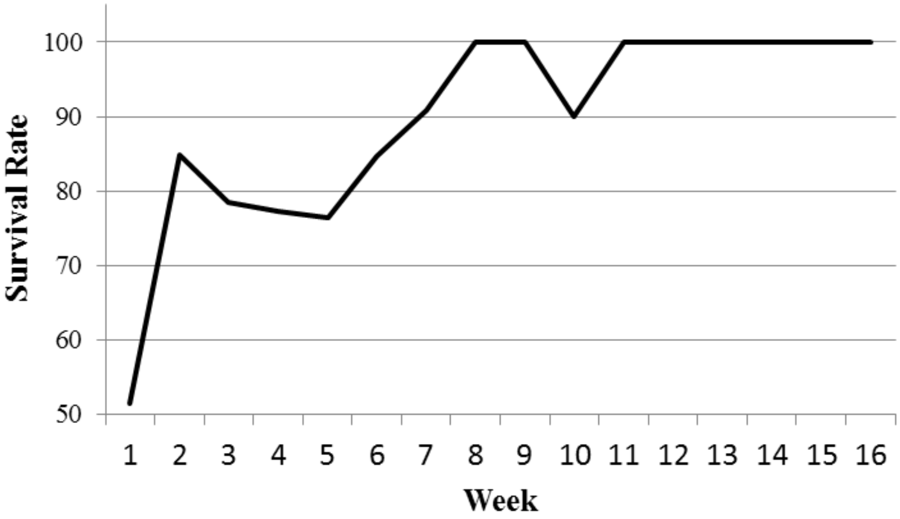

Figure 1. Weekly survival estimates for radiocollared neonate white-tailed deer at Fort Bragg Military Installation, North Carolina, 2011-2012.

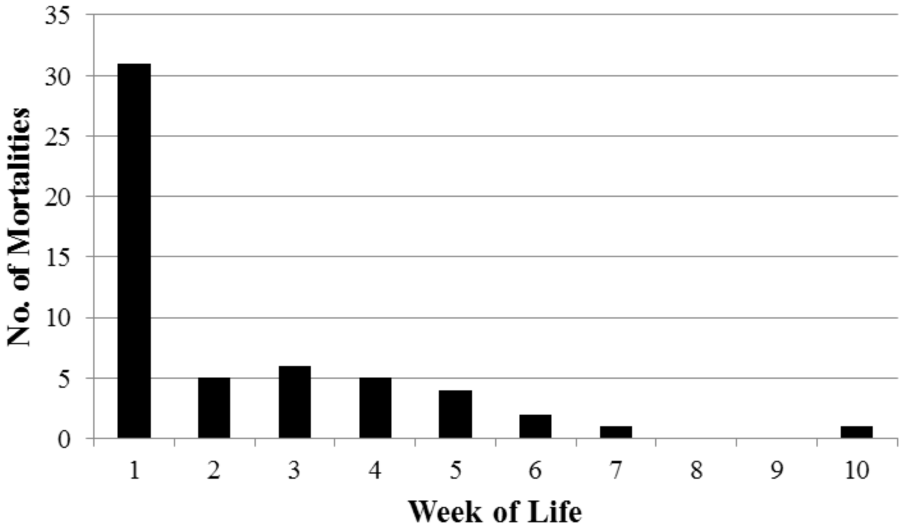

Figure 2. Number of mortalities among radiocollared neonate white-tailed deer by week of life at Fort Bragg Military Installation, North Carolina, 2011-2012.

Table 1. Set of competing models (within 2 ΔAICc of top model) that includes biological covariates influencing neonatal white-tailed deer survival at Fort Bragg Military Installation, North Carolina, 2011-2012.

Model[a]	ΔAICc	AICw	No. parameters
S(t + sib)	0.0	0.181	9
S(t)	0.088	0.173	8
S(t + sib + dob)	0.237	0.161	10
S(t + sex)	0.755	0.124	9
S(t + dob)	1.658	0.079	9
S(t + sex + sib + dob)	1.808	0.073	11

[a] t = time effect allowed to vary weekly; sib = sibling status; dob = Julian date of birth

Table 2. Summed Akaike weights for each biological covariate affecting neonatal white-tailed deer survival at Fort Bragg Military Installation, North Carolina, 2011-2012.

Biological Covariate[a]	Total Akaike Weight
Sibling status (sib)	0.415
Julian date of birth (dob)	0.313
Sex (sex)	0.197

[a] Birth weight did not appear in any competing models

Table 3. Set of competing models (within 2 ΔAICc of top model) that include vegetative covariates influencing neonatal white-tailed deer survival in the first 10 days of life at Fort Bragg Military Installation, North Carolina, 2011-2012.

Model[a]	ΔAICc	AICw	No. parameters
S(t + spp)	0.0	0.176	5
S(t)	0.102	0.168	4
S(t + fb + spp)	1.029	0.105	6
S(t + fb)	1.175	0.098	5
S(t + nspp)	1.220	0.096	5

[a] t = time effect allowed to vary weekly; spp = species diversity; fb = distance to firebreak; nspp = weighted index (Nudds score × species diversity)

Table 4. Summed Akaike weights for each biological covariate affecting neonatal white-tailed deer survival in the first 10 days of life at Fort Bragg Military Installation, North Carolina, 2011-2012.

Biological Covariate[a]	Total Akaike Weight
Species diversity (spp)	0.282
Distance to firebreak (fb)	0.204
Weighted index (nspp)[b]	0.096

[a] Nudds score did not appear in any competing models

[b] Weighted index = Nudds score × species diversity

Table 5. Causes of mortality among radiocollared white-tailed deer neonates at Fort Bragg Military Installation, North Carolina, 2011-2012.

	2011		2012		Total	
Cause of Mortality	n	%	n	%	n	%
Coyote predation	12	54.5	18	54.5	30	54.5
Starvation	5	22.7	11	33.3	16	29.1
Bobcat predation	3	13.6	2	6.1	5	9.1
Unknown[a]	2	9.1	1	3.0	3	5.5
Vehicle	0	0.0	1	3.0	1	1.8

[a] Includes non-depredated, non-starved neonates

CHAPTER 2

Setting an evolutionary trap: the hider strategy becomes maladaptive for white-tailed deer neonates in the presence of a novel predator

Abstract

An evolutionary trap occurs when an organism makes a decision that was formerly adaptive but now results in a maladaptive outcome. Often, evolutionary traps are induced by rapid, anthropogenic environmental changes, with non-native species introductions being a leading cause. The recent introduction and establishment of coyotes (*Canis latrans*) into the southeastern United States has the potential to change white-tailed deer (*Odocoileus virginianus*) population dynamics through direct predation and behavioral adaptation. Recent evidence indicates that in some areas, coyote predation is a significant source of neonatal mortality; however, the extent to which predation pressure shapes white-tailed deer behavioral responses is unknown because large canid predators have been absent in the region for nearly 100 years. We used movement rate and bedsite characteristics of radiocollared neonatal white-tailed deer to evaluate their antipredator strategies in the context of novel predation risk in a homogenous, fire-maintained ecosystem. We determined that neonate bedsites had greater plant cover values compared to random sites ($Z = 7.26$; $p < 0.001$), which indicated bedsite selection was consistent with white-tailed deer evolutionary strategy. We performed a viability selection analysis using known fates of neonates to determine the selection gradient of coyote predation on neonate movement rate and plant cover and diversity at bedsites. Interestingly, greater neonate movement rate and bedsites in less dense cover were favored by natural selection, meaning neonates that moved less and

bedded in denser cover were predisposed to greater risk of predation. These results are counter to expected anti-predator strategies in white-tailed deer and exemplify how an adaptive response can become maladaptive when anthropogenic changes induce an evolutionary trap.

Introduction

An evolutionary trap occurs when an anthropogenic change in the environment causes an organism to make a decision that was formerly adaptive but now results in a maladaptive outcome (Schlaepfer et al. 2002). Decision-making rules (i.e., 'Darwinian algorithms'; Cosmides and Tooby 1987) are expected to be adaptive because over evolutionary time they rely on cues correlated with reproductive success and survival (Williams and Nichols 1984). However, Darwinian algorithms are only as complex as necessary to enhance reproductive success and survival where species evolved; they are not so complex as to provide advantages in all introduced circumstances (Schlaepfer et al. 2002). Thus, when environments are altered, formerly reliable cues might not be associated with adaptive outcomes and organisms may be 'trapped' by their evolutionary responses to the cues, which results in reduced reproductive success or survival (Schlaepfer et al. 2002).

Humans may now be the most important biotic selective force on earth (Palumbi 2001), as they have altered nearly every environment at unprecedented rates and extents (Vitousek et al. 1997). In anthropogenically altered environments, evolutionary traps are important mechanistic explanations for the declines of populations and species (Schlaepfer et al. 2002; Sherman and Runge 2002). Additionally, anthropogenic disturbances can benefit non-native species (Byers 2002). The evolutionary trap concept is useful for understanding interactions between native and non-native species because non-natives can create novel ecological contexts to which the responses of native species may not be adaptive (Callaway and Aschehoug 2000; Shea and Chesson 2002).

The recent introduction and expansion of coyotes (*Canis latrans*) in the southeastern United States (Parker 1995) provides an opportunity to evaluate the potential for evolutionary traps to operate in a novel predator-prey dynamic. In the region, white-tailed deer (*Odocoileus virginianus*) have been without a large canid predator since 1900 (Young and Goldman 1944) and coyotes are recent, non-native additions to the landscape, having occupied the area primarily by anthropogenic means during the past 10-40 years (Hill et al. 1987, Gompper 2002). Before the arrival of coyotes, white-tailed deer persisted for decades with low predation risk (except for humans), but recent evidence indicates that direct predation of coyotes on neonates (Kilgo et al. 2012, Chitwood et al. in review) and adults (Chitwood et al. in press) can be substantial and likely affect local deer population density.

Though direct predation is clearly of interest in the coyote-deer dynamic, our understanding of behavioral responses of deer is lacking. Predation pressure should elicit changes in deer behavior that reduce direct predation risk (e.g., increased vigilance, altered space use), but how these changes affect deer populations in non-lethal ways is unknown. Deer vigilance has been studied using camera traps (Lashley et al. 2014), but in the context of predation risk, space use and movement ecology are unstudied. Therefore, we evaluated the behavior of neonatal white-tailed deer in the presence of a novel, non-native predator. Because neonates rely on crypsis as the primary means of predator avoidance at young ages, high predation risk should exert pressure for neonates to move less and use cover (DeYoung and Miller 2011). Thus, our objective was to determine if novel coyote selection pressure on neonate space use and movement elicited expected anti-predator behaviors. Because of high predation risk at our study site, we hypothesized that neonates would be more likely to survive if they had lower movement rates and relied on greater plant cover and diversity at bedsites.

Study Area

We conducted our study at Fort Bragg Military Installation (hereafter, Fort Bragg; 40,500 ha), which was owned by the U.S. Department of Defense and located in the Sandhills physiographic region of central North Carolina. Open longleaf pine (*Pinus palustris*) forests dominated the uplands, and they were managed with growing-season prescribed fire on a 3-yr fire-return interval. The understory of longleaf forests was primarily turkey oak (*Quercus laevis*) and wiregrass (*Aristida* spp.). Densely vegetated drainages that burned less frequently were interspersed throughout the landscape. An extensive, drivable firebreak network facilitated the implementation of the large-scale fire regime, while providing access for military vehicles (Lashley et al. 2014). The fire regime resulted in homogeneous uplands, which relegated dense cover to the unburned drainages (~11% of land area at Fort Bragg; Lashley et al. 2014).

Deer population density was relatively low (2-4 deer/km^2) at Fort Bragg. Hunting occurred from the first Saturday in September through 1 January in the accessible areas. Deer density decline was apparent beginning in 1989, with harvest records standardized by hunter effort showing a 30-60% reduction in deer at Fort Bragg. Though deer density estimates should be interpreted with caution, Imperio et al. (2010) demonstrated hunter harvest success was positively correlated to density of ungulates. Total hunter harvest fell from a high of 1261 in 1989 to a low of 164 in 2013 (Fort Bragg Wildlife Branch, unpublished data). Though hunter effort has changed over the years, deer hunters currently harvest deer in 1 out of 33 hunts, compared to 1 out of 15 hunts in the 1980s (J. Jones, Fort Bragg Wildlife Branch, personal communication). The apparent decline in deer density was commensurate with the initiation and establishment of coyotes at Fort Bragg, which were first documented in 1989 and were considered well-established by the mid-1990s (J. Jones, Fort Bragg Wildlife Branch, personal communication). Bobcats (*Lynx rufus*) were the only other documented predator of neonate deer at Fort Bragg (Chitwood et al. in review).

Methods

During January-May, 2011-1012, we captured adult females using tranquilizer guns. We GPS-collared (Wildcell, Lotek Wireless Inc., Newmarket, Ontario, Canada; fix rate = 2.5 hrs) all females captured in 2011, but in 2012, some females received GPS-collars, while the rest received VHF only (Model 2510B, Advanced Telemetry Systems, Isanti, MN). We deployed vaginal implant transmitters (VIT; Model M3930, Advanced Telemetry Systems) to facilitate capture of neonates. The VITs contained a temperature-sensitive switch to detect expulsion from the vaginal canal and a precise-event timer to log the time (in 30-minute intervals) passed since parturition. Implant procedures followed Bowman and Jacobson (1998) and Carstensen et al. (2003), except that we did not trim protruding antennas (Kilgo et al. 2012). We immobilized deer with Telazol (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN), xylazine hydrochloride (2.5 mg/kg; Congaree Veterinary Pharmacy, Cayce, SC), and ketamine hydrochloride (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN) in

2-cc transmitter darts. At 80-minutes post-injection, we antagonized the xylazine hydrochloride with tolazoline hydrochloride (10 mg/kg; Midwest Veterinary Supply, Burnsville, MN) and monitored the deer until recovery. Deer capture and handling was approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (10-143-O).

We monitored VIT signals intensively (≤ every 8 hours) during the fawning season (see Chitwood et al. in review for details) and allowed ≥ 2 hours after the parturition time derived from the VIT timer before initiating a search. The time delay provided time for grooming and initial bonding between female and neonate(s). When we located neonates, we used latex gloves to deploy expandable breakaway radiocollars (Diefenbach et al. 2003; Model M4210, Advanced Telemetry Systems) equipped with a motion-sensitive mortality switch on a 4-hr delay. We estimated age of opportunistically captured neonates using new hoof growth (Sams et al. 1996) and behavior.

We monitored neonates intensively to increase the chances of recovering remains and evidence of predators (coyote or bobcat) when mortalities occurred (see Chitwood et al. in review for details). We assigned final cause of mortality based on field evidence and predator DNA, if necessary (see Chitwood et al. in review). We relocated neonates via homing once every 24-hr period for the first month of life, at all times of day or night. Thereafter, we relocated neonates every other day through 12 weeks of age. We checked the location of the adult female and did not approach if she was in close proximity to the neonate. We approached neonates quietly to minimize disturbance but close enough for a visual relocation (with ambient light or with the aid of forward looking infrared). Once we located the bedded neonate, we took a GPS point, noted the actual bedsite's bearing and distance from the GPS point, and took detailed field notes defining the location of the bedsite. This approach allowed us to minimize disturbance to the neonate, while maximizing our success for returning to the exact bedsite for subsequent data collection.

Because neonates are highly susceptible to predation early in life, particularly in the first week (Kilgo et al. 2012, Chitwood et al. in review), we determined movement rate and vegetative cover at bedsites for the first 10 days of life. We used ArcMap 10 to calculate movement distances (in meters) for each neonate for the first 10 days of life using its sequential points. We calculated movement rate for each neonate by dividing the cumulative distance moved by the number of days it lived (i.e., m/day). We measured vegetative structure at known neonate bedsites using a modified vegetation profile board (Nudds 1977). We estimated percent cover from 0 – 2 m in 4 50-cm height categories by assigning visual obstruction in each height category as 0%, 1 – 20%, 21 – 40%, 41 – 60%, 61 – 80%, or 81 – 100%. We placed the board at plot center (i.e., in the bedsite) and viewed it at a height of 1-m, from 10 m away, along bearings of 0°, 120°, and 240°. We averaged estimates from the 4 height categories to provide 1 number for percent cover along each bearing. Additionally, along each bearing, we recorded the number of plant species contributing to the coverage of the board. We determined final Nudds board scores and final plant diversity scores by taking the average of the 3 profile bearings at each bedsite and then averaging across all bedsites (Chitwood et al. in review).

To confirm that neonates were selecting bedsites consistent with our evolutionary understanding of the species (i.e., using dense cover), we used a Wilcoxon signed-rank test to compare bedsite cover values against random, unused sites. We chose unused sites by taking a random bearing and distance (>20 m and <100 m) from the known bedsite. To test for viability selection on neonate behaviors based on coyote depredation, we calculated selection gradients (Lande and Arnold 1983). We used binomial logistic regression to determine beta values and used standard least squares regression to determine *p*-values. We conducted all statistical analyses in JMP Pro 10 (SAS Institute Inc., Cary, North Carolina). We included neonates for which we had movement and bedsite data and compared those that survived the first 10 days against those that were depredated by coyotes within the first 10 days. Thus, we tested for viability selection by calculating selection gradients for neonate movement rate and cover and plant diversity at bedsites.

Results

In 2011, we monitored 28 VITs, of which all were paired with GPS collars, and in 2012, we monitored 25 VITs, 7 of which were paired with GPS collars. We radiocollared 59 neonates via VITs (23 in 2011 and 36 in 2012). Additionally, we added 6 neonates (4 in 2011 and 2 in 2012) to our sample via opportunistic encounters. Cumulative survival was low (14%), with 9 neonates surviving the 16-week study period (see Chitwood et al. in review). Coyote predation was the leading cause of mortality, accounting for 30 neonate deaths (see Chitwood et al. in review). For 4 of the coyote depredations, we were unable to obtain a movement rate because they were killed within 2 days of birth or we lost access to bedsites (due to prescribed fire or military activity); thus, they were excluded from analysis.

Nudd’s board cover values at neonate bedsites ($\bar{x}$ = 3.24, SE = 0.08, n = 325) were greater ($Z = 7.26$, $p < 0.001$) than those from random, unused sites ($\bar{x}$ = 2.42, SE = 0.08, n =

326). Selection analysis of 35 neonates (9 survivors + 26 coyote depredations) revealed that greater neonate movement in the first 10 days of life was favored by natural selection (i.e., coyote predation was biased toward neonates that moved less; Table 1). Additionally, neonate use of bedsites with lower Nudd's board cover values was favored by natural selection (i.e., coyote predation was biased toward neonates selecting denser cover; Table 1). Behaviors associated with neonate selection of bedsite plant diversity did not show evidence of selection by coyote predation (Table 1).

Discussion

Intuitively, neonates should minimize space use and movement because they evolved to rely on cryptic coloration (Lent 1974) and lack of scent (Johnson 1951, Mech 1984, Linnell et al. 2004) to avoid detection by predators, particularly at young ages. Strong selection for anti-predator traits likely explains the fact that when alarmed, neonate white-tailed deer and red deer (*Cervus elaphus*) exhibit bradycardia and reduced respiration (Epsmark and Langvatn 1979, 1985; Jacobsen 1979); white-tailed deer less than 45-days-old exhibit bradycardia in response to recorded wolf howls (Moen et al. 1978). Additionally, neonate pronghorn (*Antilocapra americana*) tended to be depredated most at 11-20 days of age (see Byers and Byers 1983 for discussion), which represented a "window of vulnerability" when they could not outrun predators but displayed increased activity. Similarly, Litvaitis and Shaw (1980) suggested risk was greatest after the first couple weeks of life when white-tailed deer fawns began moving more. Given that a hiding strategy is advantageous for young ungulates, abandoning the strategy at a young age is counter-intuitive. We should expect that neonates would move less under high predation risk, but our data indicated that moving more conferred greater survival, while moving less predisposed neonates to depredation.

Our study site is a fairly open, homogenous landscape where frequent prescribed fire has the effect of isolating the densest cover along fairly linear, low-lying drainages. With little heterogeneity on the landscape (see Lashley et al. 2014), coyotes hunting for neonates in cover are relegated to those same drainages. As hiders, young neonates should benefit from bedsites with the most cover, but if coyotes are able to thoroughly hunt the limited cover available, high predation rates on fawns should be expected. Thus, the hiding strategy evolutionarily adapted for neonatal white-tailed deer fails them at our study site, providing evidence for evolutionary trap.

Adult female behavior may be a crucial component in understanding the predator-prey dynamic, particularly with respect to neonates. Though we did not evaluate fine-scale movements or behaviors of adult females, they may serve as cues for coyotes (or other predators) to search cover for hiding neonates. Similarly, it is possible that coyotes cue on parturition behavior, which contributes to direct mortality of the female or her resulting neonates. On the same study site, Chitwood et al. (in press) documented 3 adult females depredated by coyotes during the fawning season and speculated that pregnant females may have been vulnerable targets for coyotes. Predation pressure from coyotes on adult females could be just as important as pressures exerted on neonates. For example, behavioral cues from the female may override any benefit to reduced neonate movement by prompting coyotes to search in areas where females spend the most time or leave the most scent.

At our study site, the relative novelty of coyotes as predators of deer and the intense prescribed fire regime represent the types of anthropogenically induced changes that can create evolutionary traps for otherwise well-adapted organisms. The heart of evolutionary traps is that past selection pressures shaped behaviors that were adaptive in the past (Robertson et al. 2013). In our case, white-tailed deer neonates fell victim to an evolutionary trap, as evidenced by the strong selection against the previously adaptive hider strategy. Other research has documented similar effects of non-native predators transforming formerly adaptive behaviors into maladaptive ones (e.g., Igual et al. 2007), so evolutionary traps might be a useful framework for predicting and managing the potential impact(s) of non-native species introductions (Schlaepfer et al. 2005).

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Table 1. Selection gradient (β') of coyote depredation on neonate white-tailed deer behaviors at Fort Bragg Military Installation, North Carolina, 2011-2012.

Behavior	β'	SE	*p**
Movement Rate	0.17	0.07	< 0.01
Bedsite Cover	-0.15	0.08	0.03
Bedsite Plant Diversity	0.07	0.08	0.18

*$\alpha = 0.05$

CHAPTER 3

White-tailed deer population decline and potential management scenarios in the presence of a novel predator

Abstract

Recent localized declines in white-tailed deer (*Odocoileus virginianus*) populations in the southeastern United States have been linked to increasing predation pressure from coyotes (*Canis latrans*), a novel predator to the region. Studies have documented coyotes as the leading cause of mortality for neonates, and one study documented coyotes as a mortality factor for adult females. However, no study has used field-based vital rates to conduct sensitivity analyses or model deer population trajectories under potential management strategies. We used low, medium, and high values of fawn survival, adult female survival, and fecundity data collected from Fort Bragg Military Installation, North Carolina to demonstrate the current declining population trajectory for deer ($\lambda = 0.905$; low $\lambda = 0.788$, high $\lambda = 1.003$). Consistent with other studies of ungulates, we determined adult female survival was the most sensitive and elastic vital rate. Further, for three potential management ("what if") scenarios, we projected the population for 10 years using estimated vital rates. Reducing adult female harvest ($\lambda = 0.935$; low $\lambda = 0.875$, high $\lambda = 1.002$) and coyote removal ($\lambda = 0.995$; low $\lambda = 0.898$, high $\lambda = 1.081$) reduced the current population decline, while combining both approaches ($\lambda = 1.024$; low $\lambda = 0.898$, high $\lambda = 1.141$) resulted in population increases. Our data indicate that for low-density deer populations with heavy predation pressure on neonates, protecting adult females from harvest may not completely offset population declines. Coyote removal might be a necessary strategy due to the possibility of

increasing very low fawn survival, which appears to be the most important vital rate in our study. However, managers may have to start with reductions in adult female harvest because coyote removal would have to be continuous and consistently effective, making it an impractical management approach by itself.

Introduction

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

Coyote predation on white-tailed deer, particularly neonatal fawns, can be high (e.g., Cook et al. 1971, Bartush and Lewis 1981, Whittaker and Lindzey 1999, Vreeland et al. 2004). Ballard et al. (2001) concluded that coyotes can be a significant source of mortality for deer, and Ballard et al. (1999) suggested coyotes could replace wolves as deer predators in parts of northeastern North America, where they depredate adults in winter and neonatal fawns. Coyote predation on neonates may be compensatory to other mortality factors (Bartmann et al. 1992, Bishop et al. 2009), or additive (and therefore limiting; Messier et al. 1986, Patterson et al. 2002), but most research related to coyote impacts on deer has been conducted either in the historic western range or in northeastern North America where winter severity contributes to predation susceptibility (Gompper 2002). Only recently have direct assessments of coyote impacts been conducted in the forested landscapes and milder climate of the southeastern U.S. Though effects of coyote predation on deer may vary across the southeastern U.S. landscape, evidence is mounting that neonate survival is severely affected in some areas (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, M. C. Chitwood, unpublished data). In addition, recent evidence indicates that coyotes could become an important source of mortality for adult deer, particularly females (Chitwood et al. in press *a*). Thus, deer population dynamics could be changing and alternative management strategies might warrant consideration (Kilgo et al. 2010).

Despite establishment of coyotes in the southeastern U.S. and evidence from other regions that coyotes can impact deer populations, wildlife professionals have remained relatively unconcerned about potential effects (Kilgo et al. 2010). Kilgo et al. (2010) surmised the lack of concern could stem from the belief that coyotes are not significant predators of deer in the southeastern U.S. or from the perception that deer are too abundant to worry about impacts. Due to mild climate and low mortality from winter nutritional stress, hunter harvest is believed to drive the dynamics of most southeastern U.S. deer populations (Kilgo et al. 2010). However, Kilgo et al. (2010) presented data from South Carolina that indicated declining deer recruitment commensurate with the increasing population of coyotes. Thus, the potential for coyote predation to impact deer populations in the region warrants consideration of adaptive changes in management where impacts are significant.

However, better estimates of vital rates are needed to construct a framework for deciding which management strategies are most likely to influence population growth positively.

Understanding the influences of select vital rates (e.g., neonate survival, adult female survival, fecundity) on population dynamics is crucial for maximizing success of conservation efforts, particularly with sensitive or declining species. Demographic analyses, including sensitivity analyses of matrix population models, provide valuable insight into which vital rates have the greatest influence on population growth, are most variable, and should be targeted by managers (Wisdom et al. 2000, Reed et al. 2002, Mills 2007). Analytical sensitivity uses reproductive value and stable age distributions (or stable stage distributions, SSD) to quantify how a small, equal change in any stage-specific vital rate will change asymptotic population growth rate (i.e., the λ provided by a matrix at SSD; Mills and Johnson 2013). Analytical elasticity rescales sensitivity to account for proportional change in λ, given an incremental proportional change in a vital rate (Mills and Johnson 2013). These analyses have informed management of numerous species with economic value or conservation concern, including sea turtles (Crouse et al. 1987), tortoises (Reed et al. 2009), amphibians (Biek et al. 2002), waterfowl (Hoekman et al. 2002, Coluccy et al. 2008), big game (Raithel et al. 2007, Johnson et al. 2010), upland game birds (Clark et al. 2008, Sandercock et al. 2008, Devers et al. 2009, Taylor et al. 2012), and migratory waterbirds (Grear et al. 2009). Although white-tailed deer are not of conservation concern, their wide distribution and popularity among big game hunters make them a valuable commodity. In the context of coyote predation impacts on white-tailed deer vital rates in the southeastern U.S., no comprehensive population models or sensitivity analyses have been conducted, both of which are necessary to identify key vital rates and improve management decisions. Thus, our objectives were to assess the relative importance of stage-specific vital rates in a declining deer population with heavy predation pressure from coyotes and to present several management options (i.e., "what if" scenarios) and demonstrate their potential to impact deer population estimates via underlying changes in vital rates.

Study Area

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

Deer population density was relatively low (~6 deer/km^2) at Fort Bragg. Hunting occurred from the first Saturday in September through 1 January in the accessible areas. Deer density decline was apparent beginning in 1989, with harvest records standardized by hunter effort showing a 30-60% reduction in deer at Fort Bragg by 2010. Although deer density estimates should be interpreted with caution, Imperio et al. (2010) demonstrated hunter harvest success was positively correlated to density of ungulates. At Fort Bragg, total hunter harvest fell from a high of 1261 in 1989 to a low of 163 in 2003; currently, hunter harvest is around 250-300 deer per year. Though hunter effort has changed over the years, deer hunters currently harvest deer in 1 out of 33 hunts, compared to 1 out of 15 hunts in the

1980s (J. Jones, Fort Bragg Wildlife Branch, personal communication). The apparent decline in deer density was commensurate with the initiation and establishment of coyotes at Fort Bragg, which were first documented in 1989, were considered well-established by the mid-1990s (J. Jones, Fort Bragg Wildlife Branch, personal communication), and now represent the leading cause of neonatal deer mortality (M. C. Chitwood, unpublished data). Bobcats (*Lynx rufus*) were the only other documented predator of neonate deer at Fort Bragg (M. C. Chitwood, unpublished data).

Methods

Model Structure

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

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

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

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

Fecundity for yearlings and adults was calculated as follows:

$$F_i = \mathrm{B_i} \cdot S_i,$$

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

Assumptions

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

Model Development

To determine λ and analytical sensitivities and elasticities, we parameterized our 3x3 population matrix using vital rates derived from radiocollar-based field studies at Fort Bragg (see Chapter 1). We parameterized the base model (i.e., the "Current Scenario") using current vital rates at Fort Bragg. However, to incorporate variability into our projections, we followed an approach used by Merrill et al. (2003), where we used low, medium, and high values for all parameters (Table 1) to represent the range of possible population trajectories. Medium parameter values represented our mean predictions, unless otherwise noted. Thus, our Current Scenario model with medium parameter values was:

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

All values associated with fawn survival and adult survival and fecundity were based solely on data collected at Fort Bragg (see Chapter 1; Table 1). We determined fawn and adult survival using known-fate modeling in Program MARK (White and Burnham 1999); analysis of adult survival incorporated a staggered entry approach (Pollock et al. 1989). We determined the number of neonates produced per female from documented births (via vaginal implant transmitters; M. C. Chitwood, unpublished data). For simplicity in the matrix, we assumed a 1:1 male-to-female neonate ratio. Due to small annual sample sizes of yearlings, we incorporated variation in yearling vital rates by using values reported in the literature (Table 1). We estimated starting population size for female fawns, yearlings, and adults using density and sex ratio estimates from Fort Bragg's trail camera survey data (unpublished) following the methods of Jacobson et al. (1997). We executed the matrix in R 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria) to determine the stable stage distribution (SSD) and then ran the matrix at SSD to determine λ, sensitivities, and elasticities and to project population sizes for 10 years.

Manipulating Vital Rates Under "What If" Scenarios

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

Scenario 1: Reduce Female Harvest

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

Scenario 2: Coyote Removal

Intensive predator removal has been evaluated as a potential management strategy to mitigate impacts of coyotes, particularly on neonates (e.g., VanGilder et al. 2009, Kilgo et al. in press). Recent evidence from South Carolina indicated that effects of coyote removal on neonate survival were highly variable over a 3-year removal period (-11 - 125% increase), with a mean response of 68% increase (Kilgo et al. in press). Thus, for the Coyote Removal Scenario, we assigned low fawn survival the same as the Current Scenario, used a 68% proportional increase as the medium fawn survival, and used 125% proportional increase as the high fawn survival (Table 2). Additionally, due to documented coyote depredations on adult females at Fort Bragg (Chitwood et al. in press *a*), we recalculated adult female survival to reflect protection of ~7% of the females on the high end. We changed yearling survival proportionately to adult survival.

Scenario 3: Combined

This scenario combined vital rate changes from the previous 2 scenarios. Assuming additive effects of coyotes and hunter harvest, this scenario represented the most extreme potential for changing λ. We used the same fawn survival parameters from the Coyote Removal Scenario (Table 2). We recalculated adult female survival to reflect protection of

~15% of the females on the high end. We changed yearling survival proportionately to adult survival.

Results

Using medium values for all parameters (Table 1), the Current Scenario projected a growth rate of $\lambda = 0.905$ (with low vital rates $\lambda = 0.788$; with high vital rates $\lambda = 1.003$), meaning the deer population was declining annually by ~9-10% (Figure 2). The Reduce Female Harvest Scenario (Figure 3) and Coyote Removal Scenario (Figure 4) predicted declining populations as well, with medium vital rates projecting $\lambda = 0.935$ (low $\lambda = 0.875$; high $\lambda = 1.002$) and $\lambda = 0.995$ (low $\lambda = 0.898$; high $\lambda = 1.081$), respectively. The Combined Scenario (Figure 5) predicted an increasing population, with $\lambda = 1.024$ (low $\lambda = 0.898$; high $\lambda = 1.141$). For all scenarios, the most sensitive and elastic vital rate was adult female survival (Table 3). Population projections for 10 years under all scenarios indicated a wide range of outcomes, from nearly 10% decline under current vital rates to over 2% growth under the Combined Scenario (Figure 6).

Discussion

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

Our results should be interpreted with caution and extrapolated to other deer populations carefully because they are conditional on the assumptions we used to parameterize our matrices. Three important points should be considered: 1) we assumed density-independence, 2) we assumed our Combined Scenario was additive, and 3) we included no environmental uncertainty. The Fort Bragg deer population was clearly low-density, so our assumption of density-independence was defensible. However, many deer populations exist at or near nutritional carrying capacity, which could provide opportunities for density-dependent feedbacks to occur. In those situations, estimates of λ would be impacted and misleading elasticity values could result (Grant and Benton 2000). Similarly, the assumption of additive effects in our Combined Scenario is simplistic and illustrative but could overlook more complicated feedbacks. However, based on limited data from the southeastern U.S., coyote predation appears to be an additive source of mortality for neonates (Kilgo et al. in press). Moreover, in South Carolina, neonate mortality from coyotes remained high (Kilgo et al. 2012) even as the deer population declined to a level where female harvest was reduced to offset declines (Kilgo et al. 2010). Future research will need to examine potential additive effects of coyote predation on adult deer. Finally, we did not include environmental uncertainty in our models. Many factors (e.g., rainfall, drought, food abundance) could influence vital rates, but elasticity values for our mean projections should be accurate in the presence of stochastic environmental fluctuations (Grant and Benton 2000). Thus, our analysis should be robust to the potential impacts of environmental uncertainty without sacrificing our interpretation of mean population dynamics (Merrill et al. 2003).

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

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

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

Our most extreme scenario assumed hunter harvest and coyote depredation of adult females were additive. At Fort Bragg, the assumption of additive mortality resulted in fairly high annual survival for adult females (0.859), potentially climbing to 0.917 on the high end. Numerous other studies have reported survival rates of white-tailed deer females around 0.9 in the absence of hunting (see DeYoung 2011 for review). Thus, when adult female mortality from hunters and coyotes are additive (and managers are able to trap coyotes intensively and annually), it is possible that population growth rates could respond quite positively. As mentioned above, adult female survival rates will vary in their response to female harvest reduction depending on the amount by which harvest can be reduced. Additionally, although coyote removal provides the greatest potential impact to deer population growth (through increased fawn survival), the highly variable response of fawn survival to the removal and the high cost of implementation make it unlikely as a large-scale mitigation strategy. As a final consideration, when vital rates are at their extremes, predictions of future growth rate based on elasticities of a mean matrix can be misleading and should be interpreted with care (Mills et al. 1999). Mills et al. (1999) suggest that studies using analytical elasticity analysis should explicitly consider the range of variation possible for different vital rates and that simulation methods are a useful approach. Our study attempted to include a wide range of observed variation, albeit a combination of true process variance and estimation error (see Gould and Nichols 1998). Perhaps as additional studies of deer in the context of coyotes estimate vital rates across diverse temporal and spatial scales, future research can pursue a simulation-based approach (e.g., Life-Stage Simulation Analysis; Wisdom et al. 2000), which can include numerous vital rate estimates and correct for sampling variability. If mitigating coyote impacts on deer populations at a large scale becomes necessary, managers will need strategies based on vital rate data from deer populations of varying densities and coyote impacts. Until that time, our data indicate that for low-density deer populations with heavy predation pressure on neonates, protecting adult females from harvest may not be a magic bullet. Coyote removal may need to be implemented in conjunction with the protection of adult females due to the possibility of increasing fawn survival, which appears to be the most important vital rate in our study. However, until the trade-off between cost and effectiveness of coyote trapping improves, reducing female harvest is the most cost-efficient and logical strategy for managers to implement.

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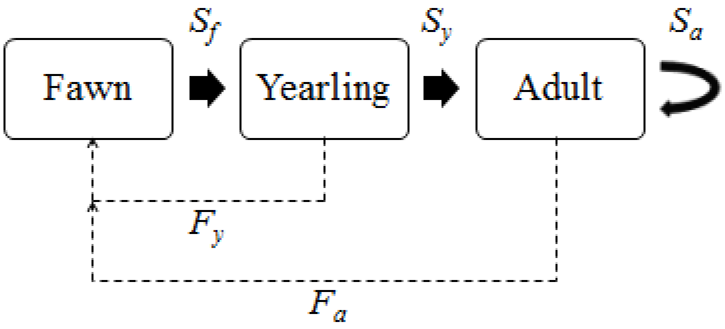

Figure 1. Life-stage model for white-tailed deer showing 3 stages: Fawn, Yearling, and Adult. Survival between stages is represented by *S* and fecundity for yearlings and adults is represented by *F*.

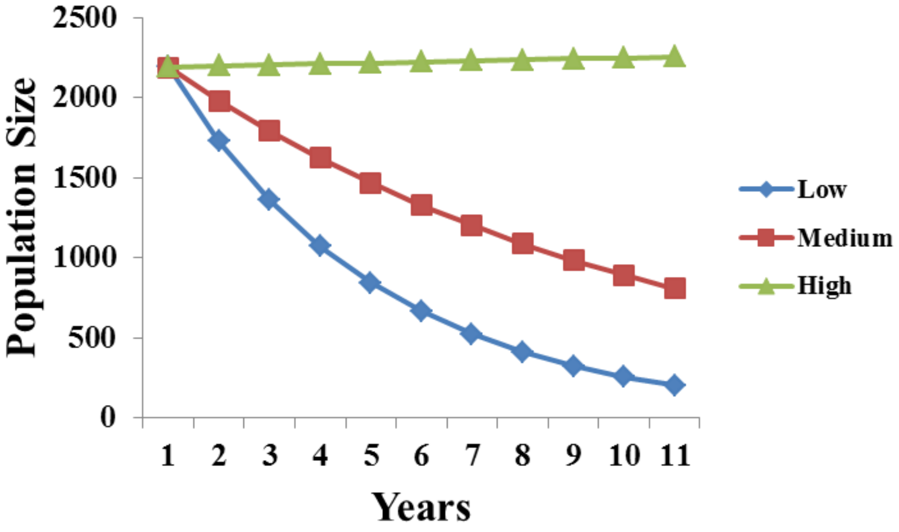

Figure 2. Predicted white-tailed deer population sizes after 10 years at current vital rates at Fort Bragg Military Installation, North Carolina, USA.

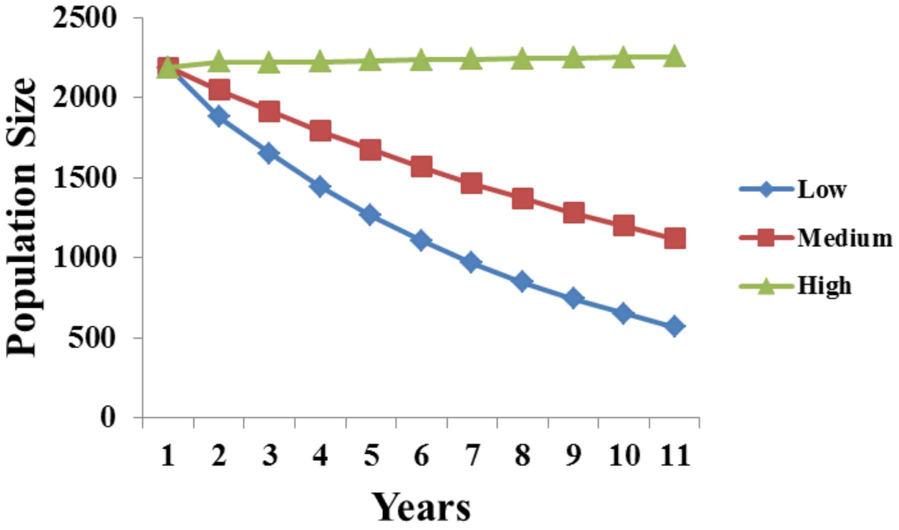

Figure 3. Predicted white-tailed deer population sizes after 10 years of reduced female harvest at Fort Bragg Military Installation, North Carolina, USA.

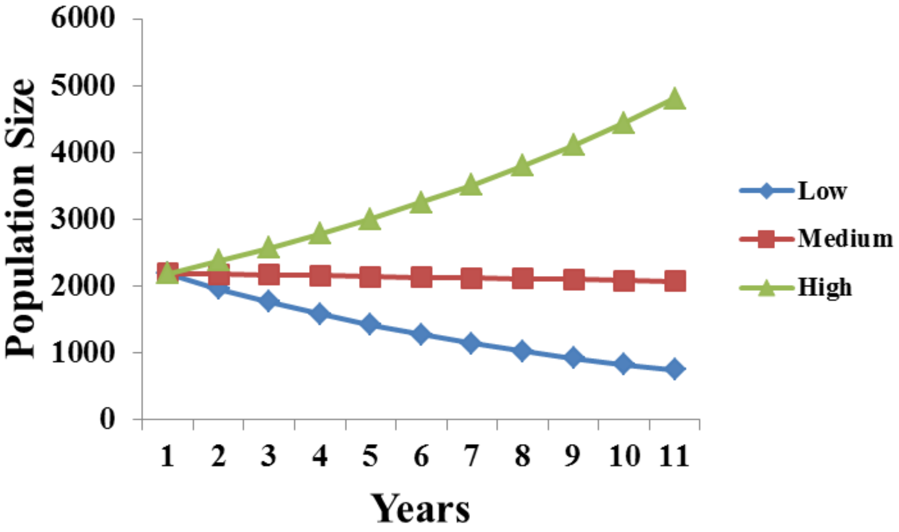

Figure 4. Predicted white-tailed deer population sizes after 10 years of coyote removal at Fort Bragg Military Installation, North Carolina, USA.

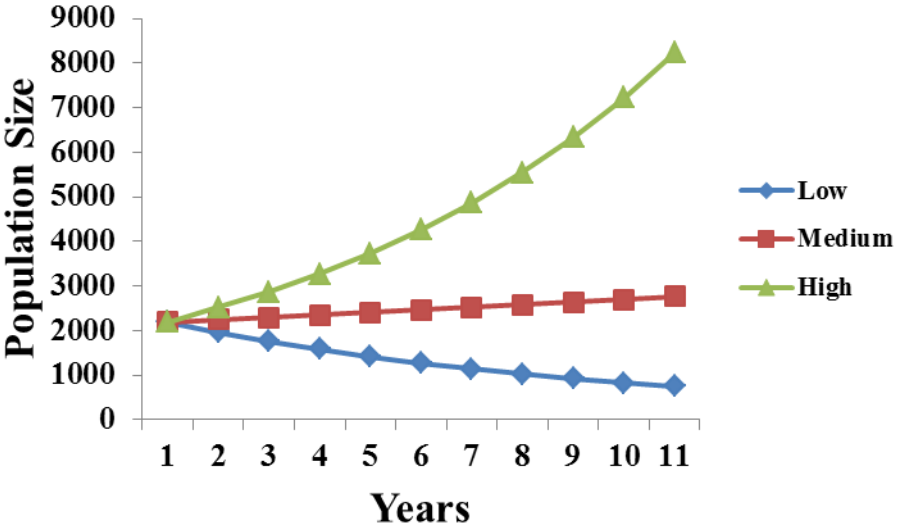

Figure 5. Predicted white-tailed deer population sizes after 10 years of reduced female harvest combined with coyote removal at Fort Bragg Military Installation, North Carolina, USA.

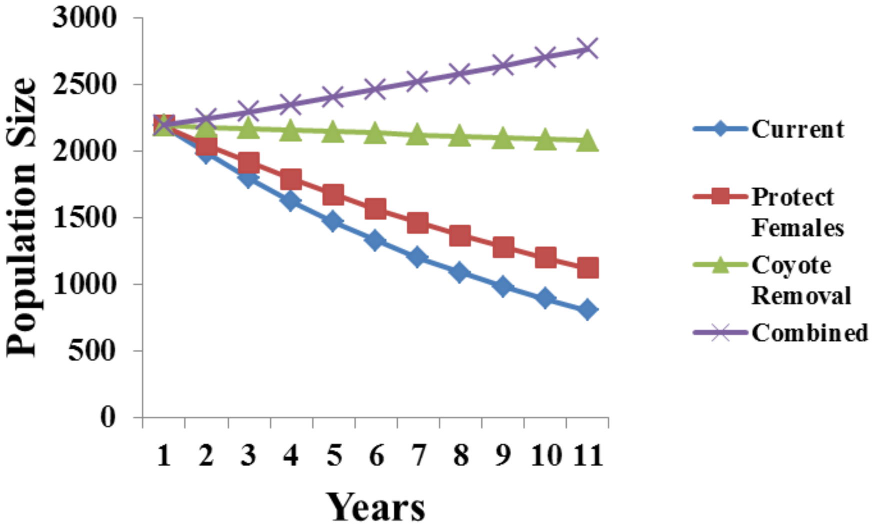

Figure 6. Predicted white-tailed deer population sizes after 10 years of current management, reducing female harvest, removing coyotes, and combining protection of females with coyote removal at Fort Bragg Military Installation, North Carolina, USA. All projections are based on “medium” vital rates for each scenario.

Table 1. Female parameter values used in “Current” matrix. Unless otherwise noted, we used medium values as mean predictions. Due to low sample sizes of yearlings in our study, we assigned low and high yearling birth rates using values reported in other studies from the southeastern U.S. (see Ditchkoff 2011). Similarly, we assigned all survival rates for yearlings based on values reported in other studies (see DeYoung 2011). All other parameter estimates were obtained from field data collected at Fort Bragg Military Installation, North Carolina, 2011-2013.

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

Table 2. Female survival parameters used in “what if” scenario matrices. Unless otherwise noted, we used medium values as mean predictions. Birth rates are not included in this table, as we used the same birth rates already reported in Table 1. All other parameter estimates were manipulated from survival values reported in Table 1, as described in text.

“What if” Scenario	Stage (parameter)	Low	Medium	High
Reduce Female Harvest	Fawn (S_f)	0.105	0.141	0.185
	Yearling (S_y)	0.775	0.804	0.833
	Adult (S_a)	0.801	0.831	0.861
Coyote Removal	Fawn (S_f)	0.141	0.237	0.317
	Yearling (S_y)	0.775	0.804	0.832
	Adult (S_a)	0.801	0.831	0.860
Combined	Fawn (S_f)	0.141	0.237	0.317
	Yearling (S_y)	0.775	0.831	0.887
	Adult (S_a)	0.801	0.859	0.917

Table 3. Medium vital rates (Table 1), sensitivities, and elasticities for all scenarios of the white-tailed deer population at Fort Bragg Military Installation, North Carolina, USA, 2011-2013.

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