SURVIVAL, MOVEMENT, AND HABITAT SELECTION OF ADULT WHITE-TAILED DEER IN SOUTHERN DELAWARE

by

Jacob M. Haus

A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology and Wildlife Ecology

Fall 2017

SURVIVAL, MOVEMENT, AND HABITAT SELECTION OF ADULT WHITE-TAILED DEER IN SOUTHERN DELAWARE

by

Jacob M. Haus

Approved: ____

Jacob L. Bowman, Ph.D.
Chair of the Department of Entomology and Wildlife Ecology

Approved: ____

Mark W. Rieger, Ph.D.
Dean of the College of Agriculture and Natural Resources

Approved: ____

Ann L. Ardis, Ph.D.
Senior Vice Provost for Graduate and Professional Education

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ____
Jacob L. Bowman, Ph.D.
Professor in charge of dissertation

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ____
W. Gregory Shriver, Ph.D.
Member of dissertation committee

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ____
Kyle P. McCarthy, Ph.D.
Member of dissertation committee

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ____
Bronson K. Strickland, Ph.D.
Member of dissertation committee

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ______________________________

Stephen L. Webb, Ph.D.
Member of dissertation committee

ACKNOWLEDGMENTS

I would like to start by thanking my advisor, Dr. Jacob Bowman. Jake has not only been an excellent advisor and mentor, but his commitment to my professional development has gone well beyond the scope of this research, and I am forever grateful. I appreciate the valuable time, effort, and assistance provided to me by the rest of my committee: Drs. Greg Shriver, Kyle McCarthy, Stephen Webb, and Bronson Strickland. I would like to thank the staff of the Delaware Division of Fish and Wildlife who were involved with the project, particularly Joe Rogerson. My fellow graduate students, both past and present, have made this experience incredibly enjoyable. I am grateful to Justin Dion, my counterpart on the deer project who somehow tolerated my need to control all aspects of not only my own research, but too often his as well. I was fortunate to have some of the most talented and committed technicians working for me; this research would not have been possible without them. I am especially thankful to lead technicians Andy Orlando, Kevin Lamp, and Miranda Reinson for their dedication and leadership. The level of support provided to me by Kristen Suchanec has been unwavering and undeserved; no person should have to learn that much about deer biology against her will.

Finally, I am so grateful for my family: Mike, Beth, and Mary, for making me the person that I am today. My sister took a frustrating amount of enjoyment from

challenging both my beliefs and my patience every chance she had, which I begrudgingly admit has made me a better man and a better scientist. My mom always encouraged me to be curious, learn new things, explore new places, and never settle for anything less than my best effort. Thank you for always being my biggest fan. My dad passed down a passion for the outdoors and taught me a love and respect of wildlife that led me to where I am today. My favorite place in the world will always be whatever chunk of woods we are chasing deer in together. I am so proud to be your son and brother, and any achievement of mine is a testament to the support that you have all given me. I love you all very much.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Chapter 1 of this dissertation examines survival of subadult male white-tailed deer (*Odocoileus virginianus*) in southern Delaware. Increasing male age structure in white-tailed deer populations has become an important objective for many state managers and private landowners seeking to improve hunter satisfaction while maintaining appropriate deer densities. Limiting mortality in the subadult age class is often the primary consideration, and regional differences in climate, habitat, regulations, and hunter behavior complicate understanding of how specific factors influence the risk of mortality. I used Cox proportional hazard modeling to examine the effects of mean distance to road, mean distance to habitat edge, dispersal behaviors, and landownership on the risk of mortality of a collared population of subadult males ($n = 61$) in Sussex County, Delaware, USA. Annual survival averaged 0.60 (95% confidence interval = 0.49 – 0.73), with hunter harvest accounting for 79% of all mortalities. The best approximating supported model for risk of mortality included covariates for landownership (public versus private; $P < 0.01$) and mean distance to habitat edge ($P = 0.01$), with mortality risk increasing on public land and in closer proximity to habitat edge. Increased mortality risk due to habitat fragmentation is well documented in white-tailed deer; however, the effect of landownership has not been quantified, especially when hunter objectives and harvest behaviors differ between landownership types. I observed annual survival rates of 0.75 (95%

confidence interval = 0.62 – 0.89) for deer exclusively on private land during the hunting season, and 0.37 (95% confidence interval = 0.18 – 0.73) for deer that utilized public land during the hunting season. Survival rates on private land were comparable to those of other regions actively managing male age structure (0.72 in Mississippi), although hunter harvest on public land may limit subadult male survival throughout the region.

Chapter 2 focuses on habitat selection in adult male and female white-tailed deer. Individual white-tailed deer can vary in their use of resources and habitats as a function of sex, age, experience, and resource availability. Such individual heterogeneity in habitat use can complicate management efforts, as general management practices may be ineffective for specific objectives at localized scales. I examined heterogeneity in fall and winter habitat selection and functional response using individual conditional logistic step selection models for adult white-tailed deer in southern Delaware. I used fractal analysis to determine the scale at which animals perceived and responded to the landscape, and modeled step selection using covariates for cover type, development, elevation roughness, distance to edge habitat, and distance to road. Magnitude and directionality of selection coefficients were variable among individuals within the same sex. I did not observe uniform individual selection coefficients in any habitat covariate for either sex, and variability in individual selection coefficients was greater in males. Selection coefficients for open habitat ($P = 0.03$) and distance to road ($P = 0.04$) were both a function of increasing proportion of open habitat within the home range. Distance to edge habitat was the only landscape covariate where individual selection coefficients were a function of age ($P = 0.03$), with older deer avoiding habitat edges. Individual models explain heterogeneity in habitat selection that is often overlooked using population level fixed-effect models. Managers attempting to influence harvest success via habitat and population management should be aware of the substantial heterogeneity in habitat use among individual deer before implementing costly practices that may not be appropriate for their specific objectives.

Chapter 1

FACTORS INFLUENCING MORTALITY RISK OF SUBADULT MALE WHITE-TAILED DEER IN DELAWARE

Introduction

Understanding the collective effects of harvest and non-harvest mortality is critical to effective management of hunter harvest on a white-tailed deer (*Odocoileus* virginianus) population (DelGiudice et al. 2002, Brinkman et al. 2004). Knowledge of the factors influencing mortality risk is necessary to the success of any deer management program with the goal of influencing age structure (Dusek et al. 1992, DelGiudice et al. 2002). Traditional harvest management involved liberal take of antlered males; however, a shift from more traditional harvest management practices has placed an emphasis on the recruitment of males into older age classes through proper habitat and population management, which often includes liberal harvest of females (Hamilton et al. 1995). Within unmanaged populations, male white-tailed deer mortality rates vary among age classes, with hunter harvest generally the greatest source of mortality among subadult (1 – 2 year old) males (Nelson and Mech 1986, Van Deelen et al. 1997, Bowman et al. 2007) and older age males being more susceptible to natural mortality (Ditchkoff et al. 2001). Survival rates vary widely among regions, with an annual survival of ≥ 0.72 for subadult males in Mississippi (Bowman et al. 2007) and as low as 0.25 in West Virginia (Campbell et al. 2005). Considerable variation in agency objectives, deer abundance, human social factors, management philosophies, and hunting traditions explain much of the regional discrepancies in harvest (Hansen 2011), however deer behavior and use of the landscape also have implications for an individual's susceptibility to harvest and therefore, survivorship (Ditchkoff et al. 2001, Little et al. 2014). Males protected from harvest at young ages generally can be recruited into older age classes in managed populations (Bowman et al. 2007, Webb et al. 2007*b*).

In general, mortality risk for game species is greater on public than private lands due to higher public land hunter densities (Root et al. 1988, Small et al. 1991). For example, Male red deer (*Cervus elaphus*) that increased use of refuge habitat at the onset of the hunting season had greater survival rates than males who did not change their habitat use in response to hunting pressure (Lone et al. 2015). Similarly, elk (*Cervus canadensis*) appear to transition from public to private land in response to hunting pressure (Conner et al. 2001). White-tailed deer typically exhibit strong site fidelity once an adult range is established (Webb et al. 2007*a*, 2010), despite increased hunting pressure (Marantz et al. 2016), but will alter their behavior during periods of hunting pressure to avoid detection by hunters (Little et al. 2014, 2016), likely by maximizing use of refuges within their home ranges (Kilpatrick et al. 2002, Rhoads et al. 2013, Padiè et al. 2015). The degree to which male white-tailed deer alter movement and behavior seems to be a function of the intensity of hunting pressure (Karns et al. 2012, Little et al. 2016). Heavy hunting pressure on public land may result in fewer available refuges and an increased susceptibility to harvest in subadult male white-tailed deer (Hansen et al. 1986) and males with home ranges consisting primarily of public land will likely have less available refuge compared to males whose home ranges consist primarily of private land.

Males are especially vulnerable to harvest during dispersal from their natal range (Roseberry and Klimstra 1974, Nelson and Mech 1986). Howard (1960) described dispersal as a permanent emigration from an individual's natal range to an area of potential reproduction. In white-tailed deer, dispersal behavior is typically biased towards subadult males (Purdue et al. 2000, Diefenbach et al. 2008). Dispersal can be instigated by either female aggression in the spring or intrasexual competition during the breeding season (Long et al. 2008) and is considered a mechanism of inbreeding avoidance (Wolff et al. 1988, Pusey and Wolf 1996). Natal range philopatry is not uncommon however, and on average, 20 – 50% of subadult males do not disperse (Long et al. 2005, 2008; McCoy et al. 2005). No mechanism has been identified as a definitive predictor of dispersal in individual white-tailed deer. Shields (1982) suggests some degree of philopatry and inbreeding is the result of selection for local adaptation; however, Hölzenbein and Marchinton (1992) found that natal range philopatry was more common among males orphaned as fawns, and led to higher survival rates due to the risk associated with dispersal. Subadult males with larger antlers may be more prone to dispersal than subadult males with relatively small antlers (McCoy et al. 2005, Shaw et al. 2006), and a study of roe deer (*Capreolus capreolus*) fawns found that future dispersers had greater energetic budgets compared to future philopatric fawns (Debeffe et al. 2014). Larger antlers and greater energetic budgets among dispersers suggests that dispersal may pose a high degree of risk for subadult males.

Vehicle collisions are a common source of deer mortality (Storm et al. 2007, Munro et al 2012). Risk of mortality due to vehicle collision is a function of both road density and traffic patterns (Gibbs and Shriver 2002, Ng et al. 2008), and is highly variable among regions. Susceptibility to harvest may also increase with proximity to roads, as there is a strong negative correlation between density of deer hunters and distance from the nearest road (Diefenbach et al. 2005). Similarly, landscape fragmentation has implications for mortality risk, with increased fragmentation being associated with larger home range sizes (Walter et al. 2009), longer dispersal distances (Long et al. 2005), and increased susceptibility to hunter harvest (Foster et al. 1997, Karns et al. 2016).

Wildlife managers in the mid-Atlantic region are currently lacking information on both overall survival rates and factors influencing risk of mortality in subadult males; information that is necessary to manage increasing male age structure on both public and private lands. My objective for this study was to identify and examine the factors (landownership, dispersal behaviors, mean distance to road, and mean distance to habitat edge) associated with increased risk of mortality in subadult male white-tailed deer. I hypothesize that risk of mortality will be greater; 1) for males using public land during the hunting season, with increased proportion of public land use increasing risk of mortality, 2) for dispersers, with longer dispersal distances associated with increased risk, and 3) for deer in closer proximity to roads and habitat edges.

Study Area

I conducted my research on private and publicly owned lands in Sussex County, Delaware (Figure 1.1). Sussex County is located on the coastal plain bordered on the north by Kent County, Delaware, on the east by the Atlantic Ocean, and on the south and west by Maryland. I focused capture efforts near the central and eastern portion of the county to limit the occurrence of animals leaving the study area due to movements outside the home range. Sussex County was 41% agricultural, 15% developed, 22% upland forest, and 22% forested wetland. The most common agriculture crops in Sussex County were corn, soybeans, and wheat (USDA 2012). The 30-year average (1980 – 2010) for daily temperatures in Sussex County ranged from -3.1 to 6.8°C in January and 19.2 to 30.3°C in July (Georgetown; National Oceanic and Atmospheric Administration [NOAA] 2017). Annual precipitation in Sussex County averaged 119 cm (1980 – 2010, Georgetown; NOAA 2017). The deer density in Sussex County was estimated to be 19.4 deer/km^2 in 2009 (DDFW 2009).

The hunting season in Delaware was open from 1 September – 31 January each year of the study with a mixture of primitive and modern weapons allowed (Table 1.1). Hunters may harvest ≤ 2 antlered males with any combination of weapons per year; however, at least 1 antlered male must have an outside antler spread > 38 cm.

Sussex County lacks a population of natural predators (i.e. coyote [*Canis latrans*], bobcat [*Lynx rufus*], black bear [*Ursus americanus*]) sufficient to affect white-tailed deer survival rates (personal communication, J. E. Rogerson, Delaware Fish and Wildlife).

Methods

I captured and collared 61 males (6 – 10 months old) during the winters (December – April) of 2014 – 2015 (n = 30) and 2015 – 2016 (n = 31) using drop nets, rocket nets, and netted cage traps (Clover 1956, Schemnitz et al. 2012). I used an intramuscular injection of xylazine (0.5 mg/kg; Conner et al. 1987, Rosenberry et al. 1999) to sedate all captured deer. After capture, I placed a blindfold over the eyes of each deer to minimize stress. Each deer received 2 self-piercing, numbered metal ear tags (Model #1005-49, National Band and Tag Company, Newport, KY) and 2 white, plastic button cattle tags (3 cm diameter) with black numbers (Allflex USA Incorporated, Dallas, TX). I recorded measurements of shoulder height, hind limb length, total length, and chest girth (Bowman et al. 1998) and estimated the age of each deer according to tooth replacement and wear (Severinghaus 1949). I affixed all subadult males with a 375 g expandable very high frequency (VHF) radio-collar with an 8-hour mortality sensor (M2510B; Advanced Telemetry Systems, Isanti, Minnesota) in the 148 – 151 MHz range. I reversed all deer with an intramuscular injection of tolazoline (3.0 mg/kg; Kreeger et al. 1986), an antagonist for xylazine. I used an injection of vitamin E (0.1 mg/kg selenium and 2.8 mg/kg vitamin E) to counteract signs of capture myopathy. I monitored all vital signs (body temperature, heart rate, and respiration) until the animal left the capture site under their own power. The University of Delaware Institutional Animal Care and Use Committee approved all trapping and handling procedures (#1260).

In order to monitored survival, dispersal distance, and proximity to roads and habitat edge, I located deer once per week from the time of capture until death or collar failure. To determine animal location, I used a handheld R410 receiver (Advanced Telemetry Systems) and a 3-element yagi antenna to obtain ≥ 3 bearings from fixed telemetry stations within 20 minutes to minimize location error due to animal movement. I entered bearings and station locations into the computer program LOAS (Location of a Signal; Ecological Software Solutions, Hegymagas, Hungary) to estimate animal location and error polygons. All location fixes were recorded during daylight hours while males would have been available for harvest in the hunting season.

I physically located any animal whose bearings had changed by $< 5\%$ from the previous location to confirm that a mortality events had not gone undetected due to mechanical failure of the mortality sensor. Upon detection of a mortality signal, I located the deer and performed a field necropsy to determine the likely cause of mortality. I classified mortality cause as vehicle collision, harvest mortality (including wounding loss and illegal harvest), or natural mortality (Garner et al. 1976). Due to small sample size in non-harvest mortalities ($n = 3$ vehicle collisions, $n = 2$ natural mortalities), I did not differentiate between causes of mortality during survival analysis. A non-capture related mortality event (deer vehicle collision) that occurred during the study period but within 14 days of capture (DelGiudice et al. 2005) was included in survival analysis (Norton et al. 2016). Data from deer with unknown fates were right censored at the last known location fix (n = 2 collar failures). I used midpoint-interval censoring (Kalbfleisch and Prentice 1980) to estimate the date of mortality for deer that did not have a known date (i.e. a wounding loss or natural mortality). Interval censoring has been criticized for potentially biased event times (Lindsey and Ryan 1998), but is considered reasonable if the interval time scale is not wide relative to the study period (Law and Brookmeyer 1992). A weekly monitoring interval resulted in time-to-event data that was accurate to ± 3 days for animals whose event time was not known precisely (n = 9).

Previous research has shown that telemetry studies provide unbiased survival estimates for white-tailed deer and the presence of VHF collars does not influence hunter harvest selection (Buderman et al. 2014, Wiskirchen et al. 2017). I informed all landowners and hunters on properties adjacent to capture sites about the possibility of encountering collared deer and encouraged hunters not to let the presence of the collar influence their harvest decision. Additionally, I published an annual article in the Delaware hunting regulations handbook describing the objectives of the study with further encouragement to ignore collars during harvest decisions.

I loaded telemetry locations into ArcMap 10.2 (Environmental Systems Research Institute, Inc., Redlands, CA) and generated buffers around location fixes equal in area to the corresponding error polygon generated in LOAS (mean = 2.05 ha, SD = 1.73 ha). I defined dispersal as a permanent emigration from a natal area to an adult area, such that pre-dispersal and post-dispersal locations did not overlap (Kenward et al. 2001, 2002; Long et al. 2005, Lutz et al. 2015) and the median x-y locations for pre-dispersal locations and post-dispersal locations were ≥ 1 km apart. I calculated dispersal distance as the linear distance (km) between median x-y pre-dispersal locations and median x-y post-dispersal locations (Kenward et al. 2002).

I overlaid deer location buffers on the 2011 National Land Cover Database (Homer et al. 2015) and the United States Census Bureau road layers for Kent and Sussex Counties, Delaware, USA. I reclassified the land cover raster to include classifications for forested, open, and developed areas (Table 1.2). I developed raster layers the United States Census Bureau road layer for Sussex and Kent Counties to 30 m resolution and removed all non-paved roadways from the data. Non-paved roads are uncommon in Sussex County and typically limited to private field access lanes. I calculated the average distance from point buffers to both the nearest habitat edge and nearest roadway cell for all individual deer. I used county parcel data to identify all regions in the study area open to public hunting and created a binomial dummy variable for public land use. Deer that had ≥ 1 buffer during the hunting season located entirely within a parcel open to public hunting were considered available for harvest on public land and were given a value of 1. I gave deer that were not available for harvest on public land a value of 0. Properties classified as open to public hunting were not subject to antler based selective-harvest criteria in excess of state regulations.

I used package ‘survival’ in program R for survival analysis (Therneau 2015). I used a study-based time scale (1 May [0] – 30 April [364]) for both years (Fieberg and

DelGiudice 2009). I used the Kaplan-Meier estimator (Kaplan and Meier 1958) to calculate a baseline annual survival curve with the Greenwood variance estimator to calculate 95% confidence intervals. I tested for a difference in survival between years using a log-rank test. I modeled the effect of covariates on annual survival using the Cox proportional hazard model (Cox 1972, Therneau and Grambsch 2000). Covariates included: study year, dispersal distance (km), a dummy variable for dispersal (1 = dispersed, 0 = did not disperse), average distance to habitat edge (m) for each deer, average distance to road (m) for each deer, a dummy variable for availability of harvest on public land (1 = available, 0 = not available), and the proportion of point buffers that fell entirely within public lands during the hunting season. I did not include point buffers partially located on public land as deer may have been near the border but not using public land, and partial overlap was rare (n = 16 points) and not likely to change model inference. I modeled all main effects individually, and formulated several *a priori* multivariate models. I limited the number of covariates in multivariate models to not exceed 1 predictor per 10 mortality events (Fieberg and DelGiudice 2009). I checked all models to assure the assumption of proportionality among hazard rates was satisfied (Grambsch and Therneau 1994). I compared a global model, null model, and all candidate models using AIC corrected for small sample size (AIC_c; Hurvich and Tsai 1989, Burnham and Anderson 2002). I used the number of mortality events as the sample size for calculation of AIC_c values. The models with the lowest AIC_c value were considered to have more support and be more parsimonious than models(i) with $\Delta_i AIC_c$ ($\Delta_i AIC = AIC_{ci} - AIC_c min$) ≥ 2 (Burnham and Anderson 2002, Posada and Buckley 2004). While a model with $\Delta_i AIC_c \leq 2$ is not necessarily indicative of a substantial level of empirical support (Arnold 2010), I used $\Delta_i AIC_c \leq 2$ as a threshold to identify competitive models.

Results

I observed a 55% dispersal rate for subadult males (n = 33), with a mean distance of 6.8 km (range = 1.7 – 19.8). Most dispersal events (85%) occurred during the fall (1 October – 30 November) when males were ~18 months old. The remaining 15% of dispersals occurred during late spring (15 April – 30 June) when males were ~12 months old. Twenty-five percent (n = 15) of deer were available for harvest on public land during the hunting season. Of the deer available for harvest on public lands, the average proportion of points that fell entirely within public property was 0.53 (range = 0.07 – 0.93). The average distance from buffer to road was 242.8 m (range = 17.5 – 603.5), and the average distance from buffer to edge was 52.2 m (range = 1.3 – 232.9).

I did not observe a difference in survival between years (P = 0.19), so I pooled survival data from both years for analysis. Annual survival (with 95% confidence interval) combined over the 2 periods was 0.60 (0.49 – 0.73; Figure 1.2). Hunter harvest was the most common source of mortality for subadult males (79% of all mortality), followed by vehicle collision (13%) and natural mortality (8%). The Cox model including covariates for availability of harvest on public land and average distance of point buffers to habitat edge received the most support, and no other models were competitive (Table 1.3). The binomial dummy variable for availability of harvest on public land was included in the 3 best approximating models, however the model including proportion of point buffers that were located on public land was not competitive. Models including individual main effects for year and distance to road both received less support than the null model. After checking for derivations in proportionality, I observed no violations in assumptions for any model. An examination of the hazard ratios for the best approximating model (Table 1.4) revealed a significant ($P < 0.01$) increase in mortality risk for deer that were available for harvest on public land (Figure 1.3) and a significant ($P = 0.01$) negative relationship between mortality risk and average distance from buffer to edge (Figure 1.4). Estimates of annual survival (at the population mean for average distance to habitat edge) were 0.37 (0.18 – 0.73) for deer that were available for harvest on public land (Figure 1.5), and 0.75 (0.62 – 0.89) for deer that were not available for harvest on public land (Figure 1.6).

Discussion

I observed mean and maximum dispersal distances that were comparable to subadult males in the mid-Atlantic region, including Pennsylvania and Maryland (Rosenberry et al. 1999, Diefenbach et al. 2008). The overall dispersal rate (55%) was also similar to rates reported in Pennsylvania (58%; Long et al. 2008); however, I observed a greater proportion of fall dispersal (85%) relative to spring dispersal (15%) than has been reported elsewhere. Spring dispersal is thought to be influenced by population structure (Hölzenbein and Marchinton 1992; Long et al. 2005, 2008) with spring dispersal becoming less common as density of adult females decreases, and fall dispersal more common as density of adult males increases (Shaw et al. 2006, Long et al. 2008). The seasonality of dispersal timing I observed may suggest strong male-male competition in the study area (Rosenberry et al. 1999), with limited female aggression towards subadult males. Dispersal has been proposed as a potential driver for increased mortality in subadult males (Nelson and Mech 1986), particularly non-hunting mortality (McCoy et al. 2005), due to increased energetic expenditure and the exploration of novel habitats. Additionally, previous research has reported increased susceptibility to harvest in subadult males during fall dispersal (Roseberry and Klimstra 1974, Nelson and Mech 1986). Cox models including covariates for either dispersal or dispersal distance were not competitive with the best approximating model however, and neither covariate was significant in any model. The absence of an increased risk of mortality in dispersers may suggest a more uniform private land management paradigm throughout the study area, with low variability in survivorship between nearby private properties. Furthermore, I observed few occurrence of non-harvest mortality despite relatively high rates of fall dispersal.

Vehicle collision were similar to other studies of hunted populations. Adult male mortality due to vehicle collision as a percentage of total mortality ranged from 0% in a rural study area (Wiskirchen 2017) to 100% in an urban study area (Etter et al. 2002), although vehicle collisions typically accounted for a consistent percentage of all mortalities (14–15%) despite substantial variability in overall survival rates in populations open to hunting (Ebersole et al. 2007, Storm et al. 2007, Grovenburg et al. 2011). Kilgo et al. (2016) found a negative relationship between risk of mortality from vehicle collision and distance to road, however the effect was small and not a strong predictor of overall survival. Mean distance to road was not an important covariate in any Cox model, possibly because mortality risk due to vehicle collision was small relative to risk due to hunter harvest. Contrary to findings in Pennsylvania (Diefenbach et al. 2005), hunter effort in southern Delaware did not seem to be concentrated near roads; however, important caveats may be that I did not include unpaved roads (i.e. logging roads, farm lanes, and minimum maintenance roads) into the analysis, and that less variability in topography may facilitate hunter access in southern Delaware relative to western Pennsylvania. Mean distance to edge may be a more appropriate proxy for risk of mortality due to increased hunter density because of both the ease of access provided by unpaved roads and field edges, as well as the propensity for hunters to select areas of high visibility (Lebel et al. 2012), such as field and habitat edges.

I observed a slightly greater overall subadult male annual survival rate relative to other regions under similar management paradigms. Among regions that do not actively practice some form of QDM through selective harvest criteria intended to protect subadult males, annual survival ranged from 0.25 (Campbell et al. 2005) to 0.41 (Nelson and Mech 1986). Wiskirchen (2017) reported an annual survival of 0.82 for males < 3.5 years and no difference in survival for private and publicly owned property in Alabama, where publicly hunted property had strict selective harvest restrictions and QDM on private property is a common practice. Additionally, Bowman et al. (2007) found a similarly high rate of survival (0.72) in subadult males under a QDM management paradigm utilizing selective harvest criteria in Mississippi.

Private property parcels in the eastern United States are typically smaller than the scale of use by deer, however, which may increase risk of mortality as deer are exposed to multiple management strategies of different landowners (McCoy et al. 2005). The survival rates I observed on public land were lower and comparable to unprotected populations of subadult males in other regions. Mortality risk did not seem to be influenced by the proportion of locations that occurred on public land, but was rather a function of whether deer utilized public land at all during the hunting season. Survival rates on private land were higher and comparable to regions that actively protect subadult males via selective harvest regulations, despite the lack of such regulations in the study area, indicates greater effort by private landowners in Delaware to manage male age structure and increased opportunities to harvest quality males. Differential survival of subadult males on public and private land is intuitive but not well documented. Hansen (2011) observed lower deer densities on public lands that did not have selective harvest criteria in excess of state regulation in Missouri, and public land hunters expressed poor harvest success and dissatisfaction with the experience. Similarly, public land deer hunters in Pennsylvania were more likely to hunt with the goal of harvesting an antlered deer regardless of age class, less likely to harvest an antlerless deer, and less likely to view themselves as land managers (Stedman et al. 2008). Differences in attitudes and objectives between public and private land hunters appear to have serious implications for the risk of harvest mortality for subadult males when harvest regulations are similar between landownership types.

Management Implications

Wildlife managers often consider public land to be both a less desirable destination for white-tailed deer hunters, and to provide fewer opportunities to harvest mature males relative to private lands (Root et al. 1988, Hansen 2011). Survival of subadult males appears to be substantially reduced on public land relative to private land in southern Delaware. Mortality risk was driven by whether an individual used public land at all during the hunting season, not frequency of use; although I did not observe much variability in proportion of use between deer (proportion of use was generally uniform [~50%]). Private landowners near public hunting areas who attempt to manage male age structure should adjust harvest management and expectations accordingly. Antler based selective harvest regulations on public land may increase male age structure on a local scale, however overall survival of subadult males in southern Delaware is comparable to or exceeds that of similar regions, especially on private land. Survival of subadult males in the region is primarily driven by hunter harvest, and individuals who are not harvested have a high probability of survival into subsequent age classes.

Acknowledgements

I would like to acknowledge the Delaware Department of Natural Resources and Environmental Control and the Federal Aid in Wildlife Restoration Act for funding this project, grant number W-35-R. The U.S. Department of Agriculture National Institute of Food and Agriculture, Hatch project DEL00712 and McIntire Stennis DEL00672, also supported this work. I am grateful to J. Dion, A. Orlando, and

numerous technicians for their support with data collection. I am thankful to the landowners and sportsman in Sussex County, Delaware for their cooperation.

TABLES

Table 1.1 Hunting season dates by weapon type for the 2015 – 2016 and 2016 – 2017 white-tailed deer hunting seasons in Sussex County, Delaware, USA.

Year	Archery*	Muzzleloader	Shotgun	Special Antlerless	Handgun
2015 – 2016	1 Sep. – 31 Jan.	9 – 17 Oct. 25 – 30 Jan.	13 – 21 Nov. 16 – 23 Jan.	2, 3, 19, 23, 24, 26, 30, 31 Oct. 12 – 19 Dec.	2 – 9 Jan.
2016 – 2017	1 Sep. – 31 Jan.	7 – 15 Oct. 23 – 28 Jan.	11 – 19 Nov. 14 – 21 Jan.	1, 17, 21, 22, 24, 28, 29, 30 Oct. 10 – 17 Dec.	7 – 14 Jan.

***** Archery season includes vertical bows and crossbows

Table 1.2 Composition of 4 reclassified raster cell cover types (Open, Forest, Developed, and Water) based on the 2011 National Land Cover Database (NLCD) classification codes.

Class	Code	Description
Open		
	21	Developed, Open Space
	31	Barren Land (Rock/Sand/Clay)
	71	Grassland/Herbaceous
	81	Pasture/Hay
	82	Cultivated Crops
	95	Emergent Herbaceous Wetland
Forest		
	41	Deciduous Forest
	42	Evergreen Forest
	43	Mixed Forest
	52	Shrub/Scrub
	90	Woody Wetlands
Developed		
	22	Developed, Low Intensity
	23	Developed, Medium Intensity
	24	Developed, High Intensity
Water		
	11	Open Water

Table 1.3 Cox proportional hazard models for mortality risk of subadult male white-tailed deer in Sussex County, Delaware, USA in 2015 – 2016 and 2016 – 2017. Multivariate models that received less support than the null model are not reported.

Model	AIC_c[a]	ΔAIC_c	ω[b]
public[c] + distance to edge	170.64	0.00	0.67
public + dispersal distance	173.18	2.54	0.18
global model	175.92	5.28	0.05
public	176.05	5.41	0.04
distance to edge	176.50	5.86	0.02
proportion on public	178.24	7.60	0.01
dispersal distance	179.50	8.86	0.01
disperse[d]	183.14	12.50	0.00
null model	185.66	15.02	0.00
year	186.12	15.48	0.00
distance to road	187.30	16.66	0.00

a. Akaike's Information Criterion adjusted for small n
b. Akaike weight
c. dummy variable for public land use (1 = available for harvest on public land, 0 = not available)
d. dummy variable for dispersal (1 = dispersed, 0 = did not disperse)

Table 1.4 The covariates from the best approximating Cox proportional hazard model (public and average distance to edge) for mortality risk of subadult male white-tailed deer in Sussex County, Delaware, USA in 2015 – 2016 and 2016 – 2017, with associated log hazards (coefficients), hazard ratios, standard errors, Z-scores, and P-values.

covariate	log hazard	hazard ratio	se (log hazard)	Z	P (>|Z|)
public = 1	1.23	3.43	0.42	2.94	< 0.01
distance to edge	-0.02	0.98	0.01	-2.46	0.01

FIGURES

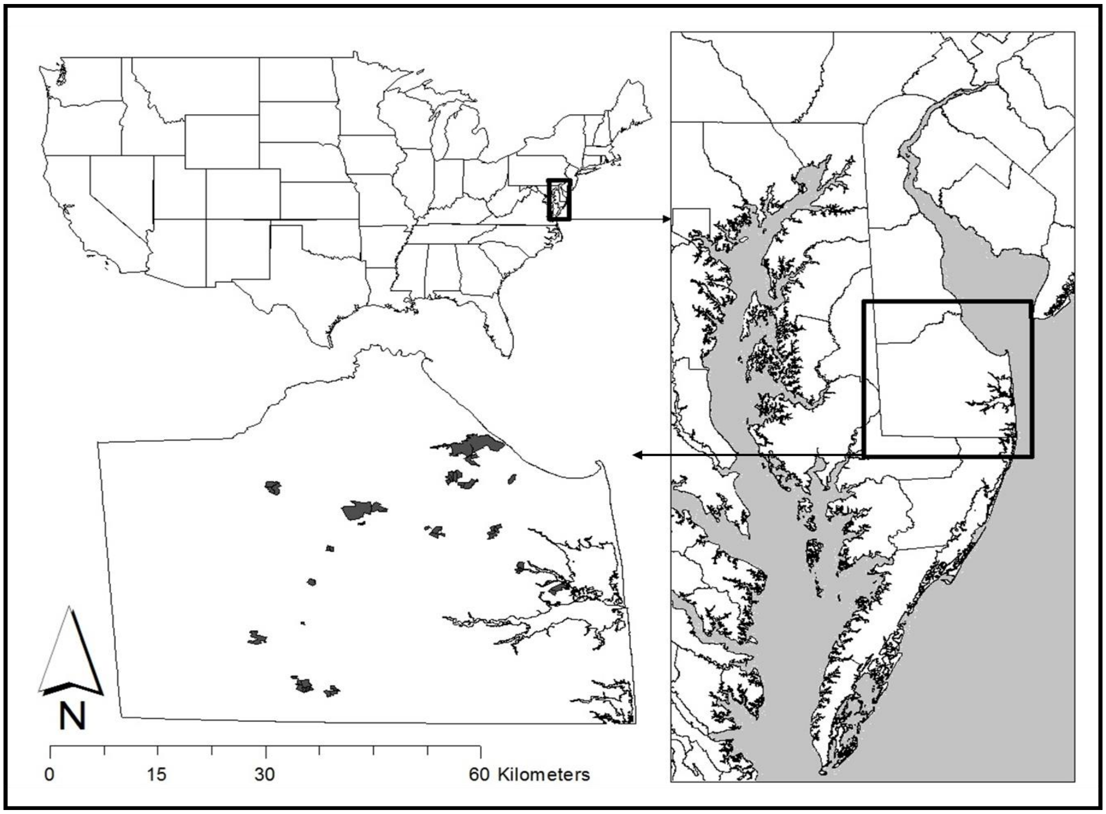


Figure 1.1 Deer were captured on a combination of public and private lands (dark gray) in Sussex County, Delaware, USA from 2014 – 2016.

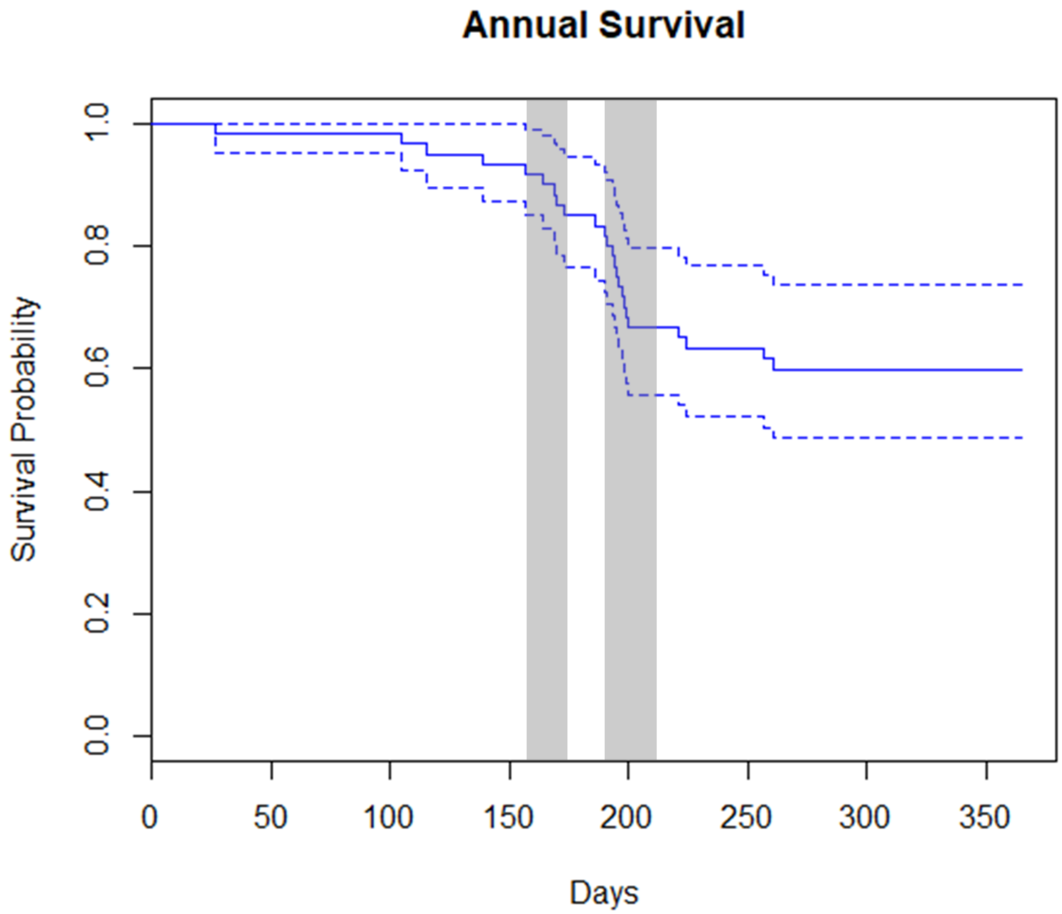


Figure 1.2 Kaplan-Meier survival curve (solid line) and 95% confidence intervals (dashed lines) of combined annual survival (1 May [day 0] – 30 April [day 364], 2015 – 2017) for subadult male white-tailed deer in Sussex County, Delaware, USA. Vertical gray bars represent the October muzzleloader season (left) and the November shotgun season (right), the two primary firearms hunting seasons in the study area.

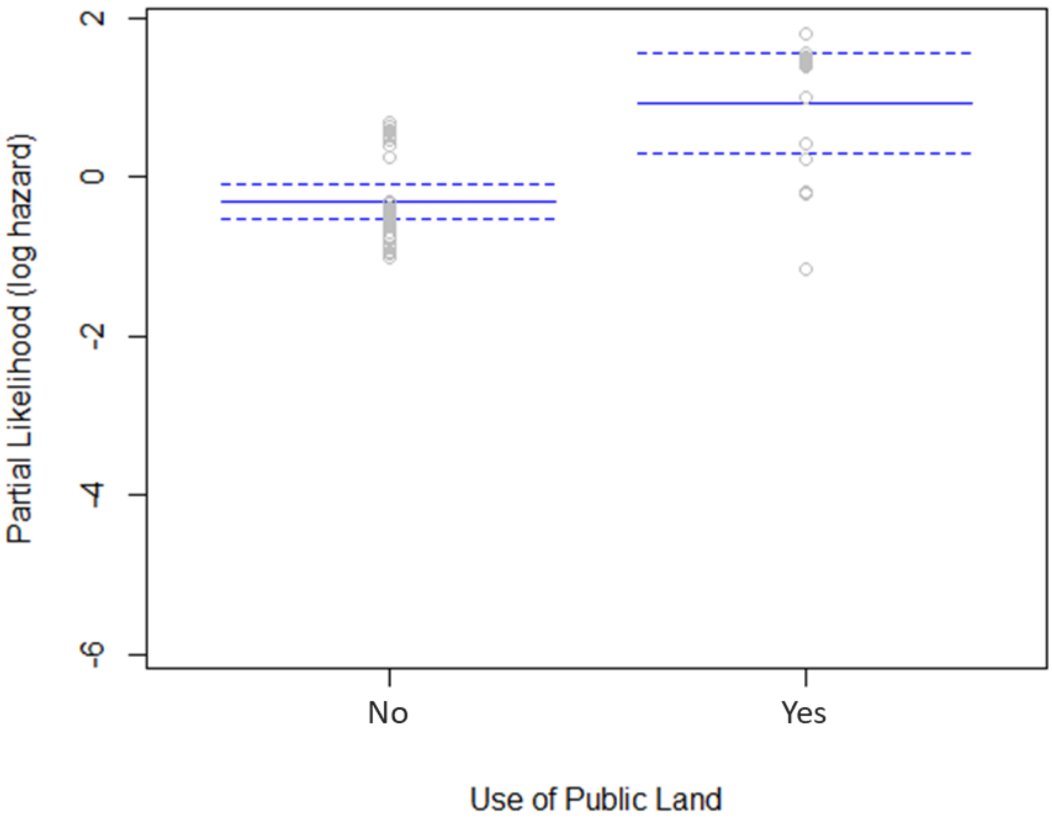


Figure 1.3 Partial Likelihood Estimate (solid) and standard error (dashed) for the log hazards (coefficients) of the use of public land in the Cox proportional hazard model for mortality risk in subadult male white-tailed deer in Sussex County, Delaware, USA from 2015 – 2017.

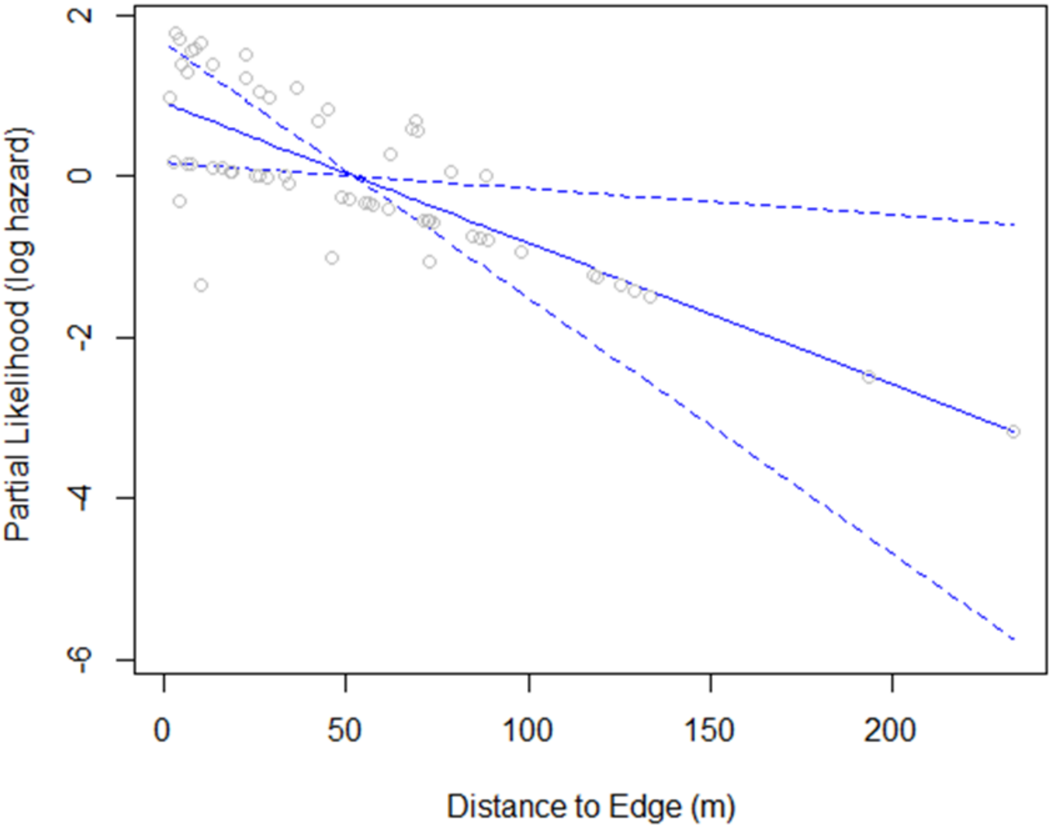


Figure 1.4 Partial Likelihood Estimate (solid) and standard error (dashed) for the log hazards (coefficients) of the average distance to habitat edge in the Cox proportional hazard model for mortality risk in subadult male white-tailed deer in Sussex County, Delaware, USA from 2015 – 2017.

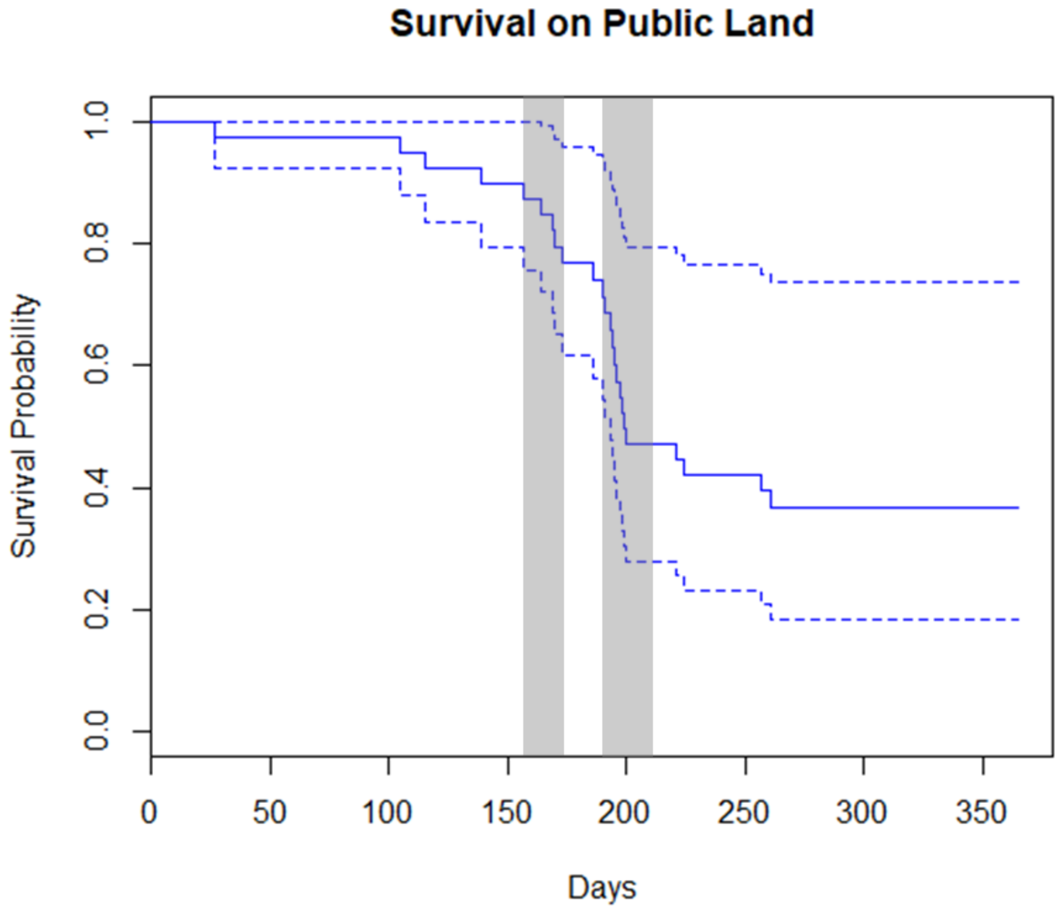


Figure 1.5 Kaplan-Meier survival estimate (solid line) and 95% confidence intervals (dashed lines) of combined annual survival (1 May [day 0] – 30 April [day 365]) for subadult deer available for harvest on public land at average values for mean distance to habitat edge in Sussex County, Delaware, USA from 2015 – 2017. Vertical gray bars represent the October muzzleloader season (left) and the November shotgun season (right), the two primary firearms hunting seasons in the study area.

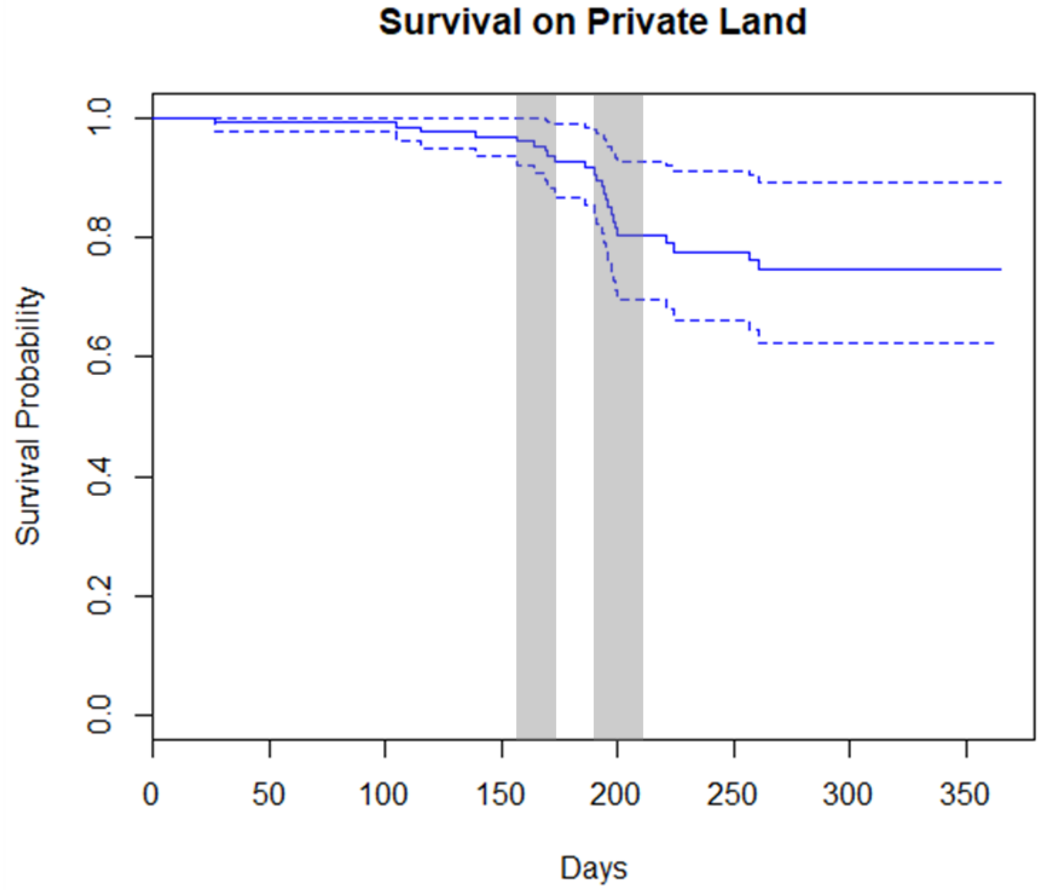


Figure 1.6 Kaplan-Meier survival estimate (solid line) and 95% confidence intervals (dashed lines) of combined annual survival (1 May [day 0] – 30 April [day 365]) for subadult deer not available for harvest on public land at average values for mean distance to habitat edge in Sussex County, Delaware, USA from 2015 – 2017. Vertical gray bars represent the October muzzleloader season (left) and the November shotgun season (right), the two primary firearms hunting seasons in the study area.

REFERENCES

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bowman, J. L., H. A. Jacobson, and B. D. Leopold. 1998. Fawn Survival on Davis Island, Mississippi after an early summer flood. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 52:397–402.

Bowman, J. L., H. A. Jacobson, D. S. Coggin, J. R. Heffelfinger, and B. D. Leopold. 2007. Survival and cause-specific mortality of adult male white-tailed deer managed under the Quality Deer Management Paradigm. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 61:76–61.

Brinkman, T. J., J. A. Jenks, C. S. DePerno, B. S. Haroldson, and R. G. Osborn. 2004. Survival of white-tailed deer in an intensively farmed region of Minnesota. Wildlife Society Bulletin 32:726–731.

Buderman, F. E., D. R. Diefenbach, C. S. Rosenberry, B. D. Wallingford, and E. S. Long. 2014. Effect of hunter selectivity on harvest rates of radio-collared white-tailed deer in Pennsylvania. Journal of Wildlife Management 78:1456–1465.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer-Verlag, New York, New York, USA.

Campbell T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2005. Population characteristics of a central Appalachian white-tailed deer herd. Wildlife Society Bulletin 33:212–221.

Conner, M.C., E.C. Soutiere, and R.A. Lancia. 1987. Drop-netting deer: costs and incidence of capture myopathy. Wildlife Society Bulletin 15:434–438.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management 65:926–940.

Cox, D. 1972. Regression models and life-tables. Journal of the Royal Statistical Society. Series B 34:187–220.

Debeffe, L., N. Morellet, N. Bonnot, J. M. Gaillard, B. Cargnelutti, H. Verheyden-Tixier, C. Vanpe, A. Coulon, J. Clobert, R. Bon, and A. J. M. Hewion. 2014. link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore. Proceedings from the Royal Society of Biological Sciences 281:20140873.

Delaware Division of Fish and Wildlife [DDFW]. 2009. Delaware Deer Density and Population Estimates.<http://www.dnrec.delaware.gov/fw/Hunting/Pages/DeerInfo.aspx> Accessed 6 May 2014.

DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66:698–717.

DelGiudice, G. D., B. A. Sampson, D. W. Kuehn, M. Carstensen Powell, and J. Fieberg. 2005. Understanding margins of safe capture, chemical immobilization, and handling of free-ranging white-tailed deer. Wildlife Society Bulletin 33:677–687.

Diefenbach, D. R., J. C. Finley, A. E. Luloff, R. Stedman, C. B. Swope, H. C. Zinn, and G. J. San Julian. 2005. Bear and deer hunter density and distribution on public land in Pennsylvania. Human Dimensions of Wildlife 10:201–212.

Diefenbach, D. R., E. S. Long, C. S. Rosenberry, B. D. Wallingford, and D. R. Smith. 2008. Modeling distribution of dispersal distance in male white-tailed deer. Journal of Wildlife Management 72:1296–1303.

Ditchkoff, S. S., E. R. Welch Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes of mortality among white-tailed deer support mate-competition theory. Journal of Wildlife Management 65:552–559.

Dusek, G. L., A. K. Wood, and S. T. Stewart. 1992. Spatial and temporal patterns of mortality among female white-tailed deer. Journal of Wildlife Management 56:645–650.

Ebersole, R., J. L. Bowman, and B. Eyler. Efficacy of a Controlled Hunt for Managing White-tailed Deer on Fair Hill Natural Resource Management Area, Cecil County, Maryland. 2007. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 61:68–75.

Etter, D. R., K. M. Hollis, T. R. Van Deelen, D. R. Ludwig, J. E. Chelsvig, C. L. Anchor, and R. E. Warner. 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. Journal of Wildlife Management 66:500–510.

Fieberg, J., and G. D. DelGiudice. 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. Ecology 90:1687–1697.

Foster, J. R., J. L. Roseberry, and A. Woolf. 1997. Factors influencing efficiency of white-tailed deer harvest in Illinois. Journal of Wildlife Management 61:1091–1097.

Garner, G., J. Morrison, and J. Lewis. 1976. Mortality of white-tailed deer fawns in the Wichita Mountains, Oklahoma. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 30:493–506.

Gibbs, J. P., and W. G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

Grambsch, P. M., and T. M. Therneau. 1994. Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika* 81:515–26.

Grovenburg, T. W., C. C. Swanson, C. N. Jacques, C. S. DePerno, R. W. Klaver, and J. A. Jenks. 2011. Female white-tailed deer survival across ecoregions in Minnesota and South Dakota. American Midland Naturalist 165:426–435.

Hamilton, J., W. M. Knox, and D. C. Guynn. 1995. How quality deer management works. Pages 7–18 *in* K. Miller and L. Marchinton, editors. Quality Whitetails. Stackpole books, Harrisburg, Pennsylvania.

Hansen, L. P. 2011. Extensive Management. Pages 409–451 *in* D. G. Hewitt, editor, Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Hansen, L. P., C. M. Nixon, and F. Loomis. 1986. Factors affecting daily and annual harvest of white-tailed deer in Illinois. Wildlife Society Bulletin 14:368–376.

Hölzenbein, S., and R. L. Marchinton. 1992. Spatial integration of maturing-male white-tailed deer into the adult population. Journal of Mammalogy 73:326–334.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63:152–161.

Hurvich, C. M. and C. L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Kalbfleisch, J. D., and R. L. Prentice. 1980. The statistical analysis of failure time data. John Wiley and Sons, New York, New York, USA.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Karns, G. R., R. A. Lancia, C. S. DePerno, and M. C. Conner. 2012. Impact of hunting pressure on adult male white-tailed deer behavior. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 66:120–125.

Karns, G. R., R. J. Gates, S. N. Matthews, J. T. Bruskotter, J. C. McCoy, and M. J. Tonkovich. 2016. Factors influencing spatial heterogeneity of female white-tailed deer harvest dynamics. Wildlife Society Bulletin 40:758–763.

Kenward, R. E., S. S. Walls, and K. H. Hodder. 2001. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. Journal of Animal Ecology 70:1–13.

Kenward, R. E., S. P. Rushton, C. M. Perrins, D.W. Macdonald, and A. B. South. 2002. From marking to modelling: dispersal study techniques for land vertebrates. Pages 50–71 *in* J. M. Bullock, R. E. Kenward, and R. S. Hails, editors. Dispersal Ecology. Blackwell Publishing, Malden, Massachusetts, USA.

Kilgo, J. C., M. Vukovich, M. J. Conroy, H. S. Ray, and C. Ruth. 2016. Factors affecting survival of adult female white-tailed deer after coyote establishment in South Carolina. Wildlife Society Bulletin 40:747–753.

Kilpatrick, H. J., A. M. LaBonte, and J. T. Seymour. 2002. A shotgun-archery deer hunt in a residential community: evaluation of hunt strategies and effectiveness. Wildlife Society Bulletin 30:478–486.

Kreeger, T. J., G. D. DelGiudice, U. S. Seal, and P. D. Karns. 1986. Immobilization of white-tailed deer with xylazine hydrochloride and ketamine hydrochloride and antagonism by tolazoline hydrochloride. Journal of Wildlife Diseases 22:407–412.

Law, C. G., and R. Brookmeyer. 1992. Effects of mid-point imputation on the analysis of doubly censored data. Statistics in Medicine 11:1569–1578.

Lebel, F., C. Dussault, A. Massé, and S. Côté. 2012. Influence of habitat features and hunter behavior on white-tailed deer harvest. Journal of Wildlife Management 76:1431–1440.

Lindsey, J. C., and L. M. Ryan. 1998. Methods for interval-censored data. Statistics in Medicine 17:219–238.

Little, A. R., S. Demarais, K. L. Gee, S. L. Webb, S. K. Riffell, J. A. Gaskamp, and J. L. Belant. 2014. Does human predation risk affect harvest susceptibility of white-tailed deer during hunting season? Wildlife Society Bulletin 38:797–805.

Little, A. R., S. L. Webb, S. Demarais, K. L. Gee, S. K. Riffell, and J. A. Gaskamp. 2016. Hunting intensity alters movement behavior of white-tailed deer. Basic and Applied Ecology 17:360–369.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stammes, and A. Mysterud. 2015. An adaptive behavioral response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour 102:127–138.

Long, E. S., D. R. Diefenbach, C. S. Rosenberry, B. D. Wallingford, and M. D. Grund. 2005. Forest cover influences dispersal distance of white-tailed deer. Journal of Mammalogy 86:623–629.

Long, E. S., D. R. Diefenbach, C. S. Rosenberry, and B. D. Wallingford. 2008. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. Behavioral Ecology 19:1235–1242.

Lutz, C. L., D. R. Diefenbach, and C. S. Rosenberry. 2015. Population density influences dispersal in female white-tailed deer. Journal of Mammalogy 96:494–501.

Marantz, S. A., J. A. Long, S. L. Webb, K. L. Gee, A. R. Little, S. Demarais. 2016. Impacts of human hunting on spatial behavior of white-tailed deer (*Odocoileus virginianus*). Canadian Journal of Zoology 94:853–861.

McCoy, J. E., D. G. Hewitt, and F. C. Bryant. 2005. Dispersal by yearling male white-tailed deer and implications for management. Journal of Wildlife Management 69:366–376.

Munro, K. G., J. Bowman, and L. Fahrig. 2012. Effect of paved road density on abundance of white-tailed deer. Wildlife Research 39:478–487.

National Oceanic and Atmospheric Administration [NOAA]. 2017. National Environmental Satellite, Data, and Information Service. NOWData. <http://mi.nws.noaa.gov/climate/xmacis.php?wfo=phi> Accessed 5 May 2017.

Nelson, M. E., and L. D. Mech. 1986. Mortality of white-tailed deer in northeastern Minnesota. Journal of Wildlife Management 50:691–698.

Ng, J. W., C. Nielsen, and C. C. St. Clair. 2008. Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. Human-Wildlife Conflicts 2:34–47.

Norton, A. S., D. J. Storm, M. A. Watt, C. N. Jacques, K. Martin, and T. R. Van Deelen. 2016. Left truncation criteria for survival analysis of white-tailed deer. Journal of Wildlife Management 80:1323–1331.

Padiè, S., N. Morellet, A. J. Mark Hewison, J. Martin, N. Bonnot, B. Cargnelutti, and S. Chamaillè-Jammes. 2015. Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos doi:10.1111/oik.02115.

Posada, D., and T. R. Buckley. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. Systematic Biology 53:793–808.

Purdue J. R, M. H. Smith, and J. C. Patton. 2000. Female philopatry and extreme spatial genetic heterogeneity in white-tailed deer. Journal of Mammalogy 81:179–185.

Pusey A. E., and M. Wolf. 1996. Inbreeding avoidance in animals. Trends in Ecology and Evolution 11:201–206.

Rhoads, C. L., J. L. Bowman, and B. Eyler. 2013. Movements of female exurban white-tailed deer in response to controlled hunts. Wildlife Society Bulletin 37:631–638.

Root, B. G., E. K. Fritzell, and N. F. Giessman. 1988. Effects of intensive hunting on white-tailed deer movement. Wildlife Society Bulletin 16:145–151.

Roseberry, J. L., and W. D. Klimstra. 1974. Differential vulnerability during a controlled deer harvest. Journal of Wildlife Management 38:499–507.

Rosenberry, C. S., R. A. Lancia, and M. C. Conner. 1999. Population effects of white-tailed deer dispersal. Wildlife Society Bulletin 27:858–864.

Schemnitz, S. D., G. R. Batcheller, M. J. Lovallo, H. B. White, and M. W. Fall, 2012. Capturing and handling wild animals. Pages 64–117 *in* N. J. Silvy, editor, The Wildlife Techniques Manual; 7th edition. Volume 1. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Shaw, J. C., R. A. Lancia, M. C. Conner, and C. S. Rosenberry. 2006. Effect of population demographics and social pressures on white-tailed deer dispersal ecology. Journal of Wildlife Management 70:1293–1301.

Shields, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State University of New York Press, Albany, USA.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1991. Predation and hunting mortality of ruffed grouse in central Wisconsin. The Journal of Wildlife Management 55:512–520.

Stedman, R. C., P. Bhandari, A. E. Luloff, D. R. Diefenbach, and J. C. Finley. 2008. Deer hunting on Pennsylvania’s public and private lands: A two-tiered system of hunters? Human Dimensions of Wildlife 13:222–233.

Storm, D. J., C. K. Nielsen, E. M. Schauber, and A. Woolf. 2007. Space use and survival of white-tailed deer in an exurban landscape. Journal of Wildlife Management 71:1170–1176.

Therneau, T. M. 2015. A package for survival analysis in S. Version 2.38.

Therneau, T. M., and P. M. Grambsch. 2000. Modeling survival data: extending the Cox model. Springer, New York, USA

United States Department of Agriculture [USDA]. 2012. National Agriculture Statistics Service. Census of Agriculture-County Profile. <http://www.agcensus.usda.gov/Publications/2012/Full_Report/Volume_1,_Chapter_2_County_Level/Delaware >. Accessed 6 May 2014.

Van Deelen, T. R., H. Campa III, J. B. Haufler, and P. D. Thompson. 1997. Mortality patterns of white-tailed deer in Michigan's Upper Peninsula. Journal of Wildlife Management 61:903–910.

Walter, W. D., K. C. VerCauteren, H. Campa III, W. R. Clark, J. W. Fischer, S. E. Hygnstrom, N. E. Mathews, C. K. Nielsen, E. M. Schauber, T. R. Van Deelen, and S. R. Winterstein. 2009. Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. Landscape Ecology 24:1405–1420.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007*a*. Scale of management for mature male white-tailed deer as influenced by home range and movements. Journal of Wildlife Management 71:1507–1512.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007*b*. Survival and cause specific mortality of mature male white-tailed deer. Journal of Wildlife Management 71:555–558.

Webb, S. L., K. L. Gee, B. K. Strickland, S. Demarais, and R. W. DeYoung. 2010. Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. International Journal of Ecology. 2010:459610.

Wiskirchen, K. H. 2017. Survival of adult white-tailed deer and movement relative to temporal patterns of predation risk. Master's Thesis, Auburn University, Auburn, Alabama, USA.

Wiskirchen, K. H., T. C. Jacobson, J. D. Sullivan, and S. S. Ditchkoff. 2017. Hunter cooperation with requests to avoid a visibly marked ungulate. Wildlife Society Bulletin 41:301–308.

Wolff, J. O., K. I. Lundy, and R. Baccus. 1988. Dispersal, inbreeding avoidance and reproductive success in white-footed mice. Animal Behavior 36:456–465.

Chapter 2

INDIVIDUAL HETEROGENEITY AND FUNCTIONAL RESPONSE IN HABITAT SELECTION AMONG ADULT WHITE-TAILED DEER

Introduction

White-tailed deer (deer; *Odocoileus virginianus*) management has become an increasingly localized practice as many individual property managers have taken a strong interest in age structures, densities, habitat use, and harvest management of the animals on their land (Hamilton et al. 1995, Jacobson et al. 2011). One of the primary objective of many management programs is to increase the quantity and quality of opportunities to harvest adult deer. An understanding of the relationships between deer and their habitat during the hunting season is a critical component of an effective management program (Morrison 2001, Anderson et al. 2012, Rhoads et al. 2013). Patterns in habitat use in adult deer are a function of resource availability, predator densities, and reproductive opportunities (Proffitt et al. 2009, Webb et al. 2011*a*, Cleveland et al. 2012), and vary between sexes (DePerno et al. 2003) and among individuals (Wagner et al. 2011, Foley et al. 2015).

Recreational hunting may be the greatest source of predation risk for adults throughout much of the range of white-tailed deer (Frid and Dill 2002, Little et al. 2015, Ciuti et al. 2012), and deer typically respond to hunting pressure by increasing use of cover habitat and refuges (Kilpatrick et al. 2002, Rhoads et al. 2013) and decreasing movement rates during high risk periods (Little et al. 2014, 2016). Similarly, deer species respond to risks associated with vehicle traffic and human activity by generally avoiding space adjacent to roads and developed areas (Rowland et al. 2000, Gagnon et al. 2007, Webb et al. 2011*a*). Wagner et al. (2010) however, demonstrated that despite avoidance of roads by deer at the population level, individuals varied in their response, and conclusions inferred from populations may not be valid at localized scales or useful to all management programs.

Individual heterogeneity in habitat selection may be a function of sex, age, previous experiences, or availability of specific habitats within an individual's home range. Age influences movement behaviors related to breeding strategy and risk aversion in adult males (Foley et al. 2015, Padiè et al. 2015), with individual heterogeneity likely having implications for survival and reproductive success (Franklin et al. 2001, Gillies et al. 2006). Understanding heterogeneity in habitat selection or response to habitat composition among groups or individual deer can provide valuable information to managers and can directly influence harvest recommendations and management success (Rhoads et al. 2013).

Habitat selection by animals are usually modeled using resource selection functions. Resource selection functions (RSFs) compare habitat characteristics at sites used by animals to those that were potentially available (Manly et al. 2002). Step selection functions (SSFs) are an extension of traditional resource selection functions that link consecutive animal locations (steps). Used steps are compared with random steps, which are characterized as available to the animal during its movement through the habitat, using a conditional approach (Duchesne et al. 2010, Thurjfell et al. 2014). SSFs pair each use step with random available steps with the same starting point drawn at from a distribution of step lengths and turning angles (Fortin et al. 2005, Thurjfell et al. 2014).

A potential complication to habitat selection analysis is the existence of a functional response in selection (Mysterud and Ims 1998, Godvik et al. 2009, Mason and Fortin 2017). Functional response is defined as the selection of a habitat differing as a function of the habitat availability within the home range. Functional responses to habitat have been reported in multiple species of cervids including roe deer (*Capreolus capreolus*; Padiè et al. 2015), caribou (*Rangifer tarandus*; Moreau et al. 2012), elk (*Cervus canadensis*; Creel et al. 2005), red deer (*Cervus elaphus*; Godvik et al. 2009, Dzialak et al. 2011*a*) and mule deer (*Odocoileus hemionus*; Anderson et al. 2012), but has not been thoroughly explored in white-tailed deer. In addition to functional responses to available habitat, selection among individuals may change as a function of age. Males of different age classes often maintain home ranges of differing size, with some studies supporting an increase in home range size as an individual matures (Nelson and Mech 1981, 1984), although more recent research suggest the opposite may be true, with more mature males generally maintaining smaller ranges than younger deer (Webb et al. 2007, Hellickson et al. 2008). While there is a paucity of research examining the effect of age on habitat use for female white-tailed deer, home range sizes for adult female roe deer vary in response to nutritional demands and reproductive status (Tufto et al. 1996), which are partially a function of age.

Fall and winter are the periods of primary interest for most white-tailed deer management programs as they correspond to the breeding season and the preponderance of mortality in both sexes. My objectives were to evaluate variability in fall and winter habitat selection between adult male and adult female deer, as well as among individuals of both sexes using individual SSFs. Additionally, I examined the functional response in habitat selection of individual deer to habitat characteristics within the home range, and how habitat selection varied with age.

Study Area

Deer were captured on private and publicly owned lands in Sussex County, Delaware (Figure 1.1). Sussex County is located on the coastal plain bordered on the south and west by Maryland, on the north by Kent County, Delaware, and on the east by the Atlantic Ocean. I focused capture efforts near the central and eastern portion of the county to increase the probability that deer could still be found on or near the primary study area. Elevations in the study area ranged from 0 – 21 m above sea level, with little regional variability. The most common agriculture crops in Sussex County were corn, soybeans, and wheat (USDA 2012). Sussex County was 41% agricultural, 15% developed, 22% upland forest, and 22% forested wetland. The 30-year average (1980 – 2010) for daily temperatures in Sussex County ranged from -3.1 to 6.8°C in January and 19.2 to 30.3°C in July (Georgetown; National Oceanic and Atmospheric

Administration [NOAA] 2017). Annual precipitation in Sussex County averaged 119 cm (1980 – 2010, Georgetown; NOAA 2017).

The deer density in Sussex County was 19.4 deer/km^2 in 2009 (DDFW 2009). The hunting season in Delaware was open from 1 September – 31 January each year with a mixture of primitive and modern weapons allowed (Table 1.1). Hunters may harvest ≤ 2 antlered males with any combination of weapons per year; however, at least 1 antlered male must have an outside antler spread > 38 cm. The State of Delaware also offers a Severe Deer Damage Assistance Program that allows qualifying landowners to harvest antlerless deer from 15 August – 15 May.

Methods

I captured and collared 48 adult white-tailed deer (≥ 18 months old) during the winters (December – April) of 2014 – 2015, and 2015 – 2016 using drop nets, rocket nets, and netted cage traps (Clover 1956, Schemnitz et al. 2012). I sedated all captured deer using an intramuscular injection of xylazine (0.5 mg/kg; Conner et al. 1987, Rosenberry et al. 1999). I placed a blindfold over the eyes of each deer to minimize stress. Each deer received 2 self-piercing numbered metal ear tags (Model #1005-49, National Band and Tag Company, Newport, KY) and 2 white plastic button cattle tags (3 cm diameter) with black numbers (Allflex USA Incorporated, Dallas, TX). I recorded measurements of shoulder height, hind limb length, total length, and chest girth (Bowman et al. 1998), and estimated the age of each deer according a combination of tooth replacement and wear (Severinghaus 1949) and body characteristics (Demarais et al. 1999) to increase accuracy of age estimates (Bowman et al. 2007). I affixed all adults with an 825 g iridium GPS collar with a 10-hour mortality sensor (G2110E; Advanced Telemetry Systems, Isanti, Minnesota). Males received collars with an expandable elastic mechanism that allowed for growth and seasonal swelling of the neck. I reversed all deer with an intramuscular injection of tolazoline (3.0 mg/kg; Kreeger et al. 1986), an antagonist for xylazine. I monitored all vital signs (body temperature, heart rate, and respiration) until the animal left the capture site under their own power. The University of Delaware Institutional Animal Care and Use Committee approved all trapping and handling procedures (#1260 and #1288).

Issues with expandable collar retention, collar failure, and early mortality resulted in data from 26 of 48 animals (12 males, 14 females) included in the final analysis. Individuals ranged from 2.5 – 6.5 years of age during the analysis. I programed collars to record a fix every hour for the duration of the Delaware hunting season (1 September – 31 January) during the 2015 – 2016 and 2016 – 2017 seasons, resulting in 77,916 location fixes (36,212 for males, 41,704 for females). I programmed all collars on males to break off remotely during the following spring to avoid animal welfare concerns in subsequent years from neck growth. Because females do not experience seasonal swelling of the neck to the same degree as males, collars were not programmed to break off until battery failure. Habitat selection analysis can be biased if habitat type influences GPS fix success or location error (Bowman et al. 2000, D’Eon et al. 2002). Mean fix rate of GPS locations for all animals was 97% (range = 92 – 100%). I removed any physically impossible locations as well as all 3-dimensional locations with position dilution of precision (PDOP) > 10 and 2-dimensional locations with PDOP > 5 (D'Eon and Delparte 2005). GPS location error and missed location fixes have negligible impact on habitat selection inference when fix rate exceeds 90% (Frair et al. 2004, Godvik et al. 2009), and habitats considered problematic for location bias (e.g. heavy canopy cover, rugged topography) are not typical of southern Delaware (Cain et al. 2005, Lewis et al. 2007, Vance et al. 2017).

I used fractal analysis to estimate the spatial scale at which deer perceived the landscape (Nams 2005, Webb et al. 2009) following procedures outlined by Dzialak et al. (2011*b*). I used an estimate of fractal dimension to quantify tortuosity of movement as a function of spatial scale of the movement path (Nams 2005). I used program Fractal 5.0 (Nams 1996) to estimate fractal dimension (*D*) using the VFractal estimator where location data for each animal were separated into movement paths of fixed length (m), and where θ was the mean turning angle between steps for a given movement path.

$$D = \frac{1}{1 + \log_2(\cos\theta + 1)}$$

I calculated scaling parameters using the distribution of step lengths for the population of deer, with a minimum path length of 5 m, a maximum of 5500 m, and 90 divisions.

I estimated the spatial scale of perception of the landscape for deer by examining the correlation of tortuosity between adjacent movement paths. When correlation was positive, path segments were smaller than the patch size perceived by the animal; when negative, path segments were approximately equal to patch size; and when correlation was zero, path segments were larger than patch size (Nams 2005, Webb et al. 2009). I therefore used the mid-point of the range of path sizes where correlation in tortuosity was generally negative as the spatial scale at which to calculate habitat covariates for the step selection functions.

I used a point-based approach in step selection modeling opposed to a path-based approach (Boyce et al. 2003). I paired each hourly use point with 10 random steps (Benson 2013) starting from the same point of origin. I generated random step points by sampling from the observed distributions of step length and relative turning angle. To avoid circularity, I generated random step points for all 26 individuals using the mean observed distributions of the other 25 individuals (Fortin et al. 2005). I considered random step points to be available habitat as defined in traditional resource selection modeling (Manly et al. 2002).

I used the spatial scale to define the number of 30 m resolution raster grid cells to include in a square moving window used to estimate landscape covariates around each point. I used a geographic information software (ArcMap 10.2; Environmental Systems Research Institute, Inc., Redlands, CA) to calculate landscape covariates from both used and available points within each moving window. I reclassified the 2011 National Land Cover Database (Homer et al. 2015) to include classifications for forested, open, and developed areas (Table 1.2). Open water was classified as non-habitat and was masked from the generation of available steps. I created a 30 m resolution road raster layer from the United States Census Bureau road data for Sussex

County and removed all unpaved roadways, as unpaved roads are uncommon in Sussex County and typically limited to private field access lanes. Landscape covariates included proportion of forested areas (forest), proportion of unforested areas (open), and proportion of developed areas (developed), and the elevation roughness (roughness), calculated as the standard deviation of elevation from a 30 m resolution digital elevation model (DEM). I also calculated the linear distance (m) from the used or available point to both the nearest road raster cell (road) and habitat edge (edge). Habitat edge was considered any change in raster cell land cover type. To aid in model convergence and to allow for coefficient comparison, I centered and standardized all covariates (X_i) separately for used and available points for each sex. I checked for correlation among all covariates for both sexes, and used an information theoretic approach to select between correlated covariates. Step selection functions were estimated using conditional logistic regression (Duchesne et al. 2010). I generated a model for each individual deer predicting probability of use using the ‘clogit’ function in package ‘survival’ (Therneau 2015) in program R (R core development team 2017).

I defined functional response as a shift in habitat selection as availability within the home range differed, and I estimated response by modeling individual selection coefficients as a function of predictors describing the available habitat in each individual’s home range. I calculated home ranges using an autocorrelated kernel density estimator (AKDE; Fleming et al. 2015, 2017) in a continuous time framework. AKDE accounts for autocorrelation in high frequency GPS location fixes when estimating home range boundaries, which results in more statistically appropriate range estimates than traditional kernel density estimators. I used the 95% maximum likelihood estimate of the AKDE home range boundary to calculate the proportion of forest, open, and developed areas available to each deer within the home range. I also calculated the density of roads and edge habitat within each home range (km/km^2). I constructed simple linear and quadratic regression (function ‘lm’ in R) to model individual β values for selection as dependent variables as a function of the habitat characteristics for each home range. I also used an analysis of variance (ANOVA; function ‘aov’ in R) to determine if there was a difference in individual selection coefficients for any covariate by age class (2.5, 3.5, and 4.5+ years old).

Results

Fractal analysis indicated correlation of tortuosity between adjacent paths versus path length averaged negative values from generally 185 – 280 m for adult males (Figure 2.1B) and 175 – 285 m for adult females (Figure 2.2B). Plots of fractal *D* versus path length suggest a transition in movement pattern corresponding to the range of negative correlation for both sexes (Figures 2.1A and 2.2A), providing additional evidence of a patch size corresponding to the scale at which adult deer perceive the landscape (Weins 1989; Webb et al. 2009, 2013; Dzialak et al. 2011*b*). Because raster cells are 30 m resolution, the area of the square moving window must be a factor of 30. I used a spatial scale of 225 m as the approximate mid-point of the ranges for both sexes resulting in a square moving window of 450 m^2 , or 15 x 15 30 m resolution raster cells, centered on each used and available points to calculate landscape covariates.

Covariates for proportion of forest habitat and proportion of open habitat were negatively correlated for both males and females. I removed the covariate for forest habitat from step selection analysis to avoid issues with correlation, as the univariate model including forest habitat resulted in a greater AIC value and was less parsimonious than the model containing the open habitat covariate (Burnham and Anderson 2002). For all used and available points prior to transformation, proportion of open habitat averaged 0.42 (range = 0.00 – 1.00), standard deviation of elevation averaged 0.40 m (0.00 – 3.00), distance to edge habitat averaged 116.33 m (0.0 – 850.58), and distance to road averaged 238.52 m (0.00 – 1537.49).

I did not observe uniform selection among males for any covariate (figure 2.3), and standard deviations of selections coefficients were large relative to the mean for all covariates. Male selection coefficients were generally positive for developed areas at the population level (mean = 0.39, Standard deviation [sd] = 0.36), but 4 of 12 individual males avoided developed areas (Table 2.3). Population averages for male selection of distance to habitat edge was negative (mean = -0.12, sd = 0.35) suggesting avoidance of areas near habitat edge, however 6 of 12 individuals selected for areas farther habitat edge. Similarly, 6 of 12 individual males selected for habitats with increased elevation roughness, with a population mean suggesting slight selection for rough elevation (mean = 0.11, sd = 0.55). The population average of selection coefficients for open habitat was positive (mean = 0.09, sd = 0.56) with 7 of 12 individual males showing a positive selection coefficient for open habitat. Eight of 12 males selected for areas farther from roads than available habitat, with a positive population level selection of distance to road (mean = 0.18, sd = 0.53).

I did not observe uniform selection for any covariate among females (Figure 2.4). Similar to males, population means of selection coefficients were positive for developed areas (mean = 0.02, sd = 0.36), negative for distance to edge (-0.08, sd = 0.34), and positive for open habitat (mean = 0.03, sd = 0.36). The direction of population average selection differed in females for selection of elevation roughness (mean =-0.09, sd = 0.54) and distance to road (mean = -0.06, sd = 0.52), however.

I observed a functional response in habitat selection in 2 candidate models (Table 2.4). No simple linear model of function response was significant. I observed a quadratic response in selection of both open habitat (Figure 2.5) and distance to road (Figure 2.6) as a function of the proportion of the home range classified as open habitat. Selection coefficients for open habitat and distance to road were both relatively strong when open habitat was rare, decreased at moderate proportions of open habitat, and increased at greater proportions of open habitat within the home range.

I did not find a correlation between selection for developed areas, elevation roughness, open habitat or distance to road and age class of adult deer, potentially due to low sample sizes of mature (≥ 4.5 years old) deer (n = 8). Selection for distance to edge habitat was a function of age (P = 0.03, F = 0.20, df = 2), however. Deer in the 2.5 year old age class were more likely to select for areas near a habitat edge, while 3.5 and ≥ 4.5 year old deer selected for habitat that was farther from habitat edge than available points (Figure 2.7). Pairwise comparisons revealed no difference in selection for distance to edge habitat between 3.5 and ≥ 4.5 year old deer (P = 0.37), but selection in 2.5 year old deer differed from 3.5 year old deer (P = 0.03) and ≥ 4.5 year old deer (P = 0.03).

Discussion

A number of biotic and abiotic factors, including but not limited to behavioral state, risk avoidance, and landscape composition complicate the spatial scale at which adult deer perceive and respond to the landscape (Morales et al 2004, Gautestad and Mysterud 2005, Pinaud 2008). Despite confounding variation throughout different regions and different analytical approaches, the spatial scale of landscape use I calculated is similar to those identified in multiple cervid species. Webb et al. (2009) used fractal analysis to identify perceived habitat patch size of 333 – 692 m for adult male white-tailed deer, while Williams et al. (2012*a*, 2012*b*), used first-passage time analysis to identify a similar scale of perception in adult white-tailed deer of both sexes. Additionally, female mule deer appeared to perceive the habitat at a scale of 284 – 413 m (Webb et al. 2013). Comparable, though slightly larger, landscape scales have been reported for elk as well (Frair et al. 2005, Dzialak et al. 2011*b*). Spatial scale of habitat perception may be slightly reduced in white-tailed deer in southern Delaware due to the high degree of fragmentation from agriculture, although the patch size used to calculate landscape covariates for SSF models appeared to be reasonable and representative of how cervids generally respond to and perceive the landscape.

Among males, I observed relatively consistent variability in individual selection coefficients across all habitat covariates, although directionality of selection was highly variable in all covariates. Eight of 12 individual males did not avoid roads, which is surprising considering the increased risk of mortality associated with roads. Mortality due to vehicle collision is a function of both road density and traffic patterns (Ng et al. 2008, Gulsby et al. 2011). Previous research has found vehicle collisions accounted for a consistent percentage of all mortalities (14 – 15%) despite substantial variability in overall survival rates in populations open to hunting (Ebersole et al. 2007, Storm et al. 2007, Grovenburg et al. 2011). Kilgo et al. (2016) found a negative relationship between risk of mortality from vehicle collision and distance to road, however the effect was small and not a strong predictor of overall survival. While roadways pose a direct but moderate risk to males through vehicle collision, an avoidance of roads may also be a function of predator avoidance, as concentration of deer hunters is negatively correlated with distance to road (Diefenbach et al. 2005) and adult males are typically under greater harvest pressure than females (Webb et al. 2014). Under landscapes with limited hunting pressure, shifts in habitat use among adult males are primarily driven by breeding behavior (Karns et al. 2012), although predator avoidance behavior has a greater influence on movement and habitat selection than does behavior related to breeding (Little et al. 2016). I did not observe an avoidance of developed areas and roads at the population level or among all males. Habitat selection in response to human activity is complex (Harju et al. 2011), and results of previous research are mixed. Deer exposed to human activity have shown immediate and prolonged avoidance of developed areas (Sawyer et al. 2006), and Webb et al. (2011*b*) found a negative correlation between human activity and survival rates in elk. In contrast, selection for parks and residential areas has also been reported (Kilpatrick and Spohr 2000, Grund et al. 2002). Developed areas in Delaware often includes regulations for mandatory safety zone buffers, and some individuals may be utilizing exurban and suburban habitats as refuges from hunting pressure (Bowman 2012). Furthermore, high levels of individual heterogeneity in male selection coefficients in less risk prone habitats may support the concept of a variation in movement behavior resulting from the presence of multiple breeding strategies (DeYoung et al. 2006, Foley et al. 2015).

Among females, I observed similar variability in individual selection coefficients among covariates, but variability was lower relative to males. The population level selection of open habitat by females is likely a function of selection for open agricultural areas for foraging. Nocturnal selection for agriculture fields by adult females during the hunting season is a common behavior in southern Delaware (Miller 2012); however, I observed no selection for open habitat in males. Sexual segregation in selection for forest habitat among deer is a well-documented behavior (Lesage et al. 2002, DePerno et al. 2003, Stewart et al. 2003), with females typically selecting for more open habitats relative to males.

The population level avoidance of elevation roughness in females relative to males is difficult to explain in a region dominated by coastal plains habitat such as southern Delaware. While I did not observe any correlation in covariates for open habitat and low elevation roughness, use of row crop fields may also be driving selection for reduced elevation roughness. Row crop is typically associated with uniform elevation, but not all open habitats are row crop, which may explain the lack of correlation between covariates. Additionally, topographical variation in southern Delaware is typically associated with patches of forested wetlands and drainages. An examination of the raw location fixes revealed that, while males did not select for or against topographical depressions associated with wetlands, females tended to remain in the uplands forests and agriculture.

Function responses in habitat selection are typically calculated using the individual selection coefficients for a habitat as a response variable, and the availability of that same habitat within an individual's home range as the explanatory variable. A response in selection for any given habitat could theoretically be a function of the availability of any number of different habitats, however. The only response in selection for habitat as a function of that same habitat's availability in the home range was for open habitat. Deer of both sexes selected for open habitat when open habitat was rare in the home range and when the home range consisted primarily of open habitat, but showed no selection or avoidance when proportion of open habitat was moderate. Because open habitat is southern Delaware is typically associated with deer food resources, such as row crop, increased selection for open areas when such habitat is rare is intuitive. Selection for open areas when such habitat is common is a function of the scale used to define selection, both the moving window for defining landscape perception and the choice of home range within the landscape by the animal (first order selection; Mysterud and Ims 1998). Selection for distance to road was also a function of proportion of open habitat in the home range, with the strongest avoidance of roads occurring in deer with relatively low and high proportions of open habitat within their range, and moderate proportions of open habitat resulting in neither selection nor avoidance of roads. Wagner et al. (2011) found that in Pennsylvania, avoidance of roads was greatest among deer with lower road densities within their range, and avoidance decreased as road density increased. While I did not observe a direct response in selection for distance to road as a function of road density, areas were open habitat is rare are likely areas of contiguous forest in which roads are not common. My results show a similar pattern in avoidance of roads until moderate proportions of open habitat within the range, but show an increase in avoidance at greater proportions of open habitat. Discrepancies in functional response to road density between regions may be attributable to differences in the extremes of road densities, with southern Delaware having a greater density of roads associated with open habitat than central Pennsylvania. Furthermore, deer may perceive roads associated with open habitat as riskier than roads in forested habitat due to the proximity of escape cover.

As deer aged, they selected for areas farther from edge habitat, likely a result of mature deer preferring interiors of more contiguous forest patches in response to hunting. While a paucity of information exists examining the effect of age on response to risk in white-tailed deer, roe deer are more likely to utilize refuges and avoid risky habitats in response to hunting pressure as they age (Padiè et al. 2015) and older boreal caribou (*R. tarandus caribou*) show an increased avoidance of roads and landscape features associated with potential wolf (*Canis lupus*) encounters (Mumma et al. 2017). Older deer may have learned how to minimize risk of mortality due of harvest as they aged.

Habitat selection analysis during the fall and winter is complicated by the simultaneous occurrence of both the hunting and breeding seasons, which can confound interpretation of results. Because such causal relationships are difficult to infer, analyses assigning specific behavioral causation to individual heterogeneity and functional responses in habitat selection should be interpreted with caution. Additionally, marginal population inference can be difficult when variability among individuals or groups is high (Sheppard et al. 2006, Gillingham and Parker 2008). Heterogeneity in habitat use and response to the landscape has direct implications for susceptibility to harvest, offspring survival, and fitness (Hamel et al. 2008, Dassault et al. 2012, Decesare et al. 2014, Lone et al. 2015, Mumma et al. 2017). While most models of habitat selection are developed to make marginal population level inference, variation in individual selection is an important and poorly understood complication to management. Even when implemented properly, the magnitude and direction of selection can be influenced by a small number of individuals (Gillies et al. 2006). Additionally, when individual variation is high and not accounted for, incorporating more individuals into a population level model will not provide additional value to managers as models will be unable to represent multiple different habitat selection strategies within the population (Gillingham and Parker 2008). Individual conditional logistic regression models provide a valuable understanding of how individual variation in white-tailed deer may affect habitat or harvest management.

Management Implications

Knowledge of individual heterogeneity and functional responses in habitat use during fall and winter will be informative to property managers attempting to influence harvest and demographics at a localized scale. Fall and winter habitat selection for adult white-tailed deer varies widely within the sexes. Property managers should understand that there is no panacea management strategy likely to be useful at a localized scale for all individual deer on a property or for either sex. Management actions targeting one sex may be generally beneficial at a large scale, but are not likely to benefit the other sex or even the majority of the target sex at a localized scale, and may even be detrimental.

Acknowledgements

I would like to acknowledge the Delaware Department of Natural Resources and Environmental Control and the Federal Aid in Wildlife Restoration Act for funding this project, grant number W-35-R. The U.S. Department of Agriculture National Institute of Food and Agriculture, Hatch project DEL00712 and McIntire Stennis DEL00672, also supported this work. I am grateful to J. Dion, A. Orlando, and numerous technicians for their support with data collection. I am thankful to the landowners and sportsman in Sussex County, Delaware for their cooperation.

TABLES

Table 2.1 Correlation matrix for landscape covariates used in step selection models for adult male white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA.

Coefficient	forest	open	developed	roughness	edge	road
forest	1.00					
open	-0.92	1.00				
developed	-0.30	-0.11	1.00			
roughness	-0.03	-0.15	0.28	1.00		
edge	0.09	-0.06	-0.10	-0.24	1.00	
road	0.28	-0.12	-0.42	-0.22	0.10	1.00

Table 2.2 Correlation matrix for landscape covariates used in step selection models for adult female white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA.

Coefficient	forest	open	developed	roughness	edge	road
forest	1.00					
open	-1.00	1.00				
developed	-0.06	0.02	1.00			
roughness	0.14	-0.14	0.08	1.00		
edge	0.41	-0.41	-0.05	0.04	1.00	
road	0.54	-0.54	-0.02	-0.18	0.40	1.00

Table 2.3 Selection coefficients from individual conditional logistic regression models of step selection for adult white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA. Models includes 12 adult males (1) and 14 adult females (2) identified by unique tag ID numbers.

Group	ID	developed	edge	roughness	open	road
(1) Males						
	636	0.80	-0.40	-0.19	-0.61	-0.56
	641	1.21	-0.24	0.14	0.02	0.49
	644	-0.21	-0.47	-0.33	-0.13	-0.18
	659	0.24	-0.67	-0.08	0.00	0.79
	668	0.24	0.36	0.31	0.54	0.56
	676	0.00	0.12	-0.47	0.21	-0.17
	680	0.06	0.04	0.11	-0.28	0.15
	688	-0.02	-0.37	0.33	0.27	-0.34
	697	-0.20	0.39	0.45	-0.38	0.04
	702	0.16	0.13	-0.52	-0.13	0.06
	705	0.81	-0.42	1.55	1.57	1.35
	717	1.61	0.03	-0.02	0.02	0.07
(2) Females						
	621	-0.48	0.06	0.86	0.16	-0.48
	711	0.02	-0.03	-0.44	0.11	0.30
	720	0.50	-0.23	-0.60	0.13	0.40
	725	0.27	0.51	-0.48	0.25	0.36
	751	-0.61	-0.18	-0.82	-1.00	-1.31
	753	-0.53	0.15	0.05	0.03	-0.54
	762	-0.03	0.11	-0.73	-0.13	-0.28
	770	-0.05	-0.05	0.78	0.14	0.40
	783	0.01	-0.24	0.06	-0.24	-0.42
	785	0.27	-1.00	-0.45	0.63	0.14
	786	0.28	-0.23	-0.06	0.18	0.45
	791	0.42	-0.04	-0.02	-0.02	-0.02
	800	-0.07	-0.09	0.53	0.26	-0.31
	814	0.36	0.21	0.11	-0.05	0.48

Table 2.4 Significant models of step selection function coefficients as functions of habitat characteristics within the home range for 26 adult white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA. Selection for open habitat (model 1) and distance to road (model 2) were a function of the availability of open habitat within the home range. Both models include 23 degrees of freedom.

Selection Coefficient	Home Range Coefficient	Estimate	Std. error	T score	P-value
(1) B_{open} ~	Intercept	0.86	0.54	1.59	0.12
	% open	-4.79	2.45	-1.96	0.06
	% open ^{2}	6.02	2.63	2.29	0.03*
(2) B_{road} ~	Intercept	1.39	0.65	2.13	0.04*
	% open	-6.46	2.94	-2.19	0.04*
	% open ^{2}	6.97	3.18	2.20	0.04*

* coefficient is significant at $\alpha = 0.05$

FIGURES

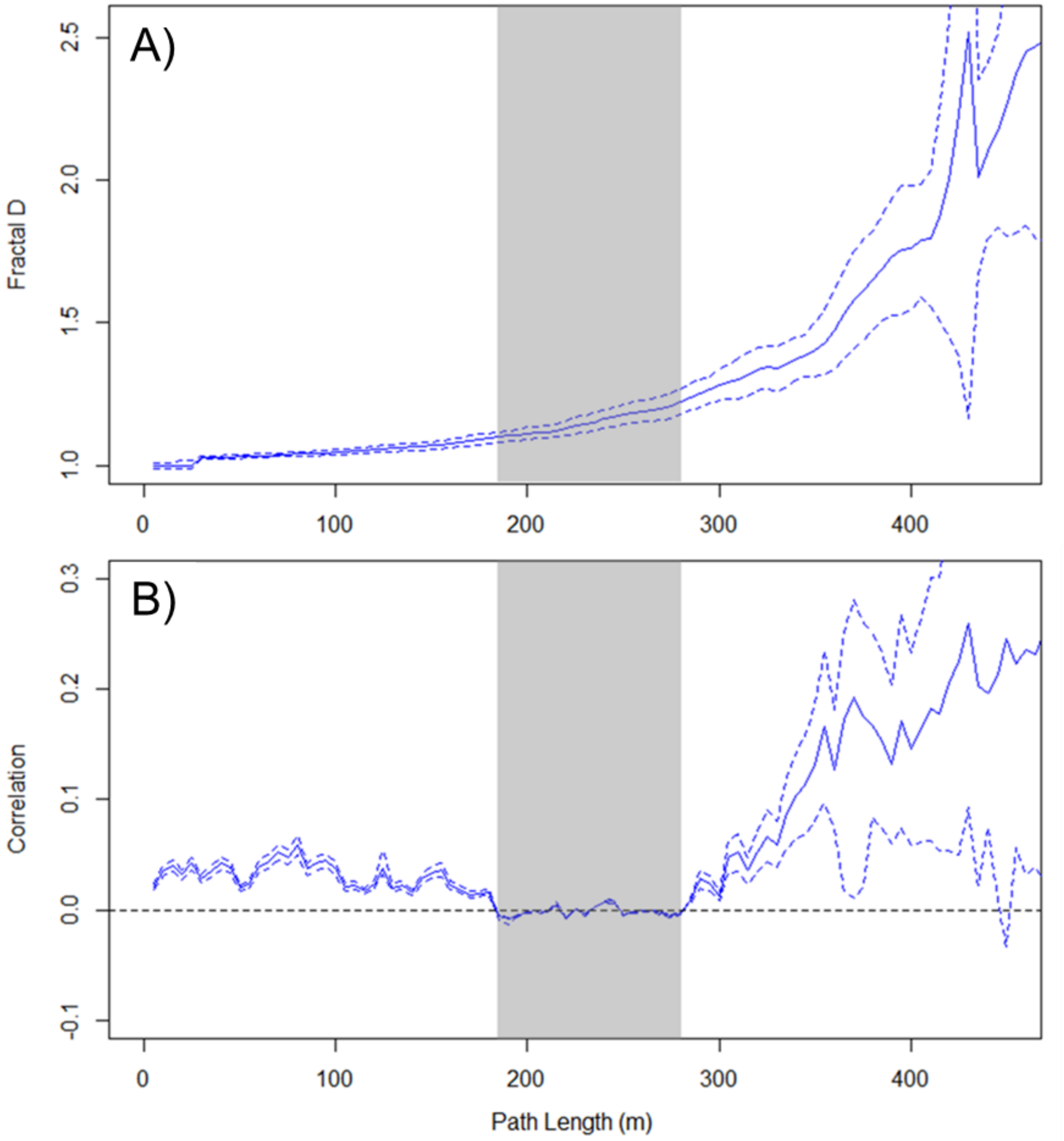


Figure 2.1 A) Mean fractal dimension and B) correlation of tortuosity for neighboring segments of the movement path at varying path lengths for adult male white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA. Vertical gray bars approximate a path length of 185 – 280 m within which correlation of tortuosity among adjacent path segments generally were negative, providing an estimate of patch size within which males were likely to perceive landscape features.

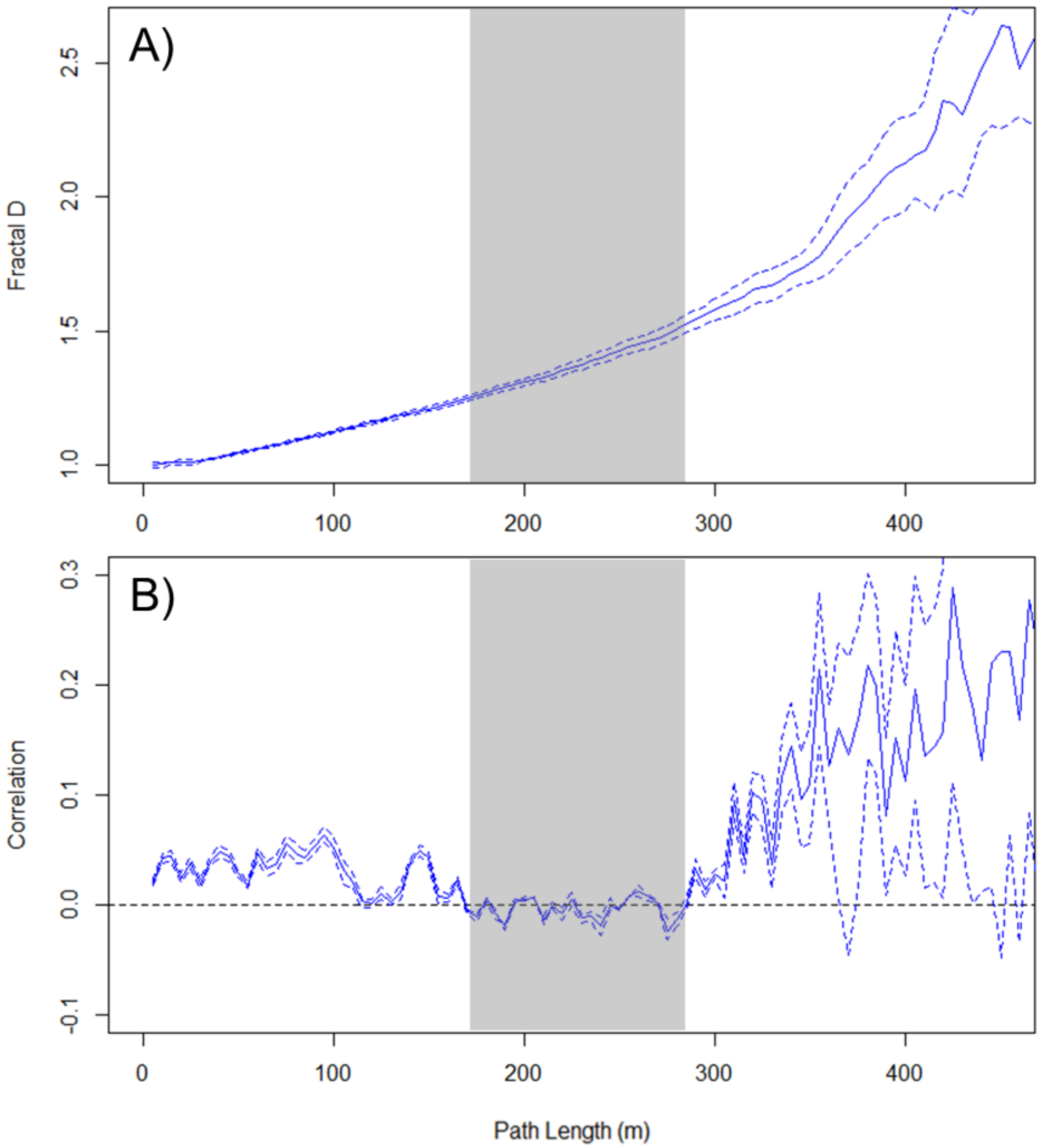


Figure 2.2 A) Mean fractal dimension and B) correlation of tortuosity for neighboring segments of the movement path at varying path lengths for adult female white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA. Vertical gray bars approximate a path length of 175 – 285 m within which correlation of tortuosity among adjacent path segments generally were negative, providing an estimate of patch size within which females were likely to perceive landscape features.

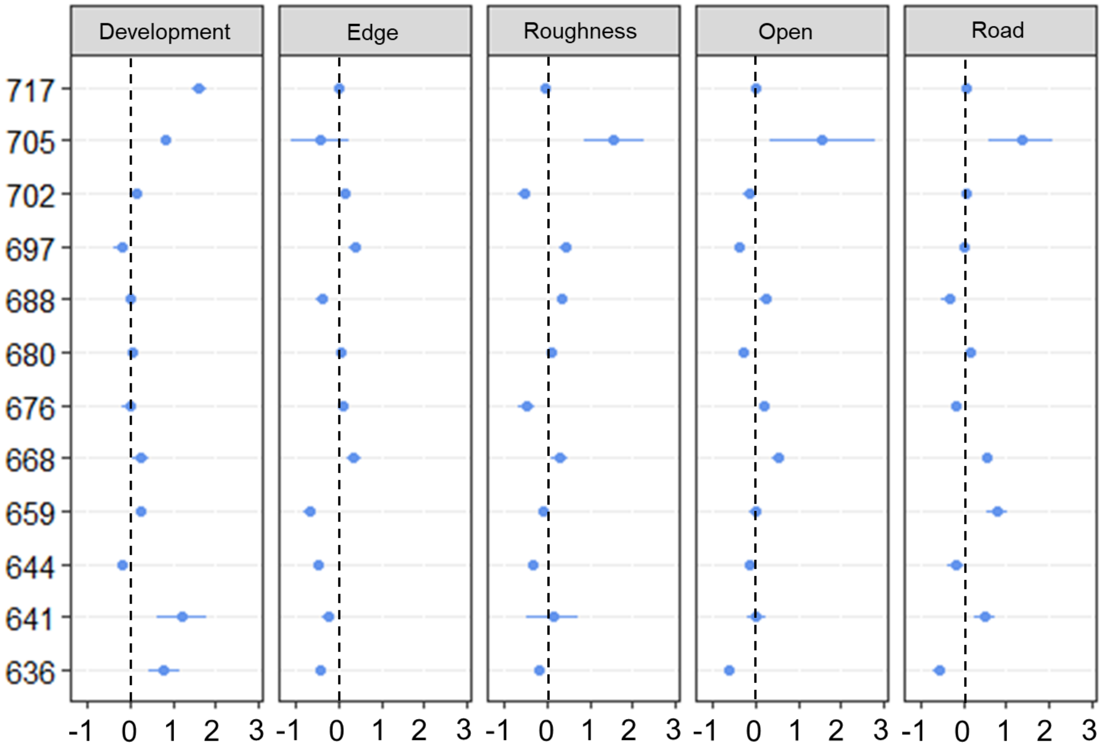


Figure 2.3 Selection coefficients (points) and 95% confidence intervals (lines) individual conditional regression step selection models for 12 adult male white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA. Values greater than 0 (dashed vertical line) represent selection of the landscape covariate, values less than 0 represent avoidance, and coefficients whose 95% confidence intervals overlap zero were interpreted as neither selection or avoidance.

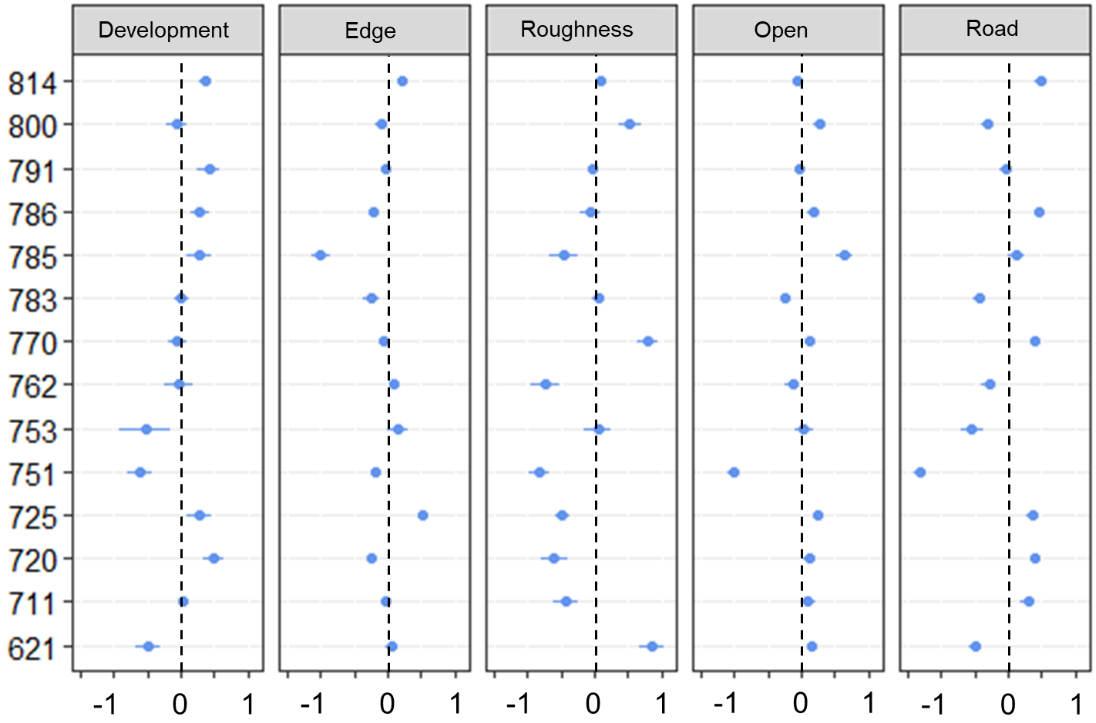


Figure 2.4 Selection coefficients (points) and 95% confidence intervals (lines) individual conditional regression step selection models for 14 adult female white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA. Values greater than 0 (dashed vertical line) represent selection of the landscape covariate, values less than 0 represent avoidance, and coefficients whose 95% confidence intervals overlap zero were interpreted as neither selection or avoidance.

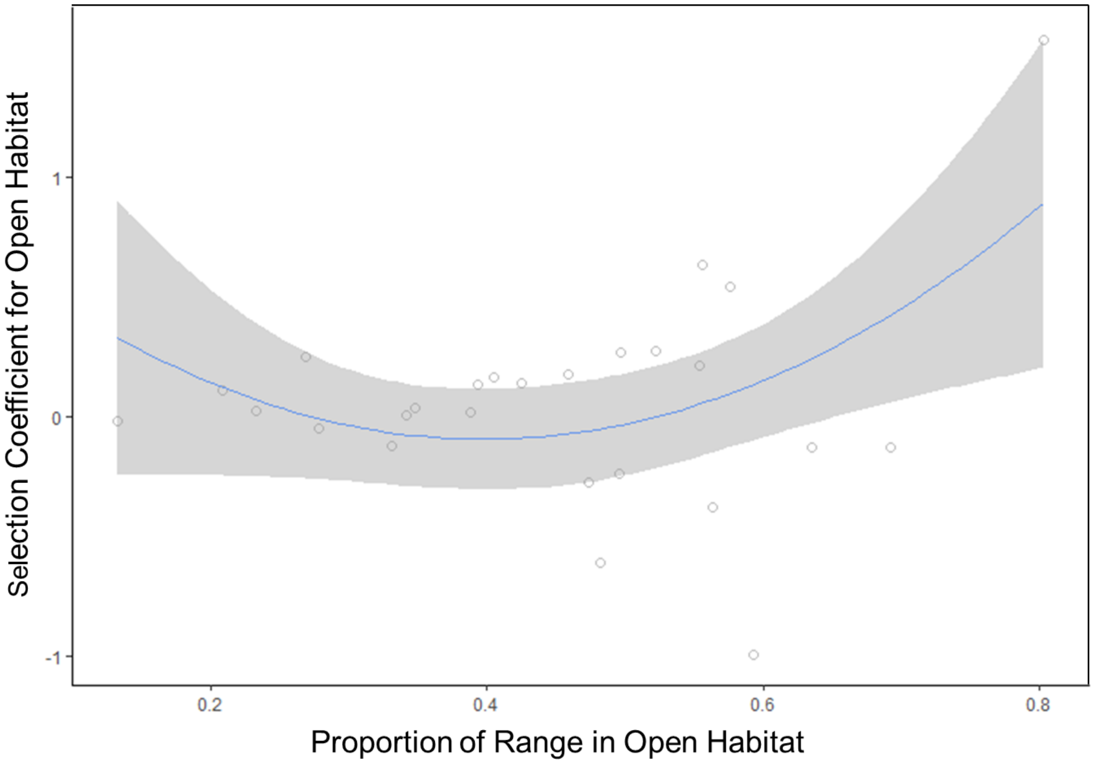


Figure 2.5 Functional response in selection for open habitat as a function of the availability of open habitat in the home range for 26 adult white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA.

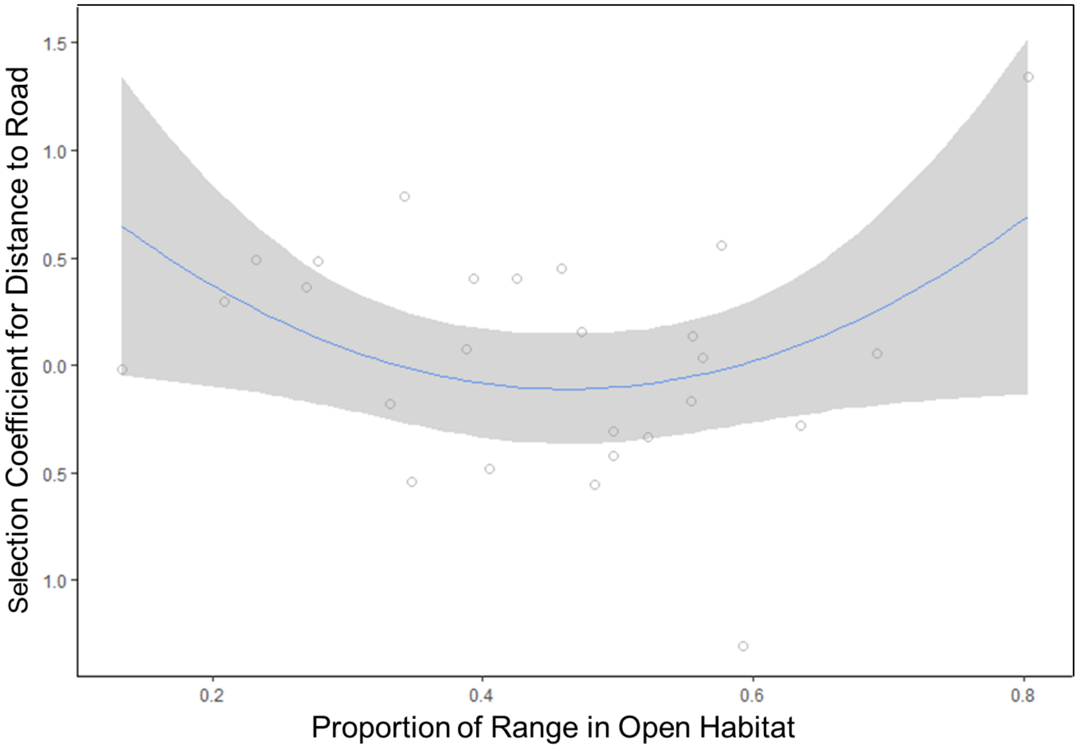


Figure 2.6 Functional response in selection for distance to road as a function of open habitat within the home range for 26 adult white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA.

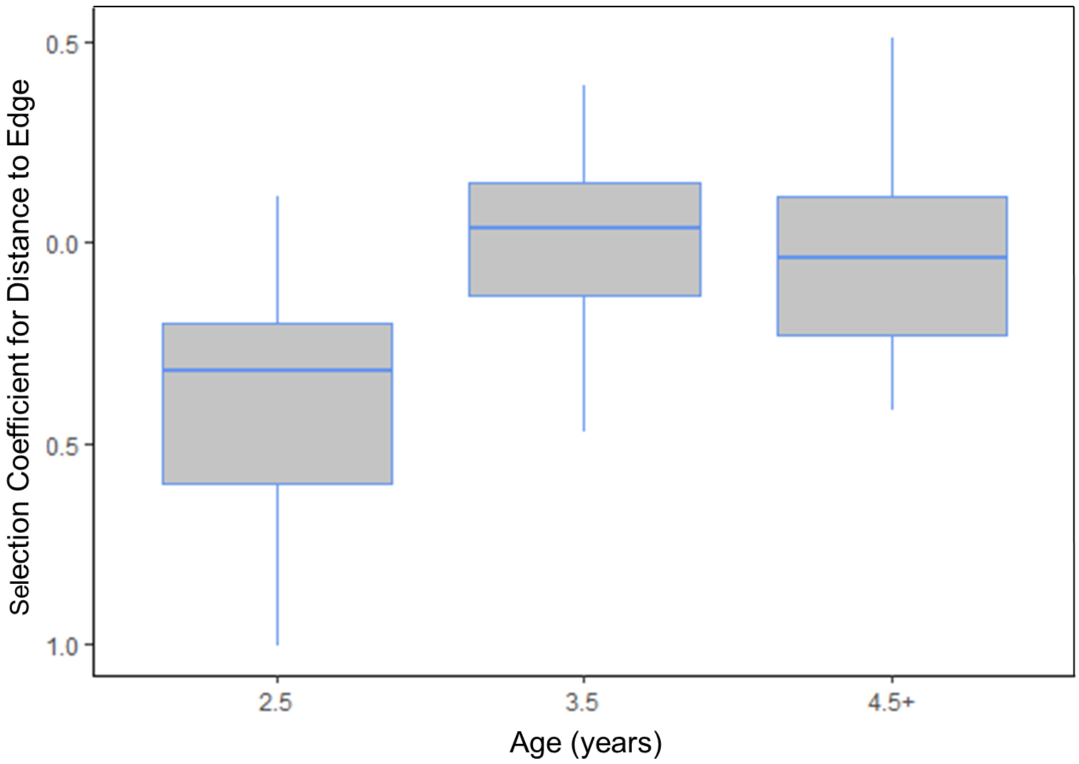


Figure 2.7 Individual step selection function coefficients for distance to habitat edge by age class (2.5, 3.5, and ≥ 4.5 years old) for 26 adult male and female white-tailed deer during the 2015 – 2016 and 2016 – 2017 hunting seasons in Sussex County, Delaware, USA.

REFERENCES

Anderson, E. D., R. A. Long, M. P. Atwood, J. G. Kie, T. R. Thomas, P. Zager, and R. T. Bowyer. 2012. Winter resource selection by female mule deer *Odocoileus hemionus*: functional response to spatio-temporal changes in habitat. Wildlife Biology 18:153–163.

Benson, J. F. 2013. Improving rigour and efficiency of use-availability habitat selection analyses with systematic estimation of availability. Methods in Ecology and Evolution 4:244–251.

Bowman, J. L. 2012. The role, size, and effectiveness of safety zones for creating refuges for white-tailed deer. Human-Wildlife Interactions 6:291–297.

Bowman, J. L., H. A. Jacobson, and B. D. Leopold. 1998. Fawn Survival on Davis Island, Mississippi after an early summer flood. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 52:397–402.

Bowman, J. L., C. O. Kochanny, S. Demarais, and B. D. Leopold. 2000. Evaluation of a new GPS collar for white-tailed deer. Wildlife Society Bulletin 28:141–145.

Bowman, J. L., H. A. Jacobson, D. S. Coggin, J. R. Heffelfinger, and B. D. Leopold. 2007. Survival and cause-specific mortality of adult male white-tailed deer managed under the Quality Deer Management Paradigm. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 61:76–61.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. M. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Écoscience 10:321–332.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer-Verlag, New York, New York, USA.

Cain, J. W., P. R. Krausman, B. D. Jansen, and J. R. Morgart. 2005. Influence of topography and GPS fix interval on GPS collar performance. Wildlife Society Bulletin 33:926–934.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behavior of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7:e50611.

Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.

Clover, M. R. 1956. Single-gate deer trap. California Fish and Game 42:199–201.

Conner, M.C., E.C. Soutiere, and R.A. Lancia. 1987. Drop-netting deer: costs and incidence of capture myopathy. Wildlife Society Bulletin 15:434–438.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

DeCesare, N. L., M. Hebbelwhite, M. Bradley, D. Hervieux. L. Neufeld, and M. Musiani. 2014. Linking habitat selection and predation risk to spatial variation in survival. Journal of Animal Ecology 83:343–352.

Delaware Division of Fish and Wildlife [DDFW]. 2009. Delaware Deer Density and Population Estimates.<http://www.dnrec.delaware.gov/fw/Hunting/Pages /DeerInfo.aspx> Accessed 6 May 2014.

Demarais, S., D. Stewart, and R. N. Griffin. 1999. A hunter’s guide to aging and judging live white-tailed deer in the Southeast. Mississippi State University Extension Service Report MSU-ES Publication 2206, Mississippi State, Mississippi, USA.

D’Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430–439.

D’Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383–388.

DePerno, C. S., J. A. Jenks, and S. L. Griffin. Multidimensional cover characteristics: is variation in habitat selection related to white-tailed deer sexual segregation? Journal of Mammalogy 84:1316–1329.

Diefenbach, D. R., J. C. Finley, A. E. Luloff, R. Stedman, C. B. Swope, H. C. Zinn, and G. J. San Julian. 2005. Bear and deer hunter density and distribution on public land in Pennsylvania. Human Dimensions of Wildlife 10:201–212.

Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. Journal of Animal Ecology 79:548–555.

Dussault, C., V. Pinard, J. Ouellet, R. Courtois, and D. Fortin. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? Proceedings from the Royal Society of Biological Sciences 279:4481–4488.

Dzialak, M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, J. P. Mudd, and L. D. Hayden-Wing, J. B. Winstead, S. L. Webb. 2011*a*. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. PLoS One 6:e14597. doi:10.1371/journal.pone.0014597

Dzialak, M. R., S. L. Webb, S. M. Harju, J. B. Winstead, J. J. Wondzell, J. P. Mudd, and L. D. Hayden-Wing. 2011*b*. The spatial pattern of demographic performance as a component of sustainable landscape management and planning. Landscape Ecology 26:775–790.

Ebersole, R., J. L. Bowman, and B. Eyler. Efficacy of a Controlled Hunt for Managing White-tailed Deer on Fair Hill Natural Resource Management Area, Cecil County, Maryland. 2007. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 61:68–75.

Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96:1182–1188.

Fleming, C. H., and J. M. Calabrese. 2017. A new kernel density estimator for accurate home-range and species-range area estimation. Methods in Ecology and Evolution 8:571–579.

Foley, A. M., R. W. DeYoung, D. G. Hewitt, M. W. Hellickson, K. L. Gee, D. B. Wester, M. A. Lockwood, and K. V. Miller. 2015. Purposeful wanderings: mate search strategies of male white-tailed deer. Journal of Mammalogy 96:279–286.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Foster, J. R., J. L. Roseberry, and A. Woolf. 1997. Factors influencing efficiency of white-tailed deer harvest in Illinois. Journal of Wildlife Management 61:1091–1097.

Franklin, S. E., G. B. Stenhouse, M. J. Hansen, C. C. Popplewell, J. A. Dechka, and D. R. Peddle. 2001. An integrated decision tree approach (IDTA) to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. Canadian Journal of Remote Sensing 27:579–592.

Friar, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41:201–212.

Frair, J. L., E. H. Merrill, D. R. Visscher. D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (Cervus elaphus) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20:273–287.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:1–16.

Gagnon, J. W., T. C. Theimer, N. L. Dodd, A. L. Manzo, and R. E. Schweinsburg. 2007. Effects of traffic on elk use of wildlife underpasses in Arizona. Journal of Wildlife Management 71: 2324–2328.

Gautestad, A. O., and I. Mysterud. 2005. Intrinsic scaling complexity in animal dispersion and abundance. American Naturalist 165:44–55.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. Joanne Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gillingham M. P., and K. L. Parker. 2008. The importance of individual variation in defining habitat selection by moose in northern British Columbia. Alces 44:7–20.

Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90:699–710.

Grovenburg, T. W., C. C. Swanson, C. N. Jacques, C. S. DePerno, R. W. Klaver, and J. A. Jenks. 2011. Female white-tailed deer survival across ecoregions in Minnesota and South Dakota. American Midland Naturalist 165:426–435.

Grund, M. D., J. B. McAninch, and E. P. Wiggers. 2002. Seasonal movements and habitat use of female white-tailed deer associated with an urban park. Journal of Wildlife Management 66: 123–130.

Gulsby, W. D., D. W. Stull, G. R. Gallagher, D. A. Osborn, R. J. Warren, K. V. Miller, and L. V. Tannenbaum. 2011. Movements and home ranges of white-tailed deer in response to roadside fences. Wildlife Society Bulletin 35:282–290.

Hamel, S., S. D Côté, J. Gaillard, and M. Festa-Bianchet. 2008. Individual variation in reproductive cost of reproduction: high-quality females always do better. Journal of Animal Ecology 78:143–151.

Hamilton, J., W. M. Knox, and D. C. Guynn. 1995. How quality deer management works. Pages 7–18 *in* K. Miller and L. Marchinton, editors. Quality Whitetails. Stackpole books, Harrisburg, Pennsylvania, USA.

Harju, S. M., M. R. Dzialak, R. G. Osborn, L. D. Hayden-Wing, and J. B. Winstead. 2011. Conservation planning using resource selection models: altered selection in the presence of human activity changes spatial prediction of resource use. Animal Conservation 14:502–511.

Hellickson, M. W., T. A. Campbell, K. V. Miller, R. L. Marchinton, and C. A. DeYoung. 2008. Seasonal ranges and site fidelity of adult male white-tailed deer (*Odocoileus virginianus*) in southern Texas. The Southwestern Naturalist 53:1–8.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Jacobson, H. A., C. A. DeYoung, R. W. DeYoung, T. E. Fulbright, and D. G. Hewitt. 2011. Management on private property. Pages 453–479 *in* D. G. Hewitt, editor, Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Karns, G. R., R. A. Lancia, C. S. DePerno, and M. C. Conner. 2012. Impact of hunting pressure on adult male white-tailed deer behavior. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 66:120–125.

Karns, G. R., R. J. Gates, S. N. Matthews, J. T. Bruskotter, J. C. McCoy, and M. J. Tonkovich. 2016. Factors influencing spatial heterogeneity of female white-tailed deer harvest dynamics. Wildlife Society Bulletin 40:758–763.

Kilgo, J. C., M. Vukovich, M. J. Conroy, H. S. Ray, and C. Ruth. 2016. Factors affecting survival of adult female white-tailed deer after coyote establishment in South Carolina. Wildlife Society Bulletin 40:747–753.

Kilpatrick, H. J., and S. M. Spohr. 2000. Spatial and temporal use of a suburban landscape by female white-tailed deer. Wildlife Society Bulletin 28:1023–1029.

Kilpatrick, H. J., A. M. LaBonte, and J. T. Seymour. 2002. A shotgun-archery deer hunt in a residential community: evaluation of hunt strategies and effectiveness. Wildlife Society Bulletin 30:478–486.

Kreeger, T. J., G. D. DelGiudice, U. S. Seal, and P. D. Karns. 1986. Immobilization of white-tailed deer with xylazine hydrochloride and ketamine hydrochloride and antagonism by tolazoline hydrochloride. Journal of Wildlife Diseases 22:407–412.

Lesage, L., M .C. Crête, J. Huot, and J. Ouellet. 2002. Use of forest maps versus field surveys to measure summer habitat selection and sexual segregation in northern white-tailed deer. Journal of Canadian Zoology 80:717–726.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effect of habitat on GPS collar performance; using data screening to reduce location error. Journal of Applied Ecology 44:663–671.

Little, A. R., S. Demarais, K. L. Gee, S. L. Webb, S. K. Riffell, J. A. Gaskamp, and J. L. Belant. 2014. Does human predation risk affect harvest susceptibility of white-tailed deer during hunting season? Wildlife Society Bulletin 38:797–805.

Little, A. R., S. L. Webb, S. Demarais, K. L. Gee, S. K. Riffell, and J. A. Gaskamp. 2016. Hunting intensity alters movement behavior of white-tailed deer. Basic and Applied Ecology 17:360–369.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stammes, and A. Mysterud. 2015. An adaptive behavioral response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour 102:127–138.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition, Kulwer Academic Publishers, Dordrecht, Netherlands.

Mason, T. H. E., and D. Fortin. 2017. Functional responses in animal movement explain spatial heterogeneity in animal-habitat relationships. Journal of Animal Ecology 86:960–971.

Miller, M. M. 2012. Resource selection and survival of female white-tailed deer in an agricultural landscape. Master's Thesis, University of Delaware, Newark, Delaware, USA.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445.

Moreau, G., D. Fortin, S. Couturier, and T. Duchesne. 2012. Multi-level functional response for wildlife conservation: the case of threatened caribou in managed boreal forests. Journal of Applied Ecology 49:611–620.

Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 6:613–623.

Mumma, M. A., M. P. Gillingham, C. J. Johnson, and K. L. Parker. 2017. Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. Ecology and Evolution. In press. doi: 10.1002/ece3.3563.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435–1441.

Nams, V. O. 1996. The VFractal: a new estimator for fractal dimension of animal movement paths. Landscape Ecology 11:289–297.

Nams, V. O. 2005. Using animal movement paths to measure response to spatial scale. Oecologia 143:179–188.

National Oceanic and Atmospheric Administration [NOAA]. 2017. National Environmental Satellite, Data, and Information Service. NOWData. <http://mi.nws.noaa.gov/climate/xmacis.php?wfo=phi> Accessed 5 May 2017.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs 11:1–53.

Nelson, M. E., and L. D. Mech. 1984. Home-range formation and dispersal of deer in northeastern Minnesota. Journal of Mammalogy 65:567–575.

Ng, J. W., C. Nielsen, and C. C. St. Clair. 2008. Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. Human-Wildlife Conflicts 2:34–47.

Padiè, S., N. Morellet, A. J. Mark Hewison, J. Martin, N. Bonnot, B. Cargnelutti, and S. Chamaillè-Jammes. 2015. Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos doi: 10.1111/oik.02115.

Pinaud, D. 2008. Quantifying search effort of moving animals at several spatial scales using first passage time analysis: effect of the structure of environment and tracking systems. Journal of Applied Ecology 45:91–99.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73:345–356.

R Development Core Team. 2017. R: A language and environment for statistical computing. Vienna, Austria.

Rhoads, C. L., J. L. Bowman, and B. Eyler. 2013. Movements of female exurban white-tailed deer in response to controlled hunts. Wildlife Society Bulletin 37:631–638

Rosenberry, C. S., R. A. Lancia, and M. C. Conner. 1999. Population effects of white-tailed deer dispersal. Wildlife Society Bulletin 27:858–864.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672–684.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 20:396–403.

Schemnitz, S. D., G. R. Batcheller, M. J. Lovallo, H. B. White, and M. W. Fall, 2012. Capturing and handling wild animals. Pages 64–117 *in* N. J. Silvy, editor, The Wildlife Techniques Manual; 7th edition. Volume 1. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Sheppard, J. K., A. R. Preen, H. Marsh, I. R. Lawler, S. D. Whiting, and R. E. Jones. 2006. Movement heterogeneity of dugongs, *Dugong dugon* (Müeller), over large spatial scales. Journal of Experimental Marine Biology and Ecology 334:64–83.

Stewart, K. M., T. E. Fulbright, D. L. Drawe, and R. T. Bowyer. 2003. Sexual segregation in white-tailed deer: responses to habitat manipulations. Wildlife Society Bulletin 31:1210–1217.

Storm, D. J., C. K. Nielsen, E. M. Schauber, and A. Woolf. 2007. Space use and survival of white-tailed deer in an exurban landscape. Journal of Wildlife Management 71:1170–1176.

Therneau, T. M. 2015. A package for survival analysis in S. Version 2.38.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2:4. doi:10.1186/2051-3933-24.

Tufto, J., R. Andersen, and J. Linnell. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65:715–724.

United States Department of Agriculture [USDA]. 2012. National Agriculture Statistics Service. Census of Agriculture-County Profile. <http://www. agcensus.usda.gov/Publications/2012/Full_Report/Volume_1,_Chapter_2_ County_Level/Delaware >. Accessed 6 May 2014.

Van Etten, R. C., D. Switzenberg, and L. Eberhardt. 1965. Controlled deer hunting in a square-mile enclosure. Journal of Wildlife Management 29:59–73.

Vance, J. A., D. S. Jachowski, A. C. Boynton, and M. J. Kelly. 2017. Importance of evaluating GPS telemetry collar performance in monitoring reintroduced population. Wildlife Society Bulletin. In print. doi:10.1002/wsb.806

Wagner, T., D. R. Diefenbach, S. A. Christensen, and A. S. Norton. 2011. Using multilevel models to quantify heterogeneity in resource selection. Journal of Wildlife Management 75:1788–1796.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007. Scale of management for mature male white-tailed deer as influenced by home range and movements. Journal of Wildlife Management 71:1507–1512.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demarais. 2009. Using fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210–1217.

Webb, S. L., M. R. Dzialak, R. G. Osborn, S. M. Harju, J. J. Wondzell, L. D. Hayden-Wing, and J. B. Winstead. 2011*a*. Using pellet groups to assess response of elk and deer to roads and energy development. Wildlife Biology in Practice 7:32–40.

Webb, S. L., M. R. Dzialak, J. J. Wondzell, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011*b*. Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. Population Ecology 53:483–493.

Webb, S. L., M. R. Dzialak, K. L. Kosciuch, and J. B. Winstead. 2013. Winter resource selection by mule deer on the Wyoming-Colorado border prior to wind and energy development. Rangeland Ecology and Management 66:419–427.

Webb, S. L., and K. L. Gee. 2014. Annual survival and site fidelity of free-ranging white-tailed deer (Odocoileus virginianus); comparative demography before (1983–1992) and after (1993–2005) spatial confinement. Integrative Zoology 9:24–33.

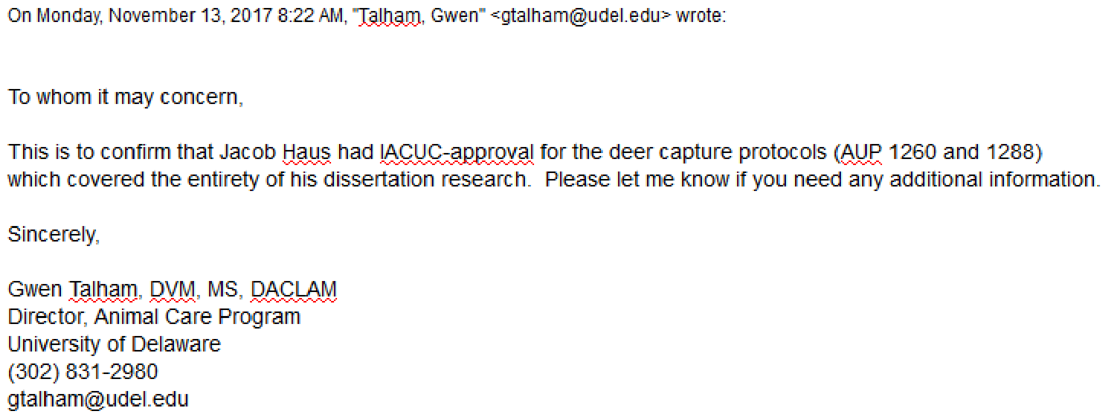
Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Williams, D. M., A. Dechen Quinn, and Porter W. F. 2012*a*. Impact of habitat-specific GPS positional error on detection of movement scales by first-passage time analysis. PLoS ONE 7:11. doi:10.1371/journal.pone.0048439

Williams, D., A. Dechen Quinn, and W. Porter. 2012*b*. Landscape effects on scales of movement by white-tailed deer in an agricultural-forest matrix. Landscape Ecology 27:45–57.

Appendix

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL OF WILDLIFE CAPTURE AND HANDLING PROTOCOLS



On Monday, November 13, 2017 8:22 AM, "Talham, Gwen" <gtalham@udel.edu> wrote:

To whom it may concern,

This is to confirm that Jacob Haus had IACUC-approval for the deer capture protocols (AUP 1260 and 1288) which covered the entirety of his dissertation research. Please let me know if you need any additional information.

Sincerely,

Gwen Talham, DVM, MS, DACLAM
Director, Animal Care Program
University of Delaware
(302) 831-2980
gtalham@udel.edu