

Factors Affecting White-tailed Deer Recruitment in Virginia

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Abstract (academic)

Deer (*Odocoileus* spp.) are an important cultural and economic resource. They are the most popular game species in the United States and the number one driver of conservation funding. On the other hand, they also cause damage to resources including to the agricultural industry, private property and to humans via deer vehicle collisions. Many areas in eastern North America have experienced a decline in white-tailed deer (*Odocoileus virginianus*) populations over the past twenty years concurrent with changes in landscape, deer harvest strategies, and increasing and expanding black bear (*Ursus americanus*) and coyote (*Canis latrans*) populations. Most studies have addressed this problem at small spatial and temporal scales and in areas where predation was assumed to be limiting population growth. We evaluated white-tailed deer fawn recruitment both directly and indirectly at relatively broader spatial and temporal scales. We studied fawn survival on Marine Corps Base Quantico in Virginia, USA from 2008–2019. We used the Kaplan-Meier estimator, and Cox-proportional hazards models to assess annual survival and factors that influence hazard risk such as sex, weather, landscape composition and configuration and food availability. On Marine Corps Base Quantico, we found an increase in red oak mast abundance increases survival and probability of fawn survival was higher during the first interval of the study (2008–2010; 0.71 [0.52–0.96]; survival probability [CI_{95%}]) than the last three intervals (2011–2013; 0.46 [0.30–0.70]; 2014–2016; 0.48 [0.35–0.66] and 2017–2019; 0.50 [0.39–0.63]). We also found that predation was the leading source of mortality. We assessed recruitment using lactation status from hunter harvest data collected by the Virginia Department of Game and Inland Fisheries during a 22-year period in 30 counties in the Appalachian

Mountains of western Virginia. We predicted lactation status as a function of landscape composition and configuration, oak mast abundance, weather, age, and predator detection rates using generalized linear mixed models. We found land cover diversity index positively and black bear detection rate negatively influenced recruitment. Age also predicted lactation status with middle-aged females (3.5–4.5 years old) having a higher lactation probability than mature (≥ 5.5 years old) age and young (2.5 years old) age class deer. Based on these findings, recruitment is likely to be greater in areas that are heterogeneous. Therefore, if an increase in recruitment is desired silvicultural practices such as fire and timber harvest could be used to permanently change land cover types. These silvicultural practices could also be used to increase the number of oaks on the landscape, and augment production of mature oaks as red oak mast abundance influenced fawn survival. Also reducing predation by manipulating predator densities could improve recruitment. Another potential option which needs further research, would be to reduce predator efficiency by increasing hiding cover for fawns.

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Abstract (public)

Deer (*Odocoileus* spp.) are an important cultural and economic resource. They are the most popular game species in the United States and the number one driver of conservation funding. Conversely, they also cause damage to resources including to the agricultural industry, private property and to humans via deer vehicle collisions. Some areas in eastern North America have experienced a decline in white-tailed deer (*Odocoileus virginianus*) populations over the past twenty years concurrent with the colonization of coyotes (*Canis latrans*) as well as changes in habitat. Therefore, we aimed to determine white-tailed deer fawn survival rates and factors affecting recruitment across a large spatial and temporal scale. Recruitment is when an individual becomes part of the reproductive population. However, for harvestable populations, recruitment is when individuals can be legally harvested for the first time. On Marine Corps Base Quantico from 2008–2019, in Virginia, USA we found that probability of fawn survival was higher during the first interval of the study (2008–2010; 0.71 [0.52–0.96]; survival probability [CI_{95%}]) than the last three intervals (2011–2013; 0.46 [0.30–0.70]; 2014–2016; 0.48 [0.35–0.66] and 2017–2019; 0.50 [0.39–0.63]). We also discovered predation was the leading cause of death and probability of survival increased with increasing red oak mast abundance. Over a large spatial (30 counties) and temporal (22 years) scale we examined fawn recruitment by predicting lactation status of female harvested white-tailed deer in the Appalachians Mountains of western Virginia. We found land cover diversity index positively and black bear (*Ursus americanus*) detection rate negatively influenced recruitment. Age also predicted lactation status with middle-aged females (3.5–4.5 years old) having a higher lactation probability than mature (≥ 5.5 years old) age and

young (2.5 years old) age class deer. Based on these findings, recruitment is likely to be greater in areas that have a mixture of land cover types. Therefore, if an increase in recruitment is desired silvicultural practices such as fire and timber harvest could be used to permanently change land cover types. These silvicultural practices could also be used to increase the number of oaks on the landscape, and augment production of mature oaks as red oak mast abundance influenced fawn survival. Also reducing predation by manipulating predator densities could improve recruitment. Overall, we found diversity of land cover types, food availability, predators, and age influences population dynamics of white-tailed deer.

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Chapter 1: Introduction

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Understanding drivers of spatial and temporal variation in demography and population dynamics of large mammals, including ungulates such as white-tailed deer (*Odocoileus virginianus*), is key to managing a species. Adult survival and fecundity vary little in relation to environmental variability (Gaillard et al. 1998, 2000). Alternatively, large mammalian neonates experience a wide variation in recruitment (0–100%) with predators causing up to 100% of the mortalities (Linnell et al. 1995). Recruitment is the number of individuals that reach sexual maturity (Porter 1991). However, for harvestable populations, recruitment is when an individual survives until the harvest period. Knowing drivers of recruitment levels on specific sites is essential to make informed management decisions (Shuman et al. 2017).

A female's nutritional condition and body mass is linked to survival of their fawn, with higher nutritional condition and body mass increasing their offspring's chance of survival (Mech et al. 1991, Monteith et al. 2014). Pregnant females require 16.4% more energy than non-pregnant females and lactation has two to three times the energetic demands of pregnancy (Robbins 1993). Therefore, breeding is timed so the last trimester of a female's pregnancy, when 75–80% of the growth of the fetus occurs, and fawning coincide with the green up when food availability tends to be greatest (Armstrong 1950, Robbins et al. 1974, DeYoung and Miller 2011). Therefore, as the nutritional condition of an individual can impact fawn recruitment, habitat quality is crucial to maintaining deer herds at desired levels.

Extrinsic factors such as weather and landscape configuration can also affect ungulate body condition, as adult and fawn white-tailed deer body condition decreased with an increase in snow depth and adult body condition decreased with an increase in rainfall in the winter in Nova

Scotia (Garroway and Broders 2005). Gaillard et al. (1996) found that roe deer (*Capreolus capreolus*) fawn body mass was inversely related to summer temperature. Landscape conditions can also influence fawn survival. For example, probability of fawn survival increased with distance from young forest and crops and decreased with distance to older forests in Louisiana (Shuman et al. 2017). Conversely, in Pennsylvania, landscape metrics did not predict fawn survival (Vreeland et al. 2004).

Predators such as coyotes (*Canis latrans*) are a significant mortality source for white-tailed deer fawns in the southeastern USA, with up to 80% of fawn mortalities attributed to coyotes in a study area in South Carolina (Kilgo et al. 2012). Predation rates of fawns by coyotes in the Midwest and Northeast are lower than in the South (Cook et al. 1971, Nelson and Woolf 1987, Kilgo et al. 2012, Nelson et al. 2015, Kilgo et al. 2019). In South Carolina, low white-tailed deer density coincided with high coyote predation which led to a decrease in recruitment rate (Kilgo et al. 2010).

Bears depredate young elk (*Cervus canadensis*), black-tailed deer (*Odocoileus hemionus columbianus*), moose (*Alces alces*), and white-tailed deer (Franzmann et al. 1980, Ballard et al. 1999, Barber-Meyer et al. 2010, Murphie and McCoy 2011) accounting for a varying degree of total neonate mortalities. Fawns are most susceptible to bear predation during their first month of life with 82% of black bear (*Ursus americanus*) predations occurring during the first week of life in Louisiana (Shuman et al. 2017). Bear predation may increase when there is less concealment cover for the neonates such as after a fire (Zager and Beecham 2006). Black bear predation varies with predation rates of 10% (New Brunswick, Canada), 33% (Pennsylvania, United States), 33% (Louisiana, United States) and 49% (Minnesota, United States; Kunkel and Mech 1994, Ballard et al. 1999, Vreeland et al. 2004, Shuman et al. 2017).

Bobcats (*Lynx rufus*) also depredate fawns. Some studies, conducted in New Brunswick, Canada, Texas, Illinois, and Georgia, United States, found bobcats were a fairly unimportant component of fawn mortalities, accounting for between 4-10% of the mortalities (Cook et al. 1971, Ballard et al. 1999, Rohm et al. 2007, Nelson et al. 2015). In other areas, such as in Louisiana and Virginia, bobcats were an important source of mortality, comprising 22–23% of the mortalities (Schwede et al. 1993, Shuman et al. 2017). Bobcats can be the dominant predator of fawns, accounting for 12 of 18 predator caused deaths in South and Cat Islands in South Carolina (Epstein et al. 1983). If a deer herd is at or above habitat carrying capacity, predation may not be important (Ballard et al. 2001) as other factors such as disease and starvation can be the primary cause of death (Dion 2018, McGovern et al. 2020).

Landscape quality, configuration and composition can impact ungulate movement and predation with risk of harvest from humans on roe deer being higher than risk of predation on roe deer from Eurasian lynx (*Lynx lynx*) in open habitats. Lynx depredated roe deer more than humans did in habitats that had dense understories (Lone et al. 2014). Mountainous terrain increased the overall risk of depredation from lynxes and humans, but it was greater from lynxes. Roe deer spent more time vigilant when close to buildings and in open areas during the hunting season which suggests predation risk is greater in those areas (Benhaiem et al. 2008). In a study of elk-wolf relationships and how landscape influences their movements, greatest elk mortality occurred in grasslands on flat areas close to roads and streams, a landscape well suited to wolves as cursorial hunters (Kauffman et al. 2007). Fawn predation by coyotes decreased with greater total edge, Shannon's diversity index, interspersion and juxtaposition index and mean patch fractal dimension index and increased with greater mean forest patch size, all indications of a

heterogeneous landscape (Gulsby et al. 2017). Therefore, predators and landscape features intersect to influence survival and space use of ungulates.

There are numerous methods to monitor recruitment including hunter-observation surveys, trail camera surveys, lactation status, and fawn survival studies (Dzięciołowski et al. 1995, Gulsby and Miller 2013, Kilgo et al. 2014). Many agencies and private landowners use recruitment rates to monitor herd health and determine harvest goals. Lactation rate is defined as the percent of females that are lactating from the total number of harvested females (Campbell et al. 2016). Obtaining lactation rates from harvested females is one of the easier methods to assess recruitment, but is not as precise as fawn survival studies which are more labor and cost intensive (Dzięciołowski et al. 1995, Gulsby and Miller 2013, Kilgo et al. 2014).

There has been a decline in recruitment rates in parts of the southeastern USA (Howze et al. 2009, Kilgo et al. 2010) and many areas in eastern North America have experienced a decline in white-tailed deer populations over the past twenty years concurrent with landscape changes, and increasing and expanding black bear and coyote populations (Howze et al. 2009, Kilgo et al. 2010, Little et al. 2018). Previous studies have been constrained to small temporal and spatial scales and in areas where predation was often assumed to be limiting population growth. Therefore, my work will address this issue at a broader temporal and spatial scale.

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Chapter 2: White-tailed Deer Fawn Survival on Marine Corps Base Quantico

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ABSTRACT

Some areas in eastern North America have restricted harvest of white-tailed deer (*Odocoileus virginianus*) because of perceived reductions in recruitment and population size over the last decade. Although the restoration of black bears (*Ursus americanus*) and the colonization of coyotes (*Canis latrans*) have likely increased fawn predation in some areas, limited information exists on how temporally dynamic resources and weather influence fawn survival. Therefore, we evaluated fawn survival, cause specific mortality, and factors influencing mortality risk on Marine Corps Base Quantico in Northern Virginia, USA from 2008–2019. We predicted fawn survival would (1) increase with an increase in oak mast abundance the fall before birth and decrease with an increase in winter severity during gestation; (2) increase with greater precipitation during the growing season; and (3) increase with greater land cover patch diversity, complexity, total edge, and vary across land cover types. We fit 248 fawns with very high frequency collars and found predation was the leading cause of mortality ($n=42$; 45%). We estimated fawn survival to 133 days during four, 3-year intervals and found survival was greater during the first interval (2008–2010; 0.71 [0.52–0.96]; survival probability [CI_{95%}]) than the last three intervals (2011–2013; 0.46 [0.30–0.70]; 2014–2016; 0.48 [0.35–0.66] and 2017–2019; 0.50 [0.39–0.63]). We found that for every unit increase (SD) in annual red oak (*Quercus* spp.) mast abundance, the mortality hazard is reduced by 27% ($\beta = -0.32$, $p = 0.01$). Whereas other research has reported the effect of female maternal nutritional condition, the longevity of our study revealed a link between fawn survival and a specific maternal resource (red oak mast) only

available during gestation. Our results highlight the importance of oak mast in eastern deciduous forests, and more broadly, overwinter maternal condition on white-tailed deer recruitment.

INTRODUCTION

To manage wildlife populations, it is imperative to understand factors influencing population dynamics over time. In large mammals, adult survival and fecundity are less sensitive to environmental conditions than neonate survival (Gaillard et al. 1998, 2000). Ungulate recruitment can vary considerably (Linnell et al. 1995) and is often driven by factors including predation, weather, food availability, and landscape composition and configuration (Garroway and Broders 2005, Farmer et al. 2006, Gulsby et al. 2017, Shuman et al. 2017, Wright et al. 2019). These factors can vary spatially and temporally and may interact in complex ways to influence neonatal ungulate recruitment. Understanding these complex relationships is important for predicting effects of changing conditions on ungulate populations and for sound management.

Kilgo et al. (2010) suggested coyote range expansion could be causing a decline in white-tailed deer (*Odocoileus virginianus*) recruitment and abundance in portions of the southeastern United States. Numerous studies across the region have demonstrated coyotes (*Canis latrans*) can be an important source of mortality for fawns and may reduce recruitment (Kilgo et al. 2012, Chitwood et al. 2015a, Nelson et al. 2015, Watine and Giuliano 2016), but their impacts seem to vary based on the predator communities with black bears (*Ursus americanus*) and bobcats (*Lynx rufus*) causing variable amounts of mortality as well (Shuman et al. 2017, Kautz et al. 2019). However, the role of predation as an additive mortality source is unknown as fawn survival can be low in the absence of fawn predators (Dion 2018) and other factors such as disease can be important (McGovern et al. 2020).

Nutritional condition of adult females including gestational condition can also influence fawn survival. Hard mast availability in eastern deciduous forests is a primary driver of white-tailed deer nutritional condition and population dynamics (Feldhamer et al. 1989, Wentworth et al. 1992). However, hard mast production can be highly variable creating stochastic resource availability for mast dependent wildlife species (Diamond et al. 2000, Greenberg 2000). In these forests, during fall, white-tailed deer diets are largely comprised of oak (*Quercus* spp.) mast. Mast availability is critical for deer energetic reserves during gestation (Harlow et al. 1975) as acorns were found to have higher energy content than most other available resources (Pekins and Mautz 1988). Oak mast abundance the preceding fall positively influences fawn body mass (Feldhamer et al. 1989, Wentworth et al. 1992, Fairbanks 1993), and body mass has often been linked to increased fawn survival (Saalfeld and Ditchkoff 2007, Shuman et al. 2017, Dion 2018).

Landscape attributes can also influence fawn survival by altering the distribution and quality of forage resources, concealment cover, and predators. At the bed site scale fawns often select areas that provide adequate thermal and concealment cover (Huegel et al. 1986, Van Moorter et al. 2009) and bed sites typically have greater visual obstruction than the surrounding area (Huegel et al. 1986, Shuman et al. 2018). However, the link between visual obstruction and survival is unclear and other vegetation attributes, such as plant diversity, may also be important (Chitwood et al. 2015b). At a broader scale, landscape composition may influence fawn survival. For example, a recent meta-analysis revealed fawn survival probabilities increased with increasing agricultural land cover (Gingery et al. 2018). However, these results may be related to regional differences that co-vary with agricultural land cover (Kilgo et al. 2019) as some studies have found contrary results such as increasing fawn survival with distance to croplands (Shuman et al. 2017) and increasing amount of woodland cover (McGovern et al. 2020). Landscape

configuration may also influence fawn survival. For example, Rohm et al. (2007) found fawn survival increased with increasing edge density. Furthermore, in South Carolina, fawn survival increased with greater patch heterogeneity (Gulsby et al. 2017), potentially because coyote abundances often decrease with increasing patch diversity (Crooks 2002, Cherry et al. 2017).

On Marine Corps Base Quantico (hereafter Quantico) coyotes were rarely detected before 1995, but abundances increased between 1995–2005 (R. T. Stamps and S. Simmons, Marine Corps Base Quantico, unpublished report). Subsequent declines in white-tailed deer harvest, and increased observations of coyotes generated questions regarding the impact of predation on the local deer population relative to other factors such as weather and resource availability (R. T. Stamps and S. Simmons, Marine Corps Base Quantico, unpublished report). While fawn survival is a highly stochastic demographic vital rate which is likely driven by temporally dynamic forces, many fawn survival studies occur at short temporal scales (i.e., <5 years; Huegel et al. 1985, Nelson and Woolf 1987, Ballard et al. 1999, Vreeland et al. 2004, Jackson and Ditchkoff 2013, McCoy et al. 2013, Shuman et al. 2017, Kautz et al. 2019, Wright et al. 2019). Therefore, many questions remain regarding how temporally dynamic variables influence fawn recruitment.

We evaluated fawn survival, cause-specific mortality, and factors influencing fawn mortality hazard by integrating 12 years of known fate survival data from individual fawns with field surveys for hard mast abundance, land cover data, and weather data. We tested the hypothesis that fawn survival would be influenced by temporally dynamic variables that influence nutritional condition during gestation and fawning. We hypothesized that nutritional condition of mothers during gestation and lactation would influence fawn survival. We predicted fawn survival would increase with greater hard mast availability during gestation and would decrease with increased winter severity. Furthermore, we predicted fawn survival would increase

with increased growing season precipitation. We tested the hypothesis that spatial variation in landscape conditions (i.e., availability of food and concealment cover resources) would influence fawn survival. We predicted fawn survival would increase with increasing patch diversity, complexity, and total edge and would vary with distance to land cover types and road density.

STUDY AREA

The study was conducted from 2008–2019 in northern Virginia, United States on Quantico (Figure 2.1) which covered 23,888.54 ha in the Piedmont and Coastal Plain physiographic provinces. It spanned parts of Stafford, Prince William, and Fauquier counties with the Potomac River on the eastern boundary (Stamps 2015). Quantico experienced humid summers and mild winters with a relatively long growing period from early March to late October (WeatherSpark, www.weatherspark.com, accessed 23 June 2019). January was the coldest month with an average low of -3°C and July was the warmest month with an average high of 31°C . Average annual precipitation was 103.60 cm with rain in the summer months and rains with occasional snow in the winter months. Quantico had elevations of 142.34 m above sea level to approximately sea level near the Potomac River and the topography was hilly with grades of generally between 2–25% (Stamps 2015). Cover types included deciduous forests (42.51%), mixed forest (26.93%), evergreen forests (7.47%), wetlands (9.06%), open land (5.60%), developed (6.56%) and open water (1.87%). Deciduous species included oaks, American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), yellow poplar (*Liriodendron tulipifer*) and hickories (*Carya* spp.). Evergreens included Virginia pine (*Pinus virginiana*) and loblolly pine (*Pinus taeda*). Wetlands included riverine, lacustrine, estuarine, and palustrine wetlands. Ground cover in open lands included grasses such as fescue (*Festuca* spp.), Indiangrass (*Sorghastrum nutans*), big blue stem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*) and clover (*Trifolium* spp.).

Average white-tailed deer density (deer/km²) calculated from three different areas of Quantico from 1992–2019 was 26.40 (SD: 19.67, C. Cook, Conservation Management Institute, unpublished report). White-tailed deer predators on Quantico included black bears, coyotes, and bobcats. Coyotes were the most detected fawn predator on Quantico with hunters reporting 0.85 ± 0.29 (mean \pm SD) observations/100 hours. Bobcats (0.03 ± 0.05) and black bears (0.05 ± 0.05) were rarely observed and black bear observation rates were much lower than other regions of Virginia such as the Appalachian Mountains where hunters' observations of black bears from 1997–2018 were $1.25 \pm 0.65/100$ hours (Fies 2019, T. Nocera, Conservation Management Institute, unpublished report). Quantico was used mainly for military training. Active land management included prescribed fire, food plot maintenance and timber harvesting. Deer hunting occurred on portions of Quantico from late September through January (Stamps 2015).

METHODS

Data Collection

We conducted a fawn survival study on Quantico from 2008–2019. Adult female deer were captured via free darting and drop-netting (Pneu-Dart, Williamsport, PA, USA; 12.19 m x 12.19 m, Wildlife Capture Services LLC, Flagstaff, AZ, USA). We darted females from vehicles and over bait sites with 2.0 cc one inch disposable darts (Pneu-dart) which delivered BAM (1.1 mg/kg butorphanol tartrate; 0.37 mg/kg azaperone; 0.44 mg/kg medetomidine; ZooPharm, Laramie, WY, USA) or Xylazine (3.3 mg/kg; Lloyd, Shenandoah, IA, USA; Henry Schein, Melville, NY, USA) and Telazol (5.1 mg/kg; Pfizer, New York, NY, USA; Zoetis, Parsippany-Troy Hills, NJ, USA). We intramuscularly injected deer captured in drop nets with Telazol (5.1 mg/kg; Pfizer; Zoetis) and Xylazine (3.3 mg/kg; Lloyd; Henry Schein). After anesthetization, we inserted temperature and/or motion activated vaginal implant transmitters (VITs; Model M3900,

Advanced Telemetry Systems, Isanti, MN, USA; Model TVIT-200, Telonics, Inc., Mesa, AZ, USA) into pregnant females using a lubricated 1.27 cm plastic applicator. We fit all captured deer with unique ear tags. Upon completion of processing, we reversed BAM with Naltrexone (0.51 mg/kg; ZooPharm) and Atipamazole (4.08 mg/kg; ZooPharm) and reversed Xylazine with Tolazoline (2 mg/kg; Lloyd) administered intramuscularly.

We captured fawns using thermal imagers during road surveys, ground searches, reported sightings of fawns and by monitoring VITs from 29 April–14 August. Upon capture we blindfolded, weighed, ear tagged and fitted fawns with very high frequency (VHF) expandable collars (Model MOD205, Telonics; Model M4210, Advanced Telemetry Systems) equipped with a 4-hour mortality sensor. We were able to calculate time since last movement for 82% of the fawns. We recorded the sex, determined age through inspection of the umbilicus, dewclaws, and gelatinous pads, and recorded the location of capture (Haugen and Speake 1958, Sams et al. 1996). All handling and capture methods followed guidelines of the American Society of Mammalogists (Sikes et al. 2016) and a Virginia Scientific Collection Permit (permit # 064873).

We monitored each fawn once daily through August and three times per week until 1 October when fawns were recruited into the harvestable population. We determined time and date of death via the collar mortality signal and conducted a mortality investigation to ascertain the cause of death. Upon arrival at the mortality site, we located the carcass, noted predator tracks, gathered any scat and hair potentially from predators and documented the findings and area with photographs. We spent at least 20 minutes at the site investigating the cause of death, and searched 100% of the area within a 30 m radius of the collar for predator sign.

If predation appeared to be the cause of death based on the presence of bruises, hemorrhaging, and signs of trauma, we followed a modified version of Vreeland et al. (2004) to

classify the mortality to a species based on field evidence (i.e., tracks, scat, hair, puncture wound location and diameter, cache site characteristics and predator feeding behavior). Black bears generally do not cache prey, while coyotes and bobcats cache their prey underneath leaves and soil. Bobcats also sometimes drag their prey to hide it and leave scrape marks around the cache site. All three of these predators can leave puncture wounds of varying lengths and locations (black bears: 0.6–1.3 cm in diameter on the skull, coyotes: 0.3–0.5 cm in diameter on the skull and/or neck, bobcats: 0.1–0.3 cm in diameter puncture wounds on the skull and neck most commonly). Black bears often leave limited fawn remains following depredation while coyotes generally leave bones intact but may decapitate the carcass, and bobcats often consume the shoulders and hind limbs but rarely the organs. When we observed hemorrhaging and puncture wounds, but did not have adequate data to assign the event to a given species, we categorized the cause of death as unknown predator. If we found evidence of caching, but no signs of hemorrhaging, we assigned the cause of death as unknown due to the possibility that the individual had been scavenged. When a carcass was intact with no obvious signs of trauma, we delivered it to the Virginia Department of Game and Inland Fisheries, for necropsy and sent tissue samples to the Southeastern Cooperative Wildlife Disease Study (Athens, GA, USA) for further examination.

Data Analysis

We used the non-parametric Kaplan-Meier estimator, a class of time-to-event model, to estimate probability of survival for fawns captured from 2008–2019. We used the age at capture of fawns ($n=212$) in days to estimate survival probability to 133 days (i.e., approximate age of our sample of fawns on 1 October when fawns were recruited into the harvestable population). Because of relatively small samples sizes in some years, we pooled years into four intervals each

encompassing three years 2008–2010, 2011–2013, 2014–2016 and 2017–2019 to estimate fawn survival. In addition, we estimated annual survival for years containing sample sizes with ≥ 18 fawns that had ages noted, which included 2013, 2015, 2016, 2017, 2018, and 2019 and pooled fawns from all years of the study (2008–2019) to estimate overall survival probability. We fit models utilizing the survival package in program R (The R Project for Statistical Computing Version 3.5.1, <https://www.r-project.org>, accessed 20 July 2018).

To evaluate factors affecting survival, we used Cox-proportional hazards models. We fit Cox-proportional hazards models using a staggered-entry method where each fawn ($n=248$) entered on a day of the study based on their capture date with 29 April as the first day and the 1 October being the last day. Some fawns did not have ages estimated at capture ($n=36$) so they were excluded from the age-based Kaplan-Meier analysis, but included in the Cox-proportional hazards models. We developed models based on our hypotheses that fawn survival would be influenced by temporally dynamic variables that impact nutritional condition during gestation and lactation, and spatial variation in landscape conditions.

We created three variables to represent nutritional condition during gestation. First, we calculated the average yearling female body mass at harvest for each hunting season prior to fawning to represent nutritional condition of the deer population during early winter. We chose to use yearling mass as yearlings are more sensitive to environmental changes and population density than adult deer (Strickland et al. 2008). Hard mast affects many aspects of deer biology in eastern deciduous forests, including body mass, and reproduction (Feldhamer et al. 1989, Wentworth et al. 1992). Therefore, to directly link fawn survival to gestational condition and a specific resource, we created two variables to represent temporal variability in oak mast abundance, an annual red oak mast abundance index and white oak mast abundance index.

During late August and early September, biologists examined 10 branches from 40 trees of each oak group distributed across Quantico and counted the number of acorns on the outside 0.3–0.5 meters of each branch to obtain the average number of acorns per tree on Quantico (Whitehead 1969). White oak surveys included white oak (*Q. alba*) and chestnut oak (*Q. prinus*), while red oak surveys included northern red (*Q. rubra*), southern red (*Q. falcata*), willow (*Q. phellos*), scarlet (*Q. coccinea*), and black oak (*Q. velutina*). We assigned the annual white oak mast abundance index and red oak mast abundance index values to each fawn from the fall prior to their birth.

Winter severity can also influence the condition of females and subsequent fawn survival (Mech et al. 1987, 1991, Garroway and Broders 2005). As such, we created a winter severity index, by totaling the number of days from 1 December–31 March with a maximum temperature under 0°C. We assigned the winter severity index to each fawn from the winter prior to birth. Precipitation can also influence food availability during late gestation and fawn rearing, a factor which can also impact a female’s nutritional condition and fawn survival (Mech et al. 1987, 1991, Michel et al. 2018). Therefore, we created a precipitation variable by averaging daily precipitation from 1 March–30 September for each year of the study. We obtained weather data from the National Oceanic and Atmospheric Administration Station, in Fredericksburg, Virginia, USA.

Landscape composition and configuration can influence female nutrition and fawn survival (Gulsby et al. 2017, Shuman et al. 2017, Gingery et al. 2018). Therefore, we created land cover variables using the 2011 National Land Cover Database (NLCD; 2011 National Land Cover Database, U.S. Geological Survey, Sioux Falls, SD, USA). We used ArcMap 10.6 (Environmental Systems Research Institute, Redlands, CA, USA) to reclassify the NLCD for the

area of inference into seven classes (Wetland, Mixed Forest, Evergreen Forest, Deciduous Forest, Open Land, Open Water, Developed; Table 2.1) that we *a priori* assumed would be important to fawn survival. We used the Euclidean distance tool in ArcMap 10.6 to create distance raster layers, which populated each cell with the distance to each cover type (Figure 2.2). We also created a road density variable by creating a road layer for the study area by merging road data managed by Quantico, the Virginia Geographic Information Network and Virginia Department of Transportation. We used this road layer in the line density tool in ArcMap with a search radius of 304.35 m. We selected this buffer size to represent the area used by fawns during their first three weeks of life (29.1 ha; Gulsby et al. 2017).

Landscape configuration may also influence fawn survival (Rohm et al. 2007, Gulsby et al. 2017). Therefore, we created landscape metrics including: 1) Shannon's diversity index, a measure of patch richness and evenness; 2) mean fractal dimension index, a measure of the complexity of the patch shapes, with simpler shapes such as circles having a lower index number than a more complex shape; and 3) total forested edge (Gulsby et al. 2017). We calculated Shannon's diversity index and mean fractal dimension index using the reclassified NLCD (Table 2.1) in FRAGSTATS 4.2 (FRAGSTATS Version 4.2, www.umass.edu/landeco/research/fragstats/fragstats.html, accessed 16 Jul 2019). We created total forested edge by reclassifying the 2011 NLCD into forested and non-forested (Table 2.2) in ArcMap 10.6 and then used the binary forested layer in FRAGSTATS 4.2. We calculated landscape metrics (Figure 2.3) in FRAGSTATS 4.2 using a moving window analysis with a four-cell rule and a 304.35 m radius window size. We selected this size (i.e., 29.1 ha window) to represent the area used by a fawn during early life (Gulsby et al. 2017). We then extracted spatial

metric values for each fawn's capture location using the Extract Multi Values to Points tool in ArcMap 10.6.

We scaled and centered all variables in program R and then tested for multicollinearity by creating a Pearson's correlation coefficient matrix to identify correlated variables ($r \geq |0.7|$). We used the following variables in the Cox-proportional hazards models: sex, annual red oak mast abundance, annual white oak mast abundance, yearling female mass, winter severity, precipitation, distance to land cover (wetland, mixed forest, deciduous forest, evergreen forest, open land, open water, developed), road density, total edge, Shannon's diversity index, and mean fractal dimension index (Table 2.3; Table 2.4). We conducted the Cox-proportional hazards analysis in program R using the survival package and the dredge function in package MuMIn to develop all possible linear and additive combinations of the variables. We chose to fit models with all possible combinations of our variables as our hypotheses, represented by our variables, were not mutually exclusive. We considered models ≤ 2 delta AICc to be competitive models (Anderson and Burnham 2002). We verified that the global and competing models met the proportional hazards assumption by using Schoenfeld residuals (Schoenfeld 1982), assessed variables via hazard ratios and z scores, and assigned significance at $\alpha < 0.05$.

RESULTS

During 2008–2019, we implanted VITs in 66 adult females. We captured and collared 248 fawns, of which 116 were females and 132 were males (Table 2.5). We captured 28 fawns by monitoring VITs and 220 opportunistically. We collared 7 sets of twins born from females implanted with VITs. For the 212 fawns, we estimated average age at capture to be 4.57 ± 3.90 days old with the average age of VIT captured fawns being 1.46 ± 0.84 days old and the average

age of opportunistically captured fawns was 5.04 ± 3.96 days old. Capture success varied across years with hours spent searching ranging from 123.00 to 205.33 hours (Table 2.6).

Survival probability to 133 days for four, three year intervals was 0.71 (CI_{95%}[0.52–0.96]) for 2008–2010, 0.46 (CI_{95%}[0.30–0.70]) for 2011–2013, 0.48 (CI_{95%}[0.35–0.66]) for 2014–2016 and was 0.50 (CI_{95%}[0.39–0.63]; Figure 2.4) for 2017–2019 indicating survival probability was lower during the last nine years of the study than the first three years. We found no significant difference in annual survival estimates from individual years, 2013 (0.59 CI_{95%}[0.40–0.88]), 2015 (0.59 CI_{95%}[0.43–0.83]), 2016 (0.41 CI_{95%}[0.21–0.78]), 2017 (0.49 CI_{95%}[0.30–0.79]), 2018 (0.46 CI_{95%}[0.30–0.70]), and 2019 (0.59 CI_{95%}[0.43–0.80]; Figure 2.5A). From 212 fawns, pooled survival including all years (2008–2019) was 0.50 (CI_{95%}[0.42–0.58]) to 133 days (Figure 2.5B). Fawn survival to two weeks was 0.76 (CI_{95%}[0.69–0.84]).

We recorded 94 fawn mortalities and found predation was the leading cause of fawn mortality ($n=42$; 45%), with 10 predation events ascribed to coyotes and two to bobcats (Figure 2.6). Other predation events ($n=30$) could not be assigned to a predator species. Unknown causes accounted for 40% ($n=38$) of mortalities and remaining mortalities (15%) were due to abandonment ($n=8$; 9%), pathology ($n=3$; 3%) which included abnormalities and infection, and other ($n=3$; 3%) which included fence entanglement and vehicle collisions. Of the 94 deaths, 40 were females and 54 were males. Of the remaining fawns, 82 were considered recruited and 72 had unknown fates due to dropped collars, collar failure, and lost contact. More than half of the mortalities occurred within the first three weeks of life with the latest mortality occurring at 19 weeks (133 days old; Figure 2.7).

Cox-proportional hazards models revealed that red oak mast abundance was an informative parameter in the 11 competing models whereas all other variables in the competing

models were uninformative ($p \geq 0.05$; Table 2.7). The null model was not within the set of competing models (Table 2.7). Therefore, we made inference on our top model which contained only red oak mast abundance and indicated that for every unit increase (SD) in annual red oak mast abundance, the hazard is reduced by 27% ($\beta = -0.32$, $p = 0.01$; Figure 2.8). Red oak mast abundance from 2007–2018 varied considerably among years with a mean of 20.06 ± 9.90 and a range of 4.10–36.48 average acorns/tree/year.

DISCUSSION

Understanding drivers of recruitment on specific sites is crucial for making informed management decisions (Shuman et al. 2017). Therefore, we examined annual variation in fawn survival and factors affecting survival on a relatively long-time scale (12 years) which revealed red oak mast abundance, a temporally dynamic resource, was the most important predictor of fawn survival. This result supported our hypothesis that nutritional condition during gestation is a strong predictor of reproductive success in deer. However, we acknowledge mast abundance may influence survival through other pathways such as increasing the abundance of small mammals thereby creating diversionary food items for fawn predators (McShea 2000). Many studies have demonstrated the link between female condition and fawn survival (Mech et al. 1987, 1991, Long et al. 2016), but few studies have linked survival to a specific resource. We found predation was the leading cause of death and coyotes were responsible for most of the predation events assigned to species. We found that survival was greater during the first interval (2008–2010) than the later intervals (2011–2013, 2014–2016, and 2017–2019). However, we did not detect differences in annual survival rates which all were in the last seven years of the study.

Mast has been linked to both adult female and fawn body condition of many cervids including white-tailed deer (Harlow et al. 1975, Feldhamer et al. 1989, Wentworth et al. 1992,

Kjellander et al. 2006). Wentworth et al. (1992) found the percentage of yearlings harvested declined two years after a poor oak mast event, suggesting a poor mast crop may lower recruitment. However, here we link red oak acorn abundance, a specific maternal resource only available before parturition, to fawn survival. This finding may indicate females were in better condition during gestation after good red oak mast years. Therefore, their fawns were likely born in better condition, receive greater maternal investment, or are better defended by their mothers. Annual red oak mast abundance was important, but annual white oak mast abundance was not, which may be due to there being a greater abundance of red oaks on Quantico. Red oak mast also persists longer on the landscape than white oak mast and therefore, may be available to females later in gestation (Ober 2017).

We also examined if winter severity and precipitation, which we believed would be linked with resource availability, would influence fawn survival. Multiple studies have demonstrated that winter severity and precipitation can influence the condition of females and subsequently fawn survival (Mech et al. 1987, 1991, Garroway and Broders 2005). However, we failed to detect these effects, perhaps because Quantico experiences a relatively mild and stable climate. Contrary to numerous studies (Rohm et al. 2007, Gulsby et al. 2017, Shuman et al. 2017, Gingery et al. 2018), we found no support for our prediction that spatially explicit landscape conditions would influence fawn survival.

Predation was the leading cause of mortality. Most mortalities occurred within the first 10 weeks of life, which is similar to other studies (Vreeland et al. 2004, Rohm et al. 2007, Shuman et al. 2017). Unlike in Louisiana, where most mortalities occurred during the first week of life (Shuman et al. 2017), in this study >50% of mortalities occurred within the first three weeks of life. Our finding that fawn survival was greater during the first interval of the study than the last

three intervals may be due to an increasing abundance of coyotes and black bears east of the Blue Ridge Mountains (Virginia Department of Game and Inland Fisheries 2013, Fies 2019) which includes Quantico. While we did not detect black bear predation of fawns, continued monitoring could be important to determine if black bear population growth results in lower fawn survival.

We observed low variation in annual survival. Pooling all years (2008–2019), fawn survival was 50%, which is slightly higher than the modeled survival rate for completely forested areas in the meta-analysis conducted by Gingery et al. (2018). However, our overall survival probability is more similar to studies conducted in the Midwest and Northeast (i.e., Illinois [59%; Rohm et al. 2007], Michigan [36%; Kautz et al. 2019], Pennsylvania [50%; Vreeland et al. 2004], and New Brunswick [56%; Ballard et al. 1999]) than the Southeast (i.e., Alabama [33% and 26%; Saalfeld and Ditchkoff 2007, Jackson and Ditchkoff 2013], Georgia [29%; Nelson et al. 2015], Louisiana [27%; Shuman et al. 2017], North Carolina [14%; Chitwood et al. 2015b], and South Carolina [23%; Kilgo et al. 2012]), where coyote predation appears to be a major source of fawn mortality.

In our study most fawns were captured via field searches. Therefore, fewer deer were monitored during their first days of life relative to other survival intervals. Despite there being fewer deer in the first days of life, our approach included some individuals captured on their first day of life ($n=36$). Therefore, our estimates can be considered reflective of fawn survival from birth to 133 days. However, the limited number of fawns included in the first days of life result in larger error estimates for those daily survival rates.

Our study provides evidence of temporal variation in survival rates as survival probabilities were lower during the last three intervals (2011–2013, 2014–2016 and 2017–2019)

than the first (2008–2010). Other research has reported the effect of female maternal nutritional condition, but due to the longevity of our study, we were able to link fawn survival to a specific maternal resource (red oak mast) only available during gestation. Our finding that red oak mast influenced survival suggests a single resource may be critical in influencing population dynamics in some areas and more broadly that nutritional condition of females during gestation can influence subsequent fawn survival.

MANAGEMENT IMPLICATIONS

In areas of eastern deciduous forests where recruitment is lower than desired, increasing the amount of red oak acorn production may increase recruitment. This could be achieved by increasing red oak abundance in the canopy via prescribed burning, timber harvesting, and crown releases (Abrams 1992, Johnson 1994, Healy 1997). These techniques would likely also enhance fawn concealment cover and forage availability. Managers could also increase resources available during gestation by maintaining food plots which, in some cases, have been successful at increasing deer herd health (Johnson et al. 1987). Reducing predator abundances may be an option to increase fawn survival, but predator control can be controversial and is not always successful (Kilgo et al. 2014, Gulsby et al. 2015). As managing fawn survival is more challenging than managing adult survival (Kilgo et al. 2014, Gulsby et al. 2015), another way to increase fawn recruitment would be to decrease antlerless harvest to maintain more reproductive females in the population.

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Table 2.1. Class names of the reclassified 2011 National Land Cover Database for the distance to cover types and landscape metrics used in the Cox-proportional hazards models to assess factors affecting fawn survival on Marine Corps Base Quantico, Virginia, USA from 2008–2019.

Class Name	Combined Classes
Wetland	Woody wetlands/emergent herbaceous wetlands
Mixed forest	Mixed forest
Evergreen forest	Evergreen forest
Deciduous forest	Deciduous forest
Open land	Barren/shrub/scrub/grassland/herbaceous/pasture/hay/cultivated crops
Open water	Open water
Developed	Open space/low intensity/medium intensity/high intensity

Table 2.2. Class names of the reclassified 2011 National Land Cover Database for the total edge variable used in the Cox-proportional hazards models to assess factors affecting fawn survival on Marine Corps Base Quantico, Virginia, USA from 2008–2019.

Class Name	Combined Classes
Forested	Deciduous forest/evergreen forest/mixed forest
Non-forested	Barren/shrub/scrub/grassland/herbaceous/pasture/hay/cultivated crops/woody wetlands/emergent herbaceous wetlands/open water/open space/low intensity/medium intensity/high intensity

Table 2.3. Category of variable (category), variable name and variable description (description) used in the Cox-proportional hazards models to assess factors affecting fawn survival from 2008–2019 on Marine Corps Base Quantico, Virginia, USA.

Category	Variable name	Description
Weather	Winter severity	Total number of days with a maximum temperature under zero degrees Celsius
	Precipitation	Average daily precipitation during the growing season
Landscape configuration	Total edge	Amount of edge*
	Shannon's diversity index	A measure of land cover patch types*
Landscape features	Mean fractal dimension index	Measures the complexity of the land cover patch shapes*
	Distance to wetland	Distance from capture location to nearest wetland
	Distance to mixed forest	Distance from capture location to nearest mixed forest
	Distance to deciduous forest	Distance from capture location to nearest deciduous forest
	Distance to open land	Distance from capture location to nearest open land
	Distance to open water	Distance from capture location to nearest open water
	Distance to developed	Distance from capture location to nearest developed area
Nutritional condition	Road density	Density of roads*
	Annual red oak mast abundance	Average acorns per red oak tree
	Annual white oak mast abundance	Average acorns per white oak tree
Biological	Yearling female mass	Average yearling female mass at harvest
	Sex	Sex of the fawn as determined at capture

* Landscape configuration and road density variables were calculated for each individual within a 29.1 ha buffered capture location as this area represents a fawn's home range during the first three weeks of life.

Table 2.4. Variables, their means, standard deviations (SD), minimum and maximum of the ranges included in the Cox-proportional hazards models for Marine Corps Base Quantico, Virginia, USA of risk to white-tailed deer fawns ($n=248$) from 2008–2019.

Variables*	Mean	SD	Minimum	Maximum
Wetland	381.42	315.03	0.00	1494.59
Open	230.39	210.56	0.00	1235.84
Mixed	78.99	102.68	0.00	573.15
Decid	51.44	71.70	0.00	379.47
Evergreen	427.08	535.55	0.00	2047.49
Water	1291.67	981.81	0.00	4080.00
Developed	133.16	203.93	0.00	1387.16
Road	4.27	2.98	0.00	18.41
Edge	2339.40	1007.63	0.00	4680.00
Frac	1.04	0.01	1.01	1.08
Sdi	1.13	0.34	0.02	1.71
Mass	29.36	1.57	26.49	31.71
Precipitation	3.59	0.77	2.59	6.09
Winter	5.79	2.76	1.00	11.00
Red	20.16	8.68	4.10	36.48
White	24.42	18.70	0.75	58.90

* Wetland=distance to wetland (m), Open=distance to open land (m), Mixed=distance to mixed forest (m), Decid=distance to deciduous forest (m), Evergreen=distance to evergreen forest (m), Water=distance to open water (m), Developed=distance to developed areas (m), Road=road density (kilometer per square kilometer), Edge=total edge (m), Frac=mean fractal dimension index, Sdi=Shannon's diversity index, Mass=average yearling female mass (kg), Precipitation=average daily precipitation during the growing season (mm), Winter=total number of days with a maximum high under 0 degrees Celsius, Red=annual red oak mast abundance index (average acorns per tree), White=annual white oak mast abundance index (average acorns per tree)

Table 2.5. Total number of fawns captured and number of fawns with ages estimated at capture by year used in the study on Marine Corps Base Quantico, Virginia, USA from 2008–2019.

Year	Number of fawns captured	Number of fawns with ages
2008	14	9
2009	18	9
2010	14	4
2011	10	4
2012	13	8
2013	19	18
2014	12	12
2015	28	28
2016	23	23
2017	31	31
2018	33	33
2019	33	33
Total	248	212

Table 2.6. Fawn search capture effort by year with number of effort hours per year (hours), number of fawns captured (fawns), and fawns captured per hour (fawns per hour) spent searching on Marine Corps Base Quantico, Virginia, USA.

Year	Hours	Fawns	Fawns per hour
2009	192.50	9	0.05
2016	123.00	16	0.13
2017	190.25	31	0.16
2018	205.33	31	0.15
2019	158.75	31	0.20
Total	869.83	118	0.69

Table 2.7. Competing models ($\Delta AICc \leq 2$) and the null model from the Cox-proportional hazards models examining the factors that affect white-tailed deer fawn survival ($n=248$) with model components (Model), number of parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta AICc ($\Delta AICc$), and model weights (W_i) on Marine Corps Base Quantico, Virginia, USA from 2008–2019. Bolded variables are informative ($p < 0.05$).

Model*	K	AICc	$\Delta AICc$	W_i
Red	1	893.266	0.000	0.004
Red + Winter	2	893.976	0.710	0.003
Red + Precipitation	2	894.606	1.339	0.002
Red + Mixed	2	894.758	1.492	0.002
Red + Road	2	894.846	1.580	0.002
Red + Sex	2	894.906	1.640	0.002
Red + Developed	2	894.930	1.664	0.002
Red + Winter + Precipitation	3	894.950	1.684	0.002
Red + Sdi	2	895.214	1.948	0.002
Red + Mass	2	895.226	1.960	0.002
Red + Wetlands	2	895.228	1.962	0.002
Null	0	899.084	5.818	0.000

* Red=annual red oak mast abundance index, Road=road density, Precipitation=average daily precipitation during the growing season, Mixed=distance to mixed forest, Wetland=distance to wetland, Developed=distance to developed areas, Winter=total number of days with a maximum high under 0 degrees Celsius, Sdi=Shannon's diversity index, Mass=average yearling female mass, Sex=sex of the fawn

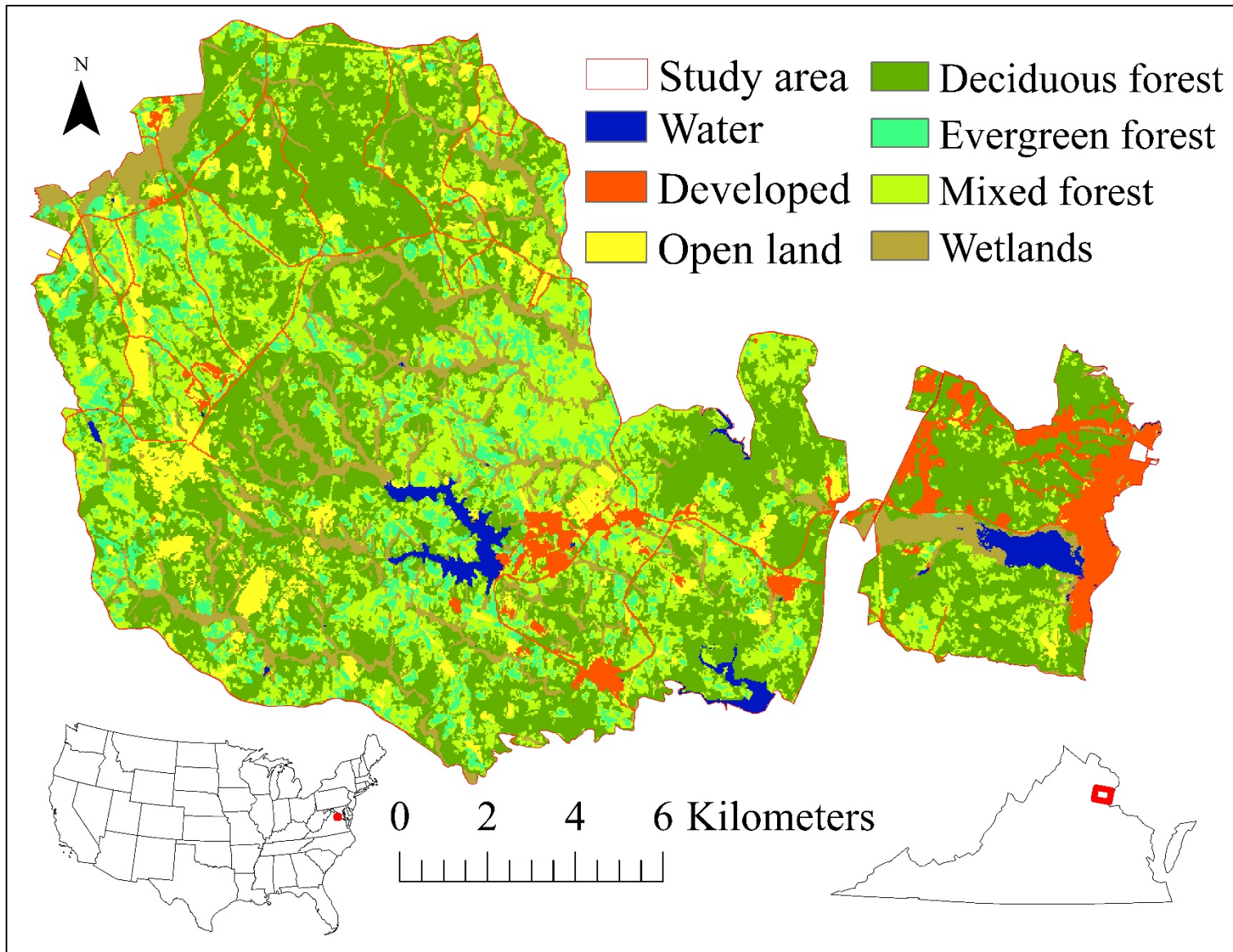


Figure 2.1. Marine Corps Base Quantico in northern Virginia, USA with open water (water), and land cover types, which include developed, open land, deciduous forest, evergreen forest, mixed forest, and wetlands.

Distance to Landscape Features

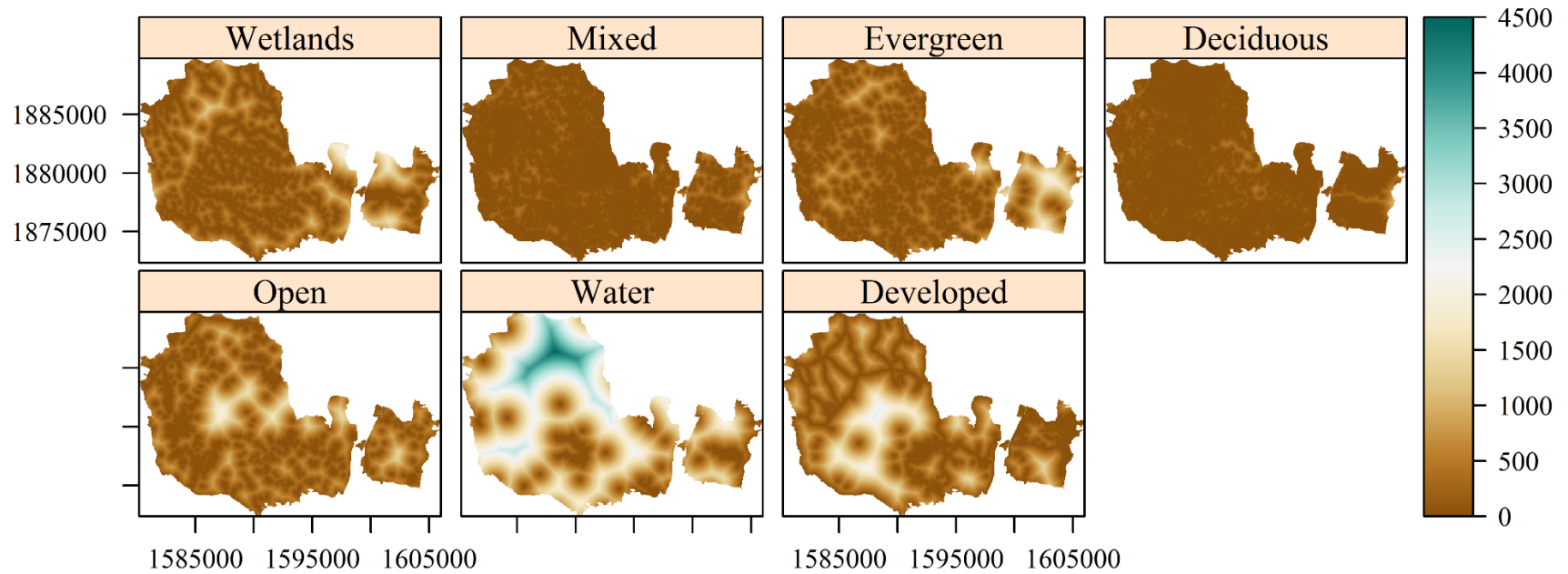
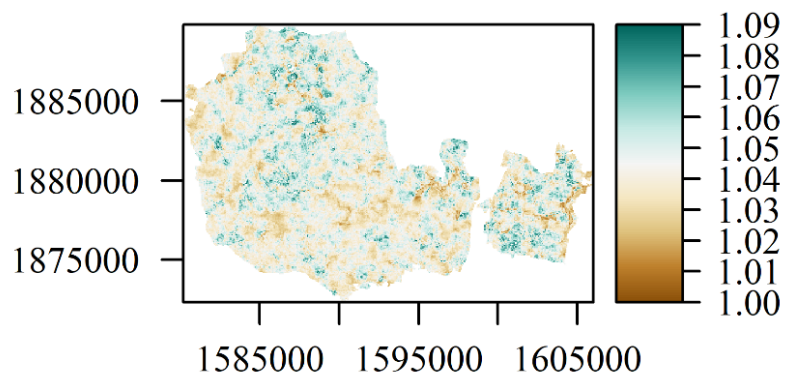
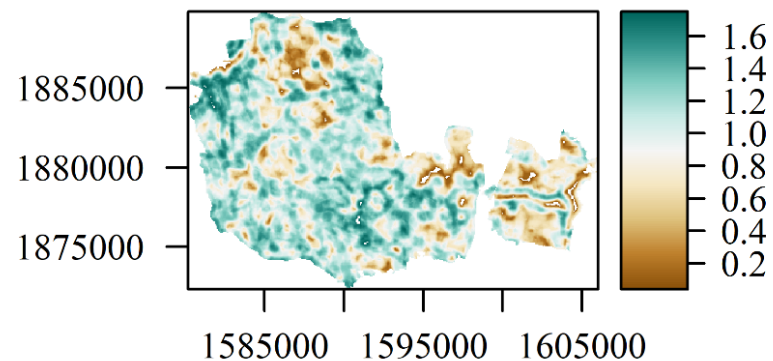


Figure 2.2. Distance in meters to wetlands (wetlands), mixed forest (mixed), evergreen forest (evergreen), deciduous forest (deciduous), open land (open), open water (water), and developed areas (developed) on Marine Corps Base Quantico, Virginia, USA.

Fractal dimension index



Shannon's diversity index



Total edge (m)

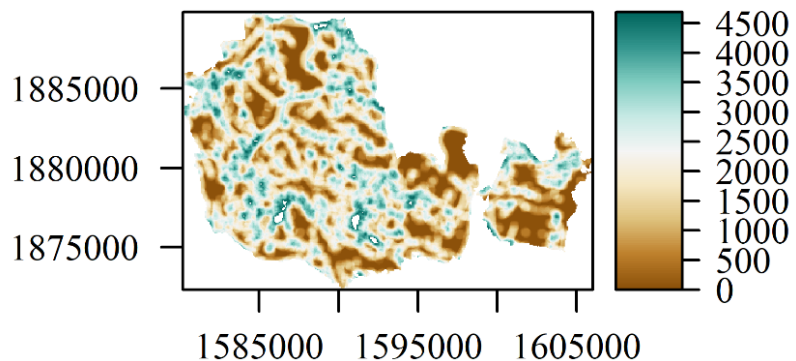


Figure 2.3. Landscape metrics which include mean fractal dimension index, Shannon's diversity index and total edge (meters) used in the Cox-proportional hazards models to assess factors affecting fawn survival on Marine Corps Base Quantico, Virginia, USA from 2008–2019.

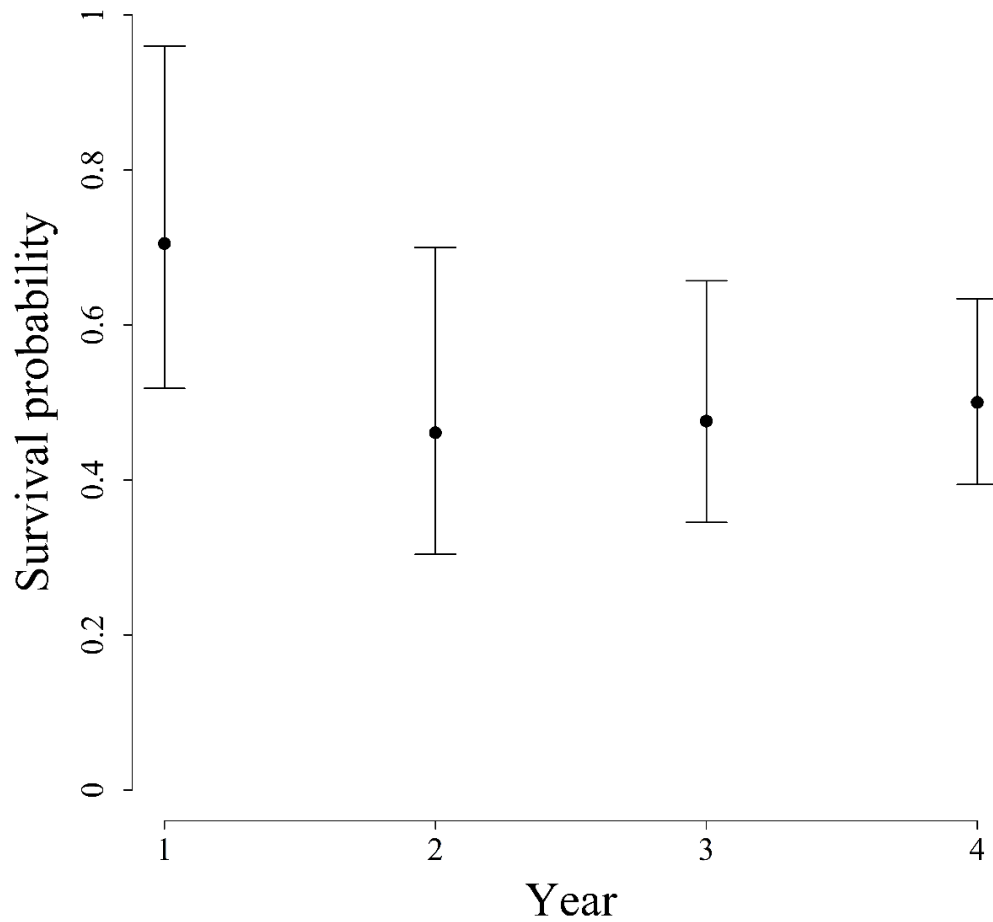


Figure 2.4. Survival estimates with 95% confidence intervals to 133 days from pooling individuals with ages by three year increments for years 2008–2010 (1), 2011–2013 (2), 2014–2016 (3), and 2017–2019 (4) of fawns on Marine Corps Base Quantico, Virginia, USA illustrating that survival was greater during the first interval of the study than the last nine years of the study.

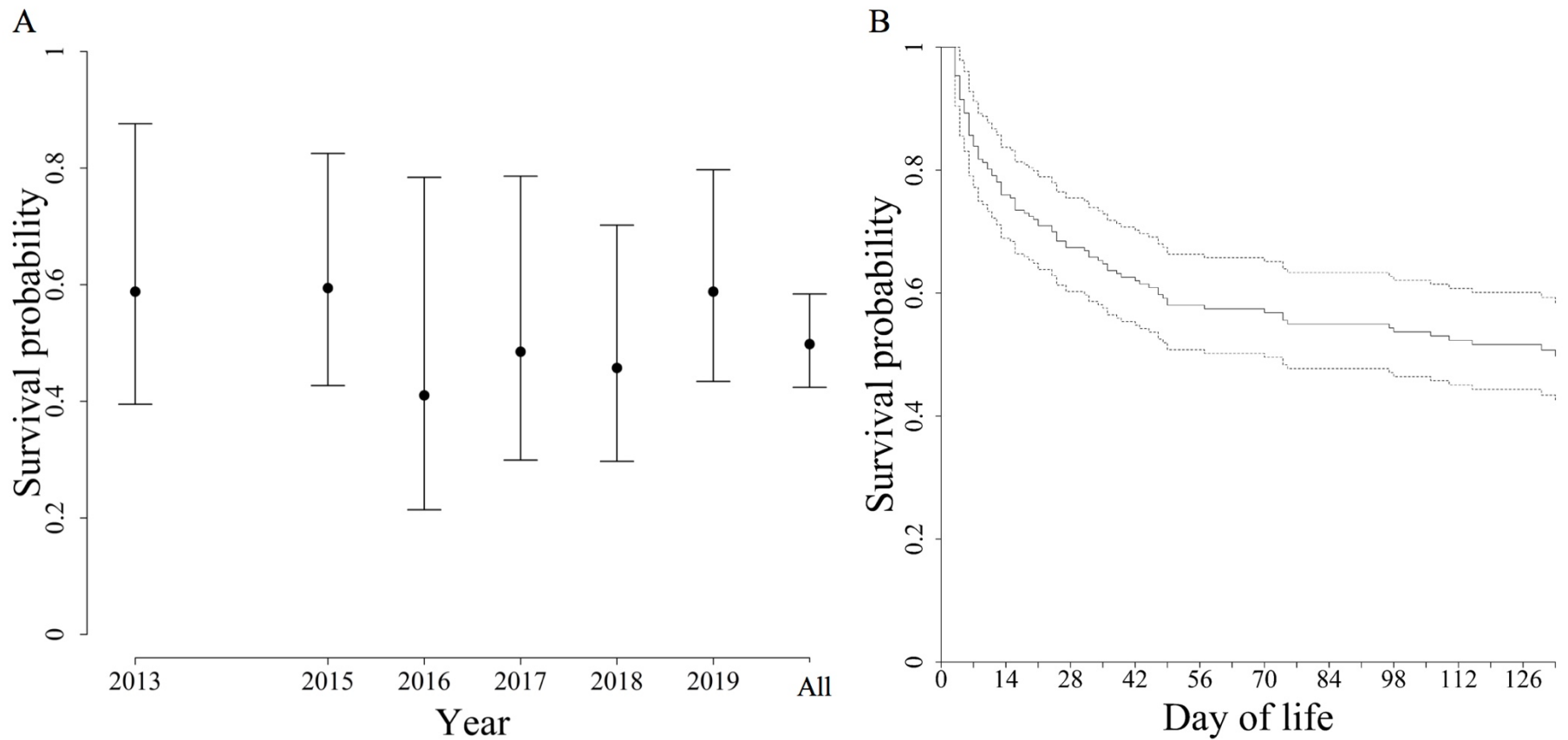


Figure 2.5. A) Survival estimates with 95% confidence intervals to 133 days by year for years 2013, 2015, 2016, 2017, 2018, 2019, and for all years (2008–2019) of fawns on Marine Corps Base Quantico, Virginia, USA **B)** Survival curve with 95% confidence intervals for all years (2008–2019) for fawns on Marine Corps Base Quantico, Virginia, USA.

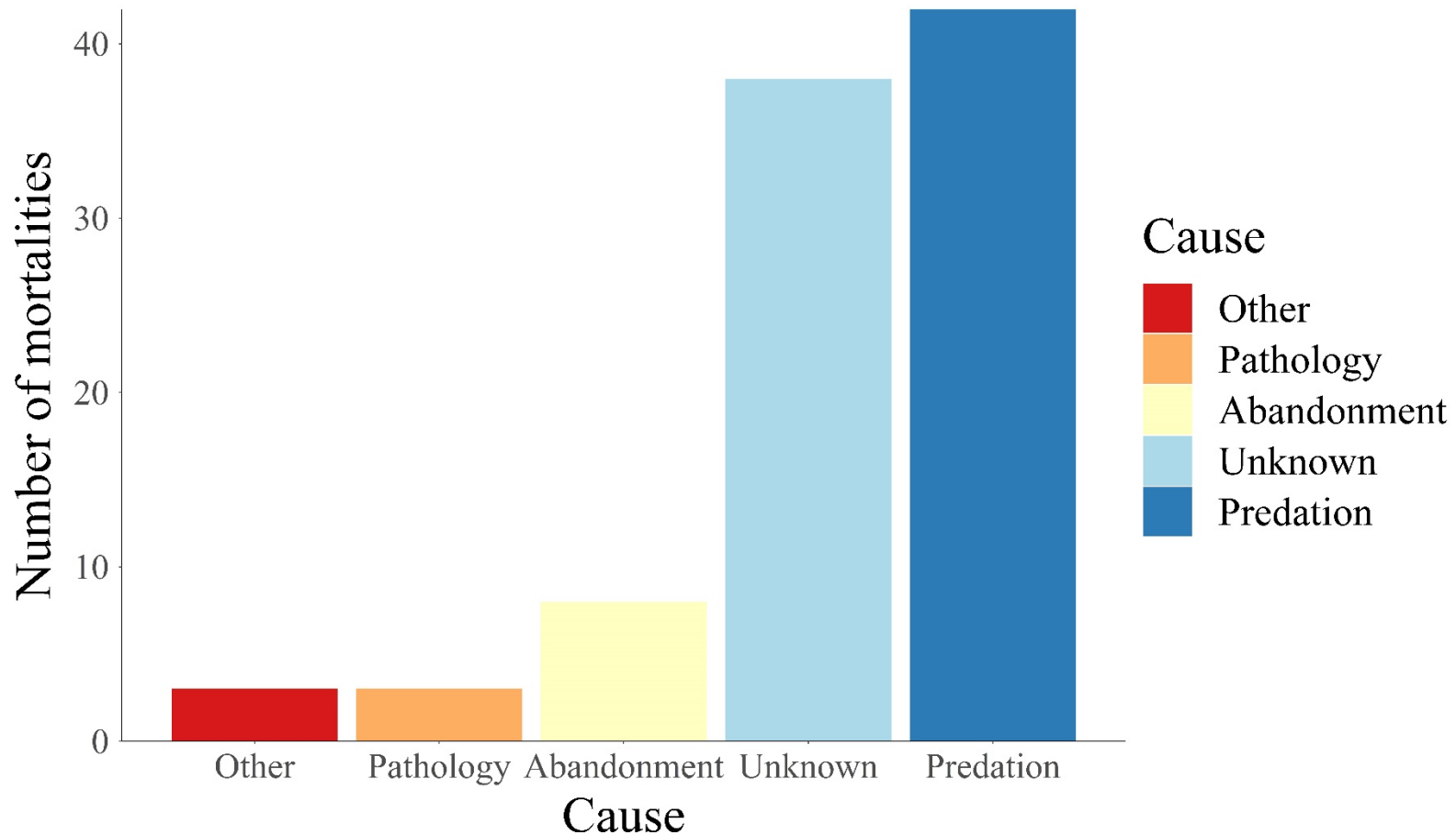


Figure 2.6. Number of mortalities ($n=94$) by cause from all 248 fawns collared with very high frequency collars on Marine Corps Base Quantico, Virginia, USA for years 2008–2019. Predation accounted for 42 mortalities with 10 predation events ascribed to coyotes and two to bobcats. Thirty-eight of the mortalities were due to unknown causes, eight were due to abandonment, three were due to pathology which included abnormalities and infection and other which accounted for three mortalities which included a fence entanglement and vehicle collisions.

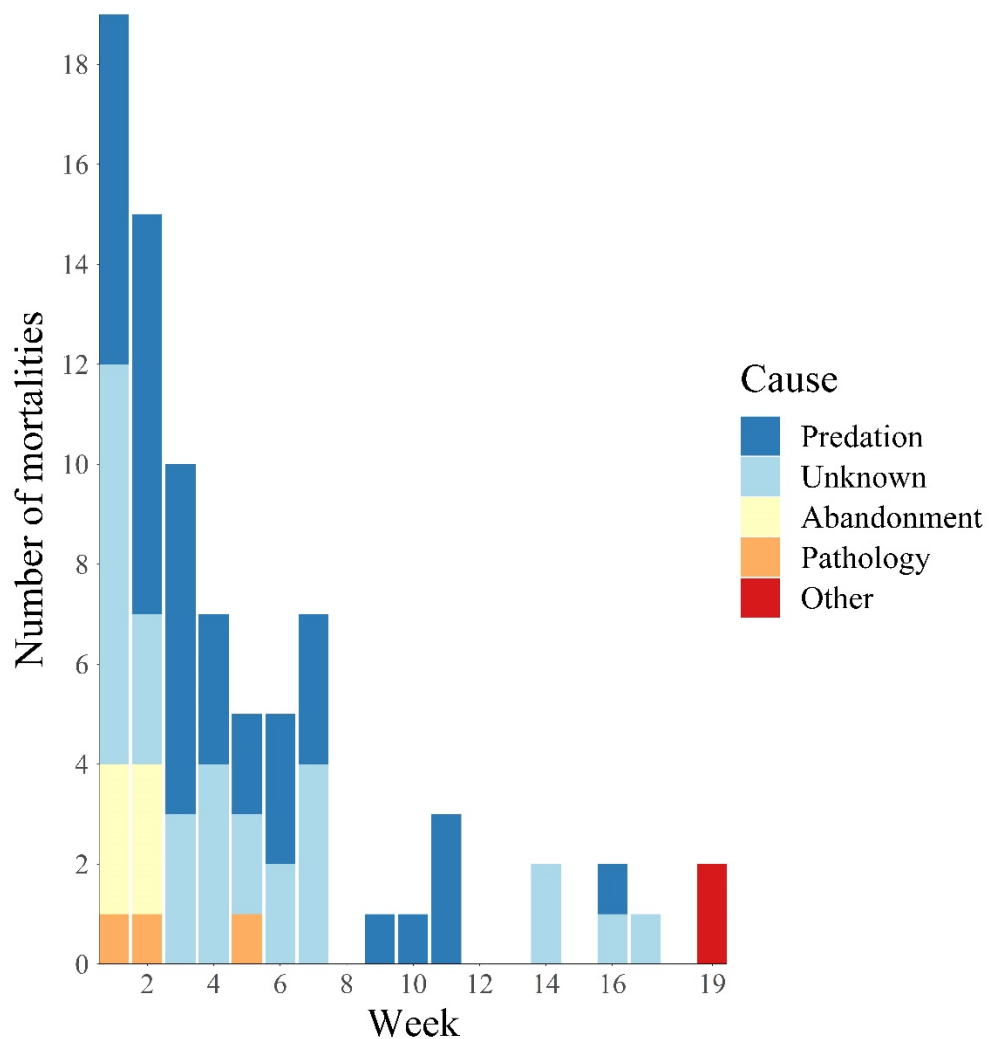


Figure 2.7. Number of fawn mortalities ($n=80$) from the 212 fawns with ages assigned by cause and week of life on Marine Corps Base Quantico, Virginia, USA for years 2008–2019. Predation included coyote ($n=10$), bobcat ($n=2$) and unknown predator ($n=27$). Pathology ($n=3$) included infection and abnormalities. The remainder of mortalities were unknown ($n=30$), abandonment ($n=6$), and other ($n=2$) which included a vehicle collision and fence entanglement.

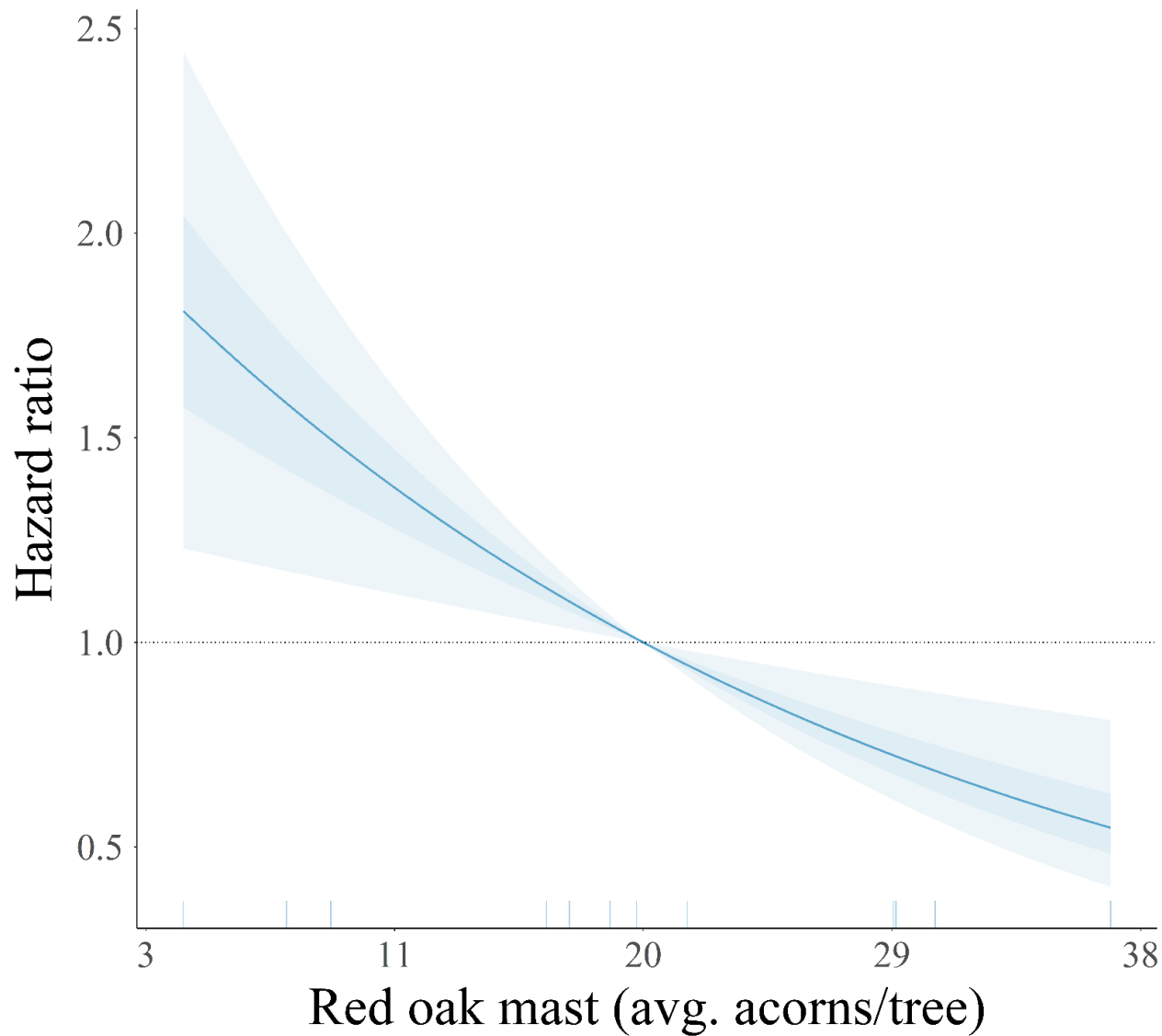


Figure 2.8. Influence of annual red oak mast abundance on the hazard ratio of white-tailed deer fawns ($n=248$) from 2008–2019 on Marine Corps Base Quantico, Virginia, USA with 50% and 95% confidence intervals with a rug plot indicating annual observed red oak mast abundance.

Chapter 3: Drivers of White-tailed Deer Recruitment in the Appalachian Mountains of Virginia

Gisèle Rosalie Aubin

ABSTRACT

During recent decades, white-tailed deer (*Odocoileus virginianus*) populations have declined in some portions of the central and southern Appalachian Mountains concurrent with changing forest conditions, increasing black bear (*Ursus americanus*) populations, and colonization of coyotes (*Canis latrans*). However, these declines are not ubiquitous across the region, and the causes are poorly understood. We investigated drivers of white-tailed deer recruitment by evaluating lactation status of 28,313 harvested adult female white-tailed deer from 30 counties in the Appalachian Mountains of western Virginia, from 1997–2018. We used generalized linear mixed models to assess our prediction that greater habitat diversity, precipitation, and mast availability would increase recruitment, while greater predator detection rates, and winter severity would decrease recruitment. We found the probability of a deer having evidence of lactation increased with habitat patch diversity at the county scale ($\beta = 0.13$, $p < 0.001$) and decreased with increasing annual black bear detection rate ($\beta = -0.09$, $p < 0.001$). Finally, middle-aged females had the highest probability of lactation indicating reproductive senescence occurs in the study population. Land use and habitat management actions that result in greater habitat diversity are likely to increase deer productivity. Manipulating black bear density through harvest is a potential management response to low white-tailed deer recruitment. However, there is growing evidence that predator richness is not a reliable predictor of fawn survival and thus examining the role of compensatory fawn mortality sources would be key in predicting the success of decreasing black bear densities to increase white-tailed deer recruitment. Our results

provide novel insight into population processes by linking environmental conditions to recruitment in a long-lived iteroparous large mammal, at broad spatial and temporal scales.

INTRODUCTION

Understanding drivers of spatiotemporal variation in populations is a key component of wildlife management. For many large mammalian species, adult female survival is the most important parameter affecting population growth rate, yet adult survival is generally high and less sensitive to environmental perturbations relative to recruitment (Gaillard et al. 1998, 2000). Neonate survival and recruitment can experience wide variations depending on predation, landscape composition and configuration, weather, and resource availability (Mech et al. 1987, Linnell et al. 1995, Farmer et al. 2006, Christianson and Creel 2014, Gulsby et al. 2017, Shuman et al. 2017). Therefore, to disentangle the complex factors driving population recruitment, long term studies over vast spatial extents are needed.

Considerable research over the past decade has focused on factors influencing white-tailed deer (*Odocoileus virginianus*) population dynamics in the eastern United States (Kilgo et al. 2010, Shuman et al. 2017, Gingery et al. 2018, Bragina et al. 2019, Kilgo et al. 2019). Deer declines are not ubiquitous in the central and southern Appalachian Mountains, but seem to transcend administrative boundaries of wildlife management agencies (Virginia Department of Game and Inland Fisheries 2015, Little et al. 2018). Changes in predator communities and landscape conditions have been suggested as broad scale drivers of purported deer declines. Appalachian landscapes have experienced substantial change over approximately the last 200 years that likely have important legacy effects on white-tailed deer populations. White-tailed deer predator populations have changed with black bears (*Ursus americanus*) being nearly extirpated in the early 1900s and then substantially increasing in some areas due to recovery

efforts during the past three decades (Unger et al. 2013, Murphy et al. 2015, Virginia Department of Game and Inland Fisheries 2013). Also, over the past century, coyotes (*Canis latrans*) colonized eastern North America and became established in the central and southern Appalachian Mountains during the 1980s–1990s (Hody and Kays 2018). Changes in habitat quality occurred due to various factors including the chestnut blight (*Cryphonectria parasitica*) which decimated chestnut abundance resulting in an approximately 34% reduction in hard mast in the Appalachians (Diamond et al. 2000).

At the beginning of the early 20th century the area was almost completely clearcut with present day forests growing during a period of fire suppression leading to mesophication, a decrease in fire tolerant shade intolerant species, and maturation of the forest (Yarnell 1998, Nowacki and Abrams 2008, Flatley et al. 2013). Also, a reduction in timber harvest over the past four decades led to a decrease in young forests and early successional habitats (Yarnell 1998, Virginia Department of Game and Inland Fisheries 2015). These factors resulted in a lowered quality forest for white-tailed deer in portions of the Appalachians. Longstanding patterns of land use in parts of the Appalachians are likely an important driver of white-tailed deer reproduction, as resource availability is greater in landscapes with admixtures of agriculture, early successional forests and mature forests, than contiguous mature forests that characterize some Appalachian landscapes (Ford et al. 1993, Kniowski 2016, Gingery et al. 2018).

Most field studies investigating white-tailed deer population vital rates in eastern North America are relatively limited in spatial and temporal scales creating a mismatch in the scale of observation and some population processes (Campbell et al. 2005, Rohm et al. 2007, McDermott 2017, Shuman et al. 2017, Kautz et al. 2019). These data gaps are particularly important in dynamic systems that can experience substantial variation in weather (Campbell and Wood

2013), predator abundance (Bozarth et al. 2011, Little et al. 2017), and resource availability (Wentworth et al. 1992). For example, in Appalachian systems, hard mast (i.e., oak [*Quercus* spp.]), is the primary food source for deer when available, however mast availability is highly variable from year to year and variation in mast abundance has been linked to nutritional condition, recruitment, and population growth (Feldhamer et al. 1989, Johnson et al. 1995, Ford et al. 1996).

We evaluated records of adult female white-tailed deer harvested from 1997–2018 in 30 Appalachian counties in western Virginia to examine factors influencing reproductive performance. Evidence of lactation at harvest indicates an individual female white-tailed deer was reproductively active and incorporates both in vivo fecundity and early fawn survival but is insensitive to litter size (Cherry et al. 2016, Campbell et al. 2016). We integrated multiple data sources including hunter observation predator surveys, mast abundance surveys, weather data, and GIS-derived landscape metrics to evaluate factors influencing lactation status in spatially and temporally referenced white-tailed deer harvest records. We used these data to test the following predictions (1) recruitment would increase in areas with greater habitat diversity and fragmentation; (2) recruitment would decrease with increasing predator detection rates; (3) weather would influence recruitment such that precipitation would increase and winter severity would decrease recruitment; and (4) recruitment would increase with mast availability.

MATERIAL AND METHODS

Study area.— Our study area comprised 30 Appalachian counties in western Virginia (Figure 3.1), located in the Blue Ridge, Ridge and Valley, and Appalachian Plateau physiographic provinces, that spanned 35,351.17 km². Nearly the entire area was clearcut by the early 20th century and current forests regenerated during an era of fire suppression resulting in

mesophication and a shift from mast producing fire tolerant forests to fire intolerant forests with fewer hard mast producing trees (Yarnell 1998, Nowacki and Abrams 2008, Flatley et al. 2013). Additionally, timber harvest was greatly reduced over the past four decades resulting in a reduction in early successional habitats and young forests (Yarnell 1998, Virginia Department of Game and Inland Fisheries 2015). Forest types included oak-hickory (*Carya* spp.), oak-pine (*Pinus* spp.), cove hardwoods, hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*) and lesser amounts of high elevation northern hardwood (e.g., sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], American beech [*Fagus grandifolia*]) and boreo-montane species. Agriculture and development interspersed the large blocks of contiguous forests primarily in the valley bottoms (Braun 1950). Elevation ranged from 93 m to 1,740 m. Long narrow chains of mountains and narrow valleys characterized the Blue Ridge and long linear ridges and broad valleys characterized the Ridge and Valley. The Appalachian Plateau physiographic province, which contained a substantial number of coalfields, had little flat land, narrow stream valleys and steep topography. From 1997–2018, across the 30 counties, the average daily low and high temperature in January were -5.1°C and 6.1°C, while in July the average daily low and high temperature were 16.5°C, and 28.7°C. During the study, mean annual precipitation was 110.30 cm. The U.S. Forest Service was the largest public landholder in these counties and managed the George Washington National Forest and Jefferson National Forest which comprised 6,831.87 km² of our study area. Virginia Department of Game and Inland Fisheries managed the Wildlife Management Areas (470.97 km²) and the National Park Service, which did not allow hunting, managed Shenandoah National Park within parts of four counties in our study area.

Data collection.—To assess recruitment, we assembled Virginia Department of Game and Inland Fisheries (VDGIF) spatially and temporally referenced adult (age \geq 2.5 years old)

female white-tailed deer harvest data from the Deer Management Assistance Program, technical check stations, and federal properties from 1997–2018. Cooperating hunters and VDGIF staff determined evidence of lactation at harvest by cutting into the udder or visual inspection (Campbell et al. 2016). Because detection of lactation can decline with time since parturition (Campbell et al. 2016), we restricted our analyses to records of harvest occurring during 1 October–30 November to minimize these effects. We included age at harvest estimated using tooth wear and replacement (Severinghaus 1949).

Analyses.— To examine the relationship between our predictor variables and white-tailed deer lactation, we used generalized linear mixed models predicting a binary response (lactating or not). We created spatially explicit variables at the county scale including percent oak forests, percent forest, forest edge density, patch interspersion and juxtaposition index, and Shannon’s diversity index of land cover types. We built temporally dynamic variables at the annual scale including bobcat (*Lynx rufus*), coyote, and black bear detection rates. We developed spatiotemporal variables at the county and annual scales including precipitation, winter severity, red oak (*Quercus* spp.) mast abundance and white oak (*Quercus* spp.) mast abundance.

To assess the effect of female age on lactation, we created an age variable with three levels, 2.5-year-old females (young), 3.5–4.5-year-old females (middle) and ≥ 5.5 years old (mature). We excluded yearlings in our analyses because they rarely produce fawns unless located in areas of low white-tailed deer density or high habitat quality (Ozoga and Verme 1982, Swihart et al. 1998). Female nutritional condition can be an important predictor of recruitment (Mech et al. 1987, 1991) and mast crops influence white-tailed deer condition, survival, and reproduction in eastern deciduous forests (Harlow et al. 1975, Feldhamer et al. 1989, Wentworth et al. 1992). Therefore, we calculated the percent oak forests for each county. We created a

binary layer by reclassifying the Atlantic Canada and Northeast U.S. Habitats layer produced by the North Atlantic Landscape Conservation Cooperative into oak forests and not oak forests (Table 3.1) in ArcMap version 10.6 (ESRI 2018). We then calculated percent oak forests for each county (Figure 3.2). To account for temporal variation in mast, we assembled the percent crown with acorns obtained by using the Greenburg and Warburton method (Greenberg and Warburton 2007) from VDGIF survey sites for each year (2007–2017). We used these data to create two metrics that described red oak mast abundance and white oak mast abundance. Red oak mast abundance included any species in the red oak group, but was dominated by northern red oak (*Q. rubra*) and included scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), and pin oak (*Q. palustris*). White oak mast abundance included any species in the white oak group but was dominated by chestnut oak (*Q. prinus*) and white oak (*Q. alba*). We used the Inverse Distance Weighted interpolation tool in ArcMap 10.6 to create continuous surfaces representing spatial variation in red and white oak mast abundance indices for each year of the study. Subsequently, we used the Zonal Statistics as Table tool in ArcMap 10.6 to obtain a value for each county and year. We assigned mast abundance (average percent crown with acorns) values from the fall before harvest to each observation occurring in 2008–2018.

Winter severity can affect female condition, which can influence maternal investment and fawn survival (Mech et al. 1987, 1991, Garroway and Broders 2005, 2007), however, the effects of winter severity on white-tailed deer recruitment is poorly understood across the long north-south gradient in Virginia (Kniowski 2016). Therefore, we acquired weather data from 32 National Oceanic and Atmospheric Administration (NOAA; National Oceanic and Atmospheric Administration n.d.) weather stations located within and around the study area to create a winter severity variable. We calculated winter severity by totaling the number of days from 1

December–31 March that were either below 0°C or had ≥ 2.5 cm of snow accumulation for each weather station and season. We then used the Inverse Distance Weighted interpolation tool in ArcMap 10.6 to obtain continuous surfaces depicting spatial variation in the winter severity index for the study area for each year. We used the Zonal Statistics as Table tool in ArcMap 10.6 to obtain an average winter severity index for each year and county. Lastly, we assigned the winter severity index from the winter before white-tailed deer harvest to each harvest observation.

To represent food availability during late gestation and lactation, we constructed a precipitation index from weather data collected from 34 NOAA stations within and around the study area, by calculating the average daily precipitation from 15 May–30 November for each of the stations and years. This period included growing season and the transition to cool season forage crops that were in the agricultural portions of the study area (United States Department of Agriculture Natural Resources Conservation Service 2017). We then interpolated the average daily precipitation for the study area using the Inverse Distance Weighted tool in ArcMap 10.6 for each year and then used the Zonal Statistics as Table tool to obtain an average daily precipitation (mm) for each county and year.

We created several metrics to reflect landscape conditions as landscape composition and configuration can affect female nutritional condition and fawn survival (Figure 3.2, Long et al. 2016, Gulsby et al. 2017, Shuman et al. 2017). We used the 2011 National Land Cover Database (NLCD) for all years because the landscape patterns, such as the extent contiguous forest is bisected by other land uses, has remained relatively unchanged at the county scale over the duration of our study period (Brandeis et al. 2018). Thus, we aimed our questions regarding the effect of landscape composition and configuration at broad scale patterns of forest and improved

land which reflect decadal land use patterns of cultivating broader valleys with ridges and narrower valleys remaining primarily forested. We created a binary layer (Forest) for each county by reclassifying the NLCD into forested, which combined Mixed Forest, Evergreen Forest, and Deciduous Forest, and non-forested which included all other categories. We then calculated the percent forest for each county by using the Forest layer. We also calculated forest edge density (meters per hectare) for each county using the Forest layer in program FRAGSTATS version 4.2 (McGarigal et al. 2012) with a four-cell rule. We created two metrics to reflect broader habitat fragmentation, Shannon's diversity index and interspersion and juxtaposition index (%). We estimated these variables at the county scale based on a 7-class landscape (Wetland, Open Land, Developed, Mixed Forest, Evergreen Forest, Deciduous Forest, and Open Water) created by reclassifying the NLCD (Table 3.2). We used FRAGSTATS 4.2 to calculate Shannon's diversity index, and interspersion and juxtaposition index using a four-cell rule for each county.

To estimate predator activity, we created annual detection rates for black bears, coyotes, and bobcats using data from annual bowhunter surveys administered during each archery white-tailed deer hunting season (October–November) by VDGIF in our study area counties (Figure 3.3). We created species-specific indices by tabulating the frequency of observations of a given predator species per 100 hours for each year. This detection rate (detections/100 hours) was likely influenced by both variations in annual abundance, and detectability of predators. Therefore, we assigned each white-tailed deer harvest record the corresponding annual detection rate index value for black bears, coyotes, and bobcats. We centered and scaled all predictor variables and then calculated Pearson correlation coefficients to test for multicollinearity ($r \geq 0.7$). We observed multicollinearity and therefore discarded percent forest and interspersion and

juxtaposition index. We retained Shannon's diversity index as we felt this variable would better reflect needed conditions for white-tailed deer. We also retained percent oak forests over percent forests as percent oak forests were a better indicator of food availability, which we believed would be crucial for female white-tailed deer condition and recruitment. In addition, we considered percent oak forests as a surrogate for oak mast abundance which allowed us to test our hypothesis about oak mast for all years of the study. We used package lmer4 version 1.1-21 (Bates et al. 2015) in program R (version 3.5.1, R Development Core Team 2018), to fit generalized linear mixed models with binomial distributions and a logistic link function predicting the binary outcome of lactation. We included all possible linear and additive combinations of scaled and centered variables that reflected our hypotheses and treated county and year as random intercept terms. Out of the competing models (≤ 2 delta AIC; Anderson and Burnham 2002) we determined the top model based on model weights and parsimony, as well as assessed variables within the models via z scores, and assigned significance at $\alpha < 0.05$.

To test our prediction more directly regarding the relationship between oak mast and recruitment, we conducted a secondary analysis that included data from annual mast abundance field surveys conducted from 2007–2017. For this analysis, we used the top model from the primary analysis and added red and white oak mast abundance to it in various combinations. We created a model set of five models. These five models retained the same model structure and random effects as the primary analysis.

RESULTS

We included 28,313 observations of harvested female white-tailed deer from 1997–2018 from 30 Appalachian counties of western Virginia. For all counties and years, mean lactation was 0.48 ± 0.50 (mean \pm SD). Mean number of harvest records per county was 943.77 ± 1007.87

and the mean number of harvest records per year was 1286.95 ± 421.54 . Of the 28,313 females, 9,382 were young, 7,966 were middle-aged, and 10,965 were mature.

From 1997–2018 participating hunters spent an average of $6,634.32 \text{ hours} \pm 2186.78$ per year conducting the bowhunter survey. Black bear detections ranged from 0.36 to 2.77/100 hours with a mean of 1.28 ± 0.65 and varied widely, but increased overtime (Figure 3.3). Coyote detections increased rapidly early in the study but stabilized then declined slightly with a range of 0.16 to 1.81/100 hours and a mean of 0.90 ± 0.45 (Figure 3.3). Bobcat detections were relatively low and stable, ranging from 0.08 to 0.41/100 hours with a mean of 0.22 ± 0.09 (Figure 3.3).

Our top model contained black bear detection rate, Shannon's diversity index, and white-tailed deer age which were all informative parameters ($p < 0.05$; Table 3.3). All other competing models (≤ 2 delta AIC) contained these variables and various combinations of other uninformative parameters ($p \geq 0.05$; Table 3.4). For every unit (SD) increase in black bear detections, probability of lactation decreased by 9% (Figure 3.4). For every unit (SD) increase in Shannon's diversity index, probability of lactation increased by 13% (Figure 3.5). We found probability of lactation to be greatest for the middle-age (3.5–4.5 years old) class, followed by young age (2.5 years old) class and mature age (≥ 5.5 years old) class (Table 3.3; Figure 3.6). Our secondary analysis included 11,126 harvest observations from 29 counties for years 2008–2018. There were three competing models (≤ 2 delta AIC), with the top model containing age, black bear detection rate and Shannon's diversity index. We did find some support for red and white oak mast abundance as these variables were in the competing models, but ultimately, both mast variables were uninformative parameters ($p \geq 0.05$) for predicting lactation status (Table 3.5).

DISCUSSION

Over a 22-year period, landscape patch diversity, black bear detection rate, and age proved to be the strongest predictors of lactation status of harvested female white-tailed deer in 30 counties in the Appalachian Mountains in western Virginia. This study area represented a larger region which has experienced a decrease in white-tailed deer populations in conjunction with a senescing forest and changing predator communities. This decrease has sparked considerable discussion of the causative factors of declining white-tailed deer densities (Virginia Department of Game and Inland Fisheries 2015, Little et al. 2018). We found support for patch diversity, a spatial variable, suggesting that increased patch diversity improved white-tailed deer recruitment potentially by enhancing nutrition or decreasing predation (Rohm et al. 2007, Gulsby et al. 2017). We also found support for temporal variation in black bear detection rates, suggesting long term recovery of black bears in western Virginia may have negatively affected white-tailed deer recruitment. However, this negative relationship between recruitment and black bear detection rate could be partially explained by maturing forests causing a decline in white-tailed deer productivity, but not hampering the growth of black bear populations (Powell et al. 1997).

White-tailed deer recruitment increased with Shannon's diversity index, a measure of patch fragmentation. In our system, Shannon's diversity index largely reflected the extent to which roads, development, and agriculture bisected large blocks of mature even-aged forests. Recruitment was lower in areas with large contiguous forests and greater in areas with more patch diversity. Therefore, areas with a lower proportion of forest and a greater proportion of other cover types, such as agriculture, generally had greater evenness and higher Shannon's diversity values. This supports the finding of Gingery et al. (2018) who demonstrated through a

meta-analysis that fawn survival increased with increasing percent agriculture in forested landscapes. Landscape fragmentation may enhance recruitment by improving female condition via increasing the variety and quality of food resources (Johnson et al. 1995). In some parts of the Appalachian Mountains the only break in forests are utility rights of ways, logging decks, and coal mines. These areas increase patch diversity and likely increase recruitment. Managers could increase deer recruitment by permanently converting forest to other patch types to diversify land cover via timber harvest and prescribed fire. However, it is unknown if the mechanism underlying the positive relationship between recruitment and patch diversity is greater food availability (Ford et al. 1993, 1994, Johnson et al. 1995, Miller et al. 2009), decreased predation (Gulsby et al. 2017) or the combined effects.

Black bear detection increased substantially during our study and white-tailed deer recruitment was negatively related to black bear detection rate. Black bears can be important predators of white-tailed deer fawns (Vreeland et al. 2004, Shuman et al. 2017) and the cause of the negative relationship between recruitment and black bear detection rate may simply be due to black bears depredating white-tailed deer fawns (Shuman et al. 2017). Additionally, black bears rely heavily on hard mast in Appalachian systems and may be an important competitor for white-tailed deer in mast-driven systems (Beeman and Pelton 1980, Reynolds-Hogland et al. 2007). Also, the negative relationship between black bears and lactation status could in part be explained by the maturing forests decreasing white-tailed deer productivity while having a smaller negative effect on black bear productivity as black bears appear to do well in Appalachian old growth forests (Powell et al. 1997). If increasing white-tailed deer densities is a management objective, managers could consider manipulating black bear densities through harvest. However, there is growing evidence that predator richness is not a strong predictor of

fawn survival (Shuman et al. 2017; Kautz et al. 2019) and thus understanding the role of compensatory fawn mortality sources would be essential in predicting the success of reducing black bear densities to increase white-tailed deer recruitment.

In our study, age influenced recruitment, with middle-aged (3.5–4.5 years old) white-tailed deer having higher lactation probabilities than young and mature white-tailed deer. In contrast, female white-tailed deer adults (≤ 15.5 years old) had no change in reproduction or fecundity in Minnesota (DelGiudice et al. 2007). These differences in findings may be due to different habitat quality and/or a herd which is substantially under the habitat carrying capacity. However, our result is similar to a finding that white-tailed deer in Alabama had the highest reproductive success from 4.5–5.5 years old (Karns et al. 2014) and that red deer (*Cervus elaphus*) success at raising offspring declines after 6–7 years old (Fisher et al. 2000).

Other predictor variables, such as coyote detection rate, did not influence white-tailed deer recruitment. However, in some systems, coyotes have a negative effect on white-tailed deer recruitment (Kilgo et al. 2010, Cherry et al. 2016). We found no support for this effect in our data, possibly due to low coyote densities in the area (Morin et al. 2016). We also suspect coyotes did not influence recruitment as our study area was largely forested which may not facilitate the cursorial hunting mode of coyotes (Crête et al. 2001, Richer et al. 2002).

Weather is often an important driver of ungulate population dynamics with evidence for positive effects of growing season precipitation (Michel et al. 2018) and negative effects of winter severity (Mech et al. 1987, Garroway and Broders 2005, 2007). We did not find any support for precipitation possibly because the Appalachian Mountains of western Virginia are relatively temperate and wet compared to some other locations. We also did not find support for

winter severity which may be due to more mild winters than in the study systems farther north (Mech et al. 1987, Garroway and Broders 2005).

We failed to detect the effect of mast abundance on recruitment despite numerous studies reporting oak mast abundance being important for female energetic requirements, and for fawn and yearling body mass (Harlow et al. 1975, Wentworth et al. 1992, Kjellander et al. 2006, Kniowski 2016). This may be due to the reduced power in the secondary analysis which included only 39% of the observations from half of the years. It is also possible that mast the previous fall did not have meaningful effects on recruitment status the following fall. Lastly, in some poor oak mast crop years there may be an abundance of other mast species such as wild grape (*Vitis* spp.) or American beech nuts that could enable white-tailed deer to compensate nutritionally to meet their energetic requirements.

There are several limitations to our retrospective and observational approach to understanding drivers of white-tailed deer recruitment, which should be acknowledged when considering our results. First, evidence of lactation is an indirect measure of recruitment that indicates that one or more fawns probably survived until recruitment (Dzięciołowski et al. 1995, Strickland et al. 2008, Campbell et al. 2016), but does not provide information on litter size and can include positive bias due to late mortality of fawns. Additionally, detectability of lactation declines with time since parturition, which may have led to under detection of females that had lactated (Campbell et al. 2016). To mitigate potential bias associated with under detection, we constrained our analyses to October and November. Additionally, our annual predator detection indices were only temporally explicit because data constraints prevented spatial representation of the data. Second, the bowhunter survey was conducted in the fall when fawns are less at risk of predation and when variation in mast may influence the behavior and detectability of predators.

Therefore, the detection rates may not reflect the activity of predators in the late spring and early summer when fawns are younger and therefore most vulnerable to predation (Shuman et al. 2017). Nonetheless, the temporal variation in black bear detection proved sufficient to detect a relationship with fawn recruitment. It is possible that due to the large scale of our study area some of the variables we found to be uninformative could be important on smaller scales. Therefore, examination of the effects of local management on white-tailed deer lactation and testing our predictions in areas with varying amounts of heterogeneity as well as known black bear densities, are important next steps to support management recommendations.

Black bear detection rate, landscape patch diversity, and age influenced the lactation status of female white-tailed deer harvested over 22 years in 30 counties in the Appalachian Mountains in western Virginia. Portions of this study area experienced a decline in white-tailed deer populations concurrent with changing predator communities and an aging forest. Our study illustrates how landscape conditions and increasing predator populations can influence population performance. Studies examining long-term data are needed to evaluate the effects of how changing environmental conditions may be impacting wildlife populations. To link these results to practice, future work should examine the efficacy of management responses to manipulate the factors we identified as influencing deer recruitment.

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TABLES AND FIGURES

Table 3.1. Class names of the reclassified Atlantic Canada and Northeast U.S. Habitats layer to create percent oak forests by county to examine factors affecting lactation from 1997–2018 in 30 Appalachian counties of western Virginia, USA.

Reclassification	Original Classes
Oak forest	Allegheny-Cumberland Dry Oak Forest and Woodland/Appalachian (Hemlock)-Northern Hardwood Forest/Appalachian Shale Barrens/Central and Southern Appalachian Montane Oak Forest/Central and Southern Appalachian Spruce-Fir Forest/Central Appalachian Alkaline Glade and Woodland/Central Appalachian Pine-Oak Rocky Woodland/Dry Oak-Pine Forest, Central Apps and Southern Piedmont/North-Central Interior Large River Floodplain/Northeastern Interior Dry-Mesic Oak Forest/Piedmont-Coastal Plain Large River Floodplain/Serpentine Barren/Woodland/South-Central Interior Mesophytic Forest/Southern and Central Appalachian Cove Forest/Southern and Central Appalachian Mafic Glade and Barrens/Southern Appalachian Low Elevation Pine Forest/Southern Appalachian Montane Pine Forest and Woodland/Southern Appalachian Northern Hardwood Forest/Southern Appalachian Oak Forest/Southern Piedmont Mesic Forest/Southern Ridge and Valley Calcareous Glade and Woodland/Southern Ridge and Valley/Cumberland Dry Calcareous Forest
Not oak forest	Acidic cliff and talus/Agriculture/Calcareous Cliff and Talus/Central Interior Highlands and Appalachian Sinkhole and Depression Pond/Circumneutral Cliff and Talus/Developed/High Allegheny Headwater Wetland/Laurentian-Acadian Freshwater Marsh/Laurentian-Acadian Wet Meadow-Shrub Swamp/North-Central Appalachian Acidic Swamp/North-Central Appalachian Large River Floodplain/North-Central Interior and Appalachian Rich Swamp/Open water/Piedmont-Coastal Plain Shrub Swamp/Plantation Forest/Riparian Forest, southeast Virginia/Shrubland/grassland; mostly ruderal shrublands, regenerating clearcuts

Table 3.2. Class names of the reclassified 2011 National Land Cover Database to create Shannon’s diversity index of land cover classes and interspersed and juxtaposition index by county to examine factors affecting lactation from 1997–2018 in 30 Appalachian counties of western Virginia, USA.

Reclassification	Original Classes
Wetland	Woody wetlands/emergent herbaceous wetlands
Mixed forest	Mixed forest
Evergreen forest	Evergreen forest
Deciduous forest	Deciduous forest
Open land	Barren/shrub/scrub/grassland/herbaceous/pasture/hay/cultivated crops
Open water	Open water
Developed	Open space/low intensity/medium intensity/high intensity

Table 3.3. The fixed effects, their estimates, standard errors, z values and p-values from the top model for the white-tailed deer harvest data (lactation) from 1997–2018 in 30 Appalachian counties of western Virginia, USA.

Fixed effects*	Estimate	Standard Error	Z value	Pr(> z)
Intercept	0.53	0.05	10.19	< 0.001
Black bear detection rate	-0.09	0.03	-3.64	< 0.001
Shannon's diversity index	0.13	0.04	3.51	< 0.001
Age mature	-1.51	0.03	-47.56	< 0.001
Age young	-0.27	0.03	-8.39	< 0.001

* Age mature=females ≥ 5.5 years old, Age young=2.5-year-old females, Age reference class=middle-aged (3.5–4.5 years old)

Table 3.4. Covariates and their respective coefficients in the competing models (≤ 2 delta AIC), number of parameters (K), along with the models ranked using Akaike’s Information Criterion (AIC), delta AIC (Δ AIC) and weight (Wi) from the generalized linear mixed models run with white-tailed deer harvest data (lactation) from 1997–2018 in 30 Appalachian counties of western Virginia, USA. Bold type represents significant variables ($p < 0.05$).

(Intercept)	Age	Be	Bo	Co	Ed	Prcp	Ws	Ma	Sdi	K	AIC	Δ AIC	Wi
0.53	+ *	-0.09							0.13	7	36092.81	0.00	0.05
0.53	+	-0.10				0.03			0.13	8	36092.95	0.14	0.05
0.53	+	-0.08	0.04						0.13	8	36093.03	0.23	0.04
0.53	+	-0.09	0.04			0.03			0.13	9	36093.09	0.29	0.04
0.52	+	-0.09			0.04				0.13	8	36093.68	0.87	0.03
0.52	+	-0.10			0.04	0.03			0.13	9	36093.83	1.02	0.03
0.52	+	-0.08	0.04		0.04				0.13	9	36093.87	1.06	0.03
0.53	+	-0.09					0.02		0.13	8	36093.88	1.07	0.03
0.52	+	-0.09	0.04		0.04	0.03			0.13	10	36093.94	1.13	0.03
0.53	+	-0.11		0.03					0.13	8	36094.15	1.35	0.03
0.53	+	-0.12		0.03		0.03			0.13	9	36094.27	1.46	0.02
0.53	+	-0.10				0.03	0.02		0.13	9	36094.31	1.50	0.02
0.52	+	-0.09			0.04		0.03		0.13	9	36094.50	1.69	0.02
0.53	+	-0.09	0.03	0.02					0.13	9	36094.53	1.72	0.02
0.52	+	-0.09						-0.02	0.12	8	36094.55	1.74	0.02
0.53	+	-0.10	0.04	0.02		0.03			0.13	10	36094.57	1.76	0.02
0.53	+	-0.08	0.03				0.02		0.13	9	36094.63	1.82	0.02
0.52	+	-0.10				0.03		-0.02	0.12	9	36094.66	1.85	0.02
0.53	+	-0.08	0.04					-0.02	0.12	9	36094.76	1.96	0.02
0.52	+	-0.09	0.04			0.03		-0.02	0.12	10	36094.79	1.99	0.02

*All pluses are bold, +=Age of female white-tailed deer (2.5, 3.5–4.5, ≥ 5.5 years old), Be=black bear detection rate, Bo=bobcat detection rate, Co=coyote detection rate, Ed=edge density, Prcp=precipitation index, Sdi=Shannon’s diversity index of land cover classes, Ma=percent oak forests, Ws=winter severity

Table 3.5. Generalized linear mixed model results ranked with Akaike’s Information Criterion with model components (Model), parameter numbers (K), Akaike’s Information Criterion (AIC), delta AIC (Δ AIC), and model weights (Wi) from all models included in the secondary analysis to determine if oak mast abundance affects lactation of white-tailed deer from 2008–2018 in 29 Appalachian counties of western Virginia, USA.

Model*	K	AIC	Δ AIC	Wi
Age + Be + Sdi	7	14265.19	0.00	0.49
Age + Be + Sdi + Wo	8	14266.77	1.58	0.22
Age + Be + Sdi + Ro	8	14267.01	1.82	0.20
Age + Be + Sdi + Wo + Ro	9	14268.67	3.48	0.09
Null	3	15242.26	977.07	0.00

*Age=age of female white-tailed deer (2.5, 3.5–4.5, \geq 5.5 years old), Be=black bear detection rate, Sdi=Shannon’s diversity index, Ro=red oak mast abundance, Wo=white oak mast abundance

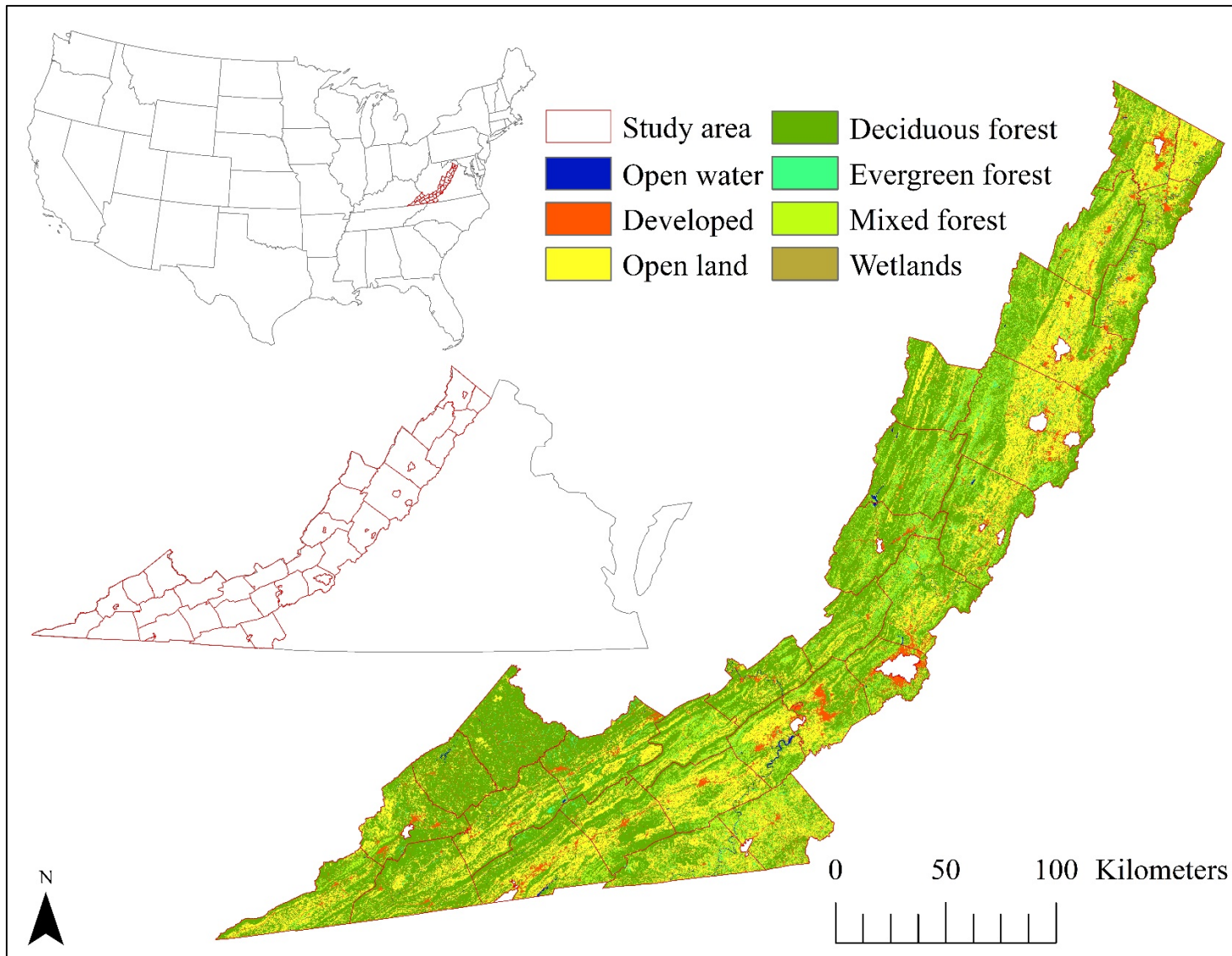


Figure 3.1. The study area included 30 counties in the Appalachian Mountains in western Virginia, USA with open water, and land cover types including developed, open land, deciduous forest, evergreen forest, mixed forest, and wetlands.

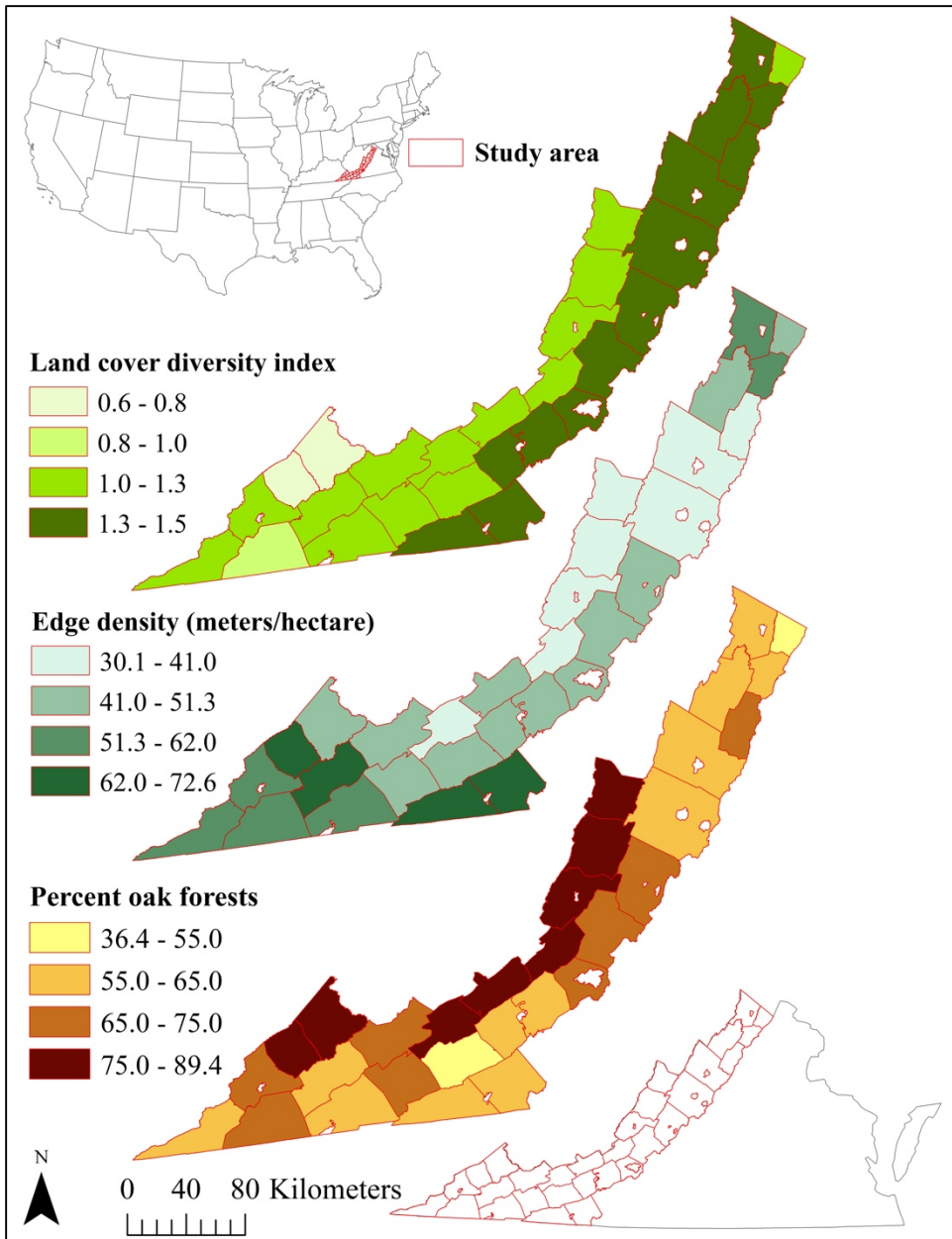


Figure 3.2. Study area, Shannon's diversity index of land cover types obtained by inputting 7 land cover classes reclassified from the 2011 National Land Cover Database by county into FRAGSTATS version 4.2 with the proportion of areal distribution among the types of patches becoming more even and/or the increasing number of patch types increasing the value of the index, edge density (meters per hectare) obtained by reclassifying the 2011 National Land Cover Database into forest versus non-forest and then inputting the layers into FRAGSTATS 4.2, and percent oak forests (%) calculated by using the Atlantic Canada and Northeast U.S. Habitats layer produced by the North Atlantic Landscape Conservation Cooperative by county in 30 Appalachian counties of western Virginia, USA.

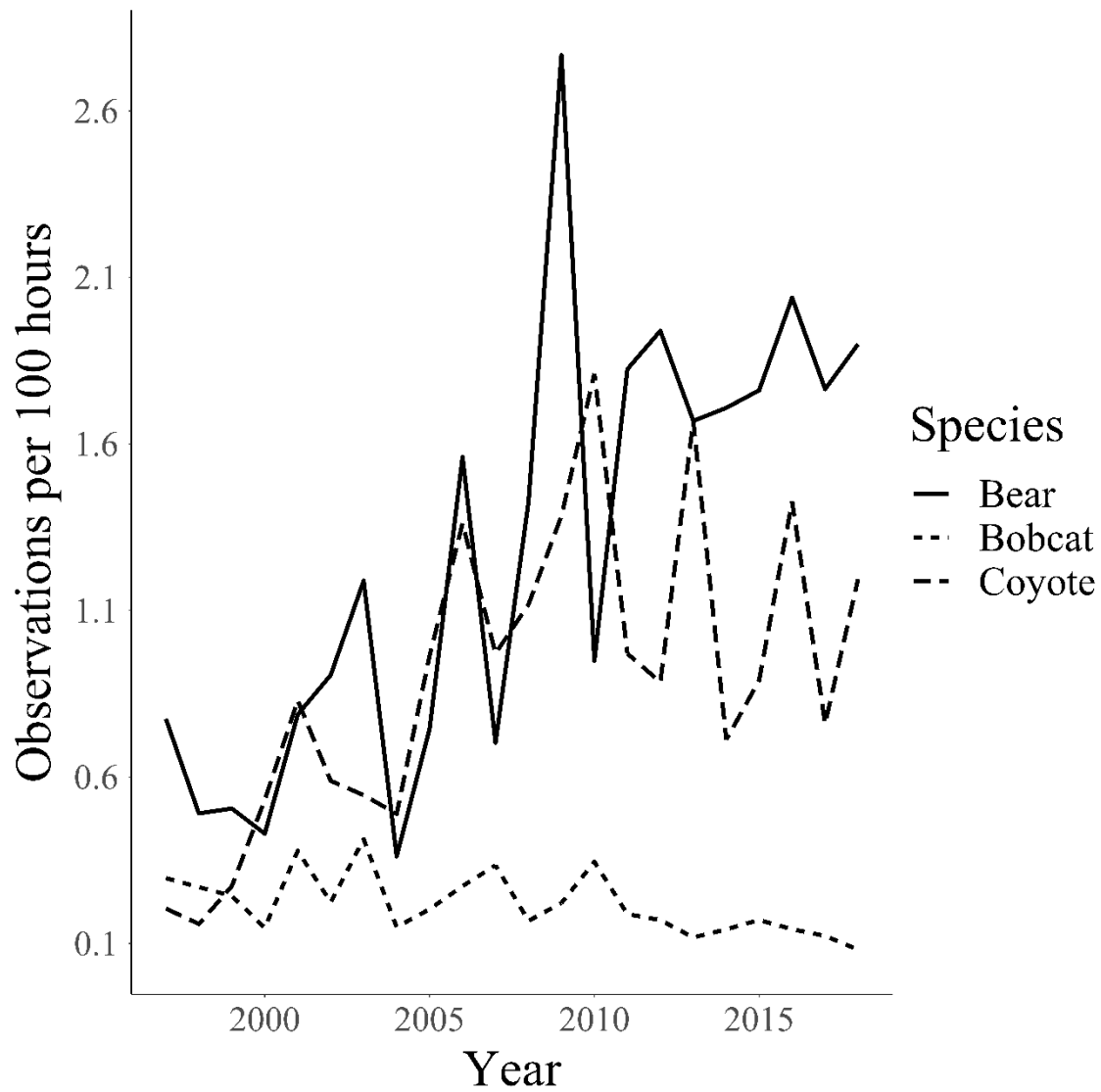


Figure 3.3. Observations of black bears, bobcats and coyotes from the bowhunter surveys per 100 hours from 1997–2018 from our study counties in western Virginia, USA with data collected by the Virginia Department of Game and Inland Fisheries.

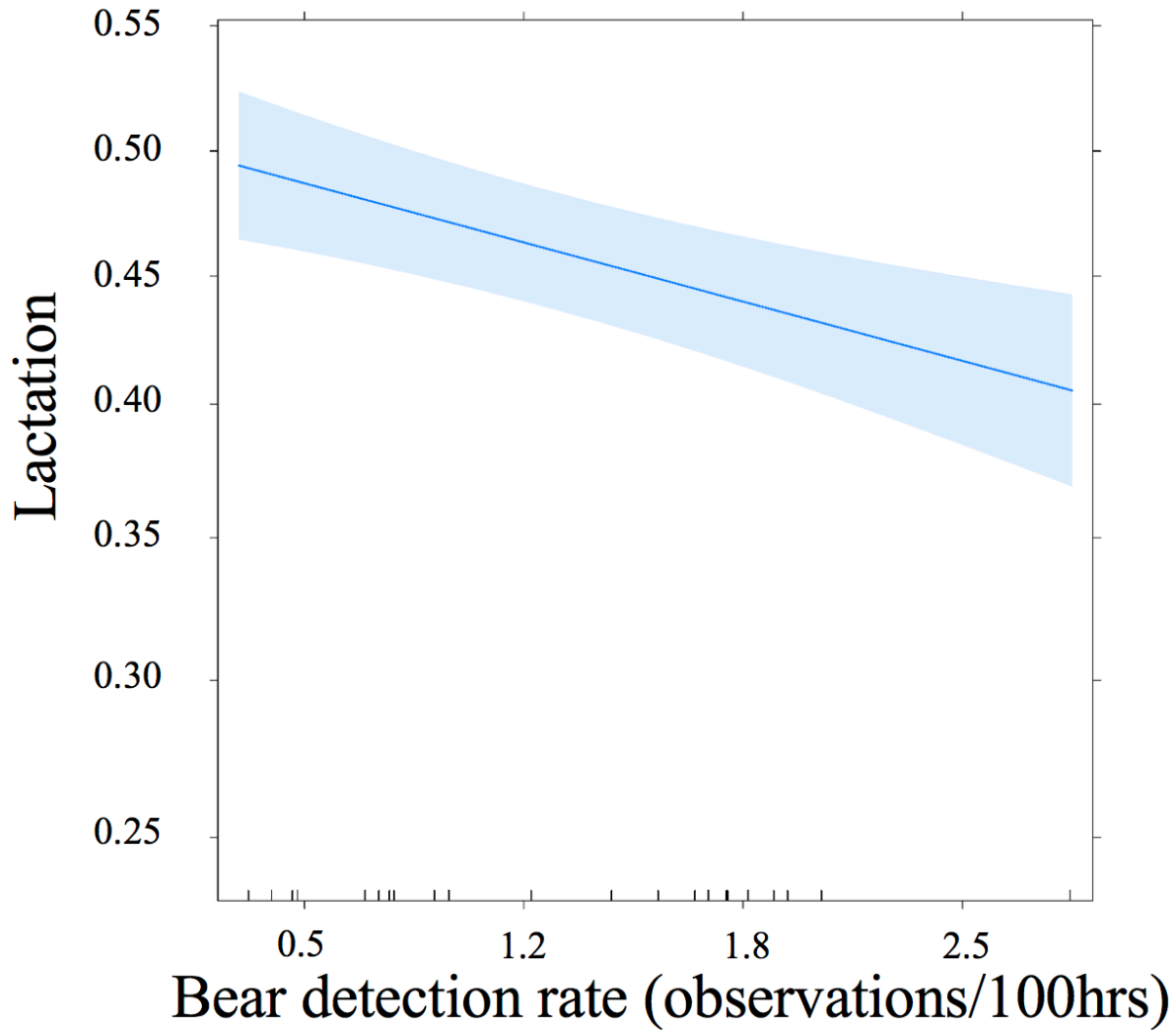


Figure 3.4. Relationship between black bear detection rate (observations/100 hours) and female white-tailed deer lactation ($n=28,313$) with 95% confidence intervals and a rug plot indicating observed black bear detection rates from 1997–2018 in 30 Appalachian counties of western Virginia, USA.

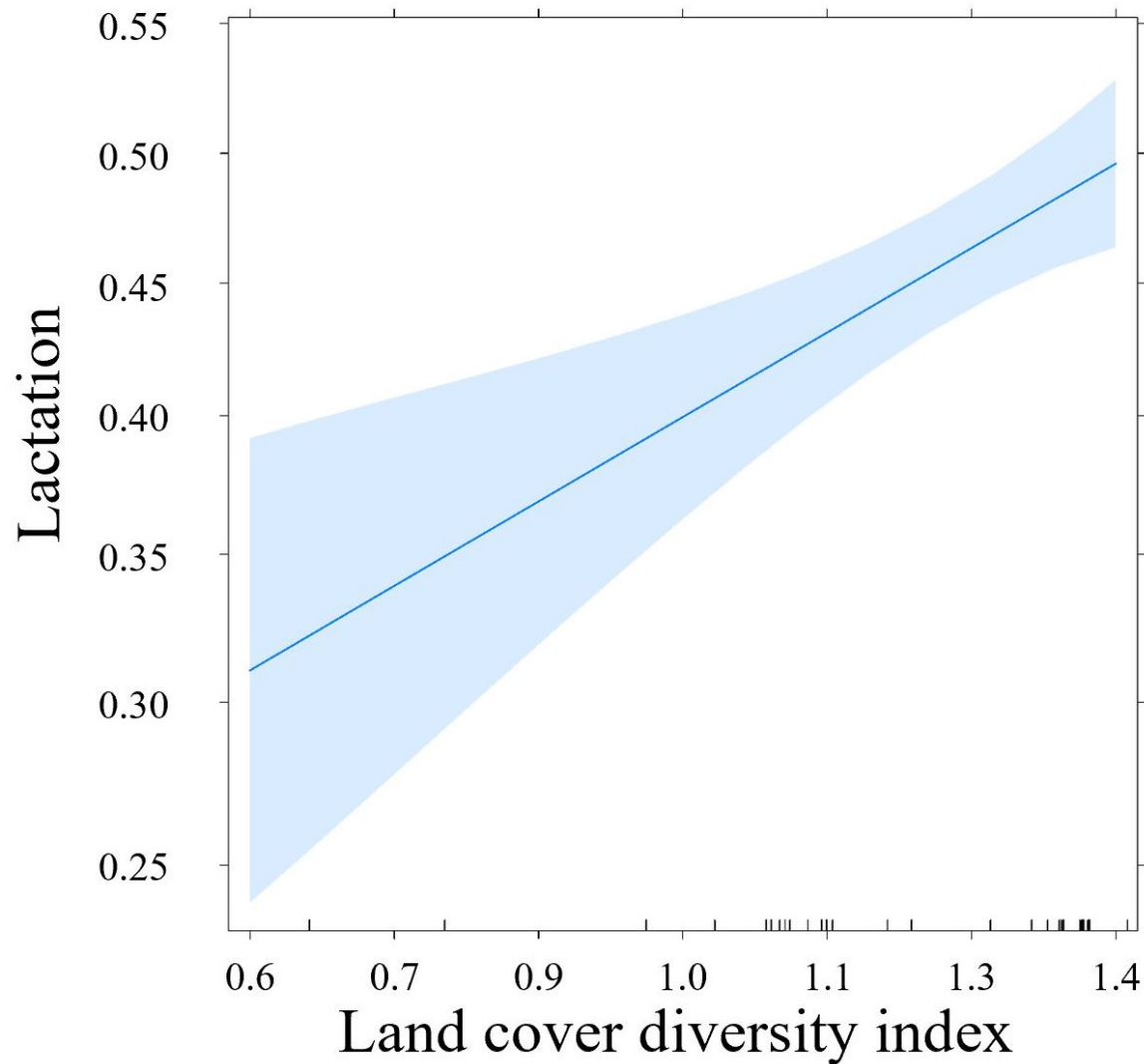


Figure 3.5. Relationship between land cover diversity index (Shannon's diversity index) and female white-tailed deer lactation ($n=28,313$) with 95% confidence intervals and a rug plot indicating observed Shannon's diversity indexes from 1997–2018 in 30 Appalachian counties of western Virginia, USA.

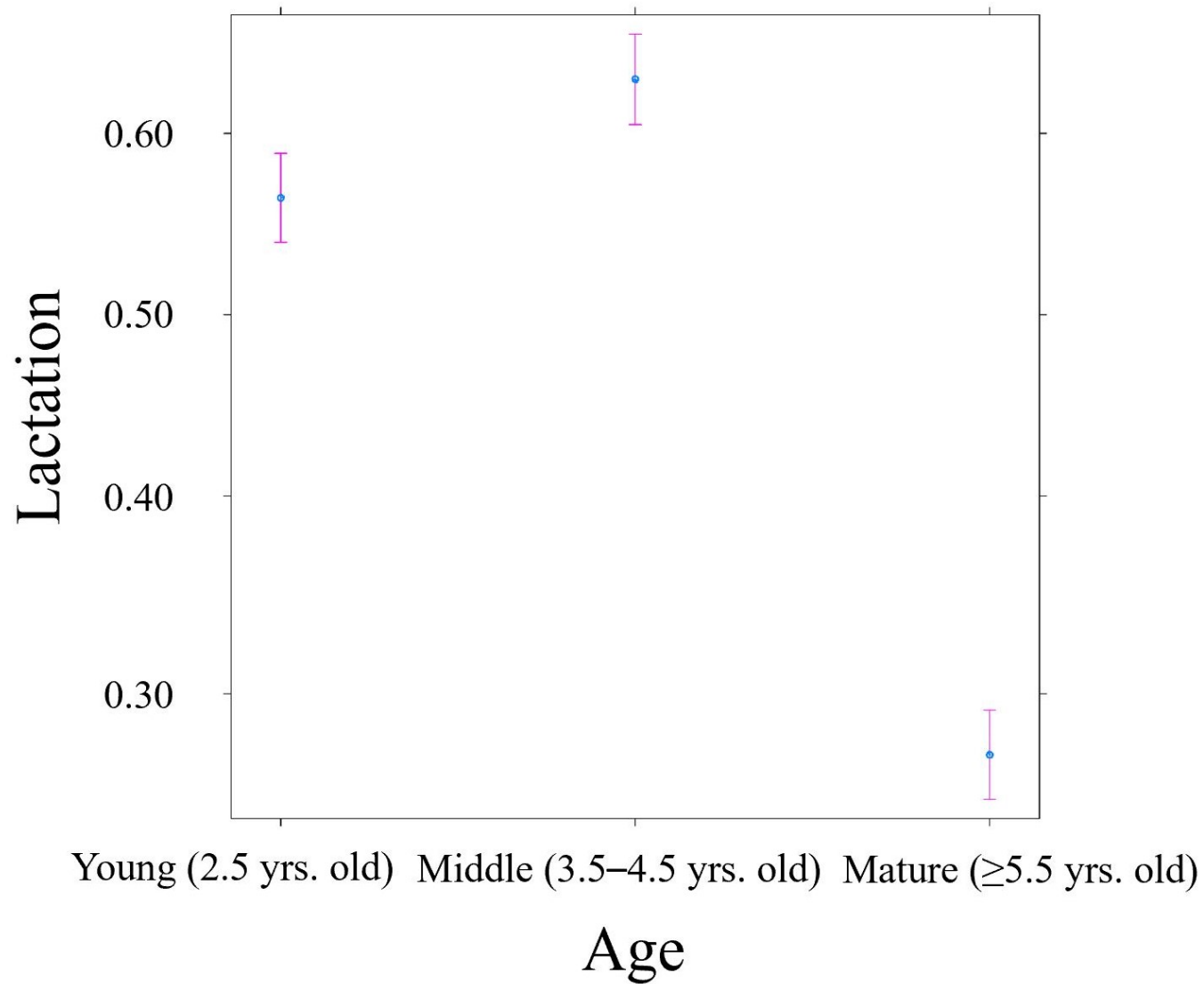


Figure 3.6. Relationship between age and female white-tailed deer lactation ($n=28,313$) with 95% confidence intervals from 1997–2018 in 30 Appalachian counties of western Virginia, USA.

Conclusion

Gisèle Rosalie Aubin

White-tailed deer (*Odocoileus virginianus*) are an important cultural and economic resource and are the largest driver of conservation funding, but they also cause economic damage to agriculture, private property and harm people in the form of deer vehicle collisions. Due to these varying impacts it is of utmost importance to understand drivers of white-tailed deer populations to be able to better manage the species at desired levels. Over the past twenty years, there has been a decline in white-tailed deer abundance in eastern North America which has occurred concurrently with expanding coyote populations (Bozarth et al. 2011, Fies 2019). There has also been an increase in bear numbers (Fies 2019, Unger et al. 2013) in many areas of the Appalachian Mountains and a degradation of the forest which stemmed from a variety of factors including the American chestnut blight, a decrease in timber harvesting and fire suppression (Yarnell 1998, Diamond et al. 2000, Flatley et al. 2013, Aldrich et al. 2014). The decline in deer numbers has been the subject of much controversy and recent research. Although studies have been conducted to determine the causes of the decline they have occurred on relatively limited spatial and temporal scales. Therefore, we studied fawn survival, mortality causes, and factors affecting survival over a 12-year period (2008–2019) on Marine Corps Base Quantico (Quantico) located in northern Virginia, USA. We found red oak mast abundance impacts survival positively and the first interval (2008–2010) of the study had a higher survival probability than the last three intervals (2011–2013, 2014–2016, 2017–2019). Predation was the leading source of mortality with most deaths occurring within 10 weeks of age. We also examined factors influencing recruitment in the Appalachian Mountains of western Virginia. We used harvest records from 22 years (1997–2018) in 30 counties from the Virginia Department of Game and

Inland Fisheries to predict lactation status, a measure of recruitment, of female deer (≥ 2.5 years old) in the Appalachian Mountains of western Virginia. We found lactation increased with increasing land cover diversity, decreased with increasing bear activity and middle-aged females had the highest lactation probability. Our findings suggest white-tailed deer recruitment is influenced by food availability, landscape characteristics, and predators. If an increase in deer numbers is so desired, managers could permanently change land cover types via such tools as fire and timber harvesting which would increase diversity of habitats. Prescribed burning and/or forestry techniques could also be implemented in order to try and increase the number of oaks on the landscape and/or to increase the amount of acorns produced by already mature oaks (Abrams 1992, Johnson 1994, Healy 1997). As bears were shown to have a negative effect on recruitment and as predators caused the largest amount of fawn deaths, managers could reduce predator numbers but before doing so it is important to examine compensatory mortality factors. Lastly reducing the number of total harvested females, leaving more individuals to reproduce on the landscape, may increase recruitment.

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