POPULATION DYNAMICS OF WHITE-TAILED DEER ON TENSAS RIVER NATIONAL WILDLIFE REFUGE, LOUISIANA

by

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(Under the Direction of Karl V. Miller and Michael J. Chamberlain)

ABSTRACT

Survival of white-tailed deer (*Odocoileus virginianus*) fawns has declined in some areas of the southeastern U.S areas, and changing predator communities may complicate deer management scenarios. During 2013-15, I monitored survival of fawns and adult females on Tensas River National Wildlife Refuge (TRNWR), Louisiana. I determined cause-specific mortality and investigated variables influencing fawn survival. I used site-specific vital rates to model population trajectories and explored potential effects of changes in fawn and adult survival rates. Predation by black bear (*Ursus americanus*) was the greatest source of fawn mortality but appears to be partitioned with predation from other species. Fawn survival was positively correlated with birth mass and closer proximity to older reforestation sites but negatively correlated with proximity to young reforestation and cropland. Under current harvest guidelines and observed fawn survival rates, deer populations on TRNWR are sustainable, but reductions in female harvest could be considered if fawn survival decreases.

INDEX WORDS: black bear, bobcat, coyote, fawn, Louisiana, neonate, *Odocoileus virginianus*, population modeling, predation, survival

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Survival of neonatal ungulates typically has a greater effect on population growth than other vital rates due to spatial and temporal variation in survival rates and greater susceptibility of fawns to limiting factors (Gaillard et al. 2000, Raithel 2007). Mortality of neonatal white-tailed deer (*Odocoileus virginianus*; hereafter deer) is sensitive to variation in numerous biological and environmental factors, including body condition at birth (Nelson and Woolf 1987, Sams et al. 1996, Carstensen et al. 2009) and habitat components (Rohm et al. 2007, Grovenburg et al. 2012), which can often affect fawn survival directly through influencing predation or indirectly by impacting growth rates (Verme 1989, Steiger 2013). In a review of literature related to neonatal mortality of ungulates, Linnell et al. (1995) reported mortality rates in northern temperate regions were variable (0-100%), suggesting that mortality rates were site-specific and difficult to extrapolate from one area to another. As a result, recruitment can vary widely across different landscapes, making it prudent to continue research to determine cause-specific mortality of fawns and effects of biological and environmental factors on deer recruitment.

Declines in deer recruitment rates due to predation on fawns have become a concern in recent years (Kilgo et al. 2010). Although a single predator species can limit fawn survival (e.g., Jackson and Ditchkoff 2013), multiple predator species can have a cumulative effect on survival (Kilgo et al. 2014) and population growth (Messier 1994). Deer in multi-predator landscapes face the challenges of variation in species-specific predator hunting strategies (Sih 2007, Sih et al. 2012) and the temporal efficacy of predation (Vreeland et al. 2004). Nationwide increases in black bear (*Ursus americanus*; Hristienko and McDonald 2007) and bobcat (*Lynx rufus*; Roberts and Crimmins 2010) populations, and the relatively recent expansion of coyote (*Canis latrans*) populations into the southeastern U.S., have led to increased apprehension about potential effects of predators on recruitment. Evidence suggests that coyotes may be a significant factor affecting deer populations in the southeastern U.S. (Kilgo et al. 2010). Therefore, identifying factors that influence fawn survival and predation risk is important to understanding deer population growth and management.

Although previous research has quantified fawn survival rates and investigated factors influencing survival, few studies have examined how fawn survival, coupled with other site-specific vital rates (e.g., adult female survival, fecundity), affected deer population growth. Moreover, information on adult female mortality in the southeastern U.S. is limited, and studies distinguishing natural from hunting mortality are lacking. Without understanding mortality rates from natural causes, it is difficult to predict how changes in harvest will influence deer populations (Robinson et al. 2014). Therefore, research quantifying adult female mortality rates from natural causes is important for informing potential management actions.

Literature Review

Fawn Survival and Cause-specific Mortality

Although many studies have explored effects of predators on white-tailed deer recruitment, most have occurred in the midwestern (Huegel et al. 1985, Nelson and Woolf 1987, Kunkel and Mech 1994, Pusateri Burroughs et al. 2006, Rohm et al. 2007, Carstensen et al. 2009), Great Plains (Garner et al. 1976, Bartush and Lewis 1981, Sams et al. 1996, Grovenburg et al. 2012), and northeastern (Mathews and Porter 1988, Ballard et al. 1999, Vreeland et al.

2004) regions of the U.S. The few studies that occurred in the southeastern U.S. documented that predation accounted for 63-90% of fawn mortalities (Epstein et al. 1985, Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015, Nelson et al. 2015). However, these studies were conducted in 2-predator systems, where coyotes and bobcats were the primary predators of fawns. No research has occurred in the southeastern U.S. in areas with 3 primary predators, specifically coyotes, bobcat, and black bear. The combined effects of multiple predators on prey survival often cannot be predicted from their individual effects (McCoy et al. 2012), and thus it is not known whether predation in multi-predator systems is additive or compensatory.

Research conducted in the midwestern U.S., where historically coyotes have been numerous, has documented minimal predation (<18%) on deer (Huegel et al. 1985, Sams et al. 1996, Brinkman et al. 2004, Pusateri Burroughs et al. 2006, Grovenburg et al. 2011), compared to more substantial predation rates in Alabama (42%; Saalfeld and Ditchkoff 2007) and South Carolina (68%; Kilgo et al. 2012). Coyotes have only recently expanded their range in the U.S. from the grassland/savannah habitat of the western states into the woodland habitat of the southeastern states. Since the first coyote in Louisiana was reported in 1949, populations have increased dramatically and expanded to cover the entire state (Goertz et al. 1975). Eastward range expansion from Texas and Arkansas into Louisiana was largely facilitated by anthropomorphic activities, extensive habitat modification and the extirpation of the native red wolf (*Canis rufus*) population that once suppressed coyote populations (Paradiso and Nowak 1971). Because of differences in the landscape, vegetation, and fauna between the southeastern U.S. and the coyote’s historic range, coyotes may also differ in their behavior and food habits. As coyote populations have increased in the southeastern U.S., there has been growing speculation that coyotes may be affecting fawn mortality and deer recruitment in the region (Kilgo et al. 2010).

It is well known that coyotes prey on deer, particularly fawns. Deer occurs in 0-60% percent of coyote scats throughout the year, with consumption peaking in summer coincident with fawning season (Andelt et al. 1987, Koehler and Hornocker 1991, Reichel 1991, Neale and Sacks 2001). In the southeastern U.S., a comparison of coyote diets in Alabama, Kentucky, Mississippi, Louisiana, Tennessee, and South Carolina, showed a wide range of occurrence of deer in stomach contents and scats (9% to 74%), varying with season and deer populations densities (Wooding 1984, Blanton and Hill 1989, Schrecengost et al. 2008, Rountree et al. 2016). Fawn mortality research echoes coyote food habits studies; numbers of fawn mortalities from coyotes ranged from 14% in Michigan to 100% in Minnesota and South Dakota (Pusateri Burroughs et al. 2006, Grovenburg et al. 2011). However, with only a few mortality studies conducted in the southeastern U.S. (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013,Chitwood et al. 2015, Nelson et al. 2015), levels of coyote predation are relatively unknown.

Removal of bobcats and coyotes can increase fawn survival and improve fawn-to-adult female ratios. In Oklahoma, fawn-to-adult female ratios increased 154% following 2 years of coyote control (Stout 1982), and in South Carolina, fawn survival rates increased an average of 68% during 3 years of coyote removal (Kilgo et al. 2014). Similarly, research on coyote and bobcat removal reported increased fawn-to-adult female ratios the year following removal of both predators in south Texas (67.5 %; Beasom 1974) and Alabama (189%; VanGilder et al. 2009). In Georgia, Gulsby et al. (2015) documented a 55% increase in fawn-to-adult female ratios following coyote removal in one study area, but found no difference in recruitment in a second study area. They concluded that coyotes may not be an important source of fawn mortality in all areas. Although these studies have shown a significant correlation between predator populations and predation on fawns, effects of predators are variable and may be influenced by climate, predator abundance, abundance of deer and alternative prey, and spatial and temporal variation in predator/prey interactions (Andelt et al. 1987, Ballard et al. 2001).

Where bobcats are sympatric with coyotes, coyotes tend to have a greater occurrence of white-tailed deer in their diets than do bobcats (Litvaitis and Harrison 1989). Bobcat predation is often thought to be insignificant (VanGilder et al. 2009) because of the low occurrence of deer in scat and stomach analyses. However, field observations (Fritts and Sealander 1978, Garner and Morrison 1980) and findings published from fawn mortality studies show that bobcats will predate fawns (Carroll and Brown 1977, Carstensen et al. 2009, Kilgo et al. 2012). In a review of research on bobcat food habits across North America, Maehr and Brady (1986) found that frequency of deer was lowest in the Southeast (0-8%), compared to the Southern Appalachians (5-18%), the West (1-20%), and the Northeast (16-35%).

In some areas bobcats are the primary predator of ungulate fawns. Two studies on barrier islands on the Atlantic Coast where coyotes were absent showed high predation on fawns by bobcats. On Cumberland Island, Georgia, deer occurred in 37% of bobcat scats, and the highest percent biomass and occurrence (44.5% and 43.5%, respectively) coincided with the fawning season (Baker et al. 2001). On Kiawah Island, South Carolina, bobcats were responsible for 57-82% of fawn mortalities (Roberts 2007). Additionally, a study on pronghorn antelope (*Antilocapra americana*) in Utah reported that bobcats killed 23% of all fawns and accounted for 93% of predation mortalities, whereas coyotes only caused 3% (Beale and Smith 1973).

Although bobcat predation on deer has been shown to be minimal in many areas, bobcats may still exert a considerable influence on some ungulate populations.

Although generally considered an opportunistic predator of neonatal ungulates (Bastille-Rousseau et al. 2011), black bears have been implicated as effective predators of ungulates. In a review of elk (*Cervus elaphus*) and moose (*Alces alces*) calf mortality in North America, predation by black or brown bear (*U. arctos*) was consistently the most important source of mortalities, contributing to 34-100% of all mortalities (Zager and Beecham 2006). White-tailed deer fawns are also a known food source of black bears (Ozoga and Verme 1982). Studies on fawn mortality in Pennsylvania, Minnesota, and New York have shown high levels of black bear predation, causing 25-60% of mortalities attributable to predation (Mathews and Porter 1988, Kunkel and Mech 1994, Vreeland et al. 2004, Carstensen et al. 2009). Both Vreeland (2004) and Mathews and Porter (1988) found that black bears were responsible for the highest percentage of fawn mortality in at least one of their study sites. Although black bear populations occur in many parts of the southeastern U.S., the occurrence of bear predation on fawns has not been documented in this region.

Protection of the Louisiana black bear (*U. a. luteolus*) from hunting and habitat improvements on Tensas River National Wildlife Refuge (TRNWR) have allowed bear populations to increase from 0.11/km^2 in the 1980s (Nowak 1986) to 0.66 bears/km^2 in 2008 (Hooker 2010). The impact of black bears on neonate ungulates tends to be positively correlated with bear density, although the relationship is not entirely proportional (Zagar and Beecham 2006). In Alaska and Canada, black bears were a significant cause of moose calf mortality when bears occurred at relatively high densities of 0.2/km^2 (Ballard 1992). On TRNWR, deer hair has been observed in bear scat at low volumes (summer-6.4%, fall-2.3%; Benson and Chamberlain

2006), but bear populations have increased to a point where they may have an effect on fawn survival.

Influence of Biological Variables on Fawn Survival

Biological factors, such as sex, birth mass, and date of birth, can influence fawn survival. Most research examining effects of sex on fawn survival has found no relationship (Vreeland et al. 2004, Saalfield and Ditchkoff 2007, Kilgo et al. 2012), but Bishop et al. (2009) documented higher survival rates of female mule deer (*O. hemionus*) fawns than male fawns. Differences in activity patterns between males and females could influence predation rates. Jackson et al. (1972) and Aanes and Anderson (1996) found that male white-tailed deer fawns and roe deer (*Capreolus capreolus*) fawns were more active than female fawns, and male white-tailed deer fawns have a high propensity to be more independent of the dam (Taber and Dasmann 1954). When fawns are young and unable to evade predators, more curious, active fawns may be more likely to be detected by predators.

Birth mass can be a critical factor in neonatal ungulate survival (Verme 1969, Thorne et al. 1976, Cook et al. 2004, Lomas and Bender 2007). Although fawn mass can be affected by other factors such as litter size, maternal age, or maternal social rank (Robinette et al. 1973, Michel et al. 2015), it is primarily a result of maternal condition (Verme 1969, Robinette et al. 1973, Cook et al. 2004, Michel et al. 2015). Maternal mass can positively influence the ability to provide increased pre- and post-natal care, and heavier offspring often have increased growth rates compared to lighter offspring (Verme 1989, Steiger 2013). The faster that a fawn grows, the sooner it will be able to escape potential predators. Nelson and Woolf (1987) and Kunkel and Mech (1994) reported that white-tailed deer fawns with lower masses at capture were more vulnerable to predation than those with higher masses at capture. Similarly, Lomas and Bender

(2007) concluded that mean birth mass was positively correlated with mule deer fawn survival rate and number of days a fawn survived.

The influence of date of birth on survival of fawns is variable. Many studies conducted where predation was a significant source of mortality on fawns have reported no effect of birth date on survival (Vreeland et al. 2004, Saalfeld and Ditchkoff 2007, Chitwood et al. 2015). Other research found that the probability of fawn survival was greatest for those born early in the season and declined for those with later birth dates (Lomas and Bender 2007, Bishop et al. 2009, Kilgo et al. 2012). This decline was attributed to stress, malnutrition, and disease on smaller, later-born young during winter or to changes in predator pressure on fawns coincident with the increased nutritional demands associated with rearing offspring. Conversely, Gregg et al. (2001) reported higher survival for pronghorn fawns born during the peak birthing period than those born during the non-peak period, and Whittaker and Lindzey (1999) documented lower survival rates for white-tailed and mule deer fawns born earlier in the season than those born later. This change in survival in relation to the peak birthing period could be attributed to the swamping effect of the greater density of fawns available during and after the peak than before it. Particularly in moderate to high density herds, the abundance of fawns during a short time period likely overwhelms predator populations, and individual fawns should be at a reduced risk of predation.

Influence of Landscape Variables on Fawn Survival

Habitat can influence fawn survival by affecting predator distribution, density, and hunting efficacy (Gese et al. 1996, Dijak and Thompson 2000). Research has shown that coyotes prefer more open habitats as opposed to forested habitats (Priest 1986, Cypher 1991, Person and Hirth 1991, Holzman et al. 1992), and Gehring and Swihart (2003) found that coyotes avoided forest patches during the summer. Coyotes rely more heavily on visual than olfactory cues when hunting, and hunting success is greater when visual stimuli are present (Wells and Lehner 1978, Wells and Bekoff 1982). Several studies concluded that coyote predation on fawns was greater in areas with lower amounts of vegetative cover (Carrol and Brown 1977, Nelson and Woolf 1987, Piccolo et al. 2010). Because coyotes are less-efficient foragers in forested landscapes than in more open habitats (Gese et al. 1996, Richer et al. 2002), fawns seeking cover in forested landscapes with abundant vegetative cover may be safer from coyote predation than those located in other habitat types. However, Kilgo et al. (2014) and Chitwood et al. (2015) found no effect of cover on coyote predation of fawns.

Bobcat habitat selection often varies seasonally (Fuller et al. 1985, Rolley and Warde 1985, Anderson 1987) and preferred habitats vary spatially. In Mississippi, bobcats selected for mature pine habitats (Chamberlain et al. 2003); whereas, habitats selected by bobcats in Arkansas were 0- to 20-year-old reforestation and mature hardwood stands (Rucker et al. 1989). However, most studies suggest that the main factor determining bobcat habitat selection is prey abundance (Hall and Newsom 1976, Rucker et al. 1989, Knick 1990, Chamberlain et al. 2003). Bobcats may select habitats with higher fawn densities or may opportunistically consume fawns located in habitats with abundant alternate prey.

Although bears consume fawns, research suggests that bears do not actively seek out fawns when foraging. In a study examining spatial patterns of black bears and several ungulate species, researchers concluded that black bears did not select for sites that had a high probability of occurrence of neonatal ungulates, but rather selected for sites with high vegetative biomass (Bastille-Rousseau et al. 2011). Female black bears in the Tensas River Basin of Louisiana selected swamp, water, agriculture, regenerating forest, and corridor habitats in summer (i.e.

during the fawning season; Benson and Chamberlain 2007). Regenerating forests were most likely selected because these habitats contained abundant soft mast resources, including blackberry (*Rubus* spp.), which represents an important food item for bears in area (Weaver 1999, Benson and Chamberlain 2006). Females also selected agricultural habitats when choosing summer home ranges, indicating that females shifted their home ranges closer to agricultural fields during summer, presumably to exploit available crops (Anderson 1997, Weaver 1999, Benson and Chamberlain 2006). Fawns using regenerating forest and agricultural habitats may be at greater risk of predation due to increased bear use of those areas.

Although several studies have quantified microhabitat characteristics of fawn bed sites (Garner et al. 1979, Huegel et al. 1986, Nelson et al. 2015) and their link to fawn survival (Chitwood et al. 2015), little is known regarding the influence of landscape factors on fawn survival. The influence of landscape characteristics on survival has been readily observed for many ungulate species. Kunkel and Pletscher (2000) concluded that moose were most vulnerable to predation in habitats that exhibited the highest wolf (*Canis lupus*) use and near trails and streams that provided an increase in wolf hunting efficiency. In Idaho, elk calf survival was higher in transitional forests with 33-66% canopy cover, which provided sufficient understory security cover for calves but was not so thick as to serve as a structural impediment to escape predators (White et al. 2010).

Vreeland et al. (2004) found that white-tailed deer fawns in Pennsylvania were >2 times more likely to survive through 9 weeks post-capture in an agricultural region than in a heavily forested region, but did not see any effect of landscape variables on survival. Conversely, studies in Illinois (Rohm et al. 2007) and South Dakota (Grovenburg et al. 2012) concluded that macrohabitat and landscape influenced fawn survival. Rohm et al. (2007) found that areas inhabited by surviving fawns were characterized by a few large forest patches adjacent to several small non-forest patches. Grovenburg et al. (2012) documented that home ranges of surviving fawns contained more grassland and wetland habitats and less forested habitat than home ranges of fawns that died. Authors of these studies hypothesized that these habitat characteristics provided fawn hiding cover and refugia from predators, and allowed dams to maintain smaller home ranges, thus increasing time for maternal care and defense.

Population Dynamics

Managers often rely on use of age ratios to index recruitment rates (DeCesare et al. 2012). However, age ratios provide limited information, and alone may be inadequate in interpreting population growth because ratios are influenced by several underlying vital rates (Caughley 1974, McCullough 1994). One alternate method for analyzing population dynamics is through radiotelemetry. The advantages of using radio-marked animals to estimate population growth include obtaining estimates of population level survival (DelGiudice et al. 2006) and reproductive rates (Grund and Woolf, Duquette et al. 2012), which may differ among animal ages. Survival and recruitment rates can then be incorporated into matrix models to estimate potential finite population growth rate (Skalski et al. 2005). Growth rate estimates derived from radiotelemetry provide more precise estimates of population growth because fate of each animal is known and age-specific variation in survival and recruitment can be directly incorporated into matrix models (Duquette et al. 2014).

Population dynamics of ungulates are complex, and how predation and resource availability affect observed growth rates has been debated (Peek 1980, Gaillard et al. 2000, Sinclair and Krebs 2003). Ungulate populations are typically characterized by high and stable survival rates of adult females, moderately variable fecundity rates, and widely variable fawn survival rates (Gaillard et al. 1998, 2000). In addition, population models have shown that population growth is affected by both the variability and elasticity of vital rates, and variable fawn survival typically has a larger effect on population change than stable adult survival (Gaillard et al. 1998). However, because of the high elasticity of adult survival, small changes in adult survival can have substantial effects on population growth (Gaillard et al. 1998).

Robinson et al. (2014) used a wide range of deer vital rates in modeling scenarios to conclude that reduced antlerless harvest was enough to offset deer population declines exacerbated by coyote predation on fawns. Robinson et al. (2014) contended that sources of mortality that occur prior to recruitment are not important for managing hunted populations as long as management objectives were met, but they acknowledged that in areas with very low recruitment (e.g., 25% fawn survival) reduced antlerless harvest may not be enough to stabilize populations. Because fawn studies in the southeastern U.S. indicate that survival is low (14-33%; Epstein et al. 1985, Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015, Nelson et al. 2015), decreases in antlerless harvest may not be sufficient to stabilize declining populations. Quantifying selected vital rates (e.g., adult female survival, fecundity) will give managers a better understanding of population trends and help inform management actions.

Objectives

To better understand the population dynamics of white-tailed deer on TRNWR, my objectives were to (1) quantify fawn survival, (2) identify causes of fawn mortality (3) determine which intrinsic characteristics and habitats influenced fawn survival, (4) estimate adult female survival, and using these data to (5) model deer population trends.

Study Area

This study was conducted on the TRNWR and adjacent private lands (hereafter Tensas) located in northeastern Louisiana in the upper Tensas River Basin. The 30,750-ha refuge was established in 1980 and was once extensively logged hardwoods and agricultural lands. Since acquisition by the United States Fish and Wildlife Service, forests on the refuge have been allowed to grow into mature bottomland hardwood and swamps, and former agricultural fields have been replanted in native hardwoods. TRNWR was bordered almost entirely by agriculture on all sides, making it an island of habitat for many species including deer and the Louisiana black bear.

The Tensas River and surrounding areas were once the location of the main channel of the Mississippi River, and remains in the western Mississippi River floodplain. Topography on Tensas was flat to slightly undulating with 0-8% slopes and elevations ranging from 17 to 23 m above mean sea level (USGS 1995). Typical of a Mississippi River floodplain, ridge/swale, oxbow lakes, and backwater swamps were present. Soils were alluvial, poorly drained but highly fertile, and were comprised mostly of the Tensas-, Sharkey-, or Alligator-series (USDA 1968). The climate of Tensas was humid subtropical. Mean annual temperature was 19°C, with mean high and low temperatures of 25°C and 12°C, respectively, and annual precipitation averaged 130 cm (NOAA 2015).

Habitats on Tensas consisted of mature bottomland hardwoods (77%), early to mid-successional hardwood plantings (20%), wetlands/open water (2%), moist-soil management areas (<1%), cropland (<1%), and administrative sites (<1%). Overstory vegetation consisted of water oak (*Quercus nigra*), willow oak (*Q. phellos*), hickory (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), and sugarberry (*Celtis* *laevigata*), with interspersed baldcypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) swamps. The understory consisted of dwarf palmetto (*Sabal minor*), poison ivy (*Toxicodendron radicans*), blackberry (*Rubus* spp.), trumpet creeper (*Campsis radicans*), and greenbrier (*Smilax* spp.). Several mast-producing species such as blackberry and pokeweed (*Phytolacca americana*) could be found in abundance along roads and edges and where forest management practices have maintained a more open canopy. Early to mid-successional hardwood plantings established for carbon credits were distributed throughout TRNWR. These plantings were initiated between 1985 and 2009. Agricultural crops grown on Tensas included corn (*Zea mays*), cotton (*Gossypium hirsutum*), soybeans (*Glycine max*) and rice (*Oryza* sp.).

Deer densities on Tensas were approximately 17-22 deer/km^2 (S. Durham, Louisiana Department of Wildlife and Fisheries, personal communication). Annual harvest during the study averaged 903 ± 55 (SE) deer per year, a decline from the average of 1,197 ± 49 (SE) deer per year in the 1990s (J. Dickson, U.S. Fish and Wildlife Service, personal communication). Since the creation of TRNWR, black bear densities on Tensas have increased from approximately 0.11/km^2 in the 1980s (Nowak 1986) to 0.36/km^2 in the late 1990s (Boerson 2003) to 0.66/km^2 in the late 2000s (Hooker 2010). Although bobcat and bear hunting on the refuge are prohibited, coyotes are considered an incidental species and may be harvested during any hunting season with the weapons legal for that day.

Thesis Format

This thesis is presented in manuscript format. Chapter 1 is an introduction and literature review of white-tailed deer fawn survival and population dynamics. Chapter 2 presents fawn survival and cause-specific mortality and identifies the biological and habitat characteristics influencing fawn survival. Chapter 3 presents adult female survival and analyzes population growth rates based on changes in vital rates. Chapter 4 provides a summary and management implications of this study.

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CHAPTER 2

SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF WHITE-TAILED DEER FAWNS ON TENSAS RIVER NATIONAL WILDLIFE REFUGE, LOUISIANA[1]

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[1] Shuman, R. M., M. J. Cherry, T. N. Simoneaux, E. A. Cooney, J. C. Kilgo, M. J. Chamberlain, and K. V. Miller. To be submitted to *Journal of Wildlife Management*.

Abstract

Changing predator communities have potential to complicate management scenarios focused on ensuring sustainable white-tailed deer (*Odocoileus virginianus*) populations. Recent research has shown that predation on fawns by coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) can limit recruitment. However, little research has been conducted in areas with 3 sympatric fawn predators such as coyote, black bear (*Ursus americanus*), and bobcat. During 2013-15, we captured 70 fawns with the aid of vaginal implant transmitters on Tensas River National Wildlife Refuge in northeastern Louisiana. We monitored fawns every 8 hours until 6 weeks of age and daily until 12 weeks of age, and assigned cause of death by using field and DNA evidence. Mean survival of fawns to 12 weeks was 0.271 (95% CI: 0.185-0.398). Of 51 mortalities, 45 (88%) were attributed to predation, 4 (8%) to starvation, 1 (2%) to natural causes, and 1 (2%) to unknown causes. We used an information theoretic approach to compare Cox proportional hazards models containing various combinations of biological and habitat covariates. Our best-supported model contained mass at birth, and distance to cropland, young reforestation (planted 2000-09), and old reforestation (planted 1985-89). Based on hazard ratios, survival increased 86% with every 1 kg increase in birth mass, which may be indicative of greater maternal investment. Survival increased 8% for every 100 m increase in distance from cropland or young reforestation, and decreased 11% with every 100 m increase in distance from old reforestation, which may be a result of spatial variation in predator densities. Our results emphasize the importance of site-specific monitoring of fawn recruitment rates in areas with burgeoning predator communities.

INDEX WORDS: black bear, bobcat, coyote, fawn, habitat, Louisiana, neonate, *Odocoileus virginianus*, predation, recruitment

Introduction

Understanding recruitment rate is critical for management of sustainable white-tailed deer (*Odocoileus virginianus*) herds and development of appropriate harvest strategies (Porath 1980). Because the life stage most susceptible to mortality is fawns, reliable estimates of their survival are vital for population modeling and herd management (Roseberry and Woolf 1991, Bowden et al. 2000). In a review of predation effects on neonatal ungulate mortality, Linnell et al. (1995) reported mortality rates of fawns in northern temperate regions were variable (0-100%), and predation accounted for 0-100% of those mortalities, suggesting that predation levels are site-specific. This recognized spatial variation in predation rates mandates site-specific research to determine cause-specific mortality of fawns and the potential impacts of predation on deer recruitment. Moreover, declines in deer recruitment rates in some areas of the southeastern U.S. (Howze et al. 2009, Kilgo et al. 2010), specifically due to predation on fawns, have become more of a concern in recent years. Fawn survival studies in this region have documented low survival rates (14-33%), with most mortalities attributed to predation (63-90%; Epstein et al. 1985, Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015a, Nelson et al. 2015). Declining populations may necessitate reduction of antlerless harvest (Robinson et al. 2014), and in areas of very low recruitment, both cessation of antlerless harvest and predator control may be necessary to offset population declines (Chitwood et al. 2015b).

Most studies examining fawn survival rates in the southeastern U.S. have implicated coyotes (*Canis latrans*) as the leading source of fawn mortality (Kilgo et al. 2014, Chitwood et al. 2015a, Nelson et al. 2015). However, these studies were conducted in 2-predator systems, where coyotes and bobcats (*Lynx rufus*) were the primary predators of fawns. No research has occurred in the southeastern U.S. in areas with 3 primary predators, specifically coyotes, bobcat, and black bear (*Ursus americanus*). The combined effects of multiple predators on prey survival often cannot be predicted from their individual effects (McCoy et al. 2012), and predation on fawns by this additional predator may be an additive or compensatory source of mortality. Fawns are a known food source of black bears (Ozoga and Verme 1982), and studies in Pennsylvania, Minnesota, and New York have shown black bears to be responsible for 25-60% of mortalities attributable to predation (Mathews and Porter 1988, Kunkel and Mech 1994, Vreeland et al. 2004, Carstensen et al. 2009). Black bears can be an important source of mortality for fawns in northern areas, but whether this same trend is present in areas of the southeastern U.S. where black bears occur is unclear.

Biological factors, such as sex, birth mass, and date of birth, can influence fawn survival (Bishop et al. 2009, Saalfield and Ditchkoff 2007). Male fawns may be more susceptible to predation (Bishop et al. 2009) based on differences in activity patterns. Jackson et al. (1972) found that male fawns were more active than female fawns, and male fawns have a propensity to be more independent of the dam (Taber and Dasmann 1954). Additionally, birth mass can be a critical factor in neonatal ungulate survival (Verme 1969, Thorne et al. 1976, Cook et al. 2004, Lomas and Bender 2007), and heavier offspring often have increased growth rates compared to lighter offspring (Verme 1989, Steiger 2013). The influence of date of birth on survival of fawns is variable. Many studies conducted where predation was a significant source of mortality on fawns have reported no effect of birth date on survival (Vreeland et al. 2004, Saalfeld and Ditchkoff 2007, Chitwood et al. 2015a), whereas other research has documented that the probability of fawn survival was greatest for those born early in the season and declined for those with later birth dates (Lomas and Bender 2007, Bishop et al. 2009, Kilgo et al. 2012). This decline was attributed to stress, malnutrition, and disease on smaller, later-born young during winter or to increases in the nutritional demand or hunting skills of predators throughout the fawning season. Conversely, Whittaker and Lindzey (1999) documented higher survival rates for white-tailed and mule deer (*O. hemionus*) fawns born later in the season than those born earlier. This could be attributed to the swamping effect as more fawns are on the landscape as the birthing season progresses. In moderate to high density deer populations, the abundance of fawns during a short time period likely overwhelms predator populations, and individual fawns should be at a reduced risk of predation (Clark and Robertson 1979, O'Donoghue and Boutin 1995, Fritts and Pearsons 2008).

Habitat characteristics affect the distribution, density, and hunting efficacy of predators (Gese et al. 1996, Dijak and Thompson 2000) and hence can influence fawn survival. Although several studies have quantified microhabitat characteristics of fawn bed sites (Garner et al. 1979, Huegel et al. 1986, Nelson 2013) and their link to fawn survival (Chitwood et al. 2015a), little is known regarding the influence of landscape characteristics on fawn survival. Vreeland et al. (2004) found that fawns in Pennsylvania were >2 times more likely to survive 9 weeks post-capture in agricultural areas than in forested areas, but did not observe any effects of landscape variables (e.g., edge density, habitat diversity) on survival. Conversely, studies in Illinois (Rohm et al. 2007) and South Dakota (Grovenburg et al. 2012) reported that landscape (e.g., edge density, patch size and density) influenced fawn survival.

Deer herds exist throughout spatially variable landscapes, with dynamic predator communities and changing habitat conditions. Predation is a complex phenomenon and, coupled with the complexity under which deer herds exist, mandates site-specific research aimed at developing science-based management programs designed to ensure the sustainability of quality deer herds. Our objectives were to (1) estimate fawn survival rates, (2) identify causes of fawn mortality, and (3) determine which biological and landscape characteristics influenced fawn survival.

Study Area

We conducted research on the Tensas River National Wildlife Refuge (TRNWR) and adjacent private lands (hereafter Tensas) located in northeastern Louisiana in the upper Tensas River Basin (Figure 2.1). The 30,750-ha refuge was established in 1980 and was once extensively logged hardwoods and agricultural lands. Since acquisition by the United States Fish and Wildlife Service, forests on the refuge have been allowed to grow into mature bottomland hardwood and swamps, and former agricultural fields have been replanted in native hardwoods. TRNWR was bordered almost entirely by agriculture on all sides, making it an island of habitat for many species including deer and the Louisiana black bear (*U. a. luteolus*).

Topography was flat to slightly undulating with 0-8% slopes and elevations ranging from 17 to 23 m above mean sea level (USGS 1995). Soils were alluvial in nature, poorly drained but highly fertile, and were comprised mostly of the Tensas-, Sharkey-, or Alligator-series (USDA 1968). The climate of Tensas was humid subtropical. Mean annual temperature was 19°C, with mean high and low temperatures of 25°C and 12°C, respectively, and annual precipitation averaged 130 cm (NOAA 2015).

Habitats on Tensas consisted primarily of mature bottomland hardwoods (77%) and early to mid-successional hardwood plantings (20%). Overstory vegetation consisted of water oak (*Quercus nigra*), willow oak (*Q. phellos*), hickory (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), and sugarberry (*Celtis laevigata*), with interspersed baldcypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) swamps. Understory consisted of dwarf palmetto (*Sabal minor*), poison ivy (*Toxicodendron radicans*), trumpet creeper (*Campsis radicans*), and greenbrier (*Smilax* spp.). Several mast-producing species such as blackberry (*Rubus* spp.) and pokeweed (*Phytolacca americana*) were abundant along roads and edges and where forest management practices have maintained a more open canopy. Early to mid-successional hardwood plantings established for carbon credits were distributed throughout TRNWR. These plantings were initiated between 1985 and 2009.Agricultural crops grown on Tensas included corn (*Zea mays*), cotton (*Gossypium hirsutum*), soybeans (*Glycine max*) and rice (*Oryza* sp.).

Deer densities on Tensas were approximately 17-22 deer/km^2 (S. Durham, Louisiana Department of Wildlife and Fisheries, personal communication). Annual harvest during the study averaged 903 ± 55 (SE) deer per year, a decline from the average of 1,197 ± 49 (SE) deer per year in the 1990s (J. Dickson, U.S. Fish and Wildlife Service, personal communication). Since the creation of TRNWR, black bear densities on Tensas have increased from approximately 0.11/km^2 in the 1980s (Nowak 1986), to 0.36/km^2 in the late 1990s (Boerson et al. 2003), to 0.66/km^2 in the late 2000s (Hooker 2010). Although bobcat and bear hunting on the refuge are prohibited, coyotes are considered an incidental species and may be harvested during any hunting season with the weapons legal for that season.

Methods

Adult Female Capture and Handling

During January-April, 2013-2015, we captured adult (≥1.5 years) females using a combination of drop nets (18.3m x 18.3m or 15.2m x 15.2m), rocket nets (12.2m or 18.3m) and darting with a tranquilizer gun (Dan-Inject, Børkop, Denmark) from a tree stand over bait. We anesthetized deer caught under nets with an intramuscular injection of ketamine hydrochloride (3.5 mg/kg; Congaree Veterinary Pharmacy, Cayce, SC) and xylazine hydrochloride (2.5 mg/kg; Congaree Veterinary Pharmacy). When darting, we used Telazol (250 mg; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine hydrochloride (225 mg; Congaree Veterinary Pharmacy) in 1-ml Pneu-Dart transmitter darts (Pneu-Dart Inc., Williamsport, PA). Once deer were located or extracted from the net, we placed them in a sternal position on an insulated mat and covered them with a blanket to aid in thermoregulation. We applied ophthalmic ointment and a blindfold and monitored vital signs at 10-minute intervals. We radio-collared (Model 2510B, Advanced Telemetry Systems, Isanti, MN), ear-tagged, and implanted each female with a temperature-activated vaginal implant transmitter (VIT; 2013 and 2015; Model M3930, Advanced Telemetry Systems) or a temperature- and light-activated VIT (2014; M3930L, Advanced Telemetry Systems; Cherry et al. 2013). Implantation procedures generally followed those described by Carstensen et al. (2003), except that we did not trim the protruding antenna (Kilgo et al. 2012). Following instrumentation, we reversed the xylazine hydrochloride with tolazoline hydrochloride (150 mg intravenous and 150 mg intramuscular; Congaree Veterinary Pharmacy) and monitored the deer until ambulatory. Capture and handling protocol was approved by the University of Georgia Institutional Animal Care and Use Committee, Permit #A2012 06-006-Y3-A2.

Fawn Capture and Monitoring

We monitored female VHF collar and VIT signals weekly from capture until June 1, daily until the first birth, and at 8-hour intervals (beginning at 0600, 1400, and 2200) until the last birth. The VITs were equipped with either a thermistor that detected and signaled a change in temperature related to expulsion of the transmitter during parturition or a thermistor and photo sensor, which detected and signaled a change in light associated with expulsion of the transmitter. In VITs with a thermistor and photo sensor, the VIT signals when it detects a change in light, a change in temperature, or both. In addition, all VITs were equipped with a timer that specified the number of 30-minute intervals that elapsed since the temperature or light change. To allow for grooming and initial bonding between the female and fawn, we waited ≥2-hours after parturition before initiating a search, but otherwise began a search with thermal imaging cameras immediately after detecting an expelled VIT. We proceeded first to the female, if not at the VIT, and then to the VIT, and recorded the location of each. If we did not locate a fawn at the VIT, we searched an area of approximately 150m between and around the female and VIT locations. If we did not find a fawn on the initial search, then we returned at 8-24-hour intervals over the following 1-3 days for additional searches. All searches lasted ≤2 hours to limit human disturbance in the area.

When we located fawns, we immediately blindfolded them and only handled them with non-scented latex gloves. We placed fawns in a cotton bag and weighed them to the nearest 0.01 kg. We determined sex and attached an expandable breakaway radio-collar (Model M4210, Advanced Telemetry Systems) equipped with a motion-sensitive mortality switch on a 4-hour delay. Fawns were then released at the capture location. We classified a litter size as twin set if two fawns were found at or near the birth site within 24 hours of parturition. To minimize the possibility of misidentifying litter size, we assigned litter size as singleton only when both the dam and fawn were found at the birth site within 6 hours of parturition, and we classified all other single fawns as unknown litter size.

To estimate survival, we monitored fawns every 8 hours (beginning at 0600, 1400, and 2200) until 6 weeks of age and once daily until 12 weeks of age. Because the greatest probability of mortality occurs during the first few weeks of life (Cook et al. 1971, Kilgo et al. 2012), we monitored fawns more intensively at younger ages. Frequent monitoring allowed for better detection of mortalities, estimation of time of death, and preservation of evidence to be used in the determination of the cause of mortality. We were able to reach most carcasses in ≤3 hours of detection (45 of 51) and all within 8.5 hours.

We estimated fawn locations every 32 hours (every fourth mortality check) from birth until 6 weeks of age via triangulation. We collected ≥3 bearings within 20 minutes (Millspaugh and Marzluff 2001) and used the maximum likelihood estimator in Location of A Signal software (version 4.0.3.8; Ecological Software Solutions LLC, Sacramento, CA) to estimate locations and accepted only locations with an error ellipse of ≤2 ha.

Fate Determination

We assigned cause of mortality based on field evidence at or near the collar or remains. We identified the predator responsible based on cache characteristics, size of feeding area, consumption patterns, and tracks or scat at the mortality site. Bobcats tend to cache remains under sticks, leaf litter, or debris without digging into the mineral soil, but if coyotes cache their prey, they typically bury it in the mineral soil (O’Gara 1978, Labisky and Boulay 1998). Black bears rarely scatter remains and tend to have 1 relatively large feeding site (1-5m) where vegetation is usually matted down (Schlegel 1976, Wade and Bowns 1984), whereas coyotes often scatter remains over a larger area (Cook et al. 1971, O’Gara 1978). Coyotes and black bears are more likely to consume the entire carcass than bobcats (Garner et al. 1976, Epstein et al. 1983, Wade and Bowns 1984). Bobcats often initiate feeding on the shoulders, whereas coyotes feed first on the viscera and hindquarters, and black bears favor the inguinal and loin areas (White 1973, O’Gara 1978). Additionally, black bears often consume ears, eyes, and tongue and invert the hide when most of the carcass is consumed (Ballard et al. 1979, Wade and Bowns 1984).

When no evidence of predation was present and the carcass was emaciated, we listed the cause of death as starvation. When no evidence of predation or emaciation was present, we listed the cause of death as natural causes. We submitted carcasses that did not exhibit signs of predation to the Southeastern Cooperative Wildlife Disease Study (Athens, GA) or Louisiana Department of Wildlife and Fisheries (Baton Rouge, LA) for full necropsy to confirm cause of death. Because of the potential for marking-induced abandonment, some researchers remove starved fawns from their samples. However, other research has suggested that the risk of marking-induced abandonment is minimal (Ozoga and Clute 1988, Carstensen Powell et al. 2005). Natural abandonment is commonly reported in deer and is attributable to various causes (Verme 1969, Langenau and Lerg 1976), and omitting starved fawns can underestimate natural mortality. Therefore, we retained starved fawns in our analyses.

To confirm our field assignment of predator species, we collected residual predator saliva for DNA identification of species. We wiped cotton swabs around bite wounds, on the head and neck of the fawn, and on the radio-collar. We swabbed ≥3 different locations on the remains of each fawn to ensure that multiple predator species would be detected if present. Wildlife Genetics International (WGI; Nelson, Canada) conducted the genetic analyses of the saliva. WGI extracted DNA from material clipped from the swab using QIAGEN DNeasy Blood and Tissue kits (Valencia, CA). The species test was a partial sequence analysis of the mitochondrial 16S rRNA gene (Johnson and O’Brian 1997). WGI first used Carnivora-specific primers to amplify the 16S sequence and then compared the sequence profiles from samples with reference data from over 125 mammalian species.

When we recovered predator DNA from the remains, even in the absence of definitive field evidence, we assigned cause of mortality to that predator species. If DNA analyses could not identify predator species or produced mixed samples, we relied on field evidence to assign predator species. If field evidence suggested predation but species could not be determined by field or DNA evidence, that cause of death was listed as unknown predator. We acknowledge that predators may have scavenged fawns that died of other causes before we could recover them; however, our intensive monitoring schedule was designed to minimize the potential for a scavenger to detect a carcass before us.

Landscape Variables

Due to variable life spans across our sample of fawns, there was considerable variability in number of relocations (*n*=1-32). Therefore, to characterize landscape variables associated with fawn survival, we calculated the distance from each fawn location to each habitat type or edge as a metric for habitat use. We classified land cover on Tensas into 7 different habitat types based on differences in vegetative species composition and tree size: mature bottomland hardwoods, young reforestation (planted 2000-08), mid-age reforestation (planted 1990-99), old reforestation (planted 1985-89), cropland, moist soil management areas, and administrative sites. We used a combination of interpretation of National Agriculture Imagery Program (NAIP) aerial imagery taken in 2013 and TRNWR forestry records (N. Renick, U.S. Fish and Wildlife Service, unpublished data) to classify habitat types and created shapefiles of each habitat type in ArcGIS 10.2 (Environmental Systems Research Institute, Inc., Redlands, CA). To facilitate the ease of distance calculations, we used the habitat layers to create distance raster layers where each 10m x 10m cell contained the distance to the nearest cell of each habitat type. In R (version 3.2, R Core Team, Vienna, Austria), we used the *raster* package to create a raster stack of all raster layers.

We then overlaid fawn locations onto the raster stack and calculated a mean distance to each habitat type and nearest edge for each fawn.

Statistical Analysis

We conducted known-fate modeling using *survival* package in R to determine survival rates and examine factors potentially affecting survival. We estimated survival rate to 12 weeks using Kaplan-Meier methods and based analysis on fawn age in days rather than a staggered entry approach (Bishop et al 2008). We estimated a 12-week survival rate rather than 16- or 26-week survival because most fawns reached 12 weeks of age by mid-October to early November, which coincided with opening of deer hunting season, when we considered fawns recruited into the hunted population.

We analyzed differences in biological factors among years using analysis of variance. We used Cox-proportional hazards survival models to investigate effects of biological factors (capture year, sex, birth mass, and Julian date of birth) and landscape variables on fawn survival. We constructed 27 a priori survival models containing various combinations of biological factors and landscape variables. For model selection, we used Akaike's Information Criterion adjusted for small sample size (AIC_c). We used Akaike weights (w_i) to evaluate the strength of evidence among competing models and considered our most plausible models to be those ≤2.0 AIC_c units from the top model (Burnham and Anderson 2002), unless they contained uninformative parameters. Models with uninformative parameters are defined as those ≤2.0 AIC_c units from the top model but contain only one additional parameter and have similar values for model deviance (Arnold 2010), and therefore we would make inference based on the most parsimonious model. We checked model assumption of proportionality by examining Schoenfeld residuals.

Results

We implanted 30 females in 2013, 32 in 2014, and 40 in 2015 with VITs. We repeatedly captured 11 females during 2 years, resulting in 102 VIT deployments among 91 individual females. We successfully captured ≥1 live fawn from 46 of the 102 VITs (45%), yielding 70 fawns (28 in 2013, 17 in 2014, and 25 in 2015). From these births, we documented 24 twin sets, 10 singletons, and 12 with unknown litter size. Reasons for failure to collar fawns from monitored VITs included transmitter failure prior to parturition (*n*=29), failure to locate fawns after apparently normal parturition (*n*=12), death of female prior to parturition (*n*=7), expulsion of VIT prior to parturition (*n*=3), stillbirth of fawns (*n*=3), loss of contact with female prior to parturition (*n*=1), and female was not pregnant when implanted (*n*=1).

Sex ratio among fawns was biased toward males (42 of 70, 60%) in all years: 15 of 28 (54%) in 2013, 9 of 17 (53%) in 2014, and 18 of 25 (72%) in 2015. Fawn mass averaged 3.00 ± 0.06 (SE) kg. Mass did not vary among years ($F_{2, 65} = 0.47$, $P = 0.63$) but did vary by sex ($F_{1, 66} = 11.33$, $P < 0.01$); males (3.14 ± 0.07 kg) weighed more than females (2.76 ± 0.08 kg). Mean date of birth was 15 July and differed across years ($F_{2, 67} = 4.22$, $P = 0.02$). In 2015, mean date of birth was earlier (10 July) than in 2013 (July 19) and 2014 (15 July). The earliest dates of birth were 5 July in 2013, 5 July in 2014, and 25 June in 2015; latest dates of birth were 8 August in 2013, 30 July in 2014, and 15 August in 2015.

Mean survival to 12 weeks was 0.271 (95% CI = 0.185-0.398). Survival rates were similar across years, and 95% confidence intervals overlapped among all years (Table 2.1). Fawn survival decreased rapidly during the first 7 days of life, with 50% (95% CI = 37.2 – 60.4%) of fawns dying during that period, whereas no fawns died after 44 days (Figure 2.2).

We identified 2 plausible models (i.e., within 2 AIC_c units) that predicted risk to fawn survival (Table 2.2). We found sex to be an uninformative parameter, and therefore the best-supported model included mass, distance to cropland, distance to young reforestation, and distance to old reforestation (Table 2.2). Based on hazard ratios, survival increased with mass, distance to cropland, and distance to young reforestation and decreased with distance to old reforestation (Table 2.3). For every 1 kg increase in birth mass, survival increased by 86%. For every 100 m increase in distance from young reforestation or cropland, survival increased by 8%, and survival decreased 11% with every 100 m increase in distance from old reforestation

Of 70 fawns, we recorded 51 mortalities: 18 in 2013, 13 in 2014, and 20 in 2015. Predation was the leading source of mortality (*n*=45; 88.2%), followed by starvation (*n*=4; 7.8%), natural causes (*n*=1; 2.0%), and unknown cause of death (*n*=1; 2.0%; Table 2.4). Based on field methods, we were able to assign predator species to 33 of 45 fawns suspected of being depredated. Mitochondrial DNA testing successfully identified predator species from 34 fawns (76%; 12 in 2013, 7 in 2014, 15 in 2015). Among this subsample, 15 were black bear, 8 were bobcat, 6 were coyote, 2 contained both black bear and bobcat DNA, 1 contained both coyote and black bear DNA, 1 contained both coyote and bobcat DNA, and 1 contained bobcat and mixed DNA (more than one species on a single swab). We assigned cause of death to both of the fawns with bobcat and black bear DNA as bobcat because we assumed it was more likely that that the fawn was scavenged by a black bear after a bobcat killed it than vice versa. We assigned cause of death to the fawn with black bear and coyote DNA as coyote because most of the carcass was buried in the mineral soil and we saw a black bear at the carcass when we arrived to assess cause of death. For the fawn with coyote and bobcat DNA and the fawn with bobcat and mixed DNA, we assigned the cause of death as unknown predator because we did not have sufficient field evidence to determine predator versus scavenger species. In all other cases, DNA identifications confirmed our field assignments. Therefore, we confidently relied on field evidence to assign predator species without DNA confirmation.

Black bear predation was the most frequent cause of mortality, accounting for 33% of all mortalities (*n*=15; Table 2.4). Coyotes accounted for 18% of all deaths (*n*=19; Table 2.4), and bobcats caused 22% of mortalities (*n*=11; Table 2.4). We were unable to assign 16% of depredated fawns (*n*=8) to a specific predator (Table 2.4). The most vulnerable time period for fawns was their first week of life, with 69% (36 of 51) of all mortality occurring during this period (Figure 2.3). Ninety-four percent (n=48) of mortalities occurred within the first month, and the remaining 3 mortalities occurred thereafter (Figure 2.3). The greatest number of mortalities caused by black bears and coyotes occurred in the first week of life, but the greatest number of mortalities caused by bobcat occurred in the third week of life (Figure 2.4)

Discussion

We observed a fawn survival rate of 27%, which was low relative to other published works in the midwestern and northeastern U.S. (70%; Nelson and Woolf 1987; 84%; Brinkman et al. 2004; 91%; Pusateri Burroughs et al. 2006; 61%; Rohm et al. 2007). However, our findings were comparable to recently published studies conducted in the southeastern U.S. For instance, survival rates were 17% and 22% in South Carolina (Epstein et al. 1985, Kilgo et al. 2012), 14% in North Carolina (Chitwood et al. 2015a), 29% in Georgia (Nelson et al. 2015), and 33% and 22% in Alabama (Saalfeld and Ditchkoff 2007, Jackson and Ditchkoff 2013). The greatest source of mortality was predation (88%) by black bear, coyote, and bobcat. Despite the uncertainty associated with assigning causes of death, our use of DNA to assign predator species helped to decrease uncertainty; DNA assignments paralleled our field assignments in all cases.

Regardless, the degree of predation we attributed to black bears, coyotes, and bobcats on Tensas may be underrepresented because of the number of mortalities where predation was evident but we could not assign the predator responsible.

Historically, studies assessing fawn survival have captured fawns using grid searches (Ballard et al. 1999, Pusateri Burroughs et al. 2006), spotlighting (Carroll and Brown 1977), observing doe behavior (Nelson and Woolf 1987, Vreeland et al. 2004), and monitoring of radio-collared females (Kunkel and Mech 1999). These methods rarely allow researchers to find fawns <24hrs old, and most captured fawns are several days up to 2 weeks old. We observed (as have others), most fawn mortality occurring during the first week of life. Hence, older fawns captured or sampled in earlier studies may have already survived a potentially critical period and likely biased estimates of fawn survival high (Gilbert et al. 2014). More recent studies have used VITs to locate fawns (Saalfield and Ditchkoff 2007, Carstensen et al. 2009, Kilgo et al. 2012), allowing a less biased assessment of fawn survival (Gilbert et al. 2014). Despite the use of VITs, we observed 3 instances where we arrived at the birth site within 2 hours of the expulsion of the VIT and did not find fawns. In each instance, the female was 100-200 m away from the VIT, and the VIT was lying at an obvious birth site still damp with placental fluid. At all 3 sites, we conducted visual searches multiple times without finding fawns, but in one instance observed a black bear within 75m of the birth site during the initial search. While it is possible that the fawns had moved away prior to our arrival, they would have had to have done so in less than 2 hours of birth. We suggest it is more plausible that these fawns were depredated prior to us being able to capture them, despite our rigorous monitoring protocol.

Predation by black bear was the greatest source of mortality (33%), consistent with studies conducted in Pennsylvania, Minnesota, and New York where predation by black bears accounted for 25-60% of mortalities attributable to predation (Mathews and Porter 1988, Kunkel and Mech 1994, Vreeland et al. 2004, Carstensen et al. 2009). Likewise, in a review of elk (*Cervus canadensis*) and moose (*Alces alces*) calf mortality, researchers reported that black bears were consistently the most important source of mortality (Zager and Beecham 2006). The density of black bears on Tensas is the highest in the state of Louisiana (Troxler 2013) and is currently at or above 0.66 bears/km^2 (Hooker 2010). The relevance of black bear predation on neonate ungulates tends to be positively correlated with bear density, although the relationship is not entirely proportional (Zagar and Beecham 2006). For instance, Ballard (1992) reported that mortality rates of elk and moose calves caused by black bears ranged from 2-50% when black bear densities were 0.016-0.570 bears/km^2, and black bears were a substantial cause of moose calf mortality when they occurred at densities of >0.2 bears/km^2.

Bobcat predation was the second greatest source of fawn mortality. Where bobcats are sympatric with coyotes, bobcat predation may be low, accounting for <10% of mortalities (Vreeland et al. 2004, Kilgo et al. 2012, Nelson et al. 2015), and coyotes tend to have a greater occurrence of deer in their diets than do bobcats (Litvaitis and Harrison 1989, VanGilder et al. 2009). However, deer can be an important prey item for bobcats in some areas (Chamberlain and Leopold 1999, Roberts 2007) and fawns provide more energy than small mammals (VanDomelen 1992). Hence, it is advantageous energetically for bobcats to consume fawns even in the presence of alternate prey. Bobcats are considered opportunistic predators (McCord and Cardoza 1982) and may exhibit a functional response to prey abundance, with increased use of preferred prey items when abundance is high (Baker et al. 2001). Bobcat predation on fawns is often low in areas of low deer densities (Kilgo et al. 2012, Chitwood et al. 2015a, Nelson et al.

2015), indicating that bobcats on Tensas are likely taking advantage of the abundance of fawns available during the birthing period.

Coyote predation on Tensas was low (18%) compared to other fawn survival studies performed in the southeastern U.S., where 42-80% of mortalities were attributed to coyotes (Saalfeld and Ditchkoff 2007, Kilgo et al 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015a, Nelson et al. 2015). The amount of coyote predation on Tensas may be a result of prey partitioning with bears and bobcats. Resource partitioning permits sympatric predators to coexist (Ricklefs 2007). Predators often partition based on food habits (Schoener 1974, Carvalho and Gomes 2004, Thornton et al. 2004, Andheria et al. 2007), but diets can converge when a resource is abundant (Schoener 1982). Fawn availability would be high initially with the pulse of fawn births, but would decline as mortality events occur. At lesser fawn densities, energetic costs of predating fawns would increase as predators expended more time searching (Krebs 1978), and predators would benefit by using other food resources (Stephens and Krebs 1986). Bears consumed fawns primarily during the first week of life but coyotes depredated fawns to 5 weeks of life. Coyote predation rates may have been higher if bears had not depredated fawns first. Alternatively, it is possible that deer populations have had more time to adapt to this novel predator. Since the first coyote in Louisiana was reported in 1949, coyote abundance in Louisiana has increased across the state, and by the 1970s, their presence was considered a permanent addition to the fauna community (Goertz et al. 1975). This colonization by coyotes is earlier than in many other parts of the southeastern U.S., where populations have only become established in the last 25 years (Kilgo et al. 2010).

Coyotes are generalist carnivores with spatially and temporally variable diets (Wooding 1984, Andelt et al. 1987, Blanton and Hill 1989, Schrecengost et al. 2008). On Tensas, the occurrence of deer increased 21% during the fawning season, whereas occurrence of lagomorphs and small mammals decreased 8% and 20%, respectively (Rountree et al. 2016). Many factors, including coyote density, deer density, abundance of alternative food sources, and vegetative hiding cover, could potentially influence the amount of coyote predation on fawns (Patterson and Messier 2000). Tensas contains a variety of habitats that provide an abundance of alternative food resources, including soft mast, lagomorphs, and small mammals. Likewise, coyotes are generalists and switch prey selection throughout the year depending on prey availability and handling time (Andelt et al. 1987, Windberg and Mitchell 1990, Rountree et al. 2016). As fawns age and become more mobile, coyotes simply shift to more easily obtainable food items (Petroelje et al. 2014).

Proximity to certain habitats may influence the ability of predators to detect and capture prey (Gese et al. 1996, Dijak and Thompson 2000). Similar to our findings, research in South Dakota found an increased probability of capture by a predator was associated with a decreased distance to agriculture and increased distance to wetland and grassland habitats (Grovenburg et al. 2012). Grovenburg et al. (2012) hypothesized that fawns were more likely to escape predation when fleeing to the thick vegetative cover of wetlands and grasslands and more likely to be captured when fleeing to agricultural fields. However, White et al. (2010) observed an increased risk of predation in elk calves in scrub-fields because the thick vegetation served as a structural impediment to escape. We speculate that the dense herbaceous vegetation and blackberry thickets in the understory of young reforestation stands on Tensas could be impeding escape of older fawns from predators.

Habitats can influence the distribution and densities of predators (King et al. 1998, Dijak and Thompson 2000). Although bobcat habitat selection varies seasonally and spatially (Fuller et al. 1985, Anderson 1987, Chamberlain et al. 2003), bobcats often prefer dense early-successional or shrubby habitats (Hall and Newsom 1976, Rolley and Warde 1985, Litvaitis et al. 1986). Because bobcat hunting behavior typically consists of stalking and attacking prey from the concealment of cover (Kruuk 1986), bobcats may be selecting early successional habitats because they contain more vegetative cover (Kolowski and Woolf 2002) or have greater prey abundance (Hall and Newsom 1976, Rucker et al. 1989, Knick 1990, Chamberlain et al. 2003). In our study, most fawn mortalities due to bobcat predation occurred within the first 3 weeks of life. Fawns are mostly sedentary during the first 2 weeks of life, but become progressively more active thereafter (Jackson et al. 1972).

Research of female black bears in the Tensas River Basin showed that they selected swamp, water, agriculture, regenerating forest, and corridor habitats in summer (i.e., during the fawning season; Benson and Chamberlain 2007). Regenerating forests were most likely selected because these habitats contain abundant soft mast resources, including blackberry, which represents an important food item for bears on Tensas (Weaver 1999, Benson and Chamberlain 2006). Female black bears on Tensas also selected agricultural habitats during summer ranges, indicating that females shifted their home ranges closer to agricultural fields during summer, presumably to exploit available crops (Benson and Chamberlain 2007). Food habits of bears in the Tensas River Basin during summer and fall are dominated by agricultural crops, particularly corn (Anderson 1997, Weaver 1999, Benson and Chamberlain 2006). Bastille-Rousseau et al. (2011) concluded that when foraging, most black bears did not select for sites that had a high probability of occurrence of neonatal ungulates, but rather, selected for sites with high vegetative biomass. It is possible that the rate of predation on fawns by black bears we observed on Tensas is a result of a high bear and deer density, in that as bears move into croplands and young reforestation areas to forage on abundant food resources, the probability of a bear opportunistically encountering and consuming a fawn increases.

Management Implications

Our study provided the first evaluation of white-tailed deer fawn survival and cause-specific mortality in areas of the southeastern U.S. with 3 sympatric predators (coyotes, black bear, and bobcat) that predate fawns. Although additional research is needed to better understand the relationship between predators and fawns in multi-predator systems across the region, our data demonstrate that black bear predation on fawns can be substantial. Current population projections indicate that predation on fawns is not limiting deer population growth on Tensas (see Chapter 3), but continued predator population growth may decrease fawn survival below sustainable levels. Black bear hunting is not permitted in Louisiana, but recent delisting of the previously threatened Louisiana black bear has given Louisiana Department of Wildlife and Fisheries authority over management and harvest regulations. Because black bear predation was the greatest source of mortality for fawns on Tensas, black bear hunting may positively influence fawn survival. However, the impact of black bear population reduction on survival of neonatal ungulates is variable (Zager and Beecham 2006). Therefore, managers would need to weigh impacts of black bear harvest on deer populations, bear populations, and public perception when evaluating harvest regulations.

Bobcat hunting and trapping are permitted in Louisiana but not on TRNWR, and managers may be able to increase fawn survival through allowing bobcat harvest on TRNWR. However, allowing harvest of bobcats may not have a considerable impact on bobcat densities or fawn predation rates. Bobcats exhibit a land tenure system, and vacancies left by harvested bobcats will likely be filled by transient or neighboring bobcats (Benson et al. 2004). Moreover, reductions in bobcat populations would require substantial hunter participation. Although coyotes on Tensas are considered an incidental species and may be harvested during any hunting season, few are harvested each year (J. Dickson, personal communication), and hunters are likely having little effect on coyote populations.

Our results indicate that fawn survival will increase as reforested areas age. However, young (1-10 years) bottomland hardwood stands are one of the most productive habitat types in Louisiana in terms of total biomass production and biomass production of preferred deer forage, but as the stands age production of preferred forage decreases (Horrell 2013). Decreases in productivity may have a negative effect on maternal body condition and fawn birth mass. Reduced fawn survival due to lower birth mass may negate any positive effect that aging stands may have on survival. Moreover, dams in lower productivity habitats may need to maintain larger home ranges to meet their nutritional needs, resulting in less time for maternal care and defense (Rohm et al. 2007). Therefore, having early successional hardwoods and cropland interspersed throughout older hardwood stands may provide a balance between decreasing predation rates and maximizing forage availability.

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Table 2.1. Annual and overall survival rates among radio-collared white-tailed deer fawns at Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

Year	n	Survival rate	SE	95% Cl
2013	28	0.357	0.091	0.217-0.587
2014	17	0.235	0.103	0.100-0.554
2015	25	0.200	0.080	0.091-0.438
Overall	70	0.271	0.053	0.185-0.398

Table 2.2. Model selection results from a Cox proportional hazard model analysis of survival of white-tailed deer fawns on Tensas River National Wildlife Refuge, Louisiana, 2013-2015. We ranked candidate models using change in Akaike's Information Criterion for small sample size (ΔAIC_c) and Akaike weights (w_i). We present only the top 5 candidate models here.

Model[a]	K[b]	AIC_c	ΔAIC_c	w_i	Deviance
Sex+mass+crop+ref10+ref30	5	365.80	0.00	0.46	354.86
Mass+crop+ref10+ref30	4	367.18	1.38	0.23	358.56
Sex+mass+crop+ref10+ref30+edge	6	368.02	2.22	0.15	354.68
Sex+mass+edge	7	370.03	4.23	0.06	363.66
Sex+mass+crop+ref10++ref20+ref30+edge	3	370.48	4.69	0.04	354.68

[a] crop, distance to cropland; ref10, distance to young reforestation; ref20, distance to mid-age reforestation; ref30, distance to old reforestation; edge, distance to edge

[b] No. of parameters

Table 2.3. Coefficients, standard errors (SE), and 95% confidence intervals (95% CI) for covariates in top Cox proportional hazard model predicting risk to white-tailed deer fawn survival on Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

				HR[b] 95% CI	
Covariate[a]	Coefficient	SE	HR[b]	Lower	Upper
Mass	-1.358	0.381	0.257	0.122	0.542
Ref10	-0.080	0.029	0.923	0.871	0.978
Ref30	0.108	0.035	1.114	1.039	1.193
Crop	-0.083	0.024	0.920	0.878	0.964

[a] crop, distance to cropland; ref10, distance to young reforestation; ref20, distance to mid-age reforestation; ref30, distance to old reforestation; edge, distance to edge

[b] HR, hazard ratio

Table 2.4. Causes of mortality among radio-collared white-tailed deer fawns at Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

	2013		2014		2015		Total	
Cause of Mortality	n	%	n	%	n	%	n	%
Predation								
Black Bear	6	33.3	6	46.2	5	25.0	17	33.3
Bobcat	5	27.8	1	7.7	5	25.0	11	21.6
Coyote	4	22.2	1	7.7	4	20.0	9	17.6
Unknown	2	11.1	4	30.8	2	10.0	8	15.7
Natural causes[a]	0	0.0	1	7.7	0	0.0	1	2.0
Unknown	1	5.6	0	0.0	0	0.0	1	2.0
Starvation	0	0.0	0	0.0	4	20.0	4	7.8

[a] Dehydration and heart failure due to multiple birth defects

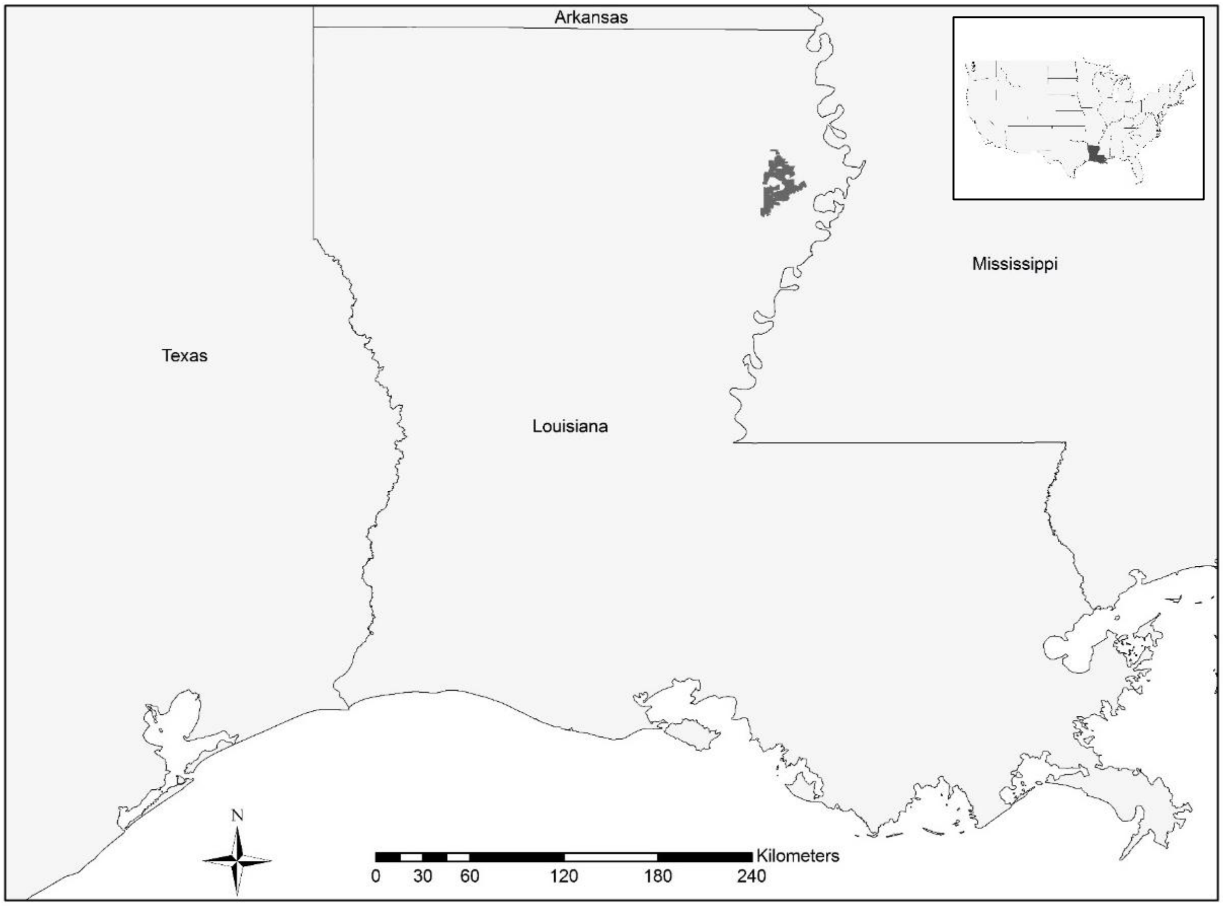

Figure 2.1. Location of Tensas River National Wildlife Refuge, Louisiana.

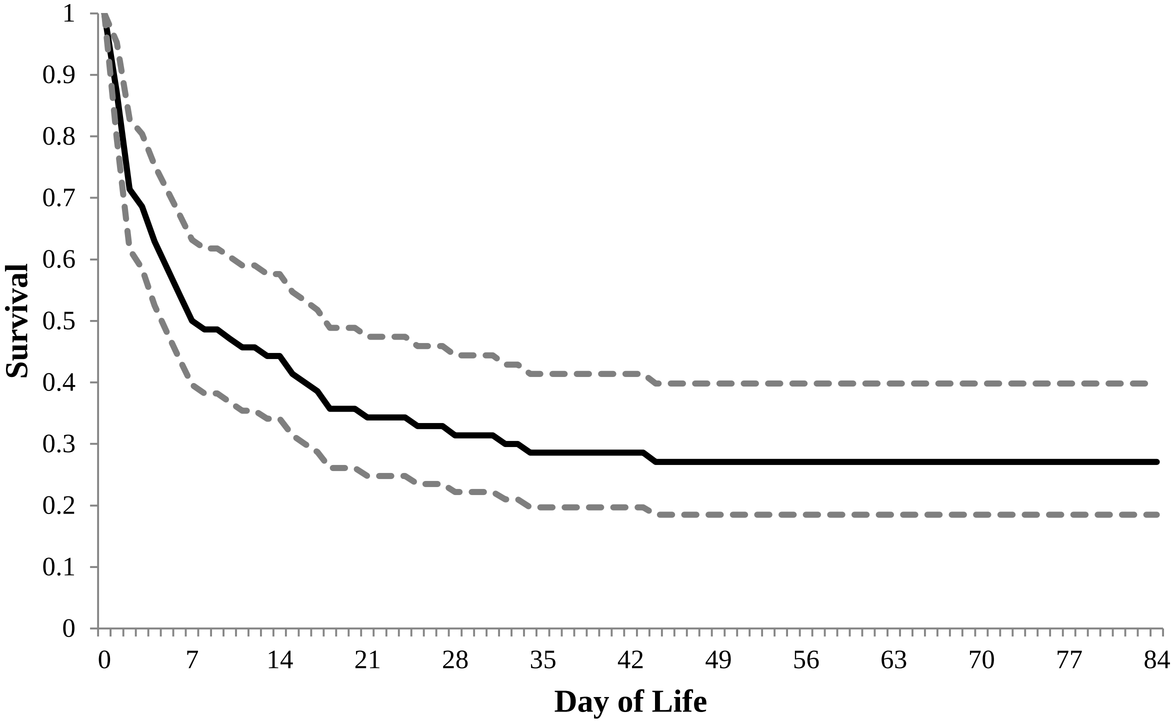

Figure 2.2. Survivorship curve for radio-collared white-tailed deer fawns from birth to 12 weeks old at Tensas River National Wildlife Refuge, Louisiana, 2013-2015. Dashed lines represent 95% confidence interval.

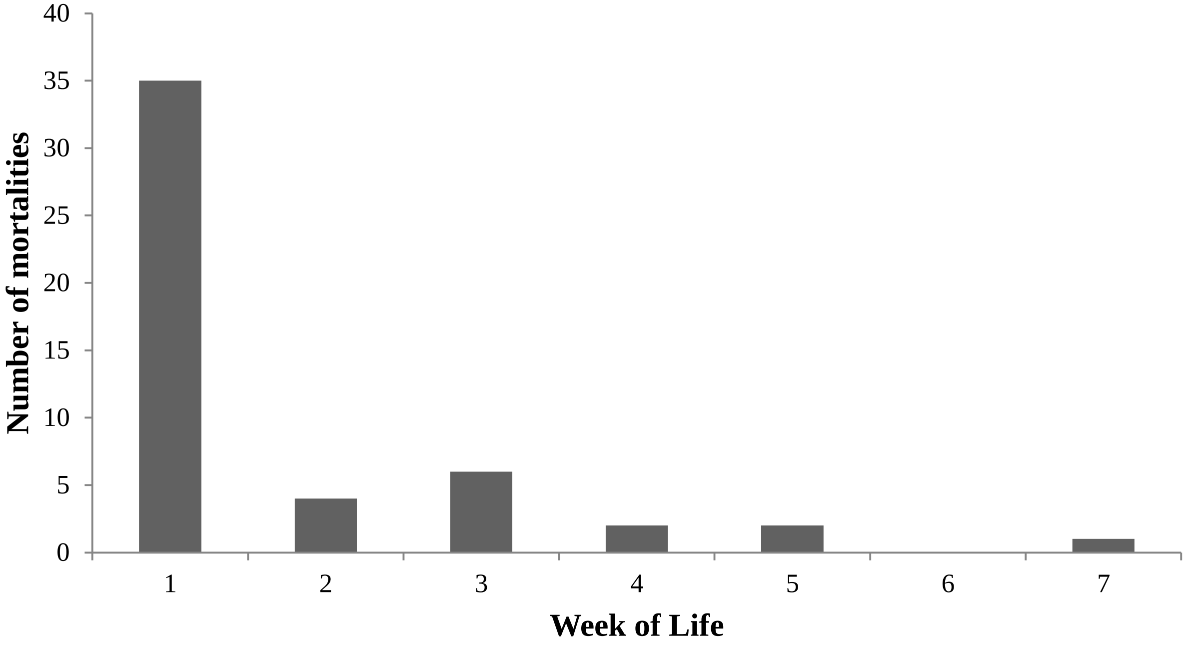

Figure 2.3. Number of mortalities by week of life among radio-collared white-tailed deer fawns at Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

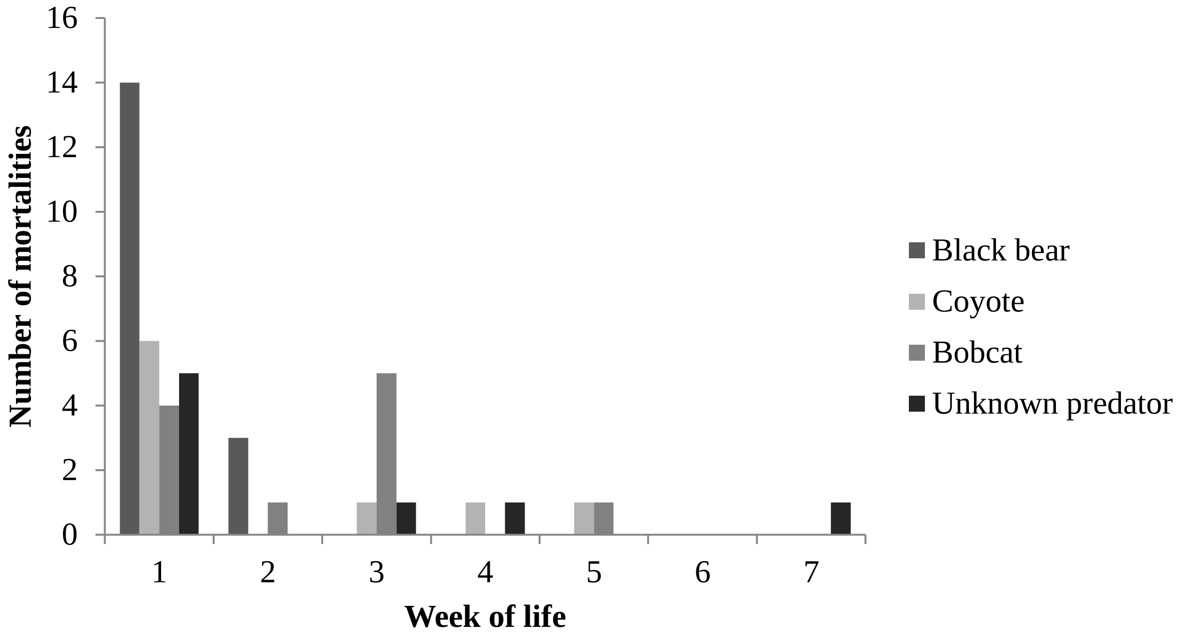

Figure 2.4. Number of predation mortalities by predator species and week of life among radio-collared white-tailed deer fawns at Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

CHAPTER 3

ADULT FEMALE SURVIVAL AND POPULATION DYNAMICS OF WHITE-TAILED DEER ON TENSAS RIVER NATIONAL WILDLIFE REFUGE, LOUISIANA[1]

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[1] Shuman, R. M., M. J. Cherry, T. N. Simoneaux, E. A. Cooney, J. C. Kilgo, M. J. Chamberlain, and K. V. Miller. To be submitted to *Journal of Wildlife Management*.

Abstract

Recent studies on white-tailed deer (*Odocoileus virginianus*) fawns in the southeastern U.S have indicated that rates of survival have declined in some areas. Vital rates, including adult female survival, fecundity, and fawn survival, can have varying effects on population growth, and few studies have used field-based vital rates to conduct sensitivity analyses or model deer population trajectories under potential changes in survival rates. During 2013-15, we radiocollared and monitored 70 mature (≥2.5 years) and 21 yearling (1.5 year-old) female deer on Tensas River National Wildlife Refuge, Louisiana (TRNWR). Annual survival averaged 0.815 (95% CI = 0.734-0.904) for mature females and 0.857 (95% CI = 0.720-1.00) for yearling females. Using observed values of fawn survival, female survival, and fecundity data from TRNWR, we estimated an increasing population trajectory ($\lambda = 1.043$). We modeled low, medium and high values for these parameters and determined that survival of mature females was the most elastic vital rate. For potential harvest intensity scenarios, we projected the population for 10 years using observed vital rates. Projections for 0% ($\lambda = 1.126$) and 10% hunting mortality ($\lambda = 1.041$) predicted increasing populations, whereas 20% ($\lambda = 0.959$) and 30% hunting mortality ($\lambda = 0.878$) resulted in population declines. Reductions in fawn survival led to population declines ($\lambda = 0.950$), but elimination of female harvest offset declines ($\lambda = 1.037$). Our results suggest that deer populations on TRNWR are sustainable under current harvest guidelines. However, reductions in female harvest may be necessary if fawn survival decreases. Alternately, reductions in predator populations may result in increased fawn survival. Therefore, managers will need to balance public perception and acceptance, economics, and population dynamics when assessing potential management strategies.

INDEX WORDS: harvest, Louisiana, mortality, *Odocoileus virginianus*, population growth, recruitment, white-tailed deer

Introduction

Population dynamics of ungulates are complex, and how predation and resource availability affect population growth has been debated (Peek 1980, Gaillard et al. 2000, Sinclair and Krebs 2002). Recognizing influences of selected vital rates (e.g., juvenile survival, adult female survival, fecundity) on population dynamics is crucial to predict population trends and inform management decisions. Ungulate populations are typically characterized by high and stable survival rates of adult females, moderately variable fecundity rates, and widely variable fawn survival rates (Gaillard et al. 1998, 2000). In addition, population growth is affected by both variability and elasticity of vital rates (Gaillard et al. 1998). As discussed by Chitwood et al. (2015a), demographic analyses, including sensitivity analyses of matrix population models, can provide 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).

Recent declines in fawn survival have been documented in many parts of southeastern U.S. (Kilgo et al. 2010), and research in some areas has shown fawn survival is low (14-33%; Epstein et al. 1985, Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015b, Nelson et al. 2015). Robinson et al. (2014) concluded that reduced antlerless harvest may be sufficient to offset projected deer population declines due to increased predation on fawns. However, they acknowledged that in areas with low recruitment (e.g., 25%) reduced antlerless harvest may not be sufficient to stabilize populations. In a recent study on an area with low fawn survival (14%), Chitwood et al (2015a) confirmed this hypothesis, concluding that protection of adult females from harvest may not completely offset projected population declines. However, no other site-specific population models or sensitivity analyses have been conducted in the southeastern U.S primarily because site-specific information on adult female survival is lacking (Robinson et al. 2014). Because vital rates can vary across the region (DeYoung 2011), we used the same methodology as Chitwood et al. (2015a) to compare projected population growth based on site-specific data from a study area in northeastern Louisiana to those determined by their study to evaluate regional variability in potential population responses to declining recruitment rates and help inform management decisions. Our objectives were to (1) determine survival of adult females, (2) estimate mortality rates attributable to natural causes and hunting, (3) assess the relative importance of stage-specific vital rates to population growth, and (4) evaluate changes in survival rates and their potential to affect deer population estimates via underlying changes in vital rates.

Study Area

The study was conducted on the Tensas River National Wildlife Refuge and adjacent private lands (hereafter Tensas) located in northeastern Louisiana in the upper Tensas River Basin. The 30,750-ha refuge was established in 1980 and was once extensively logged hardwoods and agricultural lands. Since acquisition by the United States Fish and Wildlife Service, forests on the refuge have been allowed to grow into mature bottomland hardwood and swamps, and former agricultural fields have been replanted in native hardwoods. TRNWR was bordered almost entirely by agriculture on all sides, making it an island of habitat for many species including deer and the Louisiana black bear (*Ursus americanus luteolus*).

The Tensas River and surrounding areas were once the location of the main channel of the Mississippi River, and remains in the western Mississippi River floodplain. Topography on Tensas was flat to slightly undulating with 0-8% slopes and elevations ranging from 17 to 23 m above mean sea level (USGS 1995). Typical of a Mississippi River floodplain, ridge/swale, oxbow lakes, and backwater swamps were present. Soils were alluvial, poorly drained but highly fertile, and were comprised mostly of the Tensas-, Sharkey-, or Alligator-series (UDSA 1968). The climate of Tensas was humid subtropical. Mean annual temperature was 19°C, with mean high and low temperatures of 25°C and 12°C, respectively, and annual precipitation averaged 130 cm (NOAA 2015).

Habitats on Tensas consisted of mature bottomland hardwoods (77%), early to mid-successional hardwood plantings (20%), wetlands/open water (2%), moist-soil management areas (<1%), cropland (<1%), and administrative sites (<1%). Overstory vegetation consisted of water oak (*Quercus nigra*), willow oak (*Q. phellos*), hickory (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), and sugarberry (*Celtis laevigata*), with interspersed baldcypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) swamps. The understory consisted of dwarf palmetto (*Sabal minor*), poison ivy (*Toxicodendron radicans*), blackberry (*Rubus* spp.), trumpet creeper (*Campsis radicans*), and greenbrier (*Smilax* spp.). Several mast-producing species such as blackberry and pokeweed (*Phytolacca americana*) could be found in abundance along roads and edges and where forest management practices have maintained a more open canopy. Early to mid-successional hardwood plantings established for carbon credits were distributed throughout TRNWR. These plantings were initiated between 1985 and 2009. Agricultural crops grown on Tensas included corn (*Zea mays*), cotton (*Gossypium hirsutum*), soybeans (*Glycine max*) and rice (*Oryza* sp.).

Deer densities on TRNWR were approximately 17-22 deer/km^2 (S. Durham, Louisiana Department of Wildlife and Fisheries, personal communication). Annual harvest during the study averaged 903 ± 55 (SE) deer per year, a decline from the average of 1,197 ± 49 (SE) deer per year in the 1990s (J. Dickson, U.S. Fish and Wildlife Service, personal communication). Deer hunting season on adjoining private land began with archery hunting on October 1 and lasted until January 31 with 20 days of primitive weapon hunting and 65 days of modern firearms hunting. On TRNWR, archery hunting began in early November and lasted until January 31. Deer hunting season on TRNWR also included 7 days of modern firearms hunting (2 days of youth only, 1 day antlerless only, 4 days of lottery hunts) and 2 days of primitive weapons hunting.

Methods

Female Capture

During January-April 2013-2015, we captured yearling (1.5 years) and mature (≥ 2.5 years) females using a combination of drop nets (18.3m x 18.3m or 15.2m x 15.2m), rocket nets (12.2m or 18.3m) and darting with a tranquilizer gun (Dan-Inject, Børkop, Denmark) from a tree stand over bait. We anesthetized deer caught under nets with an intramuscular injection of ketamine hydrochloride (3.5 mg/kg; Congaree Veterinary Pharmacy, Cayce, SC) and xylazine hydrochloride (2.5 mg/kg; Congaree Veterinary Pharmacy). When darting, we used Telazol (250 mg; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine hydrochloride (225 mg; Congaree Veterinary Pharmacy) in 1-ml Pneu-Dart transmitter darts (Pneu-Dart Inc., Williamsport, PA). Once deer were located or extracted from the net, we placed them in a sternal position on an insulated mat and covered them with a blanket to aid in thermoregulation. We applied ophthalmic ointment and a blindfold and monitored vital signs at 10-minute intervals. We estimated age using tooth wear and replacement (Severinghaus 1949) and the presence staining on the third premolar. We radio-collared (Model 2510B, Advanced Telemetry Systems, Isanti, MN), ear-tagged, and implanted each female with a vaginal implant transmitter (VIT; Model

M3930 or M3930L, Advanced Telemetry Systems). Radiocollars were equipped with an 8-hour mortality switch. Following instrumentation, we reversed the xylazine hydrochloride with tolazoline hydrochloride (150 mg intravenous and 150 mg intramuscular; Congaree Veterinary Pharmacy) and monitored deer until ambulatory. Capture and handling protocol was approved by the University of Georgia Institutional Animal Care and Use Committee, Permit #A2012 06-006-Y3-A2.

Female Survival

Each year, we monitored yearling and mature females weekly from capture until June 1, ≥7 times weekly June through August, and ≥1 time monthly September through January. When we detected a mortality signal, we located radiocollars as soon as possible and assigned cause of death as natural (predation, disease) or hunting-related. We used Kaplan-Meier models in the *survival* package in R (version3.2, R Core Team, Vienna, Austria) to estimate annual survival based on cause of death (i.e., natural or hunting) for yearling and mature females over monthly intervals from capture until January 14. We used a staggered-entry approach (Pollock et al. 1989) and categorized deer into groups based on 1-month capture periods with January 15 as the annual starting date.

Model Structure

To examine current population trends and effects of different harvest intensities on dynamics of the Tensas population, we used a female-based Lefkovitch matrix model (Lefkovitch 1965) with a 1-year time step:

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

Our model was composed of 3 stages, which corresponded to fawns (0-1 year old), yearlings (1-2 years old), and mature adults (≥2 years old) and included elements of fecundity (*F*) and survival (*S*) for each stage. Like Chitwood et al (2015a), we assumed that the fawn class had negligible fecundity and did not include a fecundity value for that stage (see also Dye 2007). Using the population matrix, change in population could be calculated using the equation:

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

where $\mathbf{n}(t)$ was a vector giving abundances of each stage in the population at time t and $\mathbf{A}$ was the population projection matrix. The left eigenvector of $\mathbf{A}$ gave expected relative contribution of a female in a given stage to future population growth. Following Chitwood et al. (2015a), we made several simplifying assumptions for our model: (1) density-independence, (2) geographic closure, (3) no male-limitation, (4) homogeneity of parameters for each stage, and (5) no reproductive senescence. Although Chitwood et al. (2015a) reported lower deer densities (6 deer/km^2) than those on Tensas, herd health checks performed on TRNWR in the 1990s and 2000s indicated that the herd was within nutritional carrying capacity (J. Dickson, U.S. Fish and Wildlife Service, personal communication); therefore, density-dependent feedbacks on fecundity or survival were likely to be negligible.

Model Development

We parameterized our population matrix using vital rates derived solely from radio telemetry data collected on our study site. To calculate female and yearling fecundity, we determined fecundity rate using number of fawns produced per female from documented births (via vaginal implant transmitters, see Chapter 2). Because our matrix was female-based, we included only the female portion of the fecundity rate. We assumed a 1:1 male-to-female fawn ratio, and therefore divided fecundity rates by 2. For mature females, we documented 14, 6, and

8 births with known litter size, yielding 23, 12, and 16 fawns in 2013-15; thus, mature female fecundity rates were 1.64, 2, and 2 in 2013, 2014, and 2015, respectively. For females bred as yearlings, we documented 3, 1, and 1 births with known litter size, yielding 4, 1, and 1 fawn in 2013-15, and yearling fecundity rates were 1.33, 1, and 1 in 2013, 2014, and 2015, respectively. Although the sample size for yearlings was low, fecundity data were consistent with rates documented in northeastern Louisiana (S. Durham, Louisiana Department of Wildlife and Fisheries, unpublished data). Fawn survival rates were based on estimates of fawn survival to 12 weeks (see Chapter 2). In 2013 and 2014, we monitored radiocollared fawns weekly from 12 weeks old until collar failure (approximately 6 to 9 months of age), and we did not document any natural mortality. Although there is a possibility that fawns died after censoring (e.g., after 9 months of age), we believe that the 12-week survival rate adequately estimates annual survival. Mature adult and yearling survival rates were determined as described above. We estimated starting population size for female fawns, yearlings, and mature adults using density and sex ratio estimates derived from harvest and survey data on Tensas (S. Durham, personal communication) as well as published estimates of female age structure in white-tailed deer populations (Dapson et al. 1979, Dusek et al. 1989).

We followed the approach used by Chitwood et al (2015a) to create a base model (current scenario) using current vital rates of the Tensas herd and used low, medium, and high values for all parameters (Table 3.1) to represent the range of possible trajectories and to incorporate variability and uncertainty into projections. High and low parameter values represented highest and lowest observed values, respectively, and medium parameter values represented mean observed values. We used the *popbio* package in R to determine the stable stage distribution

(SSD) and run the matrix at SSD to determine λ, sensitivities, elasticities, and to project population size for 10 years.

We then manipulated our base model to incorporate changes in vital rates. Fecundity and fawn survival rates remained unchanged, but we adjusted yearling and mature adult survival rates to reflect 0%, 10%, 20%, and 30% hunting mortality. To allow comparisons to the results from Chitwood et al (2015a), we also manipulated our base model and 0% hunting mortality scenario to include reductions in fawn survival. For these scenarios, adult survival and fecundity remained unchanged, but we used the fawn survival values reported by Chitwood et al. (2015a; Table 3.2). We constructed new matrices for each, which included adjusted vital rates (Table 3.3) based on data from our study site. As described in the construction of the base model, we used low, medium, and high values to represent the potential range of variation (Table 3.3) and for each scenario and calculated λ, sensitivities, elasticities, and population size after 10 years.

Results

We captured and radiocollared 91 individual female deer, including 70 mature adults (21, 21, and 28 in 2013-2015, respectively) and 21 yearlings (8, 9, and 4 in 2013-2015, respectively). We recaptured 11 deer following their initial capture (3 in 2014, 8 in 2015) resulting in 81 mature adults used in our analysis. Accounting for only natural mortality, mean annual survival of mature adults was 0.914 (95% CI = 0.854-0.977) and mean annual survival of yearlings was 0.952 (95% CI = 0.866-1.00; Table 3.4). Accounting for both natural and hunting mortality, mean annual survival of adults was 0.815 (95% CI = 0.734-0.904) and mean annual survival of yearlings was 0.857 (95% CI = 0.720-1.00; Table 3.4)

For current, 0%, 10% hunting mortality, and reduced fawn survival + 0% hunting mortality scenarios, the most sensitive vital rate was mature female survival, and in the reduced fawn survival, 20%, and 30% hunting mortality scenarios, the most sensitive vital rate was fawn survival (Table 3.5). The most elastic vital rate in all scenarios was mature female survival (Table 3.5).

The current scenario projected a growth rate of λ = 1.043 (low λ = 0.891, high λ = 1.182; Figure 3.1), Medium values for 0% and 10% hunting mortality scenarios predicted increasing populations (Figure 3.2A, B), projecting growth rates of λ = 1.126 (low λ = 1.026, high λ = 1.226) and λ = 1.041 (low λ = 0.938, high λ = 1.144), respectively. Both 20% and 30% hunting mortality scenarios predicted declining populations (Figure 3.2C, D), with λ = 0.959 (low λ = 0.852, high λ = 1.064) and λ = 0.878 (low λ = 0.768, high λ = 0.985), respectively. The reduced fawn survival scenario projected population declines with a growth rate of λ = 0.950 (low λ = 0.819, high λ = 1.060; Figure 3.3A), but the reduced fawn survival + 0% hunting scenario projected a growth rate of λ = 1.037 (low λ = 0.961, high λ = 1.111; Figure 3.3B),

Discussion

Knowledge of survival rates of adult females is important for managing sustainable deer herds but few studies have evaluated survival in the southeastern U.S. Our data provide estimates of yearling and mature female survival in the southeastern U.S., and to our knowledge is the first to deconstruct total mortality into natural and hunting mortality. Our non-hunting and total mortality rates for yearling (5% and 14%, respectively) and mature (9% and 18%, respectively) females were similar to those throughout the white-tailed deer range (DeYoung 2011) and to total adult female mortality in North Carolina (20%; Chitwood et al. 2015a). Previous studies in the southeastern U.S. have assumed total adult female mortality rates of 25% (South Carolina; Comer et al. 2005) and 30% (Mississippi; Gruver et al. 1984) or non-hunting mortality rate of 10% (Georgia; Keyser et al. 2006). Although we reported similar non-hunting mortality rates, we observed lower hunting mortality rates. Because mortality rates vary spatially, use of empirically derived mortality rates instead of assumed mortality rates will better inform management decisions.

We noted that survival of mature adults was the most elastic vital rate, consistent with Chitwood et al. (2015a) and other studies of large herbivores (Gaillard et al. 1998, Eberhardt 2002). Elasticity is valuable analytically, but it has limitations. Elasticities cannot always predict how population growth will change as vital rates change, and although it can be good indicator of growth-rate changes, real world management actions rarely change vital rates by the same proportionate amount determined by the sensitivity analysis (Mills et al. 1999). Vital rates with low elasticities typically have higher variance than rates with higher elasticities (Pfister 1998), and rates with low elasticities changing over wide ranges could affect growth rate as much as the vital rate ranked as most important based on elasticities alone (Gaillard et al. 1998). This underscores the importance of taking the influence of all vital rates on population growth into account when making management decisions.

Under current observed vital rates, the white-tailed deer population on Tensas is projected to be stable or slightly increase, despite low fawn survival rates (27%). Although Chitwood et al. (2015a) documented similar survival rates for mature females in North Carolina, they projected a declining deer population under current conditions ($\lambda = 0.905$; low $\lambda = 0.788$, high $\lambda = 1.003$). Robinson et al. (2014) projected declines in deer populations when fawn survival was low (23%) and adult mortality was 10% above estimates of natural mortality rates, but reported increasing populations when female mortality was reduced to 5% above natural mortality. Our findings suggest that the Tensas population is increasing despite a 10% hunting mortality rate. When we modeled populations on Tensas using current yearling and adult vital rates, but incorporating the fawn survival rates reported in Chitwood et al. (2015a), we also documented a declining population trend. However, in our study the elimination of female harvest offset the reduction of fawn survival; whereas Chitwood et al. (2015a) concluded that elimination of female harvest ($\lambda = 0.935$; low $\lambda = 0.875$, high $\lambda = 1.002$) may not completely offset population declines. Although our vital rates for adult survival were similar to Chitwood et al. (2015a) and Robinson et al. (2014), the difference in population projections is mostly likely due to the higher fecundity rates of mature adults and much higher deer densities in our study. The number of fawns being produced may exceed the consumptive capacity of predators and allows populations to be more tolerant to predation pressures.

Deer in multi-predator landscapes face the challenges of variation in species-specific predator hunting strategies (Sih 2007, Sih et al. 2012) and the temporal efficacy of predation (Vreeland et al. 2004), potentially leading to lower survival than deer in landscapes with a single predator. However, the presence of multiple predators may not dictate population growth trends. Chitwood et al. (2015a) documented coyotes (*Canis latrans*) as the only fawn predator on their North Carolina study site, but our study was conducted in an area with sympatric populations of coyotes, bobcats (*Lynx rufus*), and black bear. Although predators consumed 64% of collared fawns on Tensas (see Chapter 2), current vital rates projected an increasing population. Contrary to our results, Chitwood et al. (2015a) projected declining populations when predators consumed 54% of collared fawns (Chitwood et al. 2015b) and concluded that increases in fawn survival through coyote control had a greater impact on population growth than reduction in female harvest.

The density of deer on Tensas may influence population growth by reducing fawn predation through predator swamping. Several studies on neonatal ungulates have reported changes in survival in relation to the peak birthing period. Whittaker and Lindzey (1999) documented higher survival for white-tailed and mule deer (*O. hemionus*) fawns born later in the birthing season, and Gregg et al. (2001) determined that pronghorn (*Antilocapra americana*) fawns born during the peak birthing period had higher survival rates than those born during the non-peak period. Robinson et al. (2014) based their population projections on densities reported throughout the eastern U.S. (range = 5.4-9.2 deer/km^2), and Chitwood et al. (2015a) reported a density of 6 deer/km^2. Densities on Tensas were higher (17-22 deer/km^2), and additionally, most births (74%) on Tensas occurred during a 4-week period (July 4-July 31; see Chapter 2). The abundance of fawns during a short period likely overwhelmed predator populations, and individual fawns may be at a reduced risk of predation during the first few weeks of life when they are most likely to be predated (see Chapter 2).

Management Implications

Our results indicate that low fawn survival is not always a harbinger of deer population decline. In herds with high fecundity rates and high population densities, reduction in fawn survival may not necessitate changes in management strategies. However, managers should monitor deer herds for declines in fawn survival or increases in female mortality, as they are important variables in population change. If fawn survival continues to decrease in these areas, then reduction of female harvest would be the most practical management strategy to offset population declines. However, reduction or elimination of female harvest may influence hunter satisfaction, recruitment, or retention, and stakeholder groups may pressure management agencies to implement predator management strategies even if deer populations are stable. Although predator control may be necessary in some systems (Chitwood et al. 2015a), it can be costly or provide inconsistent results (Kilgo et al. 2014, Gulsby et al. 2015). Moreover, in multi-predator systems such as Tensas, predation may be compensatory or one predator may not cause a disproportionately greater number of mortalities than the others (see chapter 2). Hence, reductions in all predator species may be necessary to achieve increases in fawn survival. In areas with prolonged fawning periods, predators may have a disproportionate impact even if fecundity rates are high because the number of fawns available at any time during the fawning period may be insufficient to satiate predators. Therefore, managers will need to find a balance between public perception, economics, and population dynamics when assessing potential management strategies. Because predator communities, deer densities, and vital rates vary throughout the deer's range, expanded research emphasis should address regional and site-specific responses to fawn predation pressures and population resiliency to these pressures.

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Table 3.1. Values for parameters used in the population matrix based on current vital rates of white-tailed deer on Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

	Stage (parameter)	Low	Medium	High
Fecundity rates	Yearling (F_y)	0.500	0.600	0.670
	Mature (F_m)	0.820	0.910	1.000
Survival rates	Fawn (S_f)	0.200	0.271	0.357
	Yearling (S_y)	0.750	0.857	1.000
	Mature (S_m)	0.714	0.815	0.875

Table 3.2. Values for parameters used by Chitwood et al. (2015b) in their population matrix based on current vital rates of white-tailed deer.

	Stage (parameter)	Low	Medium	High
Fecundity rates	Yearling (F_y)	0.700	0.750	0.780
	Mature (F_m)	0.810	0.875	0.940
Survival rates	Fawn (S_f)	0.105	0.141	0.185
	Yearling (S_y)	0.630	0.775	0.880
	Mature (S_m)	0.721	0.801	0.854

Table 3.3. Values used for survival parameters in population matrices under different survival scenarios of white-tailed deer at Tensas River National Wildlife Refuge, Louisiana. Fecundity rates were not included because we used current scenario rates. Reduced fawn survival rates were based on those published in Chitwood et al. (2015b). All other parameter values were manipulated from natural mortality estimates.

Scenario	Stage (parameter)	Low	Medium	High
0% hunting	Fawn (S_f)	0.200	0.271	0.357
	Yearling (S_y)	0.875	0.952	1.000
	Mature (S_m)	0.875	0.914	0.944
10% hunting	Fawn (S_f)	0.200	0.271	0.357
	Yearling (S_y)	0.775	0.852	0.900
	Mature (S_m)	0.775	0.814	0.844
20% hunting	Fawn (S_f)	0.200	0.271	0.357
	Yearling (S_y)	0.675	0.752	0.800
	Mature (S_m)	0.675	0.714	0.744
30% hunting	Fawn (S_f)	0.200	0.271	0.357
	Yearling (S_y)	0.575	0.652	0.700
	Mature (S_m)	0.575	0.614	0.644
Reduced fawn survival	Fawn (S_f)	0.105	0.141	0.185
	Yearling (S_y)	0.750	0.857	1.000
	Mature (S_m)	0.714	0.815	0.875
Reduced fawn survival + 0% hunting	Fawn (S_f)	0.105	0.141	0.185
	Yearling (S_y)	0.875	0.952	1.000
	Mature (S_m)	0.875	0.914	0.944

Table 3.4. Annual survival of yearling (1.5 years) and adult (≥2.5 years) female white-tailed deer at Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

Cause of mortality	Stage	Year	*n*	Survival rate	SE	95% Cl
Natural	Yearling	2013	8	0.875	0.117	0.673-1.000
		2014	9	1.000	N/A	N/A
		2015	4	1.000	N/A	N/A
		Overall	21	0.952	0.047	0.866-1.000
	Mature	2013	21	0.905	0.641	0.788-1.000
		2014	24	0.875	0.068	0.752-1.000
		2015	36	0.944	0.038	0.873-1.000
		Overall	81	0.914	0.031	0.854-0.977
Natural + hunting	Yearling	2013	8	0.750	0.153	0.503-1.000
		2014	9	0.889	0.105	0.706-1.000
		2015	4	1.000	N/A	N/A
		Overall	21	0.857	0.076	0.720-1.000
	Mature	2013	21	0.714	0.099	0.545-0.936
		2014	24	0.875	0.068	0.752-1.000
		2015	36	0.833	0.062	0.720-0.964
		Overall	81	0.815	0.043	0.734-0.904

Table 3.5. Sensitivities and elasticities for medium vital rates in all scenarios of white-tailed deer population trends at Tensas River National Wildlife Refuge, Louisiana, 2013-2015.

Scenario	Parameter	Sensitivity	Elasticity
Current	Fawn survival	0.654	0.170
	Yearling survival	0.176	0.144
	Mature survival	0.660	0.516
	Yearling fecundity	0.044	0.025
	Mature fecundity	0.166	0.144
0% hunting	Fawn survival	0.627	0.151
	Yearling survival	0.156	0.132
	Mature survival	0.698	0.567
	Yearling fecundity	0.036	0.019
	Mature fecundity	0.163	0.132
10% hunting	Fawn survival	0.653	0.170
	Yearling survival	0.177	0.144
	Mature survival	0.660	0.516
	Yearling fecundity	0.044	0.025
	Mature fecundity	0.165	0.144
20% hunting	Fawn survival	0.678	0.191
	Yearling survival	0.201	0.158
	Mature survival	0.617	0.459
	Yearling fecundity	0.054	0.034
	Mature fecundity	0.166	0.158
30% hunting	Fawn survival	0.701	0.216
	Yearling survival	0.230	0.171
	Mature survival	0.567	0.397
	Yearling fecundity	0.067	0.046
	Mature fecundity	0.165	0.171
Reduced fawn survival	Fawn survival	0.802	0.119
	Yearling survival	0.120	0.108
	Mature survival	0.762	0.654
	Yearling fecundity	0.018	0.011
	Mature fecundity	0.l13	0.108
Reduced fawn survival + 0% hunting	Fawn survival	0.754	0.103
	Yearling survival	0.103	0.094
	Mature survival	0.795	0.701
	Yearling fecundity	0.014	0.008
	Mature fecundity	0.108	0.094

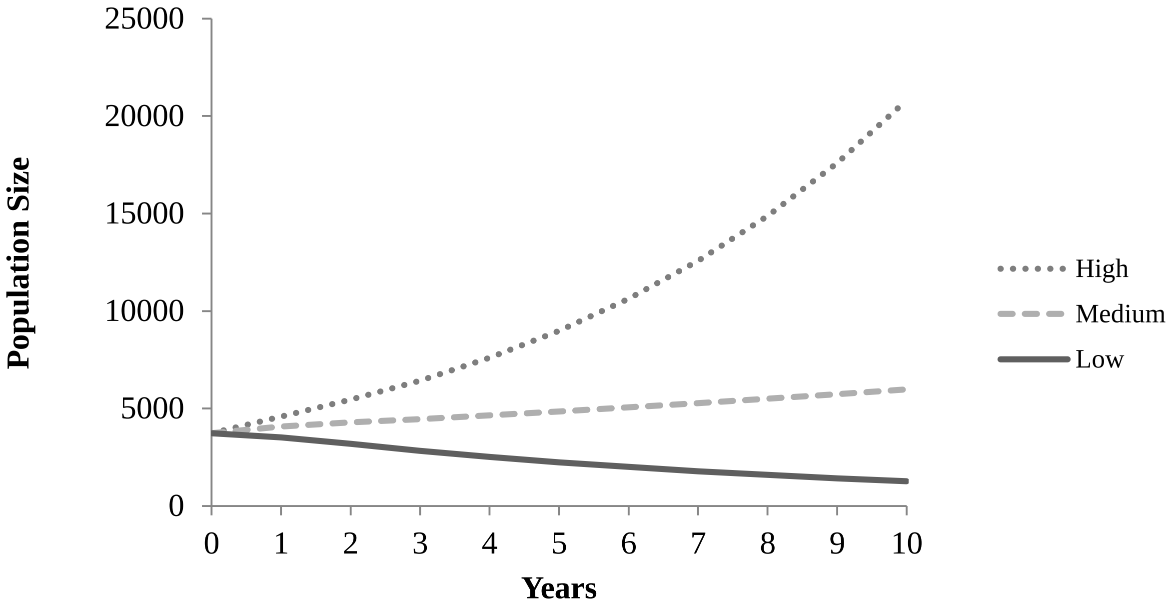

Figure 3.1. Predicted size of the white-tailed deer population after 10 years of current vital rates at Tensas River National Wildlife Refuge, Louisiana. Predicted population sizes were based on low, medium, and high vital rates.

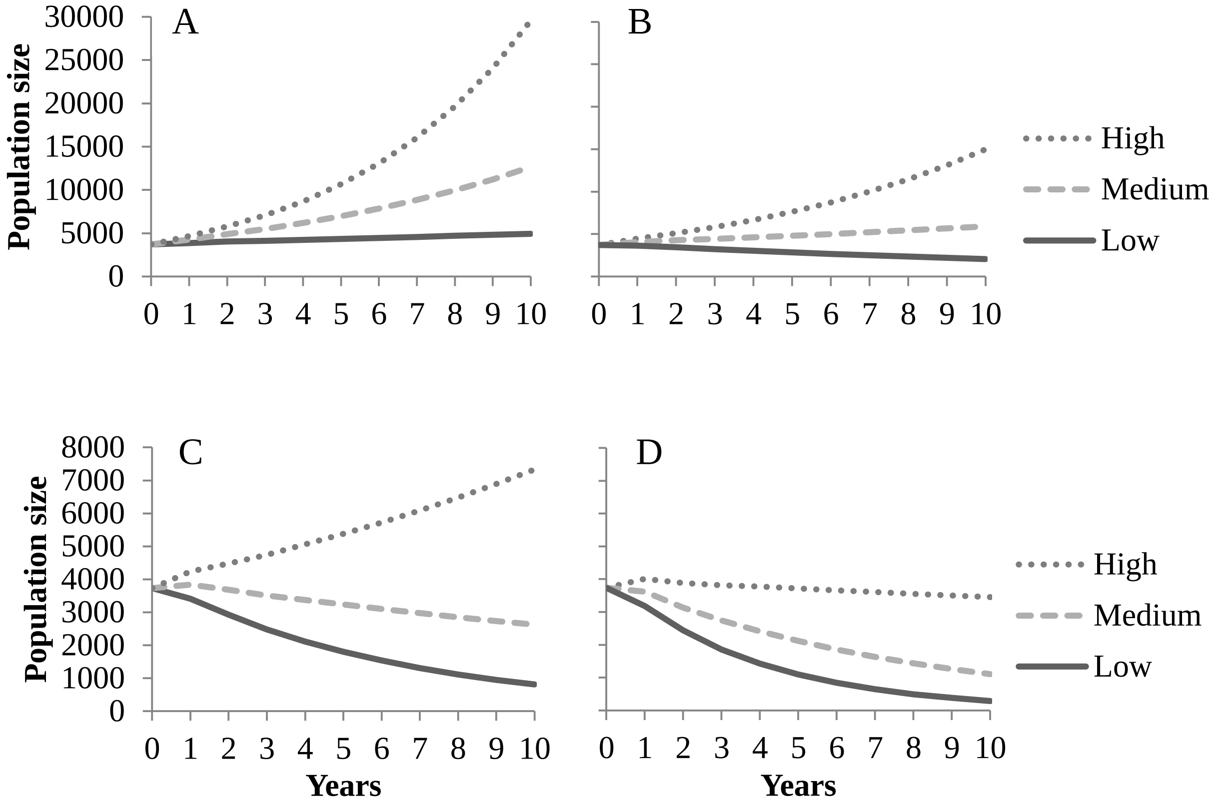

Figure 3.2. Predicted size of white-tailed deer population after 10 years of A) 0% hunting mortality, B) 10% hunting mortality, and C) 20% hunting mortality at Tensas River National Wildlife Refuge, Louisiana. Predicted population sizes were based on low, medium, and high vital rates.

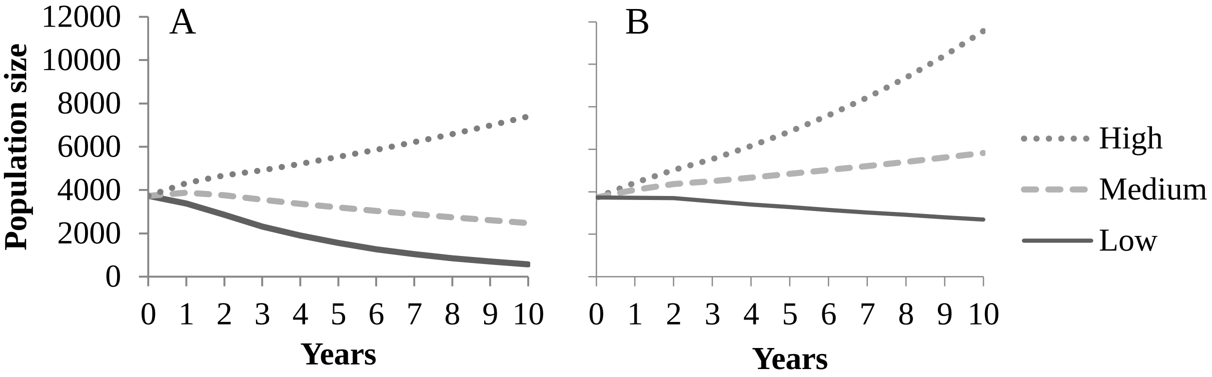

Figure 3.3. Predicted size of white-tailed deer population after 10 years of A) reduced fawn survival and B) reduced fawn survival + 0% hunting mortality at Tensas River National Wildlife Refuge, Louisiana. Predicted population sizes were based on low, medium, and high vital rates.

CHAPTER 4

SUMMARY AND MANAGEMENT IMPLICATIONS

Declines in white-tailed deer (*Odocoileus virginianus*) recruitment rates due to predation on fawns have become a concern in recent years. However, fawn survival rates are site-specific, and their influence on population growth rates can vary based on other vital rates of the population. Relatively few studies have been conducted in the southeastern U.S. examining fawn survival and cause-specific mortality, and no research in this region has occurred in areas with 3 important fawn predators. Likewise, only one other study in the southeastern U.S. has used site-specific vital rates to project population growth. Therefore, I investigated survival and cause-specific mortality of fawns in northeastern Louisiana and examined biological and landscape variables influencing survival. Likewise, I used site-specific vital rates to project current population trends and evaluated the influence of changes in survival rates of females and fawns on population growth.

My results showed that fawn survival rates were consistent with other studies conducted in the southeastern U.S., although previous studies were conducted in systems with only 2 fawn predators. In my study, black bear (*Ursus americanus*) predation was the greatest source of mortality, but my findings suggest that bears partition fawns with coyotes (*Canis latrans*) and bobcats (*Lynx rufus*). I also found that fawn survival was positively correlated with birth mass and proximity to old reforestation stands and negatively correlated with proximity to cropland and young reforestation stands. Lower survival rates of fawns located near early successional habitats is likely due to higher predator densities and greater hunting efficacy in those areas.

Although fawns near older reforested stands exhibited higher survival, closed canopy systems can have reduced deer forage availability. Therefore, having early successional hardwoods and cropland interspersed throughout older hardwood stands may provide a balance between decreasing predation rates and maximizing forage availability.

My results indicated that adult female survival was high, and changes in survival of mature (age) females would have the greatest impact on population growth. Under current observed vital rates, the deer population on Tensas is projected to be stable or slightly increasing, despite low fawn survival rates (27%). Fawn survival rates lower than those currently observed on Tensas resulted in a declining population projection, but reduction of female harvest was sufficient to offset declines. Because fawn and adult female survival rates are important variables in population change, managers should monitor deer herds for declines in fawn survival or increases in female mortality. If fawn survival continues to decrease on Tensas, then reduction of female harvest may be necessary to offset population declines.

Although my findings indicate that low fawn survival due to predation may not cause deer population decline in herds with high population densities and fecundity rates, the influence of predation on deer populations in the southeastern U.S. may depend on a myriad of factors including predator communities, habitat characteristics, and deer densities. Therefore, additional research is needed to address these differences and how they impact vital rates across the region. Understanding how predator communities and factors such as biological and habitat characteristics may influence fawn mortality and population resiliency will provide managers with a powerful tool to manage sustainable deer herds on landscapes with diverse and abundant predators.