

**Population Dynamics and Spatial Ecology of White-tailed Deer in the Central Appalachian
Mountains of Virginia**

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Abstract (Academic)

White-tailed deer (*Odocoileus virginianus*) are a highly charismatic game species with considerable ecological and economic impacts across most of their range. In the central Appalachian Mountains, deer are a keystone species in forested ecosystems. Regionally, populations vary in herd growth or decline. These fluctuations are important in that they often drive many aspects of population management and regulation, which are dependent on herd demographics. Some key population vital rates allowing better understanding of these changes in white-tailed deer herds are survival, cause-specific mortality, home-range variation, both broad and fine-scale resource selection, and ultimately population growth trends in response to changes in both population vital rates and hunter harvest regulations. In this study, I address each of these concepts within a deer population in Bath County, Virginia, that has presumably been in overall decline since the early 1990's. From June-September, 2019-2020, I monitored survival and cause specific mortality of 57 neonate white-tailed deer until 12 weeks of age. Fawn and adult female survival was 0.310 (95% CI = 0.210-0.475) and 0.871 (95% CI=0.790-0.961) respectively. During the study, I observed a total of 37 fawn mortalities and identified the cause of death using field evidence and through analyzing genetics from residual predator saliva recovered on deer carcasses. Mortalities included 28 predation events and 9 deaths from other causes (e.g., abandonment, malnutrition, or disease). Black bears accounted for 48.6% of all mortality and 64.2% of known predations within our study. My top model identified elevation as a significant predictor of fawn survival, with mortality risk increasing 20% for every 100m

increase in elevation. My model using observed vital rates predicted an increasing population of $\lambda = 1.10$ (interquartile range, IQR 1.06-1.14). The population was predicted to increase by 2% with a 10% increase in doe harvest ($\lambda = 1.02$, IQR = 0.97-1.06) but declined by 7% at 20% harvest ($\lambda = 0.93$, IQR = 0.89-0.96). I found that fawning home ranges of females that successfully reared fawns to the end of the season had significantly larger home ranges than those that were unsuccessful at higher elevations. Fawning home ranges for females with fawns increased approximately 71ha in size for every 100m increase in mean home range elevation, whereas seasonal home ranges of females without fawns decreased approximately 1.5 ha for every 100m increase in mean home range elevation. Deer selected fawn-rearing areas nearer to forested edges, open habitats, and at higher elevations, while they avoided areas near disturbed and mature forests. Within the fawn rearing area, females selected locations closer to disturbed forest, open habitats, and forested edge, while avoiding mature forest habitats, and higher elevations. Females selected birth sites with higher levels of visual obstruction. Using a step-selection method for real-time resource selection across biological seasons, we found that female deer selected for open areas during the fawning, breeding, early gestational, and late gestational seasons. During the fall breeding season, females avoided forested edge, but selected for areas at higher elevations. During early gestational seasons females selected disturbed habitats and areas at higher elevations while again avoiding forested edge. Overall, my work highlights variations in population dynamics of white-tailed deer in areas of the central Appalachian Mountains that are primarily characterized by poor habitat quality and provides novel insights into fine-scale spatial ecology of female deer across biological seasons within the region. Ultimately, while the deer population in our study was not predicted to be in decline, this work supports predation risk as being a significant factor associated with habitat quality.

Population Dynamics and Spatial Ecology of White-tailed Deer in the Central Appalachian Mountains of Virginia

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Abstract (Public)

White-tailed deer (*Odocoileus virginianus*) are a game species with extensive ecological and economic impacts across most of their range. In the central Appalachian Mountains, many populations across the region vary in terms of herd size growth, stability, or decline. These fluctuations are important in that they often drive many aspects of population management and regulation, which are dependent on the status of herd demographics. Some key population vital rates that aid us in better understanding these changes in white-tailed deer herds are survival and cause-specific mortality, home-range variation in association with habitat quality and the ability to successfully reproduce, population trends under hypothetical management scenarios, and resource selection of various habitats that are available across the landscape. In this study, I address each of these concepts within a deer population in Bath County, Virginia, which has presumably been in decline since the early 1990's. As expected, fawn survival was lower than previously reported from other study areas of the central Appalachians Mountains. Predation was the leading cause of fawn mortality, with black bears being responsible for most predation events. Fawn mortality risk was significantly associated with elevation - where fawns at higher elevations were those at greater risk. Surprisingly, the deer population in Bath County was projected to be increasing under current conditions and was also projected to be stable-to-increasing even under some hypothetical scenarios which would negatively impact population growth (i.e., 10% increase in female harvest or 17% reduction in fawn survival). Fawning home ranges of collared females which successfully reared known fawns to the end of the biological

season were significantly influenced by elevation; such that females with fawns had home ranges that increased in size with increasing elevation, whereas females without fawns had home ranges which decreased slightly in size with increasing elevation. At birth sites, females selected locations characterized by higher levels of visual obstruction compared to randomly sampled areas. Of the habitat types analyzed, both selection or avoidance of specific habitats varied across both biological season and spatial scale. Ultimately, while I found that some deer populations associated with poor quality habitats in the central Appalachians may not be in decline, deer were likely influenced greatly by habitat quality – especially pertaining to predation risk – throughout Bath County.

Dedication

To my biggest fan...My Mom.

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Chapter 1: Introduction

No other game species in North America has had such a profound effect on or importance to wildlife management as the white-tailed deer (*Odocoileus virginianus*). In many localities, their intrinsic value as a natural resource has spearheaded decades of conservation effort to increase populations, whereas in other areas, herds have become overabundant and in need of reduction. Often at the forefront of these programs, studies that focus on population vital rates, resource selection, and seasonal home range variation are foundational in providing managers with a basis for implementation of management plans.

White-tailed deer are habitat that occupy a diverse array of ecosystems in North America (Stewart et al. 2011). In forested landscapes, deer tend to select disturbed areas due to the increased quality of forage that comes with many habitat management practices (Teer 1996). This pattern may be context dependent as recently disturbed habitats may initially produce higher quantities of nutritious forage that attract deer, but lack desirable cover needed to aid in predator avoidance over an initial regrowth period (Cherry et al. 2017*a, b*). Additionally, during autumn, deer in these landscapes are often influenced by the unpredictable cyclic patterns of hard mast production (Wentworth et al. 1992, Ford et al. 1997). During summer, females are stressed with the challenges of fawn rearing and many resource selection studies focused on parturition and post-parturition seasons, as pregnant females are faced with meeting nutritional demands of lactation as well as finding fawning habitat that will provide sufficient cover to aid against cursorial predators (Lashley et al. 2015, Cherry et al. 2017*b*, Shuman et al. 2018).

Survival and recruitment of white-tailed deer populations are also driven by relationships with habitat preference and availability. Typically, these linkages are assessed regarding the reproductive chronology of the animal, when metabolic demands are higher than usual as a

response to birth and fawn rearing processes (i.e., pre-parturition, parturition, and post-parturition) (Cherry et al. 2017b, Shuman et al. 2018). However, these relationships are also influenced by predator densities and their habitat use (Cherry et al. 2017a). These interactions are paramount because it allows wildlife managers to better understand the relationships between deer and their environment and provides an understanding of factors that influence responses to management. Cherry et al. (2017b) analyzed the effects of time since fire on the selection of and within fawn rearing areas in southwestern Georgia. While areas which had been more recently burned typically provided higher quality browse, deer paradoxically selected woodlands with greater time since fire and avoided areas which had been more recently burned (Cherry et al. 2017b). They hypothesized this phenomenon to be a behavioral response to coyote (*Canis latrans*) predation in recently burned areas with reduced concealment cover. In Louisiana, fawn survival to 12 weeks increased 8% for every 100 m increase in distance from an adjacent cropland or young reforestation areas whereas survival decreased 11% for every 100 m increase in distance to old reforestation areas, which was believed to be related to spatial variation in predator distribution within the 3-predator research setting (Shuman et al. 2017).

Recruitment rates of white-tailed deer are highly dependent on the level of predation within a particular area. Researchers in the southeastern U.S. have sought to determine linkages between predation and low recruitment rates in several studies. Kilgo et al. (2012) found that coyote predation attributed between 37-80% of total fawn mortality in south-central South Carolina and suggested that if the sample was representative of the low recruitment rates across the state, current harvest levels appeared unsustainable (Kilgo et al. 2012). Chitwood et al. (2015) analyzed deer population growth trends as a response to various degrees of harvest rates and coyote removal and found that reductions in adult female harvest mortality mitigated

population declines more than coyote removal alone; however, when both scenarios worked in conjunction, the population increased (Chitwood et al. 2015). Gulsby et al. (2015) evaluated fawn recruitment rates before and after coyote removal programs on two wildlife management areas in central Georgia and found fawn recruitment rates increased from 0.65 to 1.01 fawns per adult female from pre-removal to post-removal on one site, whereas the other site had no difference in recruitment rates. These findings suggest that coyote removal efforts are somewhat variable and may provide mixed results depending on the focal area (Gulsby et al. 2015).

The central Appalachian Mountains have a rich heritage of deer hunting and many areas containing large tracts of public lands often managed to promote habitat diversity for both game and nongame species. Campbell et al. (2005) reported on survival, cause-specific mortality, and reproductive rates of deer within a high-density herd in the Unglaciated Allegheny Mountain and Plateau Physiographic province of West Virginia. Survival of fawns, yearling females, and adult females was 0.57%, 0.86%, and 0.88% respectively (Campbell et al. 2005). Additionally, they reported that out of 35 observed doe mortalities, predation was the leading cause of death ($n = 16$); in which coyotes accounted for 10, black bears (*Ursus americanus*) accounted for 3, and unidentified predators accounted for 3 female mortalities respectively (Campbell et al. 2005). Adult females (> 1.5 years old) had higher mortality rates during the winter, compared to adult males. However, both yearling and adult males had higher mortality rates during the fall compared to females of the same cohort (Campbell et al. 2005). Vreeland et al. (2004) reported fawn survival and cause-specific mortality in relation to agricultural and forested environments in Pennsylvania's Ridge and Valley physiographic province (Vreeland et al. 2004). Both 9-week (9W) and 34-week (34W) survival estimates were lower in forested environments (9W: 57.2%; 34W: 37.9%) compared to agricultural environments (9W: 72.4%; 34W: 52.9%) and the most

common source of mortality was predation at 46.2% of the 106 documented mortality events (Vreeland et al. 2004). Again, coyotes and black bears were the primary source of fawn mortality, accounting for 36.7% and 32.7% of all predation events ($n = 49$), respectively. Coyotes accounted for 62.5% and 31.7% of fawn mortality in agricultural environments and forested environments, respectively, while black bears accounted for 12.5% and 36.6% of fawn mortality in agricultural environments and forested environments, respectively (Vreeland et al. 2004). In a low-density area in eastern Kentucky, annual adult doe survival probability was at 0.89%, and the primary cause of mortality was to vehicular collisions (44% total mortalities, 8/18 events), whereas only one individual died from predation (Haymes et al. 2018). Fawn survival to four months was 43% and predation or suspected predation, all via coyotes and bobcats (*Lynx rufus*), accounted for 80% of all mortalities (McDermott 2017). Additionally, the timing of parturition was also an important factor, as estimated fawn survival to eight weeks was 48%, 66%, and 93% from the minimum, mean, and maximum observed birth dates during the study respectively (McDermott 2017).

Once known for having high deer densities, many areas of the Northern Ridge and Valley ecoregion in western Virginia have recently experienced declines in deer population numbers (VDWR 2015). This is especially true for Bath County, Virginia, where population indexes on private and public land have experienced 57% and 73% decreases respectively since 1994: the greatest declines of any other county in the state over the last 20 years (VDWR 2015). Additionally, Bath County continues to have the highest number of licensed deer hunters per capita of any other county in the state (VDWR 2015). The landscape is approximately 90% forested, with the largest landholder (51%) being the George Washington National Forest. From a habitat management perspective, Bath County historically had high levels of disturbance-based

communities due to forest management practices that promoted early successional habitat across larger portions of the landscape. Historical incidence of wildfire in the Appalachians greatly decreased from pre-European settlement to the 20th century (Lafon et al. 2017); however, prescribed fire has been applied more frequently and on larger acreages by public land managers during recent decades in the region (VDWR 2015). Annual timber harvest rates declined during the later 20th and early 21st centuries due to changing societal values since the 1990s (Oswalt et al. 2009). Ultimately, these processes have led to an overall decline in the amount of early successional habitat throughout the central Appalachians. In recent years (i.e., since 1990s), prescribed fire, timber harvest, and timber stand improvement (TSI) have all been incorporated into management plans in efforts to bolster the early-to-mid successional habitat fragmentation and to reduce the amount of mesophication occurring across the county (VDWR, 2015).

The primary goal for this study is to investigate an important deer population in Bath County, Virginia which is emblematic of public land deer herds across the Appalachian Mountains. Specifically, I sought to (1) determine drivers of survival and cause specific mortality of white-tailed deer in Bath County, Virginia, (2) model broad-scale resource selection of adult female white-tailed deer during parturition seasons across multiple orders of selection, (3) model resource selection across biological seasons using step-selection processes, and (4) evaluate how habitat quality effects spatial ecology of reproductive females during fawn rearing, using home range area as a surrogate for quality. Collectively, my research in demography and spatial ecology of white-tailed deer in the central Appalachian Mountains was designed to inform management recommendations by understanding how variations in habitat quality influence deer populations within the region.

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¹Chapter 2: Influence of Landscape Characteristics on Survival, Cause-specific Mortality, and Population Growth of White-tailed Deer in Western Virginia.

Abstract

Understanding the role of recruitment in population dynamics of white-tailed deer (*Odocoileus virginianus*) is essential in systems where resource availability fluctuates substantially. In the central Appalachian Mountains, deer are part of a complex, largely forested ecosystem that also supports three of the species' predators: black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). Our objectives were to analyze effects of landcover on survival and cause-specific mortality of neonate and adult female white-tailed deer to determine population growth trends associated with current vital rates within a deer population of central Appalachians. During 2019-2020, we captured 57 neonate deer in Bath County, Virginia, USA by monitoring 38 GPS-collared, pregnant females equipped with vaginal implant transmitters (VITs) and by conducting transect searches for recently born fawns. We estimated annual survival for adults and survival to 12 weeks of life for fawns. We used an information-theoretic approach to compare Cox proportional hazards models containing habitat features associated with fawn locations to predict neonate survival. Fawn and adult female survival was 0.310 (95% CI = 0.210-0.475) and 0.871 (95% CI=0.790-0.961) respectively. We identified a total of 37 fawn mortalities and identified the cause of death using field evidence and residual predator saliva recovered on deer carcasses. Mortalities included 28 predation events and 9 deaths from other causes (e.g., abandonment, malnutrition, or disease). Black bears accounted for

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48.6% of all mortality and 64.2% of known predations within our study. Our top model identified elevation as a significant predictor of fawn survival, with mortality risk increasing 20% for every 100m increase in elevation. We estimated population growth rates, trajectories, and elasticities using observed vital rates from our study area and hypothetical harvest scenarios. Our model using observed vital rates predicted an increasing population rate of $\lambda = 1.10$. The population was predicted to increase by 2% ($\lambda = 1.02$) with a 10% increase in doe harvest but decline by 7% ($\lambda = 0.93$) at a 20% harvest rate. We found survival to be higher near fertile valley bottoms that are often cultivated and lower along ridges characterized by shallow rocky soils. Additionally, while predation, largely driven by black bears, resulted in low fawn survival, our study suggests the population could sustain a modest increase in female harvest.

Key words: cause-specific mortality; landcover; central Appalachian Mountains; *Odocoileus virginianus*; predation; recruitment; survival; topography; *Ursus americanus*

Introduction

Gaining insight into factors that influence population dynamics is a valuable component of wildlife management. In large mammals, adult survival is typically the most important vital rate driving population growth (Gaillard et al. 2000). Adult survival is generally stable despite fluctuations in environmental conditions, as adults often sacrifice reproduction to cope with variable environments without jeopardizing their own survival. In contrast, recruitment, while less important to population growth than adult survival in most situations, can fluctuate substantially across space and time (Linnell et al. 1995) and resultantly, variation in recruitment often drives variation in population growth (Chitwood et al. 2015a, Peters et al. 2020).

Therefore, monitoring recruitment can provide valuable insight into factors that limit population growth (White and Lubow 2002).

White-tailed deer (*Odocoileus virginianus*; hereafter WTD) are an example of a large mammalian species that have higher rates of mortality early in life, where rates of fawn survival and recruitment are dependent on a plethora of biological factors. Variability in predator-prey interactions often is a function of habitat attributes that can strongly influence WTD fawn survival and recruitment (Gingery et al. 2018, Kautz et al. 2019). In a review of WTD fawn survival studies, Gingery et al. (2018) found higher fawn survival in agricultural areas than forested landscapes. However, studies have reported the opposite with fawn survival increasing with distance to cropland (Shuman et al. 2017) and decreasing with distance to wooded areas (McGovern et al. 2020). In northeastern Louisiana, fawn survival increased in areas with older reforested areas (i.e., 26 to 35 years old) and decreased near young forest (i.e., 6-15 years old) suggesting that different aspects of forest structure may also be important (Shuman et al. 2017). Typically, while variations in landscape configuration can influence preference, WTD are associated with edge habitats (DeYoung 2011). However, studies from the Midwestern US have reported both positive (Rohm et al. 2007) and negative (Wright et al. 2019) relationships between fawn survival and edge habitat density. Finer scale vegetation characteristics can also influence fawn survival including plant diversity at bed sites (Chitwood et al. 2015a).

Demographic parameters, such as fawn survival can be used to predict population growth trajectories (Wisdom et al. 2000, Reed et al. 2002). Typically, these analyses require data on several population vital rates, including population size, fecundity rates, and survival rates of yearling and adult females (Chitwood et al. 2015b, Peters et al. 2020). Historically, WTD population growth studies have found the most elastic vital rate to be adult female survival

(Robinson et al. 2014). However, other studies have found that neonate survival, if low, can significantly influence population growth (Kilgo et al. 2012, Chitwood et al. 2015b). A common goal of these models is to understand how variation in harvest or fawn survival is likely to influence population growth (Chitwood et al. 2015b, Peters et al. 2020).

The central Appalachian Mountains are dominated by mature, even-aged oak (*Quercus* spp.)-hickory (*Carya* spp.) forests and large acreages are in public ownership managed by state and federal agencies. Therefore, WTD populations often occur on large tracts of relatively undisturbed forests, intermixed with only small patches of early successional vegetative communities (i.e., disturbed areas created by prescribed fire and timber management) that are preferred by WTD (Ford et al. 1993, 1994, Campbell et al. 2004, Miller et al. 2009, Lafon et al. 2017, Lorber et al. 2018). As such, population dynamics of WTD in this region are strongly influenced by the sporadic patterns of hard mast production (Wentworth et al. 1992, Ford et al. 1993, 1994) and low acorn abundance can increase fawn mortality risk (Aubin et al. 2022). Additionally, disturbed forests are important areas for understanding predator-prey interactions among WTD populations because they influence foraging trade-offs during both gestation and fawn rearing seasons (Cherry et al. 2017b).

Within in the Appalachian Mountains WTD population dynamics vary considerably (Campbell et al. 2005, Miller et al. 2009, VDWR 2015, Gingery et al. 2018). In many areas, primarily in the northern Appalachian Mountains, WTD populations have achieved high abundances capable of hindering forest regeneration (Lesser et al. 2019). However, in some portions of the central and southern Appalachian Mountains, WTD populations have declined considerably over the decade (Little et al. 2018). These declines appear to have occurred concurrently with a reduction in timber harvest, fire suppression, mesophication, and senesce of

forests, as well as restoration of black bears (*Ursus americanus*), increases in bobcats (*Lynx rufus*), and colonization of coyotes (*Canis latrans*). The reintroduction of disturbance through prescribed fire and timber harvest has often been promoted to improve the diversity of forest conditions (Lashley et al. 2011, 2015, Harper et al. 2016). This suggestion is typically supported by the notion that disturbance will enhance wildlife habitat and reverse declines in the WTD population; however, empirical field data assessing this claim are rare. Information is needed to determine the relationship between WTD population performance and aspects inherent to the landscape such as elevation and terrain ruggedness as well as management amendable attributes such as forest successional stage and composition. Additionally, it is important to determine the influence of hunter harvest on population growth (Chitwood et al. 2015b, Peters et al. 2020).

Our objectives were to evaluate survival and cause-specific mortality of WTD within the Ridge and Valley Physiographic region of the central Appalachians and determine factors influencing these population metrics. We hypothesized that fawn mortality risk would be influenced by habitat characteristics and predicted that fawns would be at lower risk in lower elevations, where soils are deeper and cultivation is common, and in areas with more edge habitats and early successional communities. Our second objective was to estimate current population growth rates of WTD using empirical field data and to assess how those rates would change under various hypothetical scenarios that incorporate fluctuating levels of hunter harvest rates and fawn mortality. We hypothesized that adult female survival would be the most important population vital rate and predicted that fluctuations in fawn survival rates would have limited influence on population growth trajectories if female harvest rates remained unchanged.

Study Area

We conducted our research in Bath County, Virginia, USA. The county is 1,390 km² in extent and is located within the Ridge and Valley physiographic province portion of the central Appalachian Mountains in western Virginia. The county is primarily characterized by large contiguous forests along mountainous ridgelines interspersed with tracts of agricultural farmlands in the valley bottoms. Most agriculture consisted of hayfields and improved pasture with little row crop agriculture. Elevation ranges from 347m – 1,365m (Wolf and Thomas 2006). The George Washington National Forest encompasses 51% of the county and canopy composition varies in association with aspect and elevation. Xeric sites are dominated by of white oak (*Quercus alba*), chestnut oak (*Quercus prinus*), northern red oak (*Quercus rubra*), hickories (*Carya spp.*), pitch pine (*Pinus rigida*) and table mountain pine (*Pinus pungens*). Mesic sites are dominated by red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) and white pine (*Pinus strobus*). Understory communities consist of mountain laurel (*Kalmia latifolia*), wild blueberry (*Vaccinium spp.*), bear oak (*Quercus illicifolia*), rhododendron (*Rhododendron spp.*), and blackberry (*Rubus spp.*). Population density was estimated to be between 4.75-16.06 WTD/km² (Montague et al. 2017).

Research Sites

Our study was conducted on three areas in Bath County: T.M. Gathright Wildlife Management Area (GWMA), Hidden Valley Recreation Area (HVRA), and Warm Springs Mountain Nature Preserve (WSMNP). The GWMA consisted of 5,434 ha of upland hardwood forest divided into two contiguous tracts separated by Lake Moomaw and encompassing Coles, Bolar, and Allegheny Mountains. The topography of GWMA is steep with narrowly incised valleys. Small forest clearings, 1-2 ha in size were present along the ridgelines of Coles and

Bolar Mountains providing some edge and open habitat for WTD and other wildlife species. The HVRA included a diverse mix of large hayfields and gently rolling forested hills, surrounded by mountainous ridgelines. The land area of HVRA was divided into nine prescribed fire units, totaling approximately 2,780 ha. The western half of HVRA includes Back Creek Mountain with small openings on ridgelines similar to GWMA. The Nature Conservancy (TNC) owns and manages the WSMNP, which is the largest contiguous non-governmental preserve in the state of Virginia (TNC 2021). The 3,751-hectare land tract runs along the ridgetop of Warm Springs Mountain on the southeastern portion of the county and borders the George Washington National Forest and Douthat State Park. The WSMNP contains substantial areas of xeric, montane pine communities and is intensively managed, using short-return interval (3-6 year) prescribed fire (TNC 2021).

Methods

Adult Capture

From January-May during 2019 and 2020, we captured adult WTD using 17.4m x 13.1m rocket nets (Hawkins et al. 1968, Batts et al. 2006), Clover traps (Clover 1954), 6.1m x 6.1m suspended net-gun (Wildlife Capture Services LLC., Flagstaff, Arizona, USA) and dart projectors and VHF telemetry darts (Model 414 PLL, Pneu-dart Inc., Williamsport, PA, USA; Siegal-Willott et al. 2009). Once restrained in nets or traps, we administered intramuscular injections of B.A.M (Butorphanol Tartrate 27.3 mg/mL - Azaperone Tartrate 9.1 mg/mL - Medetomidine HCl 10.9 mg/mL; Zoopharm INC., Laramie, Wyoming, USA). We assessed each WTD for pregnancy using a portable veterinary ultrasound machine (KeeboMed Inc., Morton Grove, Illinois, USA; Carstensen et al. 2003) and equipped all pregnant WTD with an ATS Model G5-2D global positioning system (GPS) tracking collar (Advanced Telemetry Systems,

Isanti, Minnesota, USA). We programmed collars to collect hourly fixes for ≥ 27 months and with a continuous (24 hour) very high frequency (VHF) mortality beacon. We implanted pregnant females with ATS Model M3930 vaginal implant transmitters (VIT, Advanced Telemetry Systems, Isanti, MN, USA) having a temperature sensitive telemetry beacon that emitted a unique pulse rate upon expulsion. All VIT-implanted females received a subcutaneous injection of Meloxicam at 0.2 mg/mL (Meloxicam 5mg/mL; Putney Inc. Portland, Maine, USA) as an anti-inflammatory for pain management. At the conclusion of each workup, B.A.M were antagonized by administering injections of both atipamezole (25 mg/mL) and naltrexone HCl (50 mg/mL; Zoopharm INC., Laramie, Wyoming, USA), and the individual was monitored until full recovery.

Neonate Capture / Monitoring

Beginning in May of each capture season, we monitored females implanted with VIT using radio telemetry once daily until the first transmitter was expelled. Thereafter, VITs were checked once every 8 hours for expulsion in efforts to maximize fawn capture success (Kilgo et al. 2012, Shuman et al. 2017). When an expulsion signal was detected, we determined the amount of time since the VIT was expelled using the precise event timer (PET, Advanced Telemetry Systems, Isanti, Minnesota, USA) provided with each VIT. We did not approach fawns born ≤ 3 hours prior to when expulsion signal was first detected to allow the dams to groom and bond with their fawns. We first attempted to locate a female, before attempting to locate the VIT (Kilgo et al. 2012, Shuman et al. 2017). If the fawns were not located in the direct vicinity of the VIT, personnel searched within a 200m radius surrounding the VIT and the dam using thermal imaging scopes (Kilgo et al. 2012). If the fawns were still not found after the initial search, we attempted subsequent searches every 8- 24 hours thereafter for the next 1-3

days, using the dam's location as the focal point for searches (Kilgo et al. 2012, Shuman et al. 2017). In addition to VIT searches, we also conducted transect searches for fawns in areas WTD were frequently observed (i.e., fields and forested edges).

After fawns were located, they were immediately blindfolded to reduce stress, then placed in a cotton-mesh bag and weighed using a handheld scale. We determined sex, obtained morphometrics (i.e., chest circumference, head length, hindfoot length, shoulder length, and total length measured in centimeters), and equipped each fawn with an expandable, breakaway VHF collar (Model M4200, Advanced Telemetry Systems, Isanti, Minnesota, USA) programmed with a 4-hour mortality switch. We measured hoof growth using dial calipers of all fawns captured during transect searches to estimate age at capture (Sams et al. 1996, Brinkman et al. 2004). We recorded the capture location using a handheld GPS unit (Garmin International, Inc., Olathe, Kansas, USA). All fawns were monitored for mortality once every 8 hours (0600, 1800, 2200) for the first 4 weeks of age, then daily until 12 weeks of age.

Mortality Investigations

Fawns were immediately approached when a mortality signal was detected, and the surrounding area was assessed for signs of predation. We initially assigned a presumed predator species to each mortality based on the kill site characteristics and how the carcass was cached or consumed (O'Gara 1978, Labisky and Boulay 1998, Shuman et al. 2017). If a carcass was found, we examined remains for puncture wounds and subcutaneous hemorrhaging, particularly around the neck and skull, then swabbed remains using cotton swabs to collect residual predator saliva samples (Williams et al. 2003, Piaggio et al. 2020). We placed swabs in individual paper coin envelopes, which were allowed to air dry, and stored at room temperature. Samples were transported to the Molecular Ecology Laboratory at Texas A&M University-Kingsville for

analysis where lab personnel had no knowledge of field evidence of predator species. Before exiting the kill site, trail cameras were deployed facing the remains and left for ≥ 3 days to obtain visual confirmation of the putative predator. If a carcass was found with no obvious signs of predation, we assigned the death as other causes (e.g., starvation, abandonment). All WTD handling procedures were approved under Virginia Tech Institutional Animal Care and Use Committee (IACUC; protocol number: 17-199).

Survival Analysis

To derive initial habitat covariates used in our survival analysis, we utilized landcover data from the Virginia Geographic Information Network, which classified data using 1m aerial orthoimagery from the Virginia Base Mapping Program from 2013-2015 for the state of Virginia (VGIN 2017). We combined data from multiple sources to create a raster layer representing communities created by disturbance practices (i.e., timber harvest and/or prescribed fire). We then obtained timber harvest data from the USFS FSGeodata Clearinghouse (USDA Forest Service 2020) for federal lands and obtained timber harvest data on WMAs from Virginia Department of Wildlife Resources (VDWR). We digitized the timber harvest data pertaining to harvests that occurred on private lands during our study period by comparing USDA's National Agriculture Imagery Program (NAIP) imagery (USDA 2022) that occurred during our study. We then recorded the time of each harvest from near-real-time forest change maps, which occurred on a 24-day moving window, from the ForWarn Legacy and ForWarnII projects (Hargrove et al. 2009). We categorized all timber harvests that occurred during the last 40 years in our study area as disturbed forest, as most of our study area was characterized by older, even-aged forest.

To analyze disturbed forest created by prescribed fire, we incorporated data from previous research that analyzed the extent of fire-created canopy gaps within our study area

(Lorber et al. 2018). These data identified land patches within our study area delineating burn units and fire created canopy gaps with 0-50% canopy cover (Lorber et al. 2018). Similar to timber harvest, canopy gaps created via prescribed fire were also classified as disturbed forest. To determine the role of wildlife clearings as disturbed forest, we obtained data from the local USFS Warm Springs Ranger District and VDWR. Clearings on private lands were digitized by comparing NAIP imagery throughout the study period from 2011-2020. We again used the ForWarn Legacy and ForWarnII projects, this time to identify the time clearings were created from near-real-time forest change maps that occurred on a 24-day moving window (Hargrove et al. 2009).

To analyze forested edge habitat, we combined raster data corresponding to sub-categories of specific forest types (i.e., Northern Hardwood/Mixed/Cove, Oak Forests/Woodlands, and Pine/Oak). We then created a 40m buffer into the mature forest landcover classification that traversed adjacent habitat classifications with shorter vertical vegetation structures (i.e., open or disturbed communities). Although some edge features within our study area may have penetrated further into forested communities, we chose a 40m buffer in efforts to capture structural edge effects associated with open and shrubby understory communities influenced by light penetration (Harper et al. 2005). To represent topographic features, we created a covariate for elevation from Digital Elevation Model (DEM) data we obtained from the United States Geological Survey National Geospatial Program (USGS 2017).

We created a distance raster for each of the five habitat covariates using the Proximity tool in QGIS 3.10; where each 10m x 10m raster cell contained the Euclidian distance to each habitat type (QGIS.org, 2022). We then used the *raster* package in R (R Core Team 2020) to create a raster stack containing each landcover distance raster and extracted distance values to

each fawn's capture location. We used capture locations instead of birth site locations to incorporate fawns captured during transect searches into survival analyses.

We estimated fawn survival to 12 weeks of age using a Kaplan-Meier known-fates model (Kaplan and Meier 1958) with a daily observation interval (Bishop et al. 2008, Shuman et al. 2017). All fawns captured during transect searches were entered into survival matrix, which treated day as the monitoring interval, at their estimated age (in days) at capture. We considered fawns to be recruited into the population at the end of the 12-week monitoring period, which is approximately when individuals were incorporated into the harvestable population before the onset of fall hunting season (Shuman et al. 2017, Aubin et al. 2022). Using Cox proportional hazards models, we analyzed landcover influence on neonate survival. We constructed models that reflected our *a priori* hypotheses using both univariate and additive combinations of landcover variables. We tested each model for proportionality, and models that did not meet the proportional hazards assumption (i.e., $p < 0.05$) were excluded from analyses. Those models included univariate and additive combinations of elevation, distance to disturbed forest, and distance to forested edge. We compared models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for model selection, using Akaike weights (w_i) to determine the strength of evidence for competing models (Burnham and Anderson 2002), and made inference based on the top model while considering parsimony (Cade 2015). All survival models were fitted using the *survival* package (Therneau and Lumley 2013) in R.

Population Growth Modeling

We utilized estimated survival rates from known fate models of fawns and adult females and included fecundity data via known birth rates of captured females to determine trends in population trajectory (Chitwood et al. 2015b, Peters et al. 2020). We evaluated the effects of

various scenarios relative to management (i.e., harvest mortality) that influence vital rates (i.e., survival and fecundity) of WTD at different life stages (i.e., fawns and reproductive adult females). These scenarios determined population growth relative to current and decreased rates of neonate survival (influenced by predator management and habitat management), yearling and adult female survival (influenced by harvest management), and fecundity (influenced by habitat management). To achieve this, we utilized a female-based population matrix model structured as follows:

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

where $\mathbf{n}(t)$ was a vector of abundances at each stage in the population at time t and \mathbf{A} is a population projection matrix. We used a Lefkovitch matrix model (Lefkovitch 1965) that incorporated three stages corresponding to different age classes for fawns (0-1 years old), yearlings (1-2 years old), and mature WTD (≥ 2.5 years old) with a 1-year time step:

$$\mathbf{A} = \begin{bmatrix} 0 & F(\text{yearling}, 1 - 2 \text{ years}) & F(\text{adult}, \geq 2.5 \text{ years old}) \\ S(\text{fawn}, 0 - 1 \text{ year}) & 0 & 0 \\ 0 & S(\text{yearling}, 1 - 2 \text{ years}) & S(\text{adult}, \geq 2.5 \text{ years old}) \end{bmatrix}$$

In efforts to make comparisons to previous work, we made five simplifying assumptions about the WTD in Bath County including: (1) density-independence, (2) geographic closure, (3) no male limitation, (4) homogeneity of parameters between stages, and (5) no reproductive senescence (Chitwood et al. 2015b, Peters et al. 2020). We parameterized our model using data corresponding to vital rates from collared individuals. Additionally, fecundity for yearling and adult WTD was calculated from visual observations of litter sizes during each fawn capture event

and confirmed using supplemental data (i.e., herd health checks or harvest data) that was provided by VDWR. Based on small sample sizes of yearling females, we used the same survival rate for yearling females that we calculated for adult females (Haymes et al. 2018). We estimated yearling fecundity as a 20% reduction from our observed fecundity rate from all individuals (see Ditchkoff 2011). We divided fecundity rates by two under the assumption that the population has a 1:1 male-to-female neonate ratio (Chitwood et al. 2015b, Peters et al. 2020). We derived starting population sizes for yearling and adult female WTD from previous research conducted within Bath County (Montague et al. 2017). We then estimated adult and yearling sex ratios using trail camera data obtained throughout the three focal areas, as well as from published estimates of female age structure and harvest ratios between yearlings and adults (Dapson et al. 1979, Dusek et al. 1989).

We incorporated multiple hypothetical situations to reflect various future conditions under different management actions. We altered survival rates of adult and yearling females to reflect 0%, 10%, 20%, and 30% harvest mortality, whereby fecundity and neonate survival were not changed. Similar to Peters et al. (2020), we utilized an extremely low fawn survival rate reported in the literature (14%; 95% CI = 0.075-0.249 from Chitwood et al. 2015b), to parametrize matrix models to predict hypothetical scenarios under reduced fawn survival. Additionally, we used our unaltered adult female survival and fecundity rates while adjusting fawn survival percentages in efforts to determine adult doe harvest percentages that are sustainable under each population growth scenario. In efforts to analyze all possible combinations of vital rates, we parameterized 3×3 staged-based matrices using random values from within the 95% confidence intervals of adult, yearling, and fawn survival (Table 2.1). We computed the matrix model in R using the *popbio* package (Stubben et al. 2020) until reaching

the stable stage distribution (SSD) before calculating the population growth rate, λ . Drawing samples from these distributions, we parameterized 1,000 matrices in efforts to determine λ , sensitivities, elasticities, and project the population size for the next 10 years.

Genetic Identification of Predator Species

We used genetic data collected at fawn mortality sites to verify predator species identifications that we made based on field evidence. We extracted DNA from swabs using a commercial kit (Qiagen DNeasy, Valencia, CA), following protocols for handling non-invasive samples (i.e., extraction and PCR controls; Waits and Paetkau 2005). We amplified a portion of the mtDNA 16S rRNA gene using primers (5'–TTC TCC GAG GTC ACC CCA ACC TAA AT–3' and 5'–AGA CGA GAA GAC CCT ATG GAG CTT TAA TTA A–3') designed to detect carnivores and minimize detection of prey DNA (Kilgo et al. 2012). We amplified samples in 25- μ L reaction volumes containing 12.5 μ L of AmpliTaq Gold® 360 PCR master mix (ThermoFisher Scientific, Waltham, MA), 10 pmol of each primer, and 1.5–3 μ L DNA extract. Thermal cycling conditions were an initial denaturation at 94 °C for 10 min, followed by 40 cycles at 94 °C for 1 min, annealing at 55 °C for 1 min, extension at 72 °C for 1 min 30 sec, with a final extension at 72 °C for 5 min. We visualized PCR products via electrophoresis on 2% agarose gels containing ethidium bromide. We removed unincorporated primers and dNTPs from successful amplifications using an enzymatic method (ExoSAP-IT®, ThermoFisher Scientific), cycle-sequenced forward strands using the BigDye® Terminator V1.1 Cycle Sequencing Kit (ThermoFisher Scientific) and removed dye terminators using the DyeEx® 2.0 spin kit (Qiagen). We loaded sequencing reaction products onto a 3130xl Genetic Analyzer for separation and detection (ThermoFisher Scientific).

We imported sequences into the computer program Geneious® V10 (Kearse et al. 2012), trimmed sequences by quality score, and searched for matching sequences in GenBank. Sequences from canids can be difficult to distinguish using this region, as domestic dog (*C. familiaris*) and wolf (*C. lupus*, *C. rufus*) are identical. Coyotes in the eastern USA may have haplotypes derived from wolf or domestic dog due to past hybridization and introgression (Adams et al. 2003, vonHoldt and Aardema 2020). Previous studies used a panel of microsatellite DNA markers to conclusively identify canid samples and concluded all had nuclear DNA derived predominately from coyotes (Kilgo et al. 2012). Our main objective was to distinguish between black bear, bobcat, and canids whereby we assumed most canids in the study area were coyotes.

Results

From January-May, 2019-20, we collared and deployed VITs in 38 unique female WTD. Two females from the sample were implanted with VITs in successive years, resulting in 40 VIT deployments. We captured 32 neonates (21 in 2019 and 11 in 2020), successfully capturing ≥ 1 fawn from 22 VIT-implanted females. Reasons for failure to capture fawns from implanted females were associated with inability to locate fawns after apparent normal parturition ($n=11$), female death prior to parturition ($n=3$), or transmitter failure prior to parturition ($n=4$). Birthdates of VIT-caught fawns ranged from 6 June to 26 June in 2019 and 6 June to 11 July in 2020. Using transect searches, we captured an additional 14 fawns and 11 fawns in 2019 and 2020, respectively. Average age of opportunistically caught fawns was 3.68 days.. The HVRA was the most represented area ($n = 31$), followed by GWMA ($n = 14$) and WSMNP ($n = 12$).

We identified 37 fawn mortalities consisting of 28 predation events (75.6%) and 9 deaths from other causes (24.3%). Fawns were most susceptible to mortality within the first two weeks

of life, with 81% of mortalities occurring within that time. We identified predator DNA for 14 events (50%), 8 bear, 3 bobcat, and 3 canid. We obtained sequences from $\bar{x} = 2$ swab samples per identified event (range: 1–4), derived from the collar (57.1%), carcass or hide (32.1%), or bone fragment (10.7%). Two events yielded swabs that matched both *C. latrans* and *C. lupus* (VA-09, 3 swabs *C. latrans*, 1 swab *C. lupus*; VA-16, 1 swab *C. latrans*, 2 swabs *C. lupus*). All other events yielded 1 species. Combining both methods, black bears accounted for the majority of all fawn mortality (i.e., 48.6%), comprising 64.2% of predation events ($n = 18$), followed by bobcats ($n = 5$; 17.8%) and coyotes ($n = 3$; 10.7%). Of predation events that were genetically confirmed to a specific predator species, field diagnostics correctly identified the predator responsible for the event 100% of the time. Additionally, the genetics analysis confirmed 5 of 6 “assumed” predation events (i.e., mortality events where only a collar was found with bite punctures or tears, however a predator species could not be initially identified in the field) and therefore were able to be included in cause-specific mortality dataset.

We estimated 12-week survival to be 0.310 (95% CI = 0.210-0.457) with most mortalities occurring within the first 20 days of life (Figure 2.1). In 2019, 12-week survival was estimated to be 0.264 (95% CI = 0.153-0.455) and in 2020 fawn survival to 12 weeks was 0.394 (95% CI = 0.231-0.672). The top model predicting spatial covariate effects on fawn survival included only elevation as a meaningful predictor, carried 44.1% of the Akaike weight (w_i), and indicated that fawn mortality risk increased 20% for every 100m of elevation gain (Figure 2.2). We observed one competing model (i.e., $\Delta AIC_c \leq 2$) that included additive effects of elevation and distance to disturbed forest habitats ($\beta = -0.0002$, SE = <0.001). However, only elevation was considered a meaningful predictor because the 95% CI for disturbed forest habitats included zero (Table 2.2, 2.3).

Our population growth model using field-based vital rate estimates predicted $\lambda = 1.10$ (interquartile range, IQR = 1.06-1.14) (Figure 2.3). Additionally, we also observed a 2% increase in population trajectory ($\lambda = 1.02$, IQR = 1.00-1.07) even under a 10% increase in doe harvest. However, the population declined by 7% ($\lambda = 0.93$, IQR = 0.89-0.97) under the 20% harvest scenario and declined rapidly by 15% ($\lambda = 0.85$, IQR = 0.82-0.90) with 30% hypothetical harvest (Figure 2.4). Our model predicted a stable population ($\lambda = 0.99$, IQR = 0.96-1.03) with the current harvest rate and an approximate 17% reduction in fawn survival rate. Consequently, we observed a 4% increase in population trajectory ($\lambda = 1.04$, IQR = 1.01-1.07) when incorporating both a 17% reduction in fawn survival and no female harvest, whereas we observed a 5% declining population ($\lambda = 0.95$, IQR = 0.91-0.99) under a scenario with a 5% increase in harvest rate and a 17% reduction in fawn survival (Figure 2.5). Across all observed and hypothetical scenarios, adult female survival was the most sensitive and elastic population parameter within our model, followed by fawn survival (Table 2.4).

Discussion

In our study, we found neonate WTD survival (31%) was lower than previously reported in both forest or agriculture-dominated areas of the central Appalachians. This was in spite of the fact that our 12-week monitoring period for predicting fawn survival was less than half as long as the monitoring period from previous studies in the region (180 days; Gingery et al. 2018, Vreeland et al. 2004). Moreover, our findings of fawn survival within a 3-predator system are higher than previous studies from 2-predator systems in areas of the southeastern U.S. (Epstein et al. 1985, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015*a, b*) supporting the notion that predator species richness is not a strong predictor of survival. Coyote predation was low within our study area (10%), likely because of a low density of coyotes (Morin et al. 2016)

and a high density of black bears (Murphy et al. 2015) within our study area. As such, black bears could potentially be consuming more younger fawns than coyotes, forcing coyotes to abandon fawns as a primary prey item as they age and become more mobile (Ricklefs 2007, Petroelje et al. 2014).

Our fawn recovery rate from VIT-implanted females (53%) also was lower than in previous fawn survival studies (75%; Kilgo et al. 2012, 66%; Chitwood et al. 2015*ab*), with lower sample sizes compared to other VIT fawn survival studies (Shuman et al. 2017). However, we were able to successfully augment our sample with primarily younger age class fawns (≤ 4 days), which were still highly susceptible to mortality in our study area. Similar to other studies (Aubin et al. 2022), a portion of the neonates (43%, $n = 25$) in our sample were not monitored during the first few days of life. We note that this could produce substantial bias and overestimated survival rates from the sample (Gilbert et al. 2014). However, we reduced the potential for this bias by entering fawns captured via transect searches in the survival matrix on the interval associated with the estimated age at capture. Importantly, 56% ($n = 32$) of the sample was comprised of fawns that were captured on their first day of life so the survival intervals where mortality is high (first few days of life) are well represented in the data. As such, our estimates are representative of fawn survival from birth to 12 weeks. Previous research has shown that fawns rarely venture far from their birth sites during the first weeks of life, and most movements are maternally influenced (Marchinton and Hirth 1984, Hasapes and Comer 2017). Therefore, we concluded that landscape characteristics associated with the capture locations from the fawns captured via transect searches were representative of the landscape attributes experienced by those fawns.

We found fawn mortality risk increased with elevation. Within our study area, high elevation mature forests were interspersed with islands of early successional or open areas maintained with prescribed fire and timber harvest. In contrast, at the lower elevations, early successional or open areas are often dispersed more broadly as large pastures providing abundant foraging and cover resources for WTD. These resources are distributed in discrete patches at higher elevations and these small patches likely congregate predators and prey, particularly given two of the primary fawn predators, coyotes and black bears, are omnivorous and consume large amounts of soft mast during the fawning season (Benson and Chamberlain 2006, Cherry et al. 2016, Popp et al. 2018). The distribution and juxtaposition of early-successional habitat patches across elevational gradients is likely an important factor driving the effect of elevation on fawn mortality risk – where smaller habitat patches at ridgetops are more hazardous for fawns than more larger patches in valley bottoms. .

Our population growth model parameterized using empirical field-based estimates of vital rates predicted an increasing WTD population. Additionally, the model depicting a hypothetical 10% increase in adult female harvest and the model depicting a reduced fawn survival rate with current adult and yearling survival and fecundity predicted a stable population trajectory. Based on our findings, if vital rates used within our field-based model are representative of the WTD population in our study area, then the population is stable to increasing. One important consideration in inferring population declines from harvest data is the potential issue associated with declining hunter recruitment and, if not corrected for, hunter effort, which may both be interacting to indicate a declining population. Moreover, we did not observe any direct instances of illegal harvest, which in some settings is a significant, nor do we know if tracking collars influenced hunter behavior mortality source (Kindall et al. 2011, Wood

2018, Norman et al. 2022). Importantly, our study occurred over a short period, and it is possible the population has declined and that the years of our study were not representative of population trends occurring over the last few decades.

We acknowledge additional limitations associated with the assumptions within our population growth model, specifically as it pertains to density independence. While density dependence should always be considered, the effects increase as high-density or low-density populations fluctuate relative to their carrying capacity. Our study site was strongly characterized by poor quality habitat, with overall productivity driven primarily by variations in rainfall and oak mast production (Keyser et al. 2005, Miller and Marchinton 2007). As such, density-dependent responses were likely overshadowed in response to these conditions in our study area. Similar to other studies, we expected our hypothetical scenario of restricted harvest (i.e., 0%) to be the most likely to overestimate the population due to density-dependent responses (Peters et al. 2020). However, in terms of management, these results were still plausible in that the population would most likely still grow exponentially in the absence of harvest even if effect sizes were overestimated within the assumption of density independence. Additionally, we assumed our monitoring window (i.e., 12 weeks) for fawn survival was representative of annual fawn survival and that all fawn fecundity was zero. Research has shown that female fawns can reproduce within their first year of life under exceptionally productive conditions (Ditchkoff 2011). We note that these assumptions could have inflated the stage-based estimates for fawns. However, we posit that the combined effect of these biases was likely negligible within our study system. Moreover, while understanding the role of each of these biases is critical, we believe that the assumptions associated with these limitations allowed for comparisons of conclusions with previous research (Chitwood et al. 2015*b*, Peters et al. 2020).

Management Implications

Managing WTD in the central Appalachians can be challenging, as changes in both habitat and predator communities play important roles in population trends. Both WTD and black bears are important game species in western Virginia, requiring management regimes to meet demands on both biological and social carrying capacity within populations. In many systems, the most important vital rate manipulated by wildlife managers to increase WTD populations is female harvest; however, recent research suggests that these efforts may need to be supplemented with protection of neonate WTD in areas where fawn recruitment is low. However, WTD harvest regulations for much of the central Appalachian Mountains of Virginia are conservative (i.e., females may only be harvested with firearms on public lands in Bath County on two days throughout the entire hunting season), thus there is limited opportunity to increase adult female survival through reduced harvest opportunity. Ultimately, while WTD harvest within our study area was low relative to other portions of Virginia, our field-based population growth model predicted a stable-to-increasing population of WTD – indicating that the female population could sustain additional harvest (i.e., 10%) before resulting in decline.

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Tables

Table 2. 1. Values for parameters used in the population matrix based on estimated vital rates and hypothetical reduced fawn survival of white-tailed deer (*Odocoileus virginianus*) in Bath County, Virginia, USA, 2019-2020. The range represents the 95% confidence interval for the age-specific parameters estimated from known-fate models derived from radio-collared deer.

Vital Rate	Stage	Estimate	Model Input
Fecundity	Fawn (F_f)		0
	Yearling (F_y)		0.560
	Adult (F_a)		0.760
Observed Survival	Yearling (S_y)	0.871	0.790-0.961
	Adult (S_a)	0.871	0.790-0.961
Nonhunting Survival	Yearling (S_y)	0.927	0.866-0.992
	Adult (S_a)	0.927	0.866-0.992
Observed Fawn Survival	Fawn (S_f)	0.310	0.210-0.475
Reduced Fawn Survival ^a	Fawn (S_f)	0.141	0.075–0.249

a = Adults

y = Yearlings

f = Fawns

^a = Reported in Chitwood et al. (2015b).

Table 2. 2. Model selection results from Cox proportional hazards analysis predicting 12-week survival of white-tailed deer (*Odocoileus virginianus*) fawns in Bath County, Virginia, USA, 2019-2020. We compared models using Akaike’s Information Criterion corrected for small sample size (AICc) and ranked models based on relative differences to the top model (Δ AICc).

Model^a	<i>K</i>^b	AICc	ΔAICc	<i>w_i</i>	<i>LL</i>
elev	1	253.3	0.00	0.44	-125.615
elev + df	2	254.7	1.35	0.22	-125.173
elev + fedg	2	255.6	2.24	0.14	-125.615
elev + df + fedg	3	257.1	3.72	0.07	-125.170
df	1	257.5	4.14	0.06	-127.684
null	0	258.7	5.33	0.02	-129.336
df + fedg	2	259.3	5.94	0.02	-127.465
fedg	1	260.3	6.93	0.01	-129.080

a. elev, elevation(m); df, distance to disturbed forest; fedg, distance to forested edge habitat

b. No. parameters

Table 2. 3. Model coefficients (β), standard errors (SE), z-scores (z), and p-values (p) for models predicting landcover influence on fawn survival for white-tailed deer (*Odocoileus virginianus*) in Bath County, VA, USA, 2019-2020.

Model	Parameter	β	SE	z	p
<i>Top Model^a</i>					
	Elevation	0.002	<0.001	2.866	0.004
<i>Competing Model</i>					
	Elevation	0.002	<0.001	2.62	0.009
	Disturbed Forest ^b	-0.0002	<0.001	0.426	0.670

^a = Used for inference

^b = Distance to disturbed forest (negative values indicate higher risk at closer distances)

Table 2. 4. Sensitivities and elasticities for vital rates in all scenarios of white-tailed deer population trends in Bath County, Virginia, USA, 2019–2020.

Scenario	Parameter	Sensitivity	Elasticity
Observed	Fawn Survival	0.526	0.160
	Yearling Survival	0.170	0.135
	Adult Survival	0.679	0.545
	Yearling Fecundity	0.026	0.051
	Adult Fecundity	0.135	0.195
0% harvest	Fawn Survival	0.515	0.150
	Yearling Survival	0.159	0.129
	Adult Survival	0.698	0.569
	Yearling Fecundity	0.046	0.022
	Adult Fecundity	0.194	0.129
10% harvest	Fawn Survival	0.547	0.181
	Yearling Survival	0.193	0.147
	Adult Survival	0.637	0.490
	Yearling Fecundity	0.062	0.034
	Adult Fecundity	0.198	0.147
20% harvest	Fawn Survival	0.570	0.205
	Yearling Survival	0.222	0.160
	Adult Survival	0.589	0.429
	Yearling Fecundity	0.076	0.045
	Adult Fecundity	0.196	0.160
30% harvest	Fawn Survival	0.592	0.234
	Yearling Survival	0.254	0.172
	Adult Survival	0.531	0.360
	Yearling Fecundity	0.095	0.062
	Adult Fecundity	0.193	0.172
Reduced fawn survival	Fawn Survival	0.651	0.104
	Yearling Survival	0.107	0.094
	Adult Survival	0.793	0.700
	Yearling Fecundity	0.018	0.010
	Adult Fecundity	0.122	0.094
Reduced fawn survival and 0% harvest	Fawn Survival	0.627	0.095
	Yearling Survival	0.098	0.087
	Adult Survival	0.808	0.723
	Yearling Fecundity	0.016	0.008
	Adult Fecundity	0.120	0.087
Reduced fawn survival and 5% harvest	Fawn Survival	0.665	0.112
	Yearling Survival	0.115	0.099
	Adult Survival	0.779	0.679
	Yearling Fecundity	0.020	0.012
	Adult Fecundity	0.125	0.099

Figures

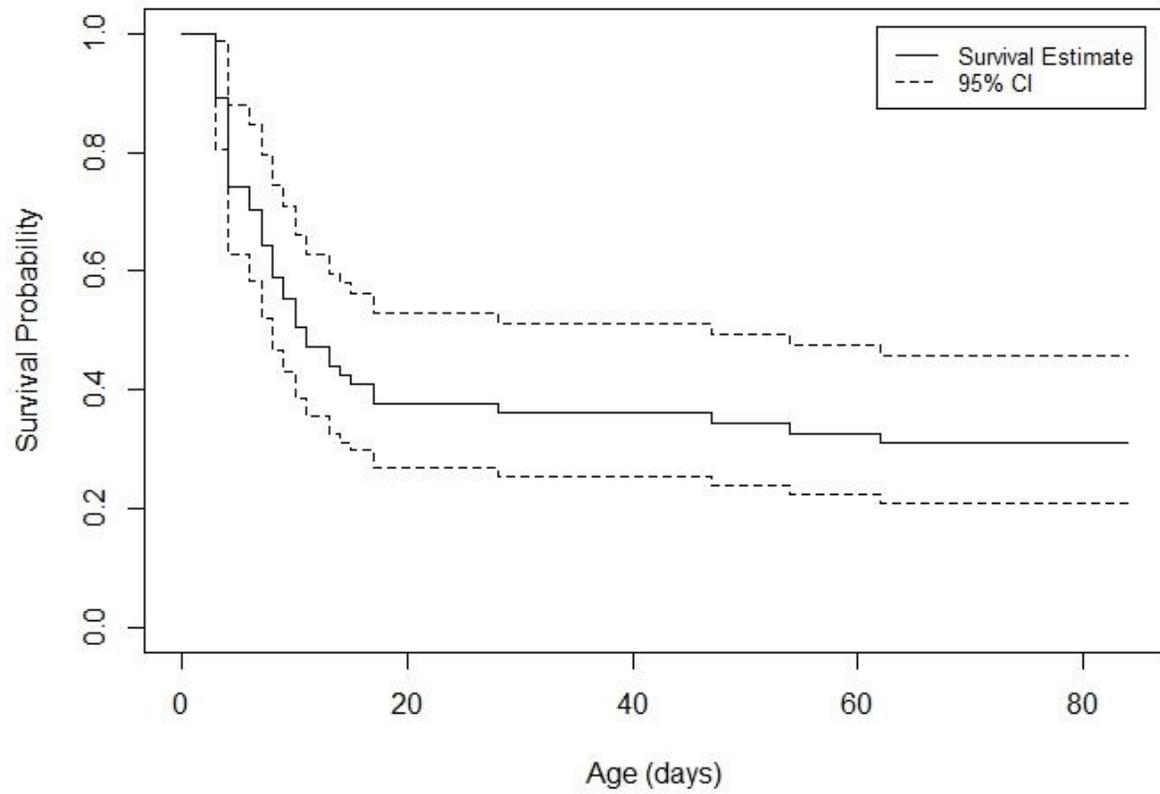


Figure 2. 1. Survival rates with 95% confidence interval of white-tailed deer (*Odocoileus virginianus*) fawns to 12 weeks of age in Bath County, VA, USA. 2019-2020.

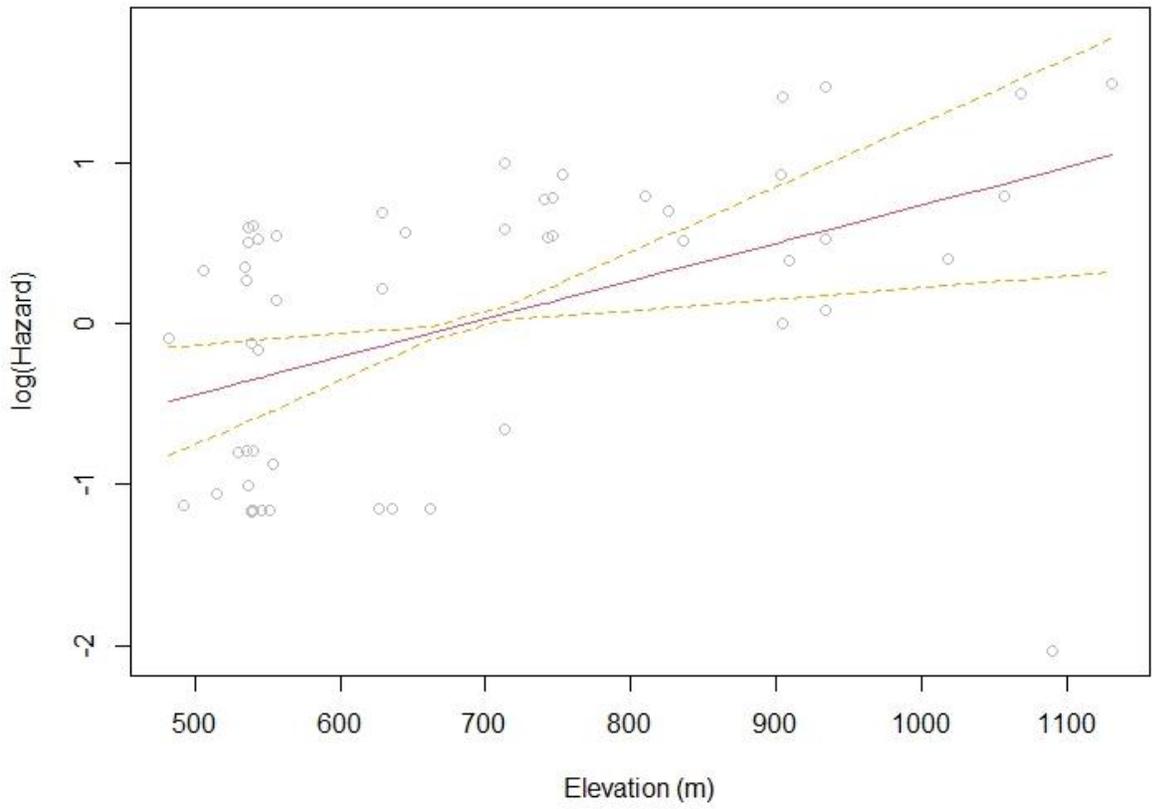


Figure 2. 2. Cox proportional hazards coefficient (red line) and 95% confidence interval (yellow dashed lines) showing the effect of elevation on white-tailed deer (*Odocoileus virginianus*) fawn survival risk in Bath County, Virginia, USA, 2019-2020.

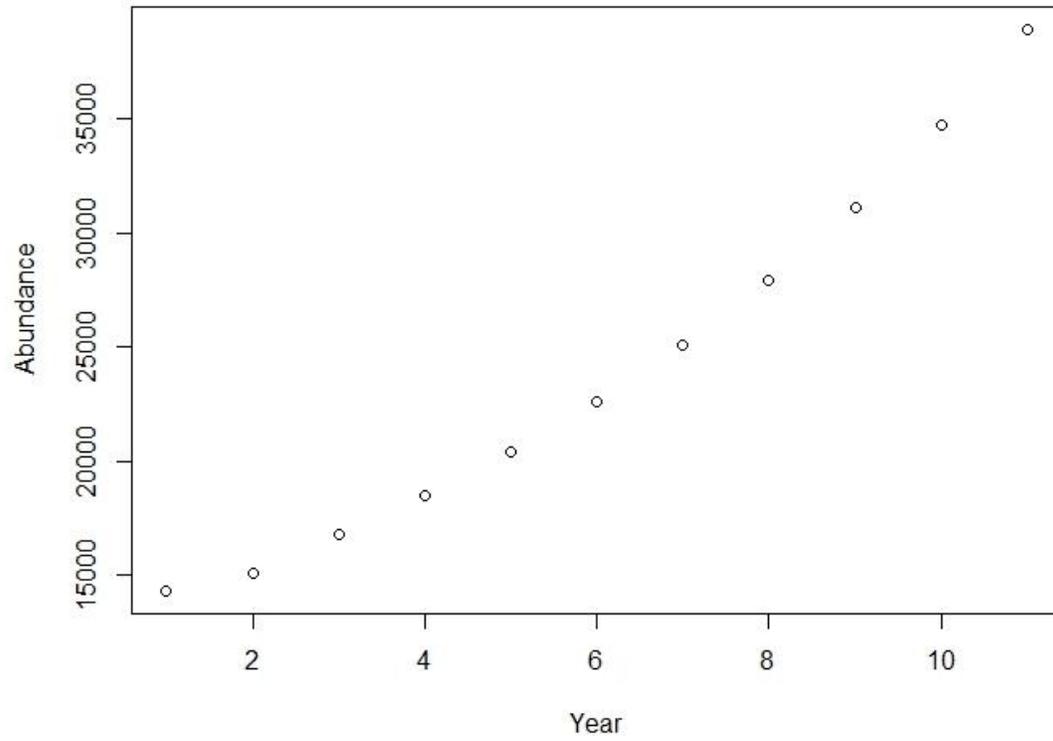


Figure 2. 3. Population trajectory of white-tailed deer (*Odocoileus virginianus*) in Bath County, Virginia, USA, using field-based estimates of population vital rates from 2019-2020.

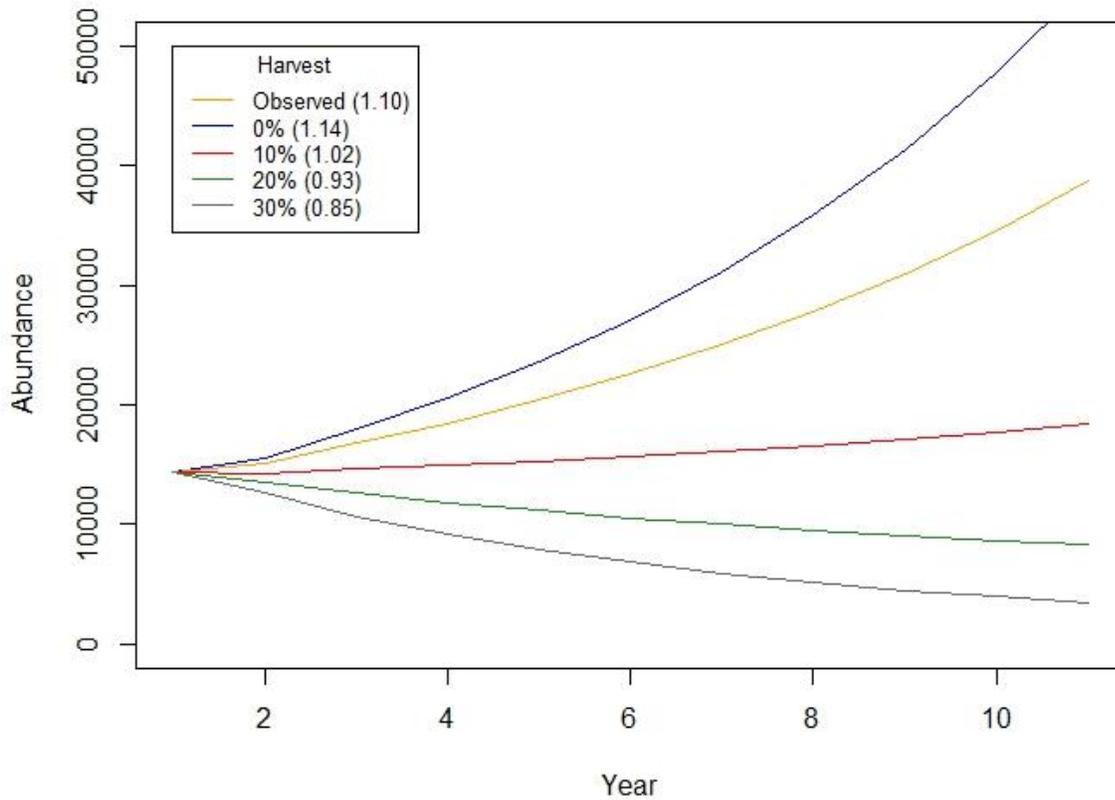


Figure 2. 4. Change in white-tailed deer (*Odocoileus virginianus*) population abundance over a 10-year period using data from our study area under current vital rates (orange line) estimated from 2019-2020 data and the hypothetical harvest regimes of 0% (blue line), 10% (red line), 20% (green line), and 30% (black line) in Bath County, Virginia, USA.

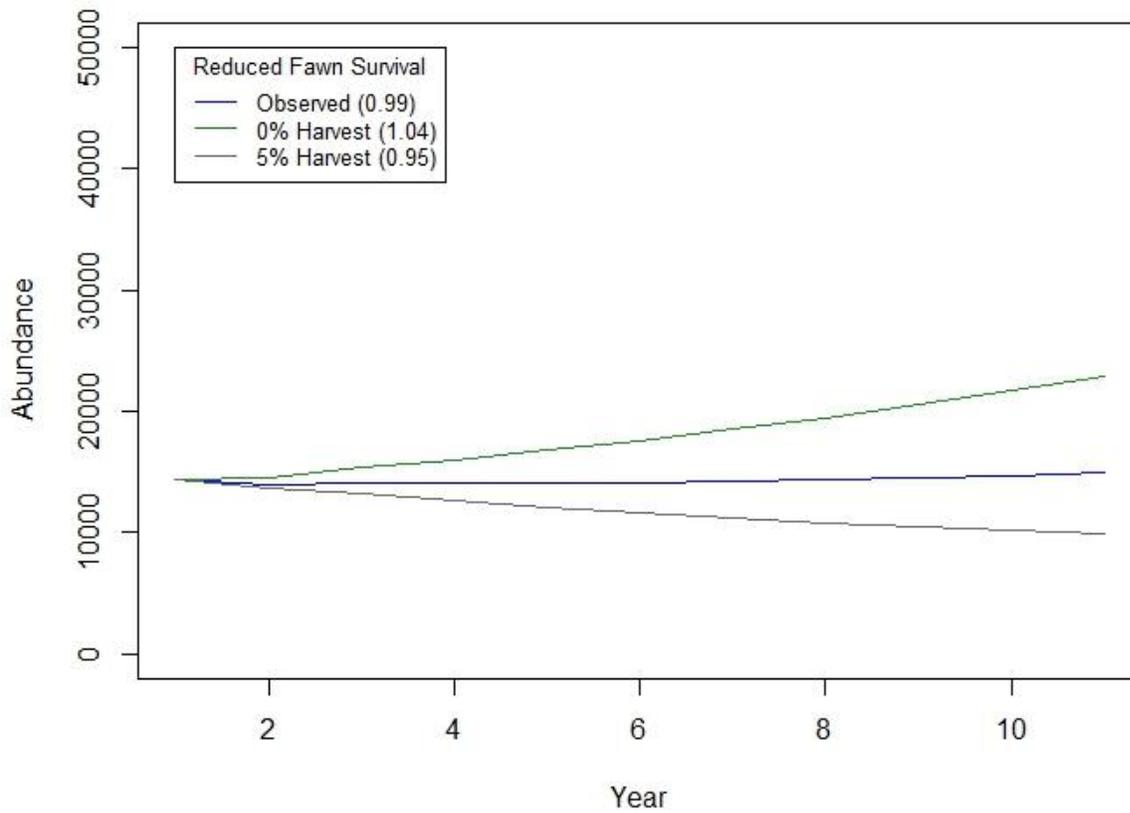


Figure 2. 5. Change in white-tailed deer (*Odocoileus virginianus*) population abundance over a 10-year period under a 17% reduction in fawn survival and (1) estimated vital rates blue line, (2) hypothetical harvest rates of 0% (green line), and (3) 5% increase from what was observed (black line) in Bath County, Virginia, USA.

²Chapter 3: Resource Selection of Adult Female White-tailed Deer During Fawning

Abstract

Resource selection analysis is a useful tool to identify critical resources required during energetically demanding seasons. For mammals, reproduction, and particularly early lactation, is a period when energetic demands and risk of predation peak. Understanding how mammals balance these demands during a critical life-history phase is a longstanding goal in ecology. White-tailed deer (*Odocoileus virginianus*) are a long-lived iteroparous species that navigate these competing demands over a wide variety of habitat types across their range. In the central Appalachian Mountains, a region dominated primarily by forested ridgelines, interspersed with disturbance-based ecological communities (i.e., timber management and prescribed fire) adjacent to largely cleared valleys, deer experience high predation risk for fawns and tremendous spatial variation in forage and concealment cover. We used dynamic Brownian bridge movement models to analyze three orders of resource selection by female white-tailed deer in the central Appalachian Mountains during the fawning season: (1) selection of fawn rearing areas from the home range, (2) selection of locations within the fawn rearing area, and (3) selection of parturition sites. We found deer selected fawn-rearing areas nearer to forested edges, open habitats, and at higher elevations, while avoiding areas near recently disturbed forests and mature forests. Within the fawn rearing area, females selected locations closer to disturbed forest, open habitats, and forested edge, while avoiding mature forest habitats, and higher elevations. Females selected birth sites with higher levels of visual obstruction. Our findings

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provide insights regarding habitat selection during an important life history process (e.g., parturition) and reinforces the importance of disturbance to female white-tailed deer during critical life stages, suggesting that female deer may be balancing the tradeoffs associated with forage quality and fawning cover by establishing fawn-rearing areas farther from disturbed forests than would be expected given their home range composition, but disproportionately using these sites within their fawn-rearing areas.

Key Words: central Appalachians, fawn, habitat, home range, *Odocoileus virginianus*, parturition, resource selection function, seasonality, white-tailed deer

Introduction

Defining areas animals select or avoid during critical biological periods can provide valuable insight regarding habitat requirements (Manly 2002). Resource selection is a hierarchical process that can highlight the complexities associated with balancing energetic demands and safety (Johnson 1980; Shuman et al. 2018). For large long-lived mammals, offspring rearing is the most energetically demanding biological season (Feldhamer et al. 2007) and a time when predation risk often peaks both for the mother and the offspring (Bled et al. 2022, Shuman et al. 2017). Females are challenged to meet increased nutritional requirements needed to sustain lactation and they need to find areas with vegetation attributes required to avoid predators (Bowyer et al. 1998; Panzacchi et al. 2010; Shuman et al. 2018). In systems with high predation risk, female ungulates often select safer but less productive environments for raising offspring, a phenomenon that has been observed in white-tailed deer (*Odocoileus virginianus*; Cherry et al. 2017), moose (*Alces alces*; Edwards 1983), caribou (*Rangifer*

tarandus; Barten et al. 2001), and mountain goats (*Oreamnos americanus*; Hamel and Cote 2007).

White-tailed deer (hereafter deer) populations are often highly influenced by habitat types and topographic attributes throughout their range (Jenkins et al. 2007; Walter et al. 2009, 2018; Dechen Quinn et al. 2013; Haus et al. 2020). During the fawning season, females balance the need to obtain adequate nutrition to support their own maintenance and lactation with minimizing risk (Hewitt 2011; Wright et al. 2021). Resource selection during fawning is often a result of the seeking areas with adequate forage and concealment cover for fawns because fawn antipredator defenses are strongly tied to concealment cover as they express behavioral (bedding between bouts of nursing and seeking thick escape cover [Grovenburg et al. 2012]), physiological (alarm bradycardia; [Jacobsen 1979]) and morphological (cryptic coloration; [Henderson et al. 2018]) adaptations that rely on avoiding detection during the limited mobility period when predation risk is greatest. During fawning, females often perceive areas with inadequate concealment cover as riskier than other areas and will display increased vigilance and decreased foraging efficiency therein (Cherry et al. 2017). In forested systems, deer tend to select recently disturbed areas due to the increased quality of forage (Teer 1996). However, during fawning, recently disturbed habitats in some areas (i.e., those treated with prescribed fire) may initially produce higher quantities of nutritious forage that attract deer, but lack desirable cover needed to aid in predator avoidance over an initial regrowth period (Cherry et al. 2017b, 2018).

The central Appalachian Mountains are characterized by high elevation ridgelines, side-slopes, and valley bottoms dominated by mature even-aged deciduous or mixed deciduous-conifer forests and are lacking in early and mid-successional communities created by disturbance. Due to decreased disturbance from timber harvest and fire (Lafon et al. 2017), and

the mesophication of forests, habitat quality for deer has declined in the region (Trani et al. 2001; Nowacki and Abrams 2008; Lafon et al. 2017; McNitt et al. 2020a). However, there has been recent interest in restoring historical disturbance regimes using fire as a surrogate for timber management (Brose et al. 2001; Lorber et al. 2018; McNitt et al. 2020a). In these systems, deer often use disturbed areas that provide new growth of high-quality forage and suitable cover to evade predators (Ford et al. 1994; Vreeland et al. 2004; Campbell et al. 2005; Miller et al. 2009; DeYoung 2011; Gingery et al. 2018).

Maternal investment associated with resource selection during the fawning season is an important ecological process for deer, as the mother's decisions during these periods can ultimately influence the survival of fawns (Duquette et al. 2014). The reintroduction of fire in areas in central Appalachian Mountains provides an excellent opportunity to evaluate the importance of ecological disturbance to deer during the critical life-history stage of fawning. We quantified selection of and within fawn-rearing areas and micro-scale selection of birth sites in a central Appalachian study system that has been the focus of fire reintroduction. We hypothesized females would select areas that meet both nutritional requirements and provide sufficient cover to successfully rear fawns. We predicted adult female deer would select fawn-rearing areas near disturbed forests and forested edges and avoid undisturbed mature forests. We predicted that female deer would select areas requiring minimal energy expenditure to traverse and that had lower risk of predation (i.e., lower elevations). Lastly, we predicted selection of birth sites would be driven by concealment cover offering increased visual obstruction.

Materials and Methods

Study Area

We conducted our research in Bath County, Virginia, USA. The county is 1,390 km² areas located within the Ridge and Valley physiographic province of the central Appalachian Mountains in western Virginia. Much of the area, particularly ridges and side-slopes, are composed of parent sandstone material and are commonly associated with highly infertile shallow soils with rugged terrain (Diefenbach and Shea 2011). The county is primarily characterized by large contiguous forests and mountainous ridgelines interspersed with agricultural in the valley bottoms. Most agriculture consisted of hayfields and improved pasture with little row crop agriculture present. Elevation ranges from 347m – 1,365m (Wolf and Thomas 2006). The George Washington National Forest encompasses 51% of the county and canopy composition varies in association with aspect and elevation. Xeric sites are dominated by white oak (*Quercus alba*), chestnut oak (*Quercus prinus*), northern red oak (*Quercus rubra*), hickories (*Carya* spp.), pitch pine (*Pinus rigida*) and table mountain pine (*Pinus pungens*). Mesic sites are dominated by red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) and white pine (*Pinus strobus*). Understory communities consist of mountain laurel (*Kalmia latifolia*), wild blueberry (*Vaccinium* spp.), bear oak (*Quercus illicifolia*), rhododendron (*Rhododendron* spp.), and blackberry (*Rubus* spp.). Population density was estimated to be between 4.75-16.06 deer/km² (Montague et al. 2017)..

Our study was conducted on three areas in Bath County including T.M. Gathright Wildlife Management Area (GWMA), Hidden Valley Recreation Area (HVRA), and Warm Springs Mountain Nature Preserve (WSMNP). The GWMA consists of 5,434 ha of upland hardwood forest divided into two contiguous tracts separated by Lake Moomaw and

encompassing Coles, Bolar, and Allegheny Mountains. Except for the ridgelines, the topography of GWMA is steep with narrowly incised valleys. A small amount of forest clearings, 1-2 ha in size are present along the ridgelines of Coles and Bolar Mountains providing forested edge and open areas for deer and other wildlife species. The HVRA includes a diverse mix of large hayfields and gently rolling forested hills, surrounded by mountainous ridgelines. The land area of HVRA is divided into nine prescribed fire units, totaling approximately 2780 ha, and fire return interval is typically every 1-3 years (S. Tanguay, personal communication). The western half of HVRA includes Back Creek Mountain, of which ridgelines also contains several 1-2 ha forest openings. The Nature Conservancy (TNC) owns and manages the WSMNP, which is the largest contiguous preserve in the state of Virginia (TNC 2021). The 3,751-hectare land tract runs along the ridgetop of Warm Springs Mountain on the southeastern portion of the county and borders the George Washington National Forest and Douthat State Park. The WSMNP contains substantial areas of xeric, montane pine communities and is intensively managed, using short-return interval (3-6 year) prescribed fire (TNC 2021).

Animal Capture and Monitoring

From January-May 2019 and 2020, we remotely anesthetized deer using dart projectors and VHF telemetry darts (Model 414 PLL, Pneu-dart Inc., Williamsport, PA, USA) (Siegal-Willott et al. 2009). We also captured adult deer throughout each study area, using 17.4m x 13.1m rocket nets (Hawkins et al. 1968; Batts et al. 2006), Clover traps (Clover 1954), and 6.1m x 6.1m suspended net-gun (Wildlife Capture Services LLC., Flagstaff, Arizona, USA) (Mattox 2008). Once restrained, we administered intramuscular injections of B.A.M (Butorphanol Tartrate 27.3 mg/mL - Azaperone Tartrate 9.1 mg/mL- Medetomidine HCl 10.9 mg/mL; Zoopharm INC., Laramie, Wyoming, USA). We assessed pregnancy status of each deer using a

portable veterinary ultrasound machine (KeeboMed Inc., Morton Grove, Illinois, USA) (Carstensen et al. 2003) and equipped all pregnant deer with an ATS Model G5-2D global positioning system (GPS) tracking collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). We programmed collars to collect hourly fixes for ≥ 24 months and with a continuous (24 hour) very high frequency (VHF) mortality beacon. We then implanted pregnant females with ATS Model M3930 vaginal implant transmitters (VIT, Advanced Telemetry Systems, Isanti, Minnesota, USA) having a temperature sensitive telemetry beacon which emitted a unique pulse rate upon expulsion. All female deer that were implanted with VITs received a subcutaneous injection of Meloxicam at 0.2 mg/mL (Meloxicam 5mg/mL; Putney Inc. Portland, Maine, USA) as an anti-inflammatory for pain management. Anesthetizing effects of B.A.M were antagonized by administering injections of both atipamezole (25 mg/mL) and naltrexone HCl (50 mg/mL) (Zoopharm INC., Laramie, Wyoming, USA), and the individual was monitored until full recovery.

Beginning in May of each capture season, VIT implanted females were monitored using radio telemetry once daily until the first transmitter is expelled (Shuman et al. 2017). Thereafter, VITs were checked once every 8 hours for expulsion in efforts to maximize fawn capture success (Kilgo et al. 2012; Shuman et al. 2017). When an expulsion signal was detected, we first determined the amount of time since the VIT was expelled using the precise event timer (PET, Advanced Telemetry Systems, Isanti, Minnesota, USA) provided with each VIT. We did not approach fawns born ≤ 3 hours prior to when an expulsion signal was first detected in efforts to allow the dam to groom and bond with her fawns.

Resource Selection Analysis

To derive resource covariates used in the resource selection function (RSF), we acquired landcover data from a variety of sources. Primarily, we utilized landcover data from the Virginia Geographic Information Network, which classified data using 1m aerial orthoimagery from the Virginia Base Mapping Program from 2013-2015 for the state of Virginia (VGIN 2022). Our final reclassified landcover covariates used in our RSF analyses included disturbed forests, forested edge, open communities, mature forest communities, and elevation.

We combined data from multiple sources to create a raster layer representing disturbed forests. We obtained timber harvest data from the USFS FSGeodata Clearinghouse (USDA Forest Service 2020) for federal lands and obtained timber harvest data on WMAs from Virginia Department of Wildlife Resources (VDWR). We digitized the timber harvest data pertaining to harvests that occurred on private lands during our study period by comparing USDA's National Agriculture Imagery Program (NAIP) imagery from 2011 through 2020 (USDA 2022). We then recorded the time of each harvest from near-real-time forest change maps that occurred on a 24-day moving window from the ForWarn Legacy and ForWarnII projects (Hargrove et al. 2009). We combined and categorized all timber harvests that occurred during the last 40 years in our study area as disturbed forest, as most of our study area was characterized by mature, even-aged forest. While we caveat that this method likely led to increased variability within this habitat designation, we believe that the differences were still substantial compared to other surrounding areas. To incorporate disturbance-based ecological communities created by prescribed fire, we included a data product provided by TNC that analyzed the extent of fire-created canopy gaps within our study area (Lorber et al. 2018). These data identified land patches within which

delineated burn units and fire created canopy gaps with 0-50% canopy cover (Lorber et al. 2018). Similar to timber harvest, canopy gaps created by fire were also classified as disturbed forest.

To map openings, we obtained data from the local USFS Warm Springs Ranger District and VDWR that identified small wildlife openings and logging decks. Clearings on private lands were hand-digitized using NAIP imagery from 2011-2020. Using the ForWarn Legacy and ForWarnII projects, we identified the time clearings were created from near-real-time forest change maps that occurred on a 24-day moving window (Hargrove et al. 2009). All new and maintained wildlife clearings were classified as open areas.

To create a characterize mature forest, we combined raster data corresponding to sub-categories of specific forest types (i.e., Northern Hardwood/Mixed/Cove, Oak Forests/Woodlands, and Pine/Oak). Then, to represent forested edge, we created a 40m buffer into the mature forest and adjacent patch which had shorter vertical vegetation structures (i.e., open, or disturbed forests). We chose a 40m buffer in efforts to capture structural edge effects associated with open and shrubby understory communities influenced by light penetration (Harper et al. 2005). To represent topographic features, we created a covariate for elevation from 10m x 10m Digital Elevation Model (DEM) data we obtained from the United States Geological Survey National Geospatial Program (USGS 2017).

Once we had obtained and organized our landcover data, we then used a distance-based approach to determine selection or avoidance of each habitat type. To do this, we created a distance raster for each of the five habitat covariates using the Proximity tool in QGIS 3.10; where each 10m x 10m raster cell contained the Euclidian distance to each habitat type (QGIS.org, 2022). We then stacked the rasters and extracted “distance-to” the locations of each deer.

We developed resource selection functions to examine selection of and within fawn rearing areas during the fawning rearing period of June-August (Clevinger et al. Chapter 2), in a use-availability framework (Johnson 1980; Manly 2002;). We characterized space use using dynamic Brownian bridge movement models (dBBMM; (Horne et al. 2007; Kranstauber et al. 2012) to estimate probabilistic utilization distributions (UDs). We chose to use dBBMMs to characterize space use because it accounts for variability in movement paths throughout the home range of the individual; compensating for behavioral variability associated with different types of movements within the model(e.g., feeding vs. excursions between two areas; Horne et al. 2007; Kranstauber et al. 2012). We used a window size of 21 steps, a margin size of 9 steps, and an 15m location error for all deer, as visual inspection indicated these settings were sufficient to identify relevant changes in behavior. To evaluate selection of the fawn rearing area, we characterized use based on all spatial covariate values occurring within each cell of the 95% fawn-rearing UD, and availability based on all spatial covariate values occurring within each cell of the cumulative 95% UD. To evaluate resource selection within the fawn rearing area, we characterized availability by generating 5 random locations per observed animal location within the 95% fawn-rearing UD. We used a generalized linear mixed model in the Program R using package *lme4* (Bates et al. 2011) to estimate selection coefficients for spatial covariates at each level of selection.

Vegetation Sampling and Birth Site Selection

We measured vegetation characteristics at birth sites and two random locations at 30m and 100m from the birth site at a random azimuth. To minimize the effect of changes with vegetation conditions due to time between births and date collection, we sampled each birth site and associated random locations ≤ 3 weeks post parturition. We measured visual obstruction

(VO) using Nudds boards by observing the board standing 15m from focal location in each of the 4 cardinal directions and recorded a 1-5 score (1=0-20% VO, 5=81-100% VO) (Nudds 1977). We averaged the scores from each of the four locations for each of the four sections of the Nudds board: 0-0.5m, 0.5-1.0m, 1.0-1.5m, and 1.5-2.0m. We then averaged of the first two sections (0-0.5m, 0.5-1.0m) to obtain a measure of visual obstruction up to 1 m (i.e., VO1) and the average of the last two sections (1.0-1.5m, and 1.5-2.0m) to obtain a measure of visual obstruction from 1m-2m (VO2). We measured canopy cover (CC) using a spherical densitometer at 0.5m off the ground to determine solar inception (Lemmon 1956). We used a wedge prism to determine basal area (BA). We estimated ground cover (GC) using a 1x1m Daubenmire frame, at center of the focal location and at 15 m from the center in each cardinal direction. We classified percent ground cover as woody, grass, vine, debris, and bare, summing the percentages of all non-bare ground cover and calculating the average percent to provide an index of cover (Daubenmire 1959). In the event that the birth sites of twin fawns are within the exact same location, we only conducted one set of measurements pertaining to the birth event (Shuman et al. 2018).

We predicted the probability that locations would be used as a birth site by fitting a series of generalized linear models (GLMs) with a logit link function. We fit models using explanatory variables including visual obstruction (VO), ground cover (GC), basal area (BA), and canopy cover (CC). We excluded correlated predictor variables from the analysis if $|r| > 0.60$ (Barbknecht et al. 2011). Due to correlation between VO1 and VO2, we opted to analyze only VO1 as a covariate of parturition site selection because this metric represented the height of vegetation <1.0m that we assumed was most important to cover for fawns and does during parturition. All modeling and data visualization was conducted in program R (R Core Team 2020).

Results

From January-May, 2019-20, we collared, and VIT implanted 39 adult female deer. Two females from the sample were implanted in both years, for a total of 41 VIT deployments. We sampled 32 birth sites and associated random locations. From their cumulative home range, females selected fawn rearing areas nearer to forested edge ($\beta = -0.2227$, $SE = 0.0038$, $p < 0.0001$), open habitats ($\beta = -0.0118$, $SE = 0.0046$, $p = 0.0102$), and at higher elevations ($\beta = 0.2529$, $SE = 0.0085$, $p < 0.0001$), while avoiding areas nearer to disturbed forests ($\beta = 0.3482$, $SE = 0.0057$, $p < 0.0001$) and mature forest habitats ($\beta = 0.2609$, $SE = 0.0033$, $p < 0.0001$) (Table 3.1). For every 100 m increase from forested edge and open habitats, probability of use decreased approximately 4.1% and 0.1% respectively. However, probability of use increased with 100 m distance away from disturbed forests and mature forests approximately by 2.1% and 9.5% respectively. Additionally, for every 100 m increase in elevation, probability of use increased 3.3% (Figure 3.1).

Within fawn rearing areas, females selected areas closer to disturbed forests ($\beta = -0.1343$, $SE = 0.0081$, $p < 0.0001$), open habitats ($\beta = -0.1420$, $SE = 0.0073$, $p < 0.0001$), and forested edge ($\beta = -0.1272$, $SE = 0.0050$, $p < 0.0001$), while avoiding mature forest habitats ($\beta = 0.0396$, $SE = 0.0045$, $p < 0.0001$), and higher elevations ($\beta = -0.1842$, $SE = 0.0149$, $p < 0.0001$) (Table 3.2). For every 100m increase from disturbed forest, forested edge, and open habitats, probability of use decreased approximately 0.6%, 1.8%, and 0.7% respectively. However, probability of use increased with 100 m distance away from mature forested habitats by approximately 0.4%. Additionally, for every 100m increase in elevation, probability of use decreased 1.6% (Figure 3.2).

Birth sites were characterized by greater visual obstruction than would be expected at random ($\beta = 0.8764$, $SE = 0.3031$, $p = 0.0038$). Birth sites were characterized by having approximately 20% more visual obstruction ($VO=4.55$) than randomly sampled sites 30m and 100m away ($VO=3.55$). No other covariates we measured were informative parameters for predicting parturition sites (Table 3.3; Figure 3.3).

Discussion

Understanding relationships between habitat composition and maternal decision making can provide valuable insight into resource requirements during critical life-history stages. Often, these processes can heavily influence survival and recruitment of species. As predicted, mature forests were avoided at the two higher orders of selection. Our results support other studies that found deer avoid mature, even-aged forest (Ford et al. 1993, 1997; Campbell et al. 2004, 2005; Miller et al. 2009; Harper et al. 2016) during fawning, likely due to lack of suitable forage and fawning cover. Conversely, we found deer selected areas at both higher orders that were nearer to forested edges and open areas. These results were expected, as deer are often characterized as an edge species (Reynolds 1966a; b; Williamson 1983; Williamson and Hirth 1985; Rohm et al. 2007). These areas are often associated with both abundant forage resources and concealment cover. Open areas, such as agricultural fields, can also be important habitats for deer during fawn rearing (Gingery et al. 2018) and often provide abundant food resources (Nixon et al. 1991; DeYoung 2011). However, in our study area, forested lands accounted for 90% of land cover and agriculture was dominated by hayfields and pasture as opposed to row crops. Therefore, it could be that these open habitats were selected because of the abundant homogenous cover they offer limits ability for predators to key into vegetation cues. Additionally, while many of these open habitats were in lower elevation valleys, they were typically near developed areas where people

and livestock were more common, potentially providing a human shield effect (Beringer et al. 1990; Fecske et al. 2002; Sollmann et al. 2016)

We found female deer responded differently to disturbed forest and elevation across orders of selection. Cross-scale disagreement in selection is often associated with tradeoffs between foraging and predation risk (Mysterud et al. 1999; Shuman et al. 2018), with some studies reporting that predation risk influences resource selection at broader scales and forage availability influences the process at finer scales (Rettie and Messier 2000; Fortin et al. 2004; Anderson et al. 2005). Disturbed forests have been associated with both high-quality deer forage (Patton 1976; Miller et al. 2009; Crimmins et al. 2010; Eby et al. 2014; Harper et al. 2016; Cherry et al. 2017b; Parker et al. 2020) but also increased predator use (Benson and Chamberlain 2007; Schrecengost et al. 2008; Boisjoly et al. 2010; Cherry et al. 2017b; a; McNitt et al. 2020a; b). Our findings suggest female deer may be balancing the tradeoffs associated with forage quality and fawning cover (Shuman et al. 2018) by establishing fawn-rearing areas farther from disturbed forests than would be expected given their home range composition, but disproportionately using these sites within their fawn-rearing areas. Fawn-rearing is primarily the season when deer would be sensitive to predation risk and avoiding these areas when establishing fawn-rearing areas may be an anti-predator defense. However, given the forage quality offered at these sites, it is not surprising that females then use these sites within the fawn-rearing area. Similarly, females established fawn-rearing areas at higher elevations within their home ranges, but within their fawn-rearing areas they disproportionately used lower elevations. Deer may have established fawn-rearing areas near ridgelines with wildlife clearings where the cost of locomotion - particularly for fawns - is lowest but use lower elevation sites within the fawn-rearing area where predation risk was lower for their accompanying fawns (Clevinger

Chapter 2). During our study, fawn mortality risk increased approximately 22% for every 100m increase in elevation (Clevinger Chapter 2) thus using lower elevations would be a way to combat this risk.

At the micro-scale, we found females selected parturition sites that maximized visual obstruction for concealment cover. Fawns are highly adapted to use concealment cover to avoid predation as indicated by behavioral (e.g., bedding between feeding, fleeing to cover; [Grovenburg et al. 2012]), physiological (e.g., alarm bradycardia; [Jacobsen 1979]), and morphological (e.g., cryptic pelage coloration; [Henderson et al. 2018]) adaptations. Choosing vegetative features that aid fawns in evading predators during the first few weeks of their lives is a critical component of successful fawn rearing (Canon and Bryant 1997; Van Moorter et al. 2009) and selecting parturition sites with dense vegetative communities is essential, not only as it pertains to visual obstruction and concealment cover, but also to suppress the airflow of scents associated with newborn fawns.

We acknowledge our habitat classifications may have contained significant variation due to methods of aggregating specific habitat management practices. For example, our “disturbed forest” was a broad class that included timber harvest and fires that occurred within the last 40 years. However, in our system, most of the landscape is even-aged forests, and the stark contrast is any stand that has been disturbed since most of the forest landscape was clearcut approximately a century ago (Nowacki and Abrams 2008; Oswalt et al. 2009). Therefore, we feel this classification of disturbed sites accurately described the process of interest. Further splitting this class into different seral stages would have required separate analyses because few deer experienced multiple disturbance types. Therefore, we suggest our approach is a reasonable method for evaluating the role of disturbance in the spatial ecology of deer.

Understanding variation in resource selection at multiple spatial scales is an important component of wildlife ecology (Johnson 1980; Manly 2002). These processes can often influence the success of critical life stages in population ecology. Similar to most large mammals, female deer experience their highest energetic demand during fawning and are heavily dependent on their surrounding environment to provide resources to sustain their dependent young (Chitwood et al. 2015; Cherry et al. 2017a; Shuman et al. 2018; Aubin et al. 2022). As such, maternal decisions are likely to be greatly influenced by life history tradeoffs between forage and predation risk. In our study, we found support for either selection or avoidance of two habitat types across scales: (1) selection of forested edge and (2) avoidance of mature forest. Our findings were expected in that each of these habitat types were associated with functional habitat attributes relative to forage and cover. Conversely, we found female deer exhibited shifts in selection of resources across scales in three habitat types including disturbed forests, open areas, and elevation. Our findings related to these habitats were also expected, as the selection or avoidance of each was likely driven by factors (i.e., forage and cover), which vary at different orders of selection when fawns are present. Concealment cover was likely the primary focus of deer during parturition seasons, such that females would shift their locations from areas of high-quality foraging to areas with high-quality concealment cover within the fawning home range (Grovenburg et al. 2012). These findings were also supported at the micro-scale, with female deer selecting parturition sites that were associated with greater concealment cover compared to randomly sampled sites.

Overall, our work highlights the habitat associations of female deer in the central Appalachians during the most energetically demanding biological season. Moreover, we report on both similarities and dissimilarities between resource selection and avoidance across two

orders of selection during fawning. Our findings magnify the roles of important habitat types across these orders in terms of not only forage quality and availability, but also cover quality and availability.

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Tables

Table 3. 1. Summary statistics of the global generalized linear mixed model, including beta coefficients (β), standard errors (SE), z-values (z), and p-values (p), predicting habitat selection of fawn rearing areas from overall home ranges of female white-tailed deer (*Odocoileus virginianus*) in Bath County, VA, USA, 2019-2020.

Model	β	SE	z	p	Int.^a
(Intercept)	-0.60847	0.21479	-2.83286	0.0046	N/A
Disturbed Forest	0.348151	0.005666	61.4495	< 0.0001	Avoided
Edge	-0.22271	0.003797	-58.6609	< 0.0001	Selected
Open	-0.01182	0.004603	-2.56839	0.0102	Selected
Mature Forest	0.260876	0.00326	80.03413	< 0.0001	Avoided
Elevation	0.252893	0.008496	29.76588	< 0.0001	Selected

^a = Interpretation

Table 3. 2. Summary statistics of the global generalized linear mixed model, including beta coefficients (β), standard errors (SE), z-values (z), and p-values (p), predicting 3rd order resource selection of landcover covariates from within fawn rearing areas of female white-tailed deer (*Odocoileus virginianus*) in Bath County, VA, USA, 2019-2020.

Model	β	SE	z	p	Int.^a
(Intercept)	-1.61705	0.039789	-40.6408	< 0.0001	N/A
Disturbed Forest	-0.13426	0.008106	-16.5617	< 0.0001	Selected
Edge	-0.12721	0.005034	-25.2721	< 0.0001	Selected
Open	-0.14195	0.007332	-19.3594	< 0.0001	Selected
Mature Forest	0.039573	0.004493	8.80759	< 0.0001	Avoided
Elevation	-0.18417	0.014914	-12.3492	< 0.0001	Avoided

^a = Interpretation

Table 3. 3. Summary statistics, including beta coefficients (β), standard errors (SE), z-values (z), and p-values (p), from generalized linear model (GLM) used to predict probability of parturition site selection of female white-tailed deer (*Odocoileus virginianus*) from vegetative and topographic characteristics in Bath County, VA, USA, 2019-2020.

Model	β	SE	z	p	Int.^a
Intercept	-4.0455	1.9955	-2.027	0.0426	N/A
Visual Obstruction	0.8764	0.3031	2.891	0.0038	Selected
Canopy Closure	0.0068	0.0078	0.865	0.3868	Not Selected
Ground Cover	-0.0409	0.0973	-0.420	0.6743	Not Selected
Basal Area	0.0009	0.0066	0.146	0.8840	Not Selected

^a = Interpretation

Figures

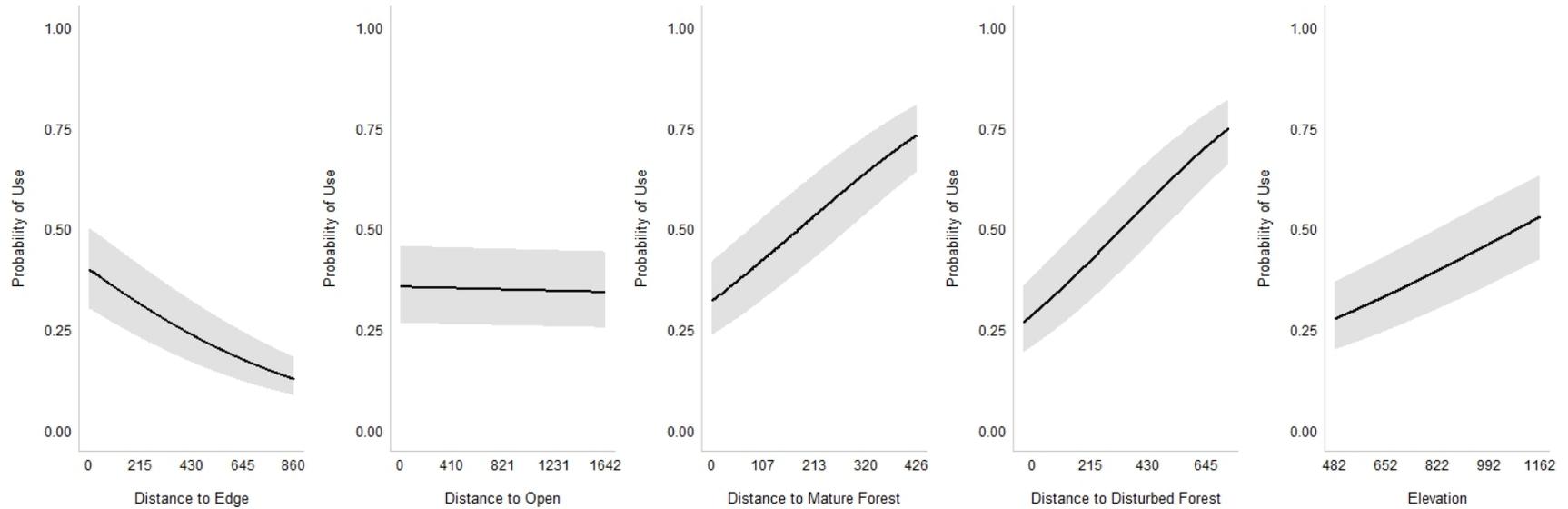


Figure 3. 1. Relative probability of use with 95% confidence interval (shaded area) of habitat types used in linear mixed regression analysis of adult female white-tailed deer (*Odocoileus virginianus*) in selecting a fawn rearing area from the overall home range during parturition seasons in Bath County, VA, USA. 2019-2020.

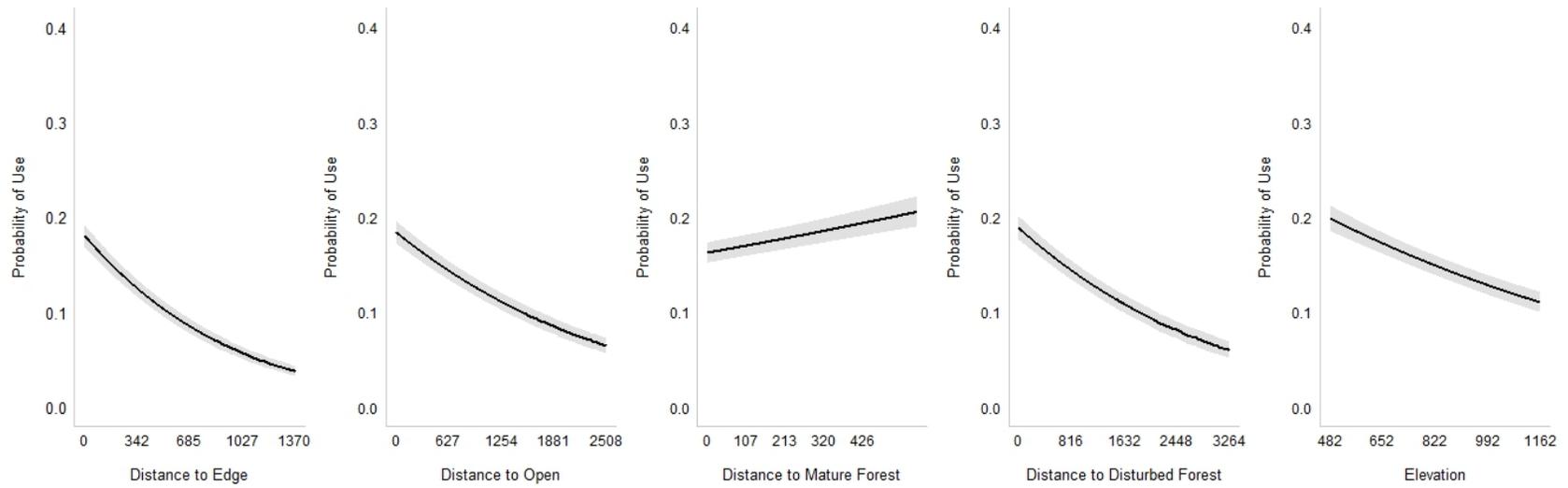


Figure 3. 2. Relative probability of use with 95% confidence interval (shaded area) of habitat types used in linear mixed regression analysis of adult female white-tailed deer (*Odocoileus virginianus*) when selecting from within the fawn rearing area during parturition seasons in Bath County, VA, USA. 2019-2020.

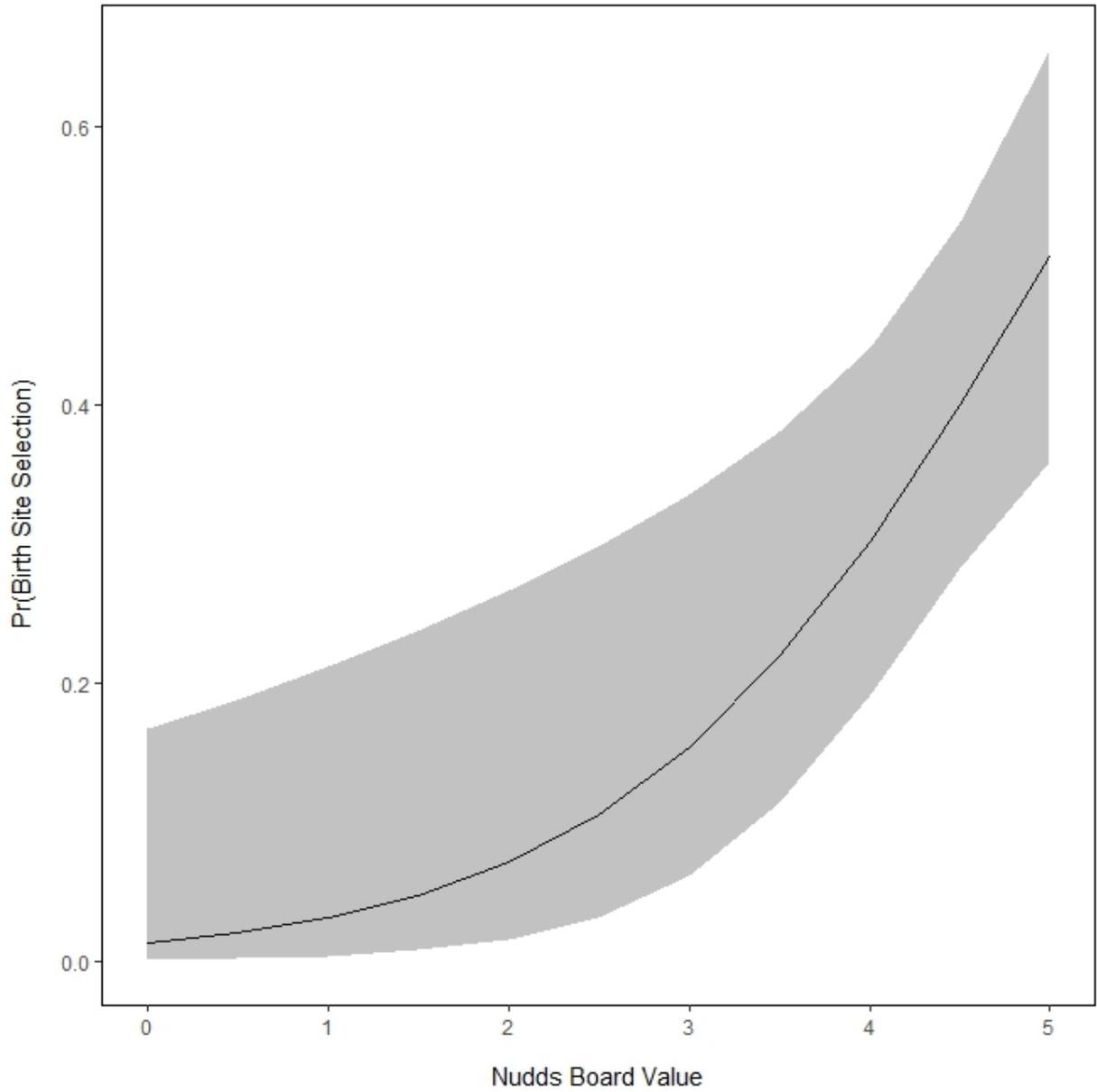


Figure 3. 3. Relative probability of birth site selection (black line) based on generalized linear regression analysis of visual obstruction score with 95% confidence interval ribbon (grey shading) of female white-tailed deer (*Odocoileus virginianus*) in Bath County, VA, USA, 2019-2020.

³Chapter 4: Influence of Elevation on Energetic Demands of Female White-tailed Deer During Parturition Season in the Central Appalachians

Abstract

Quantifying seasonal home range sizes can reveal variability within habitat quality within a given population. As such, determining habitat relationships that influence home range size during critical life periods (i.e., parturition) can provide insight into life history traits of specific wildlife populations. White-tailed deer (*Odocoileus virginianus*) are a keystone species and habitat generalist in North America. However, research is needed to better understand how topographic characteristics influence habitat quality particularly during the energetically demanding periods of reproduction. We used linear regression to analyze the effects of elevation and maternal status (with or without fawns) on home range sizes of adult female white-tailed deer during the fawning season (June-August) in the central Appalachian Mountains of western Virginia. Seasonal home ranges for females with fawns increased approximately 71 ha in size for every 100 m increase in mean home range elevation, whereas seasonal home ranges of females without fawns decreased approximately 1.5 ha for every 100 m increase in mean home range elevation. Our study highlights predation risk as a primary influencer of habitat quality on a medium sized ungulate by describing variation in maternal space use across elevational gradients.

³ This chapter was formatted for Scientific Reports
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Introduction

Understanding spatial variation in resource quality for wildlife is a longstanding goal in wildlife ecology. Variation in seasonal home range size can yield valuable insights about the relationships between animals and their environment. The habitat productivity hypothesis states that animals tend to exhibit larger home range sizes in association with overall poorer quality habitats¹. A critical assumption of this hypothesis is that animals seek to minimize the amount of space and energy required to meet their requirements for survival and reproduction. Minimizing the amount space used maximizes familiarity within the animal's home range and increases efficiency of foraging and breeding¹⁻³. Therefore, home range can be used as proxy for habitat quality as the home ranges of individuals associated with higher quality habitats tend to be smaller in size than those in poorer quality habitats¹. Additionally, within many ecosystems, forage quality and availability changes throughout the year. As a result, variation in seasonal home range size may indicate variation in habitat quality across different biological seasons^{4,5}.

White-tailed deer (*Odocoileus virginianus*; hereafter deer) are considered a keystone species, of which populations can direct the course of ecological processes associated with specific environments they inhabit⁶. As a popular game species and habitat generalist, deer have a wide-ranging geographic distribution across much of North America, and a vast amount of research has been conducted on home range characteristics of the species³. However, many populations respond differently under different habitat conditions and home range characteristics, and there is variation in seasonal movements across different regions and

environments ⁷. Further, recent studies have found that habitat quality is not only associated with resource availability, but also incorporates predation risk as a critical component of habitat quality ⁸⁻¹¹. Since predation can increase the cost of foraging it can reduce the net benefit of a given resource.

Multiple studies focusing on deer populations within fire-dominated systems of the southeastern United States have demonstrated that disturbance plays a large role in shaping habitat quality during the parturition season. Fire influences the distribution of forage, thermal refugia, and concealment cover, which are primary components of habitat quality during fawning ¹²⁻¹⁴. Often, recently burned areas provide high quality forage but inadequate concealment cover presenting reproductively active females with a tradeoff. A similar tradeoff may be a function of topographic variability in mountainous areas, where higher quality foraging occurs in areas of high predation risk ¹⁵.

The central Appalachians are a largely forested landscape with rugged, mountainous terrain. Historically, an increase in fire suppression and decrease in timber harvesting has led to a reduced amount of early successional habitat, leaving most areas primarily composed of mature, even-aged forest ¹⁶⁻²⁰. Additionally, the size and distribution of disturbances are changing, with increasing use of prescribed fire, substantial declines in timber harvest, and a reduction in the size of clear cuts ^{20,21}. Additionally, the region is also inhabited by three sympatric deer predators: coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and American black bears (*Ursus americanus*). Moreover, each of these predators have unique habitat associations that challenge fawning females to balance predation risk from a diverse predator community^{22,23}.

Home range sizes of female deer within heavily managed forests in the Allegheny Mountains of West Virginia were 3 times smaller before a ~75% population reduction and

intensive timber harvest²⁴. This suggested that home range size was inversely related to population density and intraspecific competition for preferred resources²⁴. Additionally, home ranges of both male and female deer from the same area indicated deer used areas that did not vary with topography; suggesting that other factors (e.g., social aggregations, philopatry, or food availability) were more important drivers of seasonal space use²⁵. Therefore, the energetic tradeoffs associated with traversing greater distances in rugged topography are likely less severe for females that reside in mountainous landscapes with more active habitat management that results in increased forage.

Female deer experience an increased energetic demand during late-term gestation and lactation during the fawning season^{15,26}. This is also the period when they experience the greatest predation risk to themselves and their offspring^{27,28}. For this study, we measured variation in fawning season home ranges of female deer in western Virginia. Our goal was to better understand how elevation influences females during the fawning season and to evaluate how changes in predation risk across elevational gradients may influence fawning home range size. Therefore, we analyzed the effect of elevation on fawning season home range sizes of female deer, both with and without fawns, across two fawning seasons. We hypothesized that mean elevation would significantly influence fawning home range size and predicted that dams that had fawns would have larger home ranges at higher elevations due to need for more resources? than females that did not have fawns.

Methods

We conducted our research in Bath County, Virginia, USA. The county is 1,390 km² in extent, is located within the Ridge and Valley physiographic province portion of the central Appalachian Mountains in western Virginia. The county is primarily characterized by large

contiguous forests and mountainous ridgelines interspersed with tracts of agricultural farmlands in the valley bottoms. Most agriculture consisted of hayfields and improved pasture with very little row crop agriculture. Elevation ranges from 347m – 1,365m ⁴⁰. The George Washington National Forest encompasses 51% of the county. Canopy composition varies in association with aspect and elevation. Xeric sites were dominated by white oak (*Quercus alba*), chestnut oak (*Quercus prinus*), northern red oak (*Quercus rubra*), hickories (*Carya spp.*), pitch pine (*Pinus rigida*) and table mountain pine (*Pinus pungens*). Mesic sites were dominated by red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) and white pine (*Pinus strobus*). Understory communities consist of mountain laurel (*Kalmia latifolia*), wild blueberry (*Vaccinium spp.*), bear oak (*Quercus illicifolia*), rhododendron (*Rhododendron spp.*) and blackberry (*Rubus spp.*). Deer density was estimated to be between 4.75-16.06 deer/km² ⁴¹.

We focused efforts on three separate study areas within Bath County: T.M. Gathright Wildlife Management Area (GWMA), Hidden Valley Recreation Area (HVRA), and Warm Springs Mountain Nature Preserve (WSMNP). The GWMA consisted of 5,434 ha of upland hardwood forest divided into two contiguous tracts separated by Lake Moomaw and encompassing three Coles, Bolar, and Allegheny Mountains. Except for the ridgelines, the topography of GWMA is steep with narrowly incised valleys. A small amount of forest clearings, 1-2 ha in size were present along the ridgelines of Coles and Bolar mountains providing edge and open habitat for deer and other wildlife species. The HVRA included a diverse mix of large hayfields (and gently rolling forested hills, surrounded by mountainous ridgelines. The land area of HVRA was divided into nine prescribed fire units, totaling approximately 2,780 ha. The western half of HVRA concludes at Back Creek Mountain, of which ridgelines also contains several 1-2 ha forest opening. The Nature Conservancy (TNC)

owns and manages the WSMNP, which is the largest contiguous preserve in the state of Virginia⁴². The 3,751-hectare land tract runs along the ridgetop of Warm Springs Mountain on the southeastern portion of the county and borders the George Washington National Forest and Douthat State Park. The WSMNP contains substantial areas of xeric, montane pine communities and is intensively managed, using short-return interval (3-6 year) prescribed fire (TNC, 2021).

From January-May 2019 and 2020, we remotely anesthetized deer using dart projectors and very high frequency (VHF) telemetry darts (Model 414 PLL, Pneu-dart Inc., Williamsport, PA, USA)⁴³. We also captured adult deer throughout each study area, using 17.4m x 13.1m rocket nets^{44,45}, Clover traps⁴⁶, and 6.1m x 6.1m suspended net-gun (Wildlife Capture Services LLC., Flagstaff, Arizona, USA)⁴⁷. Once restrained, we administered intramuscular injections of B.A.M (Butorphanol Tartrate 27.3 mg/mL - Azaperone Tartrate 9.1 mg/mL- Medetomidine HCl 10.9 mg/mL; Zoopharm INC., Laramie, Wyoming, USA) into each female following manufacturer's guidelines. We assessed pregnancy status of each deer using a portable veterinary ultrasound machine (KeeboMed Inc., Morton Grove, Illinois, USA)(Carstensen et al. 2003) and equipped all pregnant deer with an ATS Model G5-2D global positioning system (GPS) tracking collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). We programmed collars to collect hourly fixes for ≥ 24 months and with a continuous (i.e., 24 hour) very high frequency (VHF) mortality beacon. We then implanted pregnant females with ATS Model M3930 vaginal implant transmitters (VIT, Advanced Telemetry Systems, Isanti, Minnesota, USA) having a temperature sensitive telemetry beacon which emitted a unique pulse rate upon expulsion⁴⁸. All VIT-implanted females received a subcutaneous injection of Meloxicam at 0.2 mg/mL (Meloxicam 5mg/mL; Putney Inc. Portland, Maine, USA) as an anti-inflammatory for pain management. Anesthetizing effects of B.A.M were antagonized by administering injections of

both atipamezole (25 mg/mL) and naltrexone HCl (50 mg/mL) (Zoopharm INC., Laramie, Wyoming, USA), and the individual was monitored until full recovery.

Beginning in May of each capture season, VIT implanted females were monitored using radio telemetry once daily until the first transmitter is expelled^{33,49}. Thereafter, VITs were checked once every 8 hours for expulsion in efforts to maximize fawn capture success^{33,50}. When an expulsion signal was detected, we first determined the amount of time since the VIT was expelled using the precise event timer (PET, Advanced Telemetry Systems, Isanti, Minnesota, USA) provided with each VIT. We did not approach fawns born ≤ 3 hours prior to when an expulsion signal was first detected in efforts to allow the dam to groom and bond with her fawns. We attempted to locate the dam, followed by the VIT^{33,50}. If the fawns were not located in the direct vicinity of the VIT, personnel began searching within a 200m radius surrounding the VIT and the dam using thermal imaging scopes⁵⁰. If the fawns were not found after the initial search, subsequent searches were conducted every 8 to 24 hours thereafter for the next 1-3 days, using the dam's location as the focal point for searches^{33,50}. After the fawns were located, they were immediately blindfolded to reduce stress, then placed in a cotton-mesh bag and weighed using a handheld scale. The sex of the fawns was determined, and they were each equipped with an expandable, breakaway VHF collar (Model M4200, Advanced Telemetry Systems, Isanti, Minnesota, USA) programmed with a 4-hour morality switch. Personnel handling fawns wore non-scented latex gloves to reduce human scent. Before exiting the birth site, a location was recorded in a handheld GPS unit and the birth site was marked with piece of flagging. All fawns were monitored for mortality once every 8 hours (0600, 1800, 2200) for the first 4 weeks of age, daily thereafter until 12 weeks of age^{33,50}.

We used a dynamic Brownian bridge movement model (dBBMM) to create 95% utilization distributions (UDs) for each individual female^{13,51,52}. We used dBBMM to determine fawning season home range sizes because they are efficient in analyzing large scale, high-volume datasets by accounting for serial autocorrelation in the sequence of locations⁵³. The method involves incorporation of movement trajectories and behavioral traits associated with unique individuals and creates a probability of an animal occurring within an area, during a specific timeframe. For the model to create the utilization distributions, a Brownian motion variance parameter r (σ_m^2 , also known as the Brownian motion diffusion coefficient), which is associated with the mobility of each individual, was incorporated into the model¹³. Following a “leave-one-out method”, we used a moving window analysis with an odd number of GPS locations to identify variation in movement behaviors^{51,52,54}. Additionally, the moving window analysis also requires that a margin ≥ 3 locations surrounds each end of the window in which no behavioral changes can occur^{51,52}. We used a window size of 21 steps, a margin size of 9 steps, and an 15-m location error for all deer, as visual inspection indicated these settings were sufficient to identify relevant changes in behavior. Using data from 2019 and 2020 fawning seasons we characterized the parturition season (Jun. 1-Aug. 31) and only included deer that obtained 80% acquisition of locations for that season. We fit seasonal dBBMMs to estimate the 95% UD for each female using package *move*⁵⁵ in Program R⁵⁶.

Using Digital Elevation Model (DEM) data we obtained from the United States Geological Survey National Geospatial Program⁵⁷, we extracted elevation (m) data to all cell values within the fawn rearing home range then took the average across those cells to use in analyses. To determine the effect of elevation and maternal status on fawning season home

ranges of females, we used a linear regression model in R to predict home range size as a function of elevation, maternal status (i.e., with or without fawns), and their interaction.

Results

From January-May, 2019-20, we successfully collared and VIT implanted 38 unique females. Two females from the sample were implanted in both successive years, resulting in 40 VIT deployments. We captured 32 neonates (21 in 2019 and 11 in 2020); having successfully captured ≥ 1 fawn from 22 females. Reasons for failure to capture fawns from implanted females were associated with inability to locate fawns after apparent normal parturition (n=11), female death prior to parturition (n=3), and transmitter failure prior to parturition (n=4). From this total, only 7 females successfully reared ≥ 1 fawn to the end of their respective fawning season (August 31st), whereas 13 females were unsuccessful. Three females were not included in the analysis due to collar malfunction and one female was removed from analysis due to an extraneous home range dispersal that occurred during the fawning season.

We estimated 66 fawning season home ranges, which averaged 40.87 ha (95% CI = 31.86-49.89). We found an interactive effect of maternal success (with or without fawn at the end of the fawning season) and mean home range elevation on home range size, such that home range size increased 71.0 ha (118%) and decreased 1.4 ha (2.9%) per 100 m of elevation gain for successful and unsuccessful females, respectively (Table 4.1; Figures 4.1, 4.2).

Discussion

Gaining a better understanding of home range characteristics within wildlife populations can provide valuable insight into the habitat quality of a specific landscape for a certain species^{5,29}. We examined how elevation influenced habitat quality for female deer relative to their reproductive status. We found females that raised ≥ 1 known fawn through the fawning season

exhibited larger fawning home ranges that increased in size with elevation, whereas females without fawns exhibited smaller home ranges that did not increase with elevation. This effect is likely linked to increasing fawn predation risk associated with higher elevations, where deer in our study were likely to experience more interactions with predators, more specifically black bears^{30,31}. Black bear populations have been steadily increasing across the Appalachians³² and can be a driver of neonate mortality during the fawning season³³⁻³⁵. As such, female deer are likely influenced differently by bear populations at higher elevations than lower elevations in our study system.

In general, home ranges of female deer are smallest during the fawning season^{2,36-38} despite their high nutritional demands when lactation is a large energy expenditure^{10,15}. During fawning, dams are forced to balance the need to obtain adequate nutrition not only for themselves, but also for their offspring. These circumstances intensify when females must consider the tradeoffs associated with forage and fawning cover. At our study site, most areas lacked one of these aspects along a gradient - where one area may be more advantageous for suitable fawning cover but be less abundant with suitable forage^{12,13}. As such, the relationships between space use and habitat quality are critical to consider when the populations may be influenced by specific land attributes.

We acknowledge limitations associated with the process of assigning females to a reproductive status. As in other studies, we were often unsuccessful in locating fawns at birth sites for several reasons (e.g., equipment failure, inaccessibility to recovery locations, reduced personnel on site, etc.). We acknowledge the potential that some females were assigned as “non-fawn rearing” individuals to have in fact raised a fawn. However, these false negatives would have made differences between the groups more difficult to detect. Thus, our results of

substantial differences between the groups overcame this bias and the actual difference may have been larger than we reported.

Variation in fawning home range size is most often linked to habitat productivity⁴ and recent work has shown that predation risk should be considered as a primary component of habitat quality^{4,8-10}. We used home range size as surrogate for habitat quality, demonstrating that elevation is an important driver of habitat quality for reproductively active females but not those that lost their fawns. While forage quality is often a primary factor in predicting variation in home range size, our study area was largely characterized by mature, even-aged forest lacking considerably in preferred deer habitat. As such, forage quality likely had little influence *per se* as a component of habitat quality compared to predation risk, especially during the fawning season when maternal investment is heightened. This is especially true considering that fawn mortality risk in our study area - where black bears were a primary source of fawn mortality - increased approximately 22% for every 100 m increase in elevation (Clevinger, Chapter 2). Therefore, we posit that deer habitat is not equal in use and benefit within the central Appalachian Mountains during the fawn rearing season, in that habitat quality associated with elevation is a function of fawn mortality risk.

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Tables

Table 4. 1. Summary statistics for linear mixed effects model predicting the effect of elevation on fawning season home range sizes of adult female white-tailed deer (*Odocoileus virginianus*) that successfully reared ≥ 1 fawn to 12 weeks of age in Bath County, VA, USA, 2019-2020.

term	β	SE	<i>p</i>
Intercept	46.317	4.770	<0.001
Fawn ^a	84.434	18.469	<0.001
Elevation ^b	-2.994	3.793	0.441
Fawn*Elevation	122.202	23.293	<0.001

^a = home range size as a response to rearing ≥ 1 fawn

^b = home range size as a response to elevation

Figures

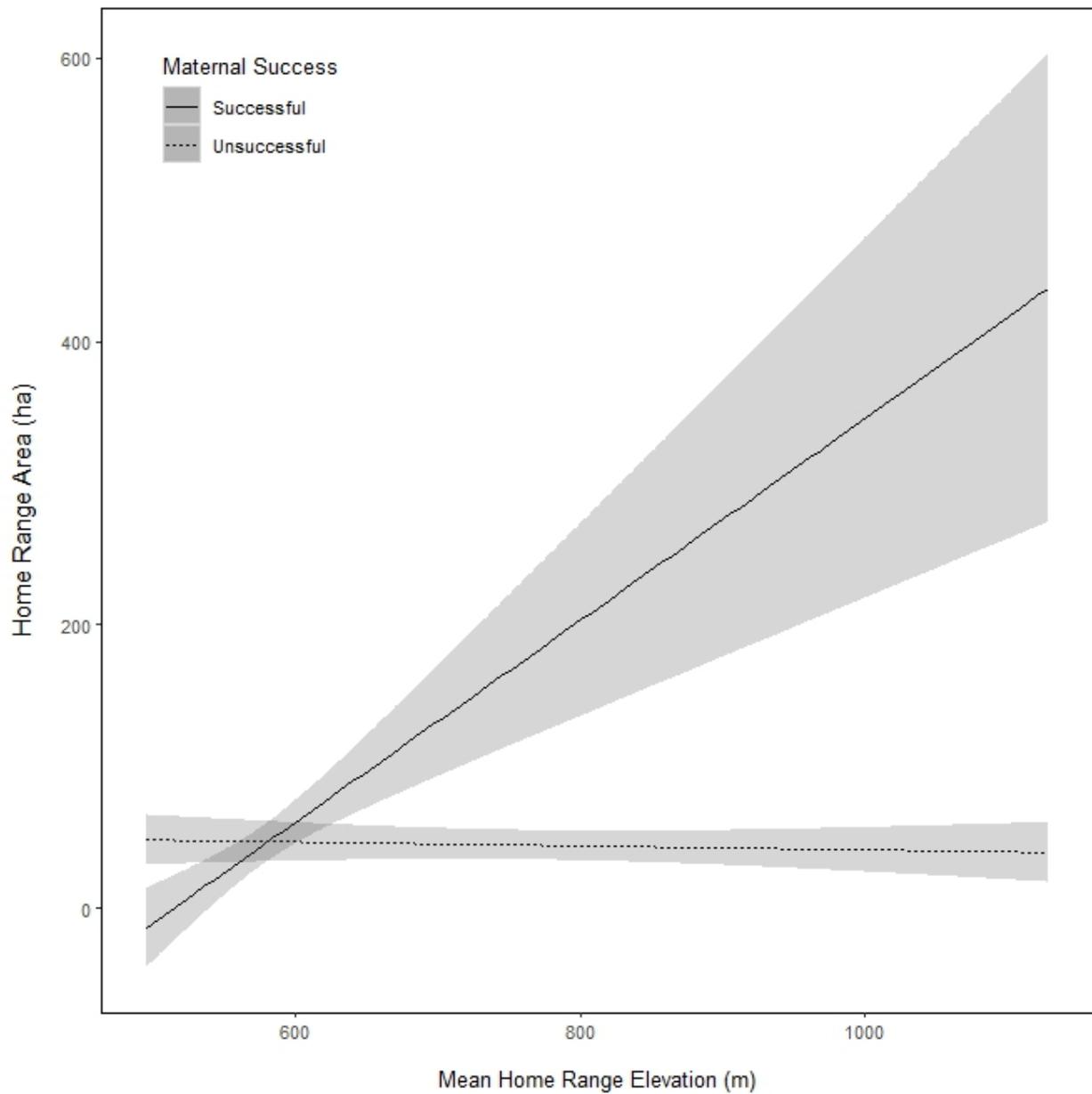


Figure 4. 1. Effect of elevation on fawning season home range sizes of adult female white-tailed deer (*Odocoileus virginianus*) that successfully reared (solid line) or unsuccessfully reared (dashed line) fawns throughout the parturition season in Bath County, VA, USA, 2019-2020.

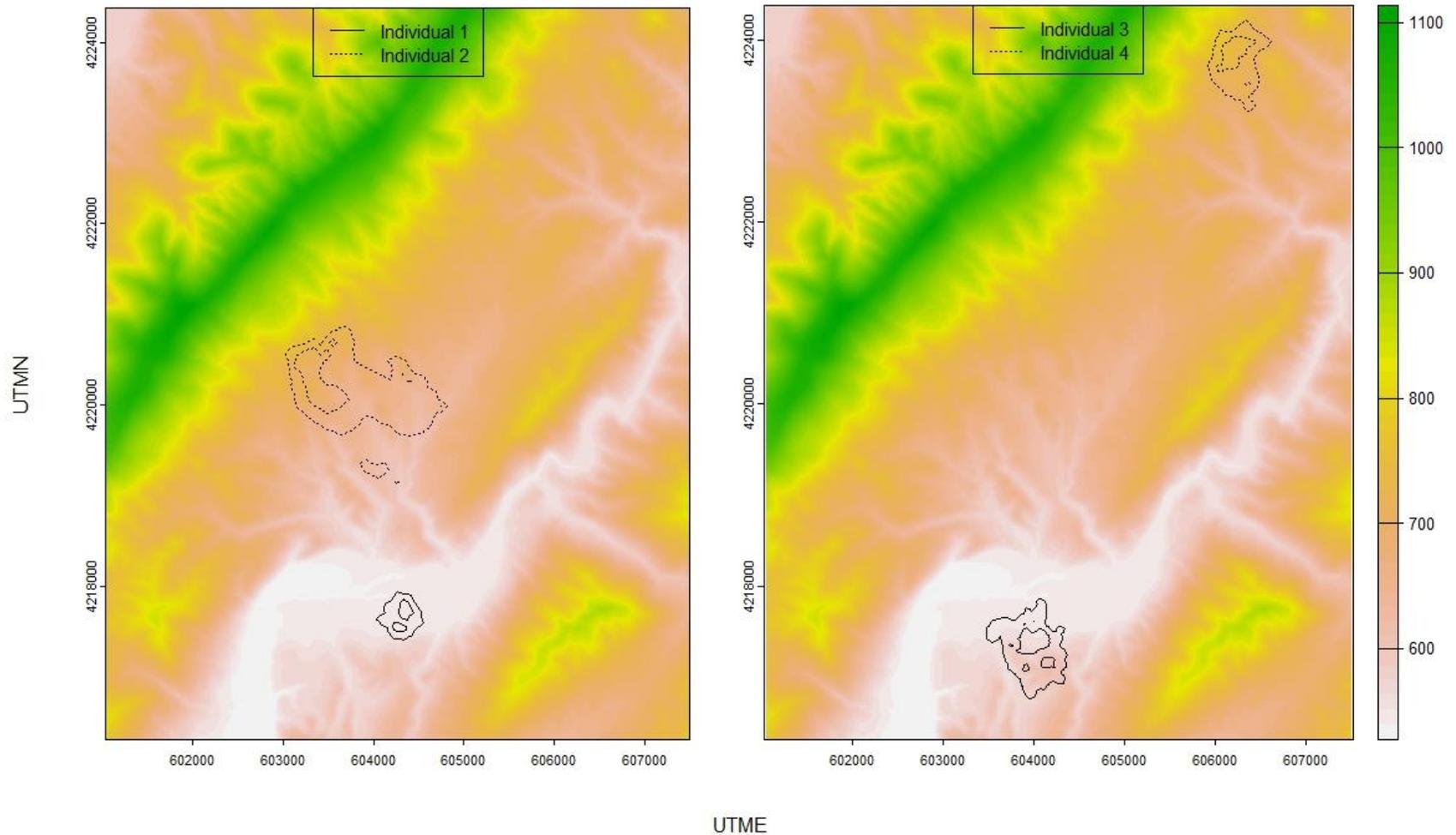


Figure 4. 2. Example of variation in elevation (m) and fawning season home range sizes (ha) of four (4) adult female white-tailed deer (*Odocoileus virginianus*) having either successfully reared at least one fawn (left) or unsuccessfully reared fawns (right) in Bath County, VA, USA, 2019-2020.

⁴Chapter 5: Resource Selection of Adult Female White-tailed Deer Across Biological Seasons in the Central Appalachian Mountains of Western Virginia

Abstract

Resource selection analysis can provide valuable insight into seasonal dynamics of habitat requirements for wildlife. In recent decades, due to disrupted disturbance regimes and mesophication, habitat quality in the Appalachian Mountains has declined for many species, including economically valuable game species such as white-tailed deer (*Odocoileus virginianus*). The landscapes of the central Appalachian Mountains are characterized by senescing mature forests that offer little benefit to white-tailed deer; however, little is known about the importance of forest disturbance to deer populations within the region. We analyzed resource selection of adult female white-tailed deer using step-selection functions across four biological seasons: breeding, early gestation, late gestation, and fawning. During the fawning, breeding, early gestation, and late gestation seasons females selected open habitats. In addition to open habitats, during the fall breeding season females avoided forested edge but selected for areas at higher elevations. During early gestation, females also selected disturbed forests and areas at higher elevations while again avoiding forested edge. During early gestation, probability of use decreased approximately 1.0% for every 100m increase from disturbed habitats and increased 8.6% for every 100m increase in elevation. However, probability of use increased 2.9% for every 100m away from forested edge. Our work provides insight into fine-scale habitat

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relationships that female deer have in a central Appalachian ecosystem and provides habitat management recommendations aimed at supporting deer populations.

Key Words: breeding, central Appalachians, fawning, gestation, habitat, home range, *Odocoileus virginianus*, seasonality, space-use, step-selection function, white-tailed deer

Introduction

Resource selection can provide valuable insight into seasonal dynamics of habitat requirements for wildlife. Resource selection decisions are thought to be the outcome of evolutionary pressures and while maladaptive decisions occur (i.e., ecological traps), particularly in rapidly changing environments, they are rare (Van Horne, 1983, Kristan, 2003). Thus, selection decisions are thought to maximize fitness and are often used to inform wildlife management. The spatial distribution of resources often changes through time and animals track these resources (Aikens et al., 2017; Drent, 1980; Merkle et al., 2016). This is often most apparent in migratory species, but similar processes likely also occur in non-migratory populations as spatial variation in resources change within a home range.

Habitat quality in the Appalachian Mountains has declined for many species in recent years as a function of altered disturbance regimes and mesophication (Harper et al., 2016; Lafon et al., 2017; Little et al., 2018). During pre-European settlement in the eastern United States, the influence of fire modified most forests within the region and created a patchwork of uneven-aged stands with high landscape level heterogeneity (Abrams and McCay, 1996; Lafon et al., 2017; Nowacki and Abrams, 2008). Intensive, exploitative timber harvest began during the early 1900s and the region experienced near complete deforestation within two decades (Davis, 2003).

Despite regeneration, the frequency and intensity of timber harvest in mature second growth stands have steadily declined since the 1990's due to changing societal perceptions and management paradigms, particularly on public lands (Oswalt et al., 2009; VDWR, 2015). Subsequent forests have primarily developed in an era devoid of intense fire-suppression and fire-intolerant species such as maple (*Acer spp.*) have proliferated and outcompeted critical mast producing species such as oaks (*Quercus spp.*), which provide a valuable food source for wildlife species (Aubin et al., 2022; Ford et al., 1997; Lafon et al., 2017; Nowacki and Abrams, 2008; Ryan et al., 2004; Trani et al., 2001; Wentworth et al., 1992). While still uncommon at the regional scale, some efforts have begun to reintroduce fire into Appalachian forests and understanding the effects of these restoration efforts on wildlife is of great interest to land managers (Brose et al., 2001; Lorber et al., 2018; McNitt et al., 2020a).

White-tailed deer (*Odocoileus virginianus*; hereafter deer) populations vary considerably across the Appalachians. For example, deer in many portions of the Allegheny Plateau physiographic region of the central Appalachian Mountains have reached densities that cause herbivory pressure capable of dramatically altering the successional trajectories and species composition in many forests (Campbell et al., 2005; Crimmins et al., 2010; Miller et al., 2009; Nuttle et al., 2014). However, deer populations in portions Blue Ridge Physiographic region of the southern Appalachian Mountains have appeared to decline below levels required to support harvest objectives in recent decades (Little et al., 2018). Within the forested Ridge and Valley Physiographic region, these declines are likely linked to poor habitat quality associated with mesophication and senesce of mature, even-aged forest communities (McShea et al., 2007; Nowacki and Abrams, 2008). Additionally, many of these areas support potentially increasing bobcat (*Lynx rufus*) populations and have experienced the recovery of black bears (*Ursus*

americanus) and a recent colonization by coyotes (*Canis latrans*). Predator risk is primary factor of habitat quality (Crawford et al., 2019; Duquette et al., 2014; Seigle-Ferrand et al., 2021) and predator communities may also influence habitat quality particularly for female deer that are more susceptible to predation than males (Cherry et al., 2015; McCullough et al., 1989). As such, research is needed to provide habitat management recommendations aimed at reversing trends of declining deer populations.

We evaluated seasonal resource selection by female deer in an area of the Ridge and Valley Physiographic region of the central Appalachian Mountains. Our study area is an ideal location for this work because, relative to the rest of the Appalachian Mountains, it has experienced a substantial reintroduction of fire as a land management tool. This area provided an excellent case study for the Appalachian Mountains and a unique opportunity to evaluate the effects of forest disturbance on deer resource selection. We hypothesized that forest disturbance would enhance deer habitat quality and predicted that deer would select disturbed forests and avoid mature forests with closed canopies and open understories. Our goal was to provide empirical support for habitat management recommendations for white-tailed deer in the region.

Methods

Study Area

Our study occurred in the Ridge and Valley physiographic province of western Virginia, in Bath County. Dominated by large tracts of mature, even-aged forest, the county is surrounded (i.e., 51% of total land area) by the George Washington National Forest (GWNF). The county is interspersed with tracts of agriculture, predominately hayfields and cattle pastures, throughout the valleys while steep hillsides and ridgelines are predominately forested. The county is 1,390 km² in extent and elevation ranges from 347 m – 1,365 m (Wolf and Thomas, 2006). Canopy

composition varies in association with aspect and elevation; with wet and dry communities producing different tree species along a gradient. Dry communities (i.e., xeric ecosystems) are predominately composed of white oak (*Quercus alba*), chestnut oak (*Quercus prinus*), northern red oak (*Quercus rubra*), hickories (*Carya spp.*), pitch pine (*Pinus rigida*) and table mountain pine (*Pinus pungens*). Predominately wet ecosystems (i.e., mesic communities) are composed of red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) and white pine (*Pinus strobus*). Understory communities consist of mountain laurel (*Kalmia latifolia*), wild blueberry (*Vaccinium spp.*), bear oak (*Quercus illicifolia*), rhododendron (*Rhododendron spp.*) and blackberry (*Rubus spp.*). Deer density was estimated to be between 4.75-16.06 deer/km² (Montague et al., 2017).

We conducted field operations in three separate areas throughout Bath County: T.M. Gathright Wildlife Management Area (GWMA), Hidden Valley Recreation Area (HVRA), and Warm Springs Mountain Nature Preserve (WSMNP). Predominately composed of forested hillsides, ridgelines, and valley drainages, GWMA (5, 434 ha in total area) is divided into two contiguous tracts. The GWMA also includes sections of three different mountains: Coles, Bolar, and Allegheny. Small, scattered forest clearings (1-2 ha in size) are commonplace along ridgelines on Coles and Bolar Mountains. In the central portion of the county, the HVRA (2780 ha in total area), is federally managed by the U.S. Forest Service (USFS). It is composed of a heterogenous mixture of habitats which includes hay pastureland, both disturbed and undisturbed forests, and several small (1-2 ha) forest clearings along the ridgelines. The HVRA has a short fire return interval (1-3 years) throughout its nine prescribed fire units (S. Tanguay., personal communication) The WSMNP is a privately owned 3,751-hectare preserve which is lies along the ridgeline of Warm Springs Mountain and is surrounded by GWNF and Douthat State Park.

The WSMNP contains substantial areas of xeric, montane pine communities and is intensively managed, using short-return interval (3-6 year) prescribed fire (TNC, 2021).

Animal Capture and Monitoring

In efforts to collect location data from deer within our study area, we remotely anesthetized adult female white-tailed deer using dart projectors and VHF telemetry darts (Model 414 PLL, Pneu-dart Inc., Williamsport, PA, USA) (Siegal-Willott et al., 2009) from January-May 2019 and 2020. Additionally, we also utilized 17.4m x 13.1m rocket nets (Batts et al., 2006; Hawkins et al., 1968), Clover traps (Clover, 1954), and 6.1m x 6.1m suspended net-gun (Wildlife Capture Services LLC., Flagstaff, Arizona, USA; Mattox, 2008) to capture female deer passively. We then restrained and anesthetized individuals via intramuscular injections of B.A.M (Butorphanol Tartrate 27.3 mg/mL - Azaperone Tartrate 9.1 mg/mL- Medetomidine HCl 10.9 mg/mL; Zoopharm INC., Laramie, Wyoming, USA). We then fitted individuals with an ATS Model G5-2D global positioning system (GPS) tracking collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). All collars were pre-programmed to collect hourly fixes for ≥ 24 months with a continuous (24 hour) very high frequency (VHF) mortality beacon. Anesthetizing effects of B.A.M were antagonized by administering injections of both atipamezole (25 mg/mL) and naltrexone HCl (50 mg/mL) (Zoopharm INC., Laramie, Wyoming, USA), and the individual was monitored until full recovery.

Step-Selection Analysis

We utilized a step-selection function (SSF) to analyze resource selection by female white-tailed deer across four biological seasons: early gestation (Dec. 1-Feb. 28), late gestation (Mar. 1-May 31), fawning (Jun. 1-Aug. 31), and breeding (Sept. 1-Nov. 30). Step-selection analysis involves linking successive animal relocations via straight-line segments or ‘used steps’

and comparing them to simulated ‘available steps’ taken from a distribution of observed step lengths and turn angles (Fortin et al., 2005; Thurfjell et al., 2014; Turchin, 1998). The primary objective of the SSF is to determine how resource covariates affect the selection of the steps. A key advantage of SSFs over other procedures such as resource selection functions is that they include movement patterns and characterize habitat availability based on the movement process without the need for estimating a home range (Johnson et al., 2008; Thurfjell et al., 2014). We simulated five available steps for every used step using the distribution of observed step lengths and turn angles derived from the entire sample of collared deer (Thurfjell et al., 2014; van Beest et al., 2012). We removed deer from the analysis if they failed to acquire 80% of the scheduled locations during a given season.

We acquired landcover data from a variety of sources to create resource variables. Primarily, we utilized landcover data from the Virginia Geographic Information Network, which classified data using 1m aerial orthoimagery from the Virginia Base Mapping Program from 2013-2015 for the state of Virginia (VGIN, 2022). Our final reclassified landcover covariates used in our SSF included disturbed forests, forested edge, open areas, mature forest, and elevation.

We combined data from multiple sources to create a raster layer representing disturbed forests. We obtained timber harvest data from the USFS FSGeodata Clearinghouse (USDA Forest Service, 2020) for federal lands and obtained timber harvest data on WMAs from Virginia Department of Wildlife Resources (VDWR). We digitized the timber harvest data pertaining to harvests that occurred on private lands during our study period by comparing USDA’s National Agriculture Imagery Program (NAIP) imagery from 2011 through 2020 (USDA, 2022). We then recorded the time of each harvest from near-real-time forest change maps that occurred on a 24-

day moving window from the ForWarn Legacy and ForWarnII projects (Hargrove et al., 2009). We categorized all timber harvests that occurred during the last 40 years in our study area as disturbed forest, as most of our study area was characterized by mature, even-aged forest. To incorporate disturbance created by prescribed fire, we included a data product provided by TNC that analyzed the extent of fire-created canopy gaps within our study area (Lorber et al., 2018). These data identified land patches within which delineated burn units and fire created canopy gaps with 0-50% canopy cover (Lorber et al., 2018). Similar to timber harvest, canopy gaps created by fire were also classified as disturbed forest.

To map openings, we obtained data from the local USFS Warm Springs Ranger District and VDWR that identified small wildlife openings and logging decks. Clearings on private lands were hand-digitized using NAIP imagery from 2011-2020. Using the ForWarn Legacy and ForWarnII projects, we identified the time the clearings were created from near-real-time forest change maps that occurred on a 24-day moving window (Hargrove et al., 2009). All new and maintained wildlife clearings were classified as open areas.

To create a mature forest variable, we combined sub-categories of Northern Hardwood/Mixed/Cove, Oak Forests/Woodlands, and Pine/Oak. To represent forested edge, we created a 40m buffer into the mature forest and adjacent patches that had shorter vertical vegetation structures (i.e., open, or disturbed forests). We chose a 40m buffer in efforts to capture structural edge effects associated with open and shrubby understory communities influenced by light penetration (Harper et al., 2005). To represent topographic features, we created a covariate for elevation from Digital Elevation Model (DEM) data we obtained from the United States Geological Survey National Geospatial Program (USGS, 2017).

Once we had obtained and organized our landcover data, we then used a distance-based approach to determine selection or avoidance of each habitat type. To do this, we created a distance raster for each of the five habitat covariates using the Proximity tool in QGIS 3.10; where each 10m x 10m raster cell contained the Euclidian distance to each habitat type (QGIS.org, 2022). We then stacked the rasters and extracted “distance-to” data to the obtained locations of each deer.

Results

From January-May, 2019-20, we GPS-collared 38 adult female white-tailed deer. Deer selected open habitats during all biological seasons (Table 5.1, Figure 5.1). During the fawning ($\beta = -0.125$, $SE = 0.050$, $p = 0.011$), breeding ($\beta = -0.145$, $SE = 0.024$, $p = < 0.001$), early gestational ($\beta = -0.153$, $SE = 0.039$, $p = < 0.001$), and late gestational ($\beta = -0.075$, $SE = 0.028$, $p = 0.007$) seasons females selected open habitats, such that for every 100m increase from open habitats, probability of use decreased approximately 2.8%, 2.3%, 3.1%, and 1.3% respectively..

Open areas were the only resource selected and no other features were avoided during the fawning season. In contrast, during the breeding season, the strongest drivers of space use were open areas, forested edges, and elevation. Females avoided forested edge ($\beta = 0.093$, $SE = 0.037$, $p = 0.013$) and selected areas at higher elevations ($\beta = 0.060$, $SE = 0.025$, $p = 0.017$). For every 100m increase from forested edge the probability of use increased by 5.7%. For every 100m increase in elevation the probability of use increased 5.0%.

During early gestation females also selected open areas, disturbed forests ($\beta = -0.084$, $SE = 0.036$, $p = 0.021$), and areas at higher elevations ($\beta = 0.112$, $SE = 0.027$, $p = < 0.001$) while avoiding forested edge ($\beta = 0.098$, $SE = 0.036$, $p = 0.007$). The probability of use decreased approximately 1.0% for every 100 m increase from disturbed forests and increased 8.6% for

every 100 m increase in elevation. However, probability of use increased 2.9% for every 100 m increase from forested edge. Besides selection of open areas, no additional habitat types were selected or avoided during the late gestational season (Figure 5. 2).

Discussion

White-tailed deer are an important game species capable of persisting in a wide range of habitat conditions (DeYoung, 2011). Within the central Appalachian Mountains, available habitats for deer include large tracts of mature, even-aged forests, sparsely interspersed with small patches of openings and early successional forests created by natural or anthropogenic disturbance. We found support for our prediction that female deer would likely select these areas across biological seasons. Interestingly, we found female deer only selected disturbed forests during the early gestation season but selected open areas during all seasons. While food availability is scarce during these overwinter periods, we posit that females may be drawn to disturbed forests during early gestation because these areas offer thermal cover from harsh winter conditions and provide attractive sources of soft mast such as wild grape (*Vitis spp.*). Therefore, disturbed forests likely provide an important cover resource and food resource required to maximize over-winter survival.

Open areas, such as maintained wildlife openings, pastures, and agricultural fields, can be highly productive areas for deer (Gingery et al., 2018; Hewitt, 2011). We found females selected these areas across all biological seasons. Within our study area, slopes and ridgelines are primarily associated with mature forests with few interspersed wildlife opens, while the valleys were mostly dominated by hayfields and pastures. These openings are likely beneficial for deer as they can provide valuable forage resources throughout the year and are also associated with high fawn survival (Gingery et al., 2018). As reported elsewhere, we found that higher elevations

were associated with lower fawn survival (Clevinger et al. Chapter 2). Creation of additional forest openings at higher elevations - particularly of larger sizes and disjunct from primary roads and trails - may improve habitat quality for deer in this mature forest landscapes.

Surprisingly, forested edge was avoided during breeding and early gestation seasons. Edges are transitional areas which deer typically select likely due to close proximity to both food and cover (Waller and Alverson, 1997; Williamson and Hirth, 1985). However, many of these areas are also selected by deer predators. In our study area, McNitt et al. (2020) found bobcats selected edge habitats and avoided interior forest (McNitt et al., 2020). Bobcats are a significant predator of adult deer in some areas (Labisky and Boulay, 1998) and in our study, we found evidence indicating bobcat predation was responsible for mortality of three adult females – one during early gestation (2/28) and two during late gestation (3/24 and 5/11) (Clevinger et al., unpublished data). Previous research has also shown that black bears select edge habitats during Autumn months, suggesting black bears may utilize habitat edges as travel corridors during these periods (Waller et al., 2014). Therefore, within our study system, we suggest the counterintuitive avoidance of forested edges could be related to higher likelihood of encountering a predator within these areas.

Lastly, we found females selected areas at higher elevations during breeding and early gestation seasons. In the central Appalachians, higher elevations are predominately forested, and ridgelines are likely utilized by deer to traverse rugged terrain (Kittle et al., 2008). The energetic demands of deer within these systems are likely elevated during the Fall, as both males and females become more active in response to mating activities (D'Angelo et al., 2005; Karns et al., 2011). Therefore, it could be that females are favoring these high-elevation corridors to conserve energy. Most of the disturbed forests within our study area is located at higher elevations and

selection for both habitat types make sense during the early gestational period as females are likely focused on finding foraging areas with abundant acorn production and thermal cover (i.e., south-facing slopes where understories are abundant in dense mountain laurel (*Kalmia latifolia*)). This is in contrast with more open valley bottoms which act as cold air sinks which lack thick understory cover during the winter months. Conversely, mating behaviors could be overshadowing the foraging response to selection of disturbed habitats during this period. Another possible explanation for selection of higher elevations during the Fall could be associated with increased human disturbance due to the onset of hunting season. Deer spatial ecology can be strongly impacted by hunting activity (Little et al., 2016; Root et al., 1988; Sullivan et al., 2018) and research has shown that deer hunters are less likely to travel further distances from roads and up steeper slopes when selecting areas to hunt (Diefenbach et al., 2005). Therefore, females within our study area may be utilizing areas at higher elevations during the Fall and Winter to reduce potential interactions with hunters.

Management Implications

Our study highlights the importance of creating and maintaining forest openings to support deer populations. The strong selection for open areas that included forest openings, pastures, and hayfields may also support predictions regarding spatial variation in population performance across the central Appalachian Mountains. Managers can expect deer populations to have higher viability in areas with larger proportions of open habitats. Additionally, we offer evidence that supports the use of prescribed fire and timber harvest to create early successional forests (Lorber et al., 2018), as these sites appear to be important areas during harsh winter conditions. Previous work suggests that certain thresholds associated with the percentage of an area treated with timber harvest can benefit both deer and forest regeneration in certain areas

(14%; Miller et al. 2009). Moreover, these applications can be extremely beneficial for a variety of other game and non-game species, including ruffed grouse (*Bonasa umbellus*; Tirpak et al., 2006), American woodcock (*Scolopax minor*; Bakermans et al., 2015), cerulean warblers (*Setophaga cerulea*; Boves et al. 2013) and golden-winged warblers (*Vermivora chrysoptera*; Klaus et al., 2001; Bakermans et al., 2015). As such, we suggest managers increase the use of both mixed-severity fire and sustainable timber harvest to enhance habitat diversity throughout the region.

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Tables

Table 5. 1. Summary statistics including beta coefficients (β), standard errors (SE), z-values (z), and p-values (p) and interpretation from step-selection analysis predicting habitat selection of female white-tailed deer (*Odocoileus virginianus*) across five (5) habitat types (open, disturbed forests, forested edge, mature forest, and elevation) during four biological seasons (i.e., fawning, breeding, early gestation, and late gestation) in Bath County, VA, USA, 2019-2021.

Season	Habitat	β	SE	z	p	Interpretation
<i>Fawning</i>						
	Disturbed					
	Forest	-0.077	0.046	-1.662	0.097	Not Selected
	Forested Edge	0.022	0.064	0.337	0.736	Not Selected
	Open	-0.125	0.050	-2.529	0.011	Selected
	Mature Forest	0.019	0.046	0.410	0.682	Not Selected
	Elevation	-0.064	0.037	-1.716	0.086	Not Selected
<i>Breeding</i>						
	Disturbed					
	Forest	-0.082	0.044	-1.872	0.061	Not Selected
	Forested Edge	0.093	0.037	2.497	0.013	Avoided
	Open	-0.145	0.024	-6.010	<0.001	Selected
	Mature Forest	-0.025	0.021	-1.151	0.250	Not Selected
	Elevation	0.060	0.025	2.380	0.017	Selected
<i>E. Gestation</i>						
	Disturbed					
	Forest	-0.084	0.036	-2.314	0.021	Selected
	Forested Edge	0.098	0.036	2.692	0.007	Avoided
	Open	-0.153	0.039	-3.904	<0.001	Selected
	Mature Forest	-0.017	0.025	-0.710	0.478	Not Selected
	Elevation	0.112	0.027	4.182	<0.001	Selected
<i>L. Gestation</i>						
	Disturbed					
	Forest	-0.051	0.038	-1.350	0.177	Not Selected
	Forested Edge	0.037	0.038	0.990	0.322	Not Selected
	Open	-0.075	0.028	-2.695	0.007	Selected
	Mature Forest	-0.051	0.029	-1.788	0.074	Not Selected
	Elevation	0.052	0.031	1.660	0.097	Not Selected

Figures

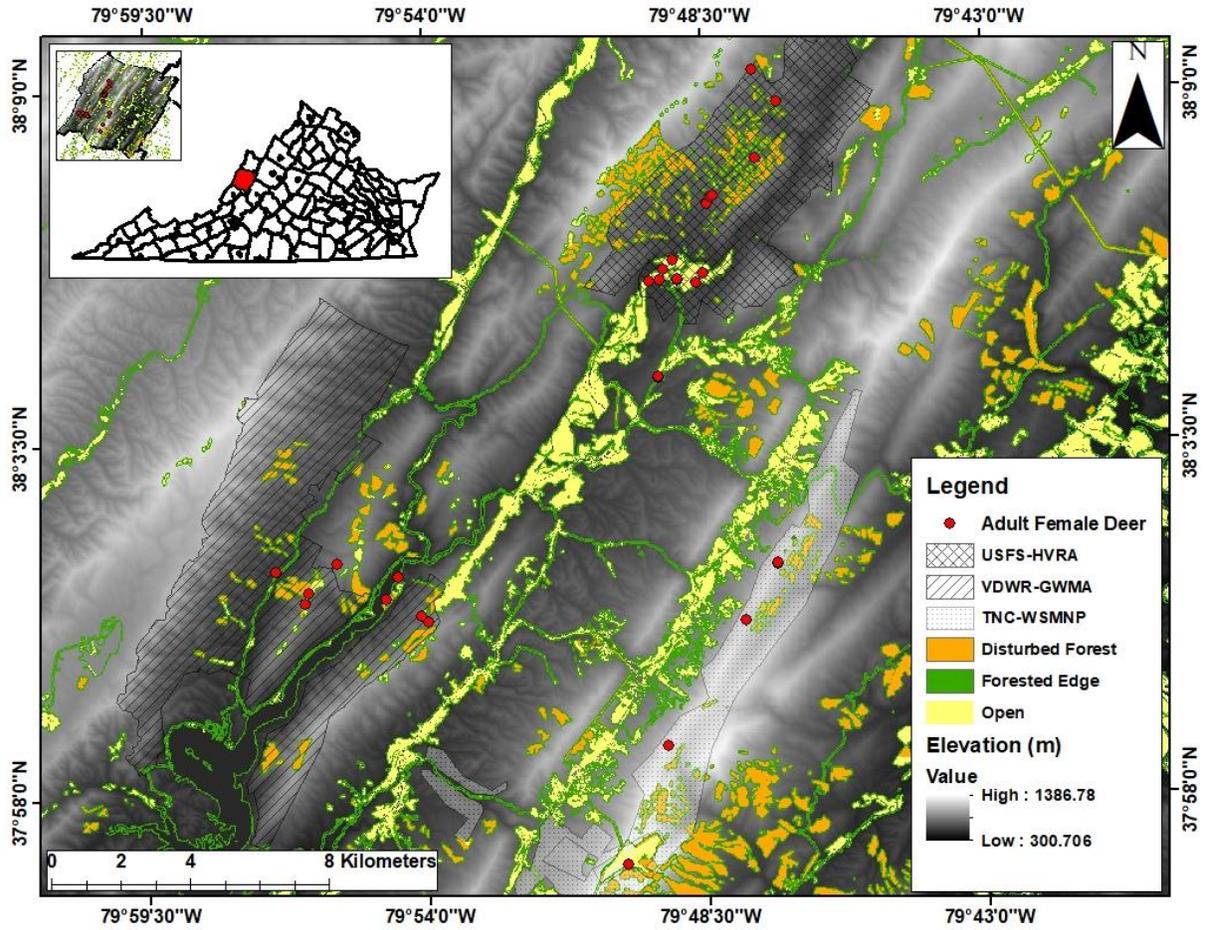


Figure 5. 1. Capture locations of adult female white-tailed deer in association to study areas, disturbed forest (i.e., early-mid successional communities; green areas), open habitats (i.e., grasslands and pasturelands; yellow areas), and elevation (m) in Bath County, VA, USA, 2019-2021.

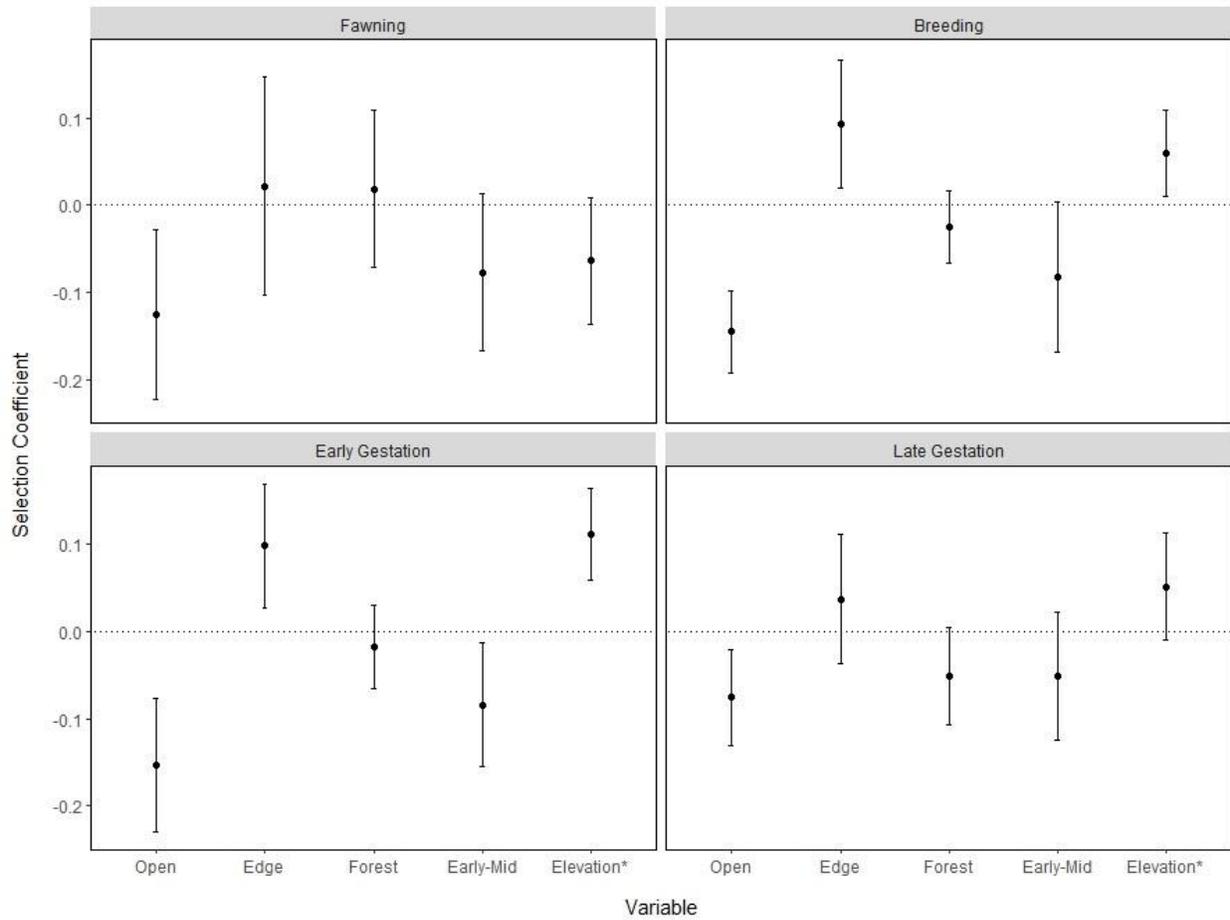


Figure 5. 2. Beta coefficients with 95% confidence intervals predicting habitat selection of adult female white-tailed deer (*Odocoileus virginianus*) across five habitat types (open, forested edge, mature forest, disturbed forest, and elevation) during four (4) biological seasons (fawning, breeding, early gestation, late gestation) in Bath County, VA, USA, 2019-2021.

Chapter 6: Conclusions

In the central Appalachians, white-tailed deer (*Odocoileus virginianus*) (hereafter deer) are a keystone species which are often a primary focus to wildlife managers (Campbell et al. 2005, DeYoung 2011). Moreover, deer herds within different parts of the region often do not share the same perceived population status (i.e., abundant or non-abundant) (Ford et al. 1994, Vreeland et al. 2004, Campbell et al. 2005, Miller et al. 2009, Montague et al. 2017, Gingery et al. 2018). Therefore, deer management strategies in the central Appalachians can be highly variable from one area to the next and careful consideration of management implications should be considered prior to implementation of any prescription. Regardless of the focal area or physiographic province (e.g., Appalachian Plateau or Ridge and Valley physiographic provinces), research suggests that disturbance communities (i.e., early successional areas) are a primary influence of deer population dynamics in the central Appalachians, where most areas are primarily characterized by mature forests long removed from the scale, frequency, and intensity of prescribed fire and timber harvest which routinely altered the landscape in years past (Harper et al. 2016, Lafon et al. 2017). In these systems today, deer populations are often highly dependent on sporadic, cyclic patterns of acorn production from mature oaks (*Quercus spp.*) during the autumnal months and understory browse during the remainder of the year (Ford et al. 1993, 1994, 1997). Coupling this with changing predator communities and declining numbers of deer hunters, changes in deer population trends within the region have warranted continued research to address these issues.

In our study, we sought to provide insights into a low-density deer population in the Ridge and Valley physiographic region of the central Appalachians which was thought to be in steady decline since the early 1990's (VDWR 2015). The focus of our work was five-fold, in that

we determined (1) both habitat-related and predator-related influences on fawn survival and cause-specific mortality, (2) both current and hypothetical (i.e., altering levels of hunter harvest and fawn survival rates) population trajectories of deer within our study area, (3) influences of specific habitat characteristics across biological seasons by identifying selection or avoidance of habitat types (i.e., forest type, disturbed areas, open communities, and elevation profile) (4) micro-scale resource selection of vegetative characteristics at fawn birth sites, and (5) variations in seasonal home range sizes of female deer relative to reproductive status during the parturition season.

Fawn survival and cause-specific mortality are common parameters of interest in deer studies across the country (Pelton 2000, Hewitt 2011, Gingery et al. 2018). Similar to other work from the central Appalachians, we found that fawn mortality within our study area was mostly attributed to predation; with black bears (*Ursus americanus*) confirmed as the primary predator (Gingery et al. 2018). Surprisingly, we did not find any significant relationships between land cover type and fawn mortality risk. However, we did find a significant association between fawn survival and elevation – where fawn survival decreases with increasing elevation. Similar to other systems, black bears within our study area were more commonly associated with high-elevation ridgelines, further away from low-elevation openings which were primarily associated with human influence and disturbance within the valleys (Young and Beecham 1986, Pelton 2000, Jones 2012). However, research pertaining to black bear space use across elevational gradients during deer parturition season would be needed to support this proposed mechanism.

Surprisingly, we found the deer population in our Bath County study was still slightly increasing and would continue to increase if an additional 10% increase in female deer harvest was sustained in the population. Moreover, we also adjusted our hypothetical population

parameters to incorporate even sharper declines fawn survival and while reducing female harvest rates to zero and predicted a slightly increasing population trajectory as well. Our population growth model yielded support for female deer harvest rate being the most sensitive and elastic vital rate within our study system (Chitwood 2014, Peters et al. 2020). In our study system, rugged, mountainous land is commonplace and without access to private land, most hunters are forced to traverse difficult terrain characterized by steep slopes and narrow ridgelines. Seeing that previous work has depicted deer populations in our study area as in decline in association with annual harvest rates (VDWR 2015), our findings support current trends in hunter recruitment and hunter effort in North America; where most hunters are (1) of older age classes and (2) less likely to venture farther from access points (Diefenbach et al. 2005, Hewitt 2011).

We utilized a resource selection function (RSF) to determine habitat selection of parturient female white-tailed deer. From a habitat standpoint, our work highlights the complexities associated with managing deer herds in the central Appalachians during the fawning season, in that we observed conflicting results in selection and avoidance of specific habitats and landcover characteristics at the 2nd and 3rd orders of resource selection. Moreover, our findings reinforce the need for fine-scale considerations of timing and placement of management practices which promote and produce preferred habitats for deer herds within the region, selecting more defined areas to conduct disturbance practices which reduce predator-prey interactions. Prior work suggests that returning low-intensity dormant or growing season fire on a 3-to-5-year interval is an effective prescription to stimulate forage for deer populations in mature, forested stands with broken canopies, while fire should be of greater intensity to produce longer-lasting forage benefits in closed canopy systems (Lashley et al. 2011, Harper et al. 2016). However, within our study area, we found that these areas are both selected and avoided by

females at different spatial scales during the parturition season. We posit that these findings are not only a function of resource selection pertaining to forage quality and availability but also fawning cover quality and availability (Cherry et al. 2017b).

At the micro-scale, we found that females selected birth sites within thick cover having increased visual obstruction. These findings reinforce the belief that thick ground cover is of primary consideration for females when fawns are most susceptible to mortality during the first few days of life, which has been documented as a response to predator pressure (Van Moorter et al. 2009, Shuman et al. 2018). Similar to other systems in the northeast and southeast, our study occurred within region of country having high numbers of neonate deer predators including not only black bears, but also coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) and fawns within our study site experienced high rates of predation (70% within the first 12 weeks of life) (Vreeland et al. 2004, Shuman et al. 2017, 2018, Gingery et al. 2018). Our findings lend support to others which have found that vegetative cover can reduce predation risk by not only providing concealment cover, but also obstruct air flow which could reduce the spread of scent used by predators which are dependent on olfactory cues to find their prey (i.e., black bears) (Wells and Lehner 1978, Shuman et al. 2018).

Like our fawn survival analyses, we found evidence supporting elevation as a significant factor in predicating parturition season home range size – where females which successfully reared fawns to the end of the biological season (i.e., 12 weeks) had significantly larger home ranges at higher elevations than those that did not. Our findings suggest predation risk is a primary factor of habitat quality (Crawford 2021, Seigle-Ferrand et al. 2021). Female deer which routinely inhabit higher elevation areas of the central Appalachians, which are associated with increased black bear activity and reduced availability of early-successional habitat, are

inevitably faced with higher energetic demands than those at lower elevations to successfully rear young. This is ultimately related to energetic demand being a function of reproductive status, where the value of resource units are lower at higher elevations because of the increased cost of foraging.

In addition to utilizing a resource selection function, we analyzed seasonal resource selection using a step-selection function (SSF). This method allowed us to characterize habitat use and availability based on movement characteristics (i.e., step lengths and turn angles) of individuals within our study area (Turchin 1998, Fortin et al. 2005, Thurfjell et al. 2014). We found open habitats (i.e., maintained wildlife clearings, hayfields, and pastures) to be of high importance to female deer, as they were selected during all biological seasons. Secondly, we found deer avoided forested edge throughout the breeding and early gestation seasons. Seeing that most deer populations have historically been characterized as edge-users which select for these transitional areas, we posit that these avoidance relationships were likely associated with varying levels of predator-prey interaction, where edge communities were likely heavily utilized by bobcats (*Lynx rufus*) (McNitt et al. 2020). We also observed selection for higher elevations throughout the breeding season and early gestational season; presumably due in response to increased human disturbances associated with Fall hunting seasons (Diefenbach et al. 2005). Disturbed forests were selected for during the early gestation season and we suggest the response was associated with a need for thermal refugia from harsh weather conditions at higher elevations (i.e., where most disturbance practices occurred across the landscape) as well as higher concentrations of residual soft mast (i.e., wild grape; *Vitis spp.*) which are attractive sources of forage to deer over winter. .

Ultimately, our study provides further insights into how deer population dynamics can fluctuate within a specific region of their geographic range. In terms of population management, for both abundant and declining herds, deer within the central Appalachians will continue to offer a conundrum to agencies until the scale of early successional habitat work and hunting impact (i.e., hunter recruitment and hunter effort) toward both predator and prey are recovered within the region. Previous research has shown that deer population dynamics are highly influenced by habitat disturbance regimes (i.e., prescribed fire and timber harvest, especially during critical biological seasons (Campbell et al. 2004, Lashley et al. 2015, Cherry et al. 2017*a*, *b*). However, our work highlights the role that landscape components (i.e., elevation) play in these processes and reinforces the need for these features to be taken into consideration during management planning.

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