

ABSTRACT

CARVER, MIKIAH RAYNE. Connecting Urbanization to Deer Ecology: Movement, Resource Selection, and Mortality Risk of White-tailed Deer Across an Urbanization Gradient (Under the direction of Dr. Nathan J. Hostetter and Dr. Christopher E. Moorman).

Cities are rapidly expanding, transforming landscapes through increased impervious surfaces, habitat fragmentation, and novel resource availability, thereby presenting both challenges and opportunities for wildlife. Given these rapid changes, understanding how wildlife movement, resource selection, and mortality risks vary across a continuum of highly urbanized to suburban, exurban, and rural areas (hereafter “urbanization gradient”) is essential for predicting responses to urbanization and developing effective wildlife conservation actions. White-tailed deer (*Odocoileus virginianus*; hereafter “deer”) are tolerant of a range of environmental conditions, including many of the landscape changes associated with urbanization, making the species an ideal model for assessing changes in behaviors and population vital rates across an urbanization gradient. Over a four-year period (January 2022 - May 2025), I monitored 202 deer (111 females; 91 males) across an urbanization gradient in Durham and Orange counties, North Carolina, to investigate how urbanization influenced deer movement, resource selection, survival, and cause-specific mortality. My study provides a foundation to inform deer management strategies as North Carolina and other regions in the eastern U.S. continue to urbanize. In Chapter 1, I used hidden Markov models and integrated step selection functions to assess the effects of impervious surface cover, forest canopy cover, proximity to roads, and time of day on various aspects of deer movement (e.g., diel activity budgets, resource selection, and step lengths). Deer adjusted their activity and movement in a manner that reduced their exposure to human disturbances. Specifically, deer avoided impervious surfaces, and the strength of selection for greater canopy cover and avoidance of roads increased with urbanization, though

these relationships varied slightly between encamped and exploratory behavioral states. In Chapter 2, I examined deer space use by analyzing how seasonal resource selection for impervious surfaces, canopy cover, and distance to roads varied across an urbanization gradient. Deer altered their selection in response to intensifying urbanization, showing stronger and more consistent selection for less developed areas with greater canopy cover as urbanization increased, whereas deer on the rural end of the gradient showed large amounts of individual heterogeneity in selection. In Chapter 3, I evaluated the effects of urbanization, sex, age, weekly movement, dispersal events, and season (harvest versus non-harvest) on weekly and annual survival and cause-specific mortality of deer using a Bayesian known-fate survival model. Causes of mortality shifted across the urbanization gradient, but annual survival was relatively stable as declines in one mortality source were offset by increases in another. In summary, deer modified their movement and resource selection in response to urbanization, reflecting behavioral plasticity that facilitates persistence across the gradient. Although annual survival remained relatively stable due to offsetting mortality causes, increasing urbanization will pose challenges for white-tailed deer population management due to public safety concerns associated with deer-vehicle collisions and restrictions on hunting in urban areas. Collectively, my research demonstrates how wildlife may respond to expanding urban development and can guide conservation strategies while mitigating negative human-wildlife interactions.

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Connecting Urbanization to Deer Ecology: Movement, Resource Selection, and Mortality Risk
of White-tailed Deer Across an Urbanization Gradient

by
Mikiah Rayne Carver

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Fisheries, Wildlife, and Conservation Biology

Raleigh, North Carolina
2025

APPROVED BY:

Dr. Nathan J. Hostetter
Committee Co-Chair

Dr. Christopher E. Moorman
Committee Co-Chair

Dr. John C. Kilgo

Dr. M. Nils Peterson

Dr. Jonathan C. Shaw

Dr. Adam J. Terando

DEDICATION

To Seth. Your endless support and quiet sacrifices have meant everything to me. I never imagined I'd convince a desert boy to trade dry heat for humidity, but you did it for me, and I'll always love you for that.

BIOGRAPHY

Growing up in a military family, I lived in many diverse areas from arid deserts to lush rainforests. My exploration as a child and young adult fostered an unquestionable appreciation for natural areas and the species that inhabit them. This affinity for the outdoors and wildlife led to my decision to pursue a B.S. in Geography and a M.S. in Wildlife and Wildlands Conservation from Brigham Young University. Combining my backgrounds in geography and wildlife conservation, I developed a strong interest in big game research, particularly in the use of tagged individuals to examine movement dynamics and habitat use across heterogeneous landscapes. This interest ultimately led me to pursue a Ph.D. at North Carolina State University.

ACKNOWLEDGMENTS

I am particularly grateful for my advisors, Nathan Hostetter and Chris Moorman, for their unmatched support, patience, and guidance. Nathan and Chris both pushed me to think critically and rigorously while offering steady support. Their combined mentorship has shaped not only my skills but also my confidence, making my graduate experience both rewarding and transformative. I am also deeply appreciative of my committee members, whose unique support and refreshing perspectives were instrumental in my development as a researcher. Special thanks to John Kilgo for his willingness to dart a few deer before the start of our first field season, a humbling experience I will not soon forget. I am equally grateful to Nils Peterson, Jon Shaw, and Adam Terando for their thoughtful challenges, and insightful questions that pushed me to think more critically and approach my research in new ways throughout my studies.

I would also like to thank my fellow colleagues for their friendships, encouragement, and support over the years. Special thanks to Jared Lamb for being an outstanding lead technician and colleague. I am grateful for your friendship, dedication, and assistance over the years. I am deeply grateful for the hard work, long hours, and dedication of the technicians and volunteers who contributed to this project. I would like to specifically thank Griffin Archambault, Anton Burt, Chase Carey, Caitlyn Connell, Emma Hense, George Goto, Elizabeth Nowlin, Evan Papst, Frederick Russell, Emma Young, Erich Wilmot, and Kyle Zampoogna for their invaluable assistance in the field. I will always cherish the experiences we shared and the lessons I learned from all of you.

I'd also like to extend my sincere thanks to everyone at the North Carolina Wildlife Resources Commission who contributed to this project in one way or another. I am especially grateful to Commissioner John Coley, Brad Howard, Chris Kreh, Heather Evans, Moriah

Bogges, April Boggs Pope, and Colleen Olfenbuttel for their support, guidance, and collaboration throughout this work. I also want to acknowledge the many staff members, biologists, and field personnel whose efforts, both in the field and behind the scenes helped make this project possible.

Lastly, I'd like to thank all my family and friends for their encouragement and support over the years. Seth, I could not have done this without you. You have been a sure foundation for me during this time of refinement and growth and I am so blessed to have you by my side. I'd also like to thank my parents. Their love, patience, and the many ways they've supported me along the way have never gone unnoticed. Last but certainly not least, A & C— the best furry office mates I could ask for. Thank you for the constant company, for reminding me to take walk breaks, and for the perfectly timed commentary during Zoom meetings.

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	ix
Chapter 1: White-Tailed Deer Adjust Movement in Response to Urbanization	1
Abstract	1
Introduction	2
Methods	5
Results	11
Discussion	13
References	18
Chapter 2: Seasonal Resource Selection by White-tailed Deer Along an Urban-Rural Gradient	37
Abstract	37
Introduction	38
Methods	41
Results	45
Discussion	47
References	51
Chapter 3: Influences of Urbanization on Survival and Cause-Specific Mortality of White-tailed Deer	64
Abstract	64
Introduction	65
Methods	66
Results	74
Discussion	78
References	84
APPENDICES	99
Appendix A: Chapter 1 Supplemental Tables and Figures	100
Appendix B: Chapter 2 Supplemental Tables and Figures	115
Appendix C: Chapter 3 Supplemental Tables and Figures	120

LIST OF TABLES

Table 1.1	Hidden Markov model comparisons for different seasonal and sex-specific groups. AIC values were calculated for five models (Null, 1, 2, 3, and 4) for each group (Female Dormant, Female Growing, Male Dormant, and Male Growing). Estimated parameter count is listed for each model under “nPars”. Delta AIC values represent the difference between each model's AIC and that of the best-fitting model (lowest AIC value) within each group. Model weights indicate the relative likelihood of each model given the data. Model 4 was the top-ranked model in all groups. Model 4 suggests variation in both time and amount of activity depending on where a deer is located along the urbanization gradient.....	28
Table 1.2	Summary of integrated step selection models used to explore the effects of behavior, landscape features, and urbanization on deer movement (step lengths and turning angles) and selection. Behavior state distinguishes between two behavior states (exploratory, encamped). Landscape features include impervious surface, canopy cover, and distance to road rasters. Urbanization is the urbanness value of an individual. Inclusion of covariates is denoted by X. See Table S4 for detailed equations.....	29
Table 1.3	Integrated step selection model comparisons for different seasonal and sex-specific groups. AIC values were calculated for five models (1-7) for each group (Female Dormant, Female Growing, Male Dormant, and Male Growing). Estimated parameter count is listed for each model under “nPars”. Delta AIC values represent the difference between each model's AIC and that of the best-fitting model (lowest AIC value) within each group. Model weights indicate the relative likelihood of each model given the data. Model 7 was the top-ranked model in all groups. Model 7 suggests deer movement and selection varies by state, landscape, and location on the urbanization gradient.....	30
Table 2.1	Numbers of white-tailed deer included in seasonal resource selection function analysis. Seasonal analyses used data collected during January 2022 to January 2025.....	60
Table 3.1	Summary of monitored individuals and fates during the study. Counts are separated by sex and age class at the time of fate. Primary causes of mortality include hunter harvest, vehicle collision, and other mortality. The other mortality category includes depredation, disease, malnutrition, poaching, predation, and unknown causes. Depredation represents an individual harvested outside of harvest season under a depredation permit. Disease and malnutrition designations were determined by the Southeastern Cooperative Wildlife Disease Study, who conducted detailed post-necropsy analyses in uncertain cases. Poaching refers to an adult male harvested illegally outside of the harvest season. Unknown cases represent collared individuals whose cause of death could not be determined. Right-censored individuals include those whose collars broke off as programmed (Breakoff), collars that failed prematurely (Collar Failure), and individuals still collared at the end of the study	

when monitoring ceased (End of Study). All right-censored individuals were alive at the time monitoring ended and thus had no confirmed mortality.....92

LIST OF FIGURES

- Figure 1.1 A) Capture locations (points) for female and male white-tailed deer overlaid on the percent impervious surface raster. The study area included Durham and Orange counties, North Carolina, USA. Urbanness values were calculated for each individual as the mean percent impervious surface in an individual's 99% autocorrelated kernel density estimated (AKDE) range distribution (purple polygon). Panels B and C show GPS locations and AKDE for B) an individual in a more urban area (urbanness value = 36.59) and (C) an individual in a more rural area (urbanness value = 0.75).....32
- Figure 1.2 Visual representation of 4 a priori hypotheses on how urbanization influences deer activity, measured as the probability of being in the exploratory state. Activity patterns are shown across a 24-hour day (x-axis) and vary with levels of urbanization (represented by different lines). Hypothesized urbanization effects include: (1) no effect, (2) a change in overall activity levels, (3) a shift in activity timing, and (4) a change in both activity levels and timing.....33
- Figure 1.3 Stable state probability plots for each seasonal and sex-specific groups based on top hidden Markov model (Model 4) parameter estimates. Colored curves depict the probability of being in the exploratory state at the end of each 2-hour fix interval over a 24-hour period for individuals representing rural (10th percentile), average (mean), and urban (90th percentile) urbanness values. Vertical dotted lines indicate the transformed sunrise and sunset times using the average double anchoring technique to account for seasonal variation in day length. Dormant season = 07:12 (sunrise) and 17:47 (sunset); Growing season = 06:35 (sunrise) and 19:51 (sunset). Gray shaded areas include ± 1 hour of the transformed sunrise and sunset times to indicate dawn and dusk, which are key times for crepuscular animals such as deer. Each prediction curve highlights when deer are likely to be in an exploratory state throughout a 24-hour period for individuals along an urbanization gradient (differing colored lines). See Table S1.5 for transition probability estimates.....34
- Figure 1.4 State based modeled selection coefficient plots for each covariate, season and sex based on the top integrated step selection function model (Model 7). The urbanization gradient (urbanness values) is plotted along the x-axis with increasing urbanization from left to right. Positive selection parameter values indicate selection for greater 1) canopy cover, 2) distance to roads, and 3) impervious surfaces (imperviousness) while negative values indicate the inverse. Dashed horizontal lines represent a neutral selection value ($\beta = 0$).....35
- Figure 1.5 Estimated step length distributions (Gamma) from the top integrated step selection function model (Model 7) for each dataset. Plots display probability density for step lengths in both the exploratory (top row) and encamped (bottom row) behavioral states. Each set of curves represent predictions for areas considered more rural (10th percentile), average (mean), or urban (90th percentile) based on urbanness values.

	For more information regarding step mean and standard deviations by state, see Table S1.7.....	36
Figure 2.1	A) Capture locations (points) for female and male white-tailed deer overlaid on the percent impervious surface raster. The study area included Durham and Orange counties, North Carolina, USA. Urbanness values were calculated for each individual as the mean percent impervious surface in an individual's 99% autocorrelated kernel density estimated (AKDE) range distribution (purple polygon). Panels B and C show GPS locations and AKDEs for B) an individual in a more urban area (urbanness value =36.59) and (C) an individual in a more rural area (urbanness value = 0.75).....	61
Figure 2.2	Urbanness values of male (left) and female (right) white-tailed deer in Durham and Orange counties, North Carolina, USA. Urbanness values were calculated as the mean impervious surface in an individual's 99% autocorrelated kernel density estimated (AKDE) range distribution for each season (See Fig. 2.1 and Methods). Higher urbanness values (urbanization gradient) correspond to more urbanized areas while lower values correspond to less urbanized areas. Box-and-whisker plots denote the median, quartiles, and 1.5 interquartile range. For additional information on AKDE size estimates by sex and season, see Fig. S2.1.....	62
Figure 2.3	Seasonal resource selection estimates for male (left) and female (right) white-tailed deer along an urban-rural gradient in Durham and Orange counties, North Carolina, USA. The x-axis represents increasing urbanization (i.e., urbanness values). Solid circles represent selection estimates (95% confidence interval), while squares indicate covariates not included in an individual's top model. Solid trend lines are fitted values as a function of the urbanization gradient (95% confidence interval). For impervious surfaces (imperviousness) and canopy cover, values >0 indicate selection, while values <0 indicate avoidance. For distance to roads, positive values indicate selection for areas farther from roads.....	63
Figure 3.1	Capture (top) and mortality (bottom) locations of male and female white-tailed deer overlaid on a percent impervious surface raster to illustrate the urbanization gradient. Mortality causes are color-coded as hunter harvest (HH, purple), vehicle collision (VC, blue), and other (green). The study area is Durham County, North Carolina, USA.....	93
Figure 3.2	Parameter estimates for (A) survival and (B) cause-specific mortality. The reference category for cause-specific mortality was set to "other" mortality, with estimates shown for hunter harvest (HH) and vehicle collision (VC).....	94
Figure 3.3	Weekly cause-specific mortality probabilities for adult and yearling male and female white-tailed deer during the harvest season. Different colors represent distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more	

	urban locations. Figures that include credible intervals are provided in Appendix C Figure S3.2.....	95
Figure 3.4	Weekly cause-specific mortality probabilities for adult and yearling male and female white-tailed deer during the non-harvest season. Different colors represent distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations. Figures that include credible intervals are provided in Appendix C Figure S3.3.....	96
Figure 3.5	Survival probability for yearling males that dispersed (purple) and did not disperse (blue) at 1-week, 2-week cumulative, and annual time intervals. Estimates represent individuals at the mean urbanization gradient value (~7.6% impervious surface within the home range). All dispersing individuals in this study were yearling males with most dispersing in the fall (n = 13) and a few dispersing in the spring (n = 3)..	97
Figure 3.6	Annual survival and cause-specific mortality probabilities for adult and yearling male and female white-tailed deer. Different colors represent survival and distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations. Figures that include credible intervals are provided in Appendix C Figure S3.5 and S3.6.....	98

CHAPTER 1: White-Tailed Deer Adjust Movement in Response to Urbanization

ABSTRACT

As urban land cover expands globally, movements of animals that persist in cities and the associated suburbs are likely to vary from those in rural environments. However, how individuals of the same species adjust their movement across an urbanization gradient remains poorly understood. We used white-tailed deer (*Odocoileus virginianus*) as a case study to investigate how individuals of an urban-tolerant species modify their movement to persist across varying levels of urbanization. From 2022-2024, we captured and collared 202 white-tailed deer (111 females; 91 males) across an urbanization gradient in Durham and Orange counties, North Carolina. We analyzed GPS collar data recorded at 2-hour intervals to assess the effects of land cover, proximity to roads, and time of day on various aspects of white-tailed deer movement (e.g., diel activity budgets, resource selection, and step lengths). Using hidden Markov models, we classified deer into two latent behavioral states (e.g., exploratory, encamped) and applied integrated step selection functions to evaluate how deer navigated the landscape. This approach enabled us to quantify the proportion of time that deer spent in each state across the urbanization gradient (i.e., diel activity budgets) and understand how anthropogenic features affected deer movement. White-tailed deer adjusted their activity and movement in a manner that likely reduced exposure to human disturbances. As urbanization increased, females exhibited increased nighttime activity and reduced daytime activity, whereas males exhibited reduced overall activity. Deer avoided impervious surfaces regardless of location on the gradient, though as urbanization increased, deer showed reduced avoidance. The magnitude of selection for greater canopy cover and avoidance of roads generally increased as urbanization increased. Resource selection differed by behavioral state, and deer in the encamped state had greater avoidance of

roads and less avoidance for impervious surfaces than deer in the exploratory state. Highlighting the behavioral flexibility of urban-tolerant species, white-tailed deer adjusted when, where, and how they moved as urbanization increased, likely to reduce exposure to human disturbance.

INTRODUCTION

Animal movements reflect trade-offs between risk and reward, and shape an individual's ability to navigate landscape changes driven by urbanization (Nathan et al., 2008; Knopff et al., 2014; Karelus et al., 2019). Urbanization can influence animal movement by introducing novel stressors such as physical barriers, changing resource availability, elevating perceived risk, and altering habitat configuration (Ditchkoff et al., 2006; Lowry et al., 2013; Knopff et al., 2014). How individual animals alter movements, if at all, in response to urbanization is key to predicting species-specific responses to landscape change (Ditchkoff et al., 2006; Doherty et al., 2021). Animal tracking studies (e.g., global positioning system [GPS] telemetry) offer powerful tools to evaluate individual movements across landscapes, enabling detailed insights into individual- and population-level responses to urbanization (Hooten et al., 2017). Studying movement of species that occur across the urbanization gradient provides opportunities to quantify the behavioral strategies some species may employ to foster persistence in urban areas (Doherty et al., 2021).

Understanding how animals adjust their activity in response to urbanization provides insight into behavioral strategies that facilitate persistence in human-dominated landscapes. Diel activity budgets (hereafter, used interchangeably with the term activity) reflect how animals adjust to shifting risks and resources in response to urban development (Van Cleave et al., 2018; Gardiner et al., 2019; Gallo et al., 2022). To evaluate these behavioral strategies, Hidden Markov movement models (HMMs) provide a framework to evaluate how animals allocate time to

different behavioral states (e.g., exploratory, encamped) in response to environmental conditions using movement data (e.g., step length, turning angle; Langrock et al. 2012; Klappstein et al., 2023). In human dominated landscapes, animals often alter their activity to avoid periods of increased human disturbance (Burger & Gochfeld, 1991; Duarte et al., 2011; Lowry et al., 2013; Gallo et al., 2022; Hansen et al., 2024). These behavioral adjustments can vary by landscape conditions, with individuals in urban settings exhibiting diel activity budgets that differ from rural conspecifics (Ditchkoff et al., 2006; Ritzel & Gallo, 2020). By examining diel activity across an urbanization gradient, we can infer how animals temporally navigate trade-offs between acquisition of resources and risk avoidance (Delisle et al., 2024; Hansen et al., 2024). These temporal adjustments reflect strategies to persist in human-altered landscapes and highlight the importance of activity timing and duration when evaluating wildlife responses to urbanization.

Examination of resource selection while accounting for behavioral state is critical for drawing meaningful conclusions relating to the effects of urbanization on wildlife (Roever et al., 2014; Karelus et al., 2019). Behavioral states mediate how and when animals interact with their environment; therefore, patterns of resource selection can vary across behavioral contexts. Human-modified environments introduce novel stressors associated with habitat fragmentation and altered distributions of food, cover, and mortality risk (Ditchkoff et al., 2006; Ritzel & Gallo, 2020). These stressors can impose biological constraints on urban-tolerant individuals by limiting access to essential resources or elevating exposure to real and perceived anthropogenic threats. In turn, these constraints often drive behavioral shifts and resource selection strategies that differ markedly from those observed in rural counterparts (Tigas et al., 2002; Ditchkoff et al., 2006; Lowry et al., 2013; Ritzel & Gallo, 2020; Delisle et al., 2024). Urban-tolerant species

may alter the timing, intensity, or spatial patterns of their movement in response to the increased availability of novel resources (e.g., ornamental plantings, small gardens, residential waste) or because traditional resources are absent or rare (Kilpatrick & Spohr, 2000; Prange et al., 2004).

As urban land cover increases globally, there is greater need to understand how wildlife movements differ along the urbanization gradient (Sol et al., 2013; Doherty et al., 2021). Herein, we examined the spatial and temporal effects of urbanization on movement of white-tailed deer (*Odocoileus virginianus*) using a multi-year GPS telemetry study conducted along an urbanization gradient in North Carolina, USA. White-tailed deer are tolerant of a range of environmental conditions, ranging from suburbs with high human densities to sparsely populated rural areas (Grund et al., 2002), making them an ideal model for assessing movement-related responses to urbanization. Previous research has demonstrated that white-tailed deer can persist in developed landscapes by modifying their movement and space use in response to habitat fragmentation and human activity across discrete landscape types (e.g., suburban, exurban, rural; Kilpatrick & Spohr, 2000; Grund et al., 2002; Rhoads et al., 2010; Dechen Quinn et al., 2013; Potapov et al., 2014). This has led to new questions about how deer movement patterns vary across a continuous urbanization gradient. Building on this foundation, our study provides a landscape-scale perspective by evaluating how deer movement is influenced by anthropogenic features across a continuous gradient. We identified key environmental predictors influencing diel activity budgets and resource selection, incorporated behavioral states, and evaluated how the strength and direction of these relationships varied along the urbanization gradient, between sexes, and across two seasons defined by plant phenology - growing and dormant. We predicted that diel activity budgets, resource selection, and step lengths would vary across the urbanization gradient and among seasons. We hypothesized that: 1) as urbanization increased, deer would

exhibit activity that minimized human interactions; 2) resource selection would vary along the urbanization gradient and reflect season- and sex-specific requirements; and 3) individual deer in more urbanized settings would exhibit shorter step lengths than their counterparts in less urbanized areas due to reduction in contiguous deer habitat. This research provides new insight into how wildlife adjust their diel activity budgets, resource selection, and step lengths in response to urban-related landscape change, contributing to our broader understanding of animal behavior in human-modified landscapes.

METHODS

Study Area

Our study was conducted from 2022 to 2025 in the Piedmont physiographic region of central North Carolina, USA, a region with a diverse urbanization gradient, ranging from rural to city-centered, high-density development, and projected urban expansion (Terando et al., 2014). We captured and monitored deer primarily in Durham County, though some individuals were captured in eastern Orange County (Fig. 1.1). The study area (approximately 77,200 ha) was characterized as a subtropical humid climate with gently rolling terrain and a mix of urban, suburban, and rural land use areas. The dominant vegetation cover was hardwood and pine forest types, including mixed hardwood-pine forest (Spooner et al., 2021). The human population of Durham County was approximately 343,628 in 2024, making it the 6th most populated county in North Carolina (U.S. Census Bureau, 2024). The central and southern portions of the study area reflected more urban areas characterized by greater levels of impervious surfaces and fragmented patches of forest. The northern part of the study area was more rural and land cover was characterized by mixed forest types, pasture, and agriculture, with low impervious surface cover (Fig. 1.1).

Capture & Collaring

We captured white-tailed deer in areas across the urbanization gradient during January-May 2022-2024 (Fig. 1.1). Deer were captured over sites baited with corn using either drop nets (Wildlife Capture Services, Flagstaff, AZ, USA) or tranquilizer dart guns with very high frequency telemetry darts (CO2 13mm Rifle, DanInject, Austin, TX, USA; Model 414 RDD, Pneu-Dart, Williamsport, PA, USA; Model F1020D, Advanced Telemetry Systems, Isanti, MN, USA) from tree stands. We used a combination of Butorphanol tartrate, Azaperone tartrate, and Medetomidine hydrochloride (BAM), in 2cc syringes/darts to immobilize deer (Wedgewood Pharmacy, Swedesboro, NJ, USA). Atipamezole and Naltrexone were used to reverse the Medetomidine hydrochloride and Butorphanol tartrate, respectively (Wedgewood Pharmacy). Female capture ceased by the end of April each year to avoid excessive stress on pregnant individuals prior to parturition. Capture methods and protocols were approved by the North Carolina State University Institutional Animal Care and Use Committee (IACUC # 21-370). Deer capture and handling was permitted by the North Carolina Wildlife Resources Commission.

We fitted captured individuals with a GPS collar (Model G5-2D; 4-hr mortality delay; Advanced Telemetry Systems) programmed to obtain locations every 2 hours, providing ~12 location fixes daily for a year. We scheduled male collars to drop off a year after deployment to ensure appropriate fit with neck swelling during only a single rut period after capture. We scheduled female collars to drop off at the end of the study. Thus, several female individuals were collared and tracked for up to three years; however, only data from the first year, with 2-hour fix rates, were used in the analysis.

Landscape Covariates

We classified the landscape using open-source geographic information system (GIS) data files (Table S1.1). Landscape covariates included percent impervious surface, percent canopy cover, and distance to roads. The impervious surface and canopy cover data were obtained from the National Land Cover Database (Dewitz, 2023). The road data layer was created by combining data from the TIGER/Line shapefile for primary roads (United States Census Bureau, 2023) and the North Carolina Department of Transportation road shapefile for secondary roads (North Carolina Department of Transportation, 2024). The two road datasets combined provided a comprehensive map of roads throughout the study area. We scaled all covariates (mean = 0, s.d. = 1) and verified that pairwise Pearson's correlation coefficients ($|r|$) were <0.7 .

Seasons

We divided the year into two distinct seasons - growing and dormant. The growing season is the period between the last spring freeze and first autumn freeze (Robeson, 2002; Linderholm, 2006), and the dormant season is all days outside of that timeframe. The growing season represents a time of active growth by herbaceous and woody plants, which in turn provide critical food and cover for white-tailed deer. Conversely, the dormant season is characterized by dormancy for most plants, lower forage availability, and less concealing cover than during the growing season. We used a statewide dataset that compiled average freeze dates from 2009-2019 to estimate the start and end dates for the growing season in the study area (NC State Extension, 2025). In the study area, the average last spring freeze occurs on 5 April, with the average first autumn freeze occurring on 4 November. Thus, we assigned the growing season as 6 April - 3 November and the dormant season as 4 November - 5 April.

Data Cleaning

We censored the first two weeks of data following collar deployment for each individual to account for possible biases in movement due to capture. We removed locations recorded less than 2 minutes from the previous location and biologically implausible points with speeds exceeding 1 m/s continuously for the 2-hr interval or step lengths greater than 3 km. Finally, we removed a small number of locations more than 4 standard deviations from the median location to censor location errors. We retained individuals with ≥ 7 days of location data for a particular season. We estimated home range crossing times of deer in this study as ~ 2.4 crossings per day (Fleming et al., 2015), thus we deemed 7 days sufficient to capture representative movement and selection patterns (Alston et al., 2023).

Urbanization Gradient

We defined a continuous urbanization gradient based on percent impervious surface (Dewitz, 2023) to describe where an individual lived along the urban-to-rural continuum. We fit individual autocorrelated kernel density estimations (AKDE) by season using the *ctmm* package in R version 4.4.1 (Fleming et al., 2015; Fleming and Calabrese, 2023; R Core Team, 2024). We then calculated the mean percent impervious surface within each individual's 99% AKDE and averaged these values across seasons to assign a single “urbanness value” (Fig. 1.1). This process avoided subjective classifications (e.g., urban, suburban, rural) and provided a continuous urbanness value reflecting an individual’s exposure to urbanization in their range distribution (Fig. 1.1).

Hidden Markov Models

We fit a series of four hidden Markov movement models (HMM; Patterson et al., 2008; Langrock et al., 2012) to test predictions of the effects of urbanization on deer diel activity budgets. All models allowed deer activity to vary by time-of-day through a series of harmonics

(Forrest et al., 2025) but imposed different assumptions for the effects of urbanization (Fig. 1.2). Specifically, Model 1 excluded urbanization, reflecting the hypothesis that activity varies by time-of-day but is constant across the urbanization gradient. Model 2 included an additive effect of urbanization on transition probabilities that allowed total activity (i.e., proportion of time spent in the exploratory state) to vary across the gradient, but the timing of activity remained constant. Model 3 included an interaction term between urbanization and time-of-day harmonics that forced total activity to remain constant across the gradient, but allowed the timing of activity to vary. Finally, Model 4 included an additive and interaction effect of urbanization where both total activity and timing of activity could vary across the gradient (Fig. 1.2). We repeated analyses for each sex and season given our objective to evaluate differences in diel activity budgets across sexes and seasons. We ranked models using Akaike's Information Criterion (AIC) to determine the most parsimonious model for each analysis (Table 1.1, Fig. 1.2, Table S1.2).

For the HMMs, we used two latent behavioral states: an exploratory state (longer step lengths, more directional) and an encamped state (shorter step lengths, increased turning angles). We included first through fourth harmonic terms of the sine and cosine of time-of-day in radians to model periodicity and capture the complex diel patterns of deer activity (Forrest et al., 2025). We transformed the time-of-day variable using a double anchoring technique to account for varying day lengths (Vazquez et al., 2019). Step lengths and turning angles were modeled using gamma and von Mises distributions, respectively (Pohle et al., 2024; Table S1.3). Finally, we used the Viterbi algorithm to post-hoc estimate the most likely behavior state for each step interval from the most parsimonious model (Zucchini et al., 2017). HMMs were fit using the *momentuHMM* package in R (McClintock & Michelot, 2018), where starting values for each

successive model (1-4) were based on results from the less complex model to promote numerical stability and model convergence. We also fit a null model without covariates to verify support for time-of-day harmonics.

Resource Selection

We used integrated step selection functions (iSSF) to investigate the effects of urbanization on step lengths, turning angles, and resource selection at the step level (Johnson, 1980; Avgar et al., 2016; Klappstein et al., 2023; Pohle et al., 2024). iSSF extend traditional step selection functions by incorporating movement metrics (e.g., step length, turning angle) directly into the resource selection analysis, relaxing the assumption that movement and resource selection are independent processes (Thurfjell et al., 2014; Klappstein et al., 2023). We fit seven models of increasing complexity to evaluate competing hypotheses on the effects of urbanization and if movement and selection varied across the urbanization gradient (Tables 1.2 and S1.4). For simplicity, we use the term *movement* in the model descriptions to reflect parameters for both step lengths and turning angles (e.g., step length, log(step length), cosine(turning angle)). All models included the HMM derived behavioral state (exploratory or encamped) on movement parameters to account for behavioral state differences. Landscape features included canopy cover, distance to roads, and impervious surfaces. Models 1-7 are summarized in Table 1.2 and Table S1.4 and briefly described here:

- M1. Behavioral state affected movement (included in all subsequent models).
- M2. Landscape features affected movement and selection.
- M3. Landscape features and behavioral state affected selection.
- M4. Landscape features affected movement and selection, selection was state dependent.
- M5. Urbanization affected movement and selection.

M6. Urbanization and landscape features affected movement and selection.

M7. Urbanization, behavioral state, and landscape features affected movement and selection.

We processed data and fit iSSF models using the AMT package (Signer et al., 2019) in R (R Core Team, 2024). We created five available steps for each used step by randomly choosing turning angles and step lengths from their respective distributions. We ranked models by AIC and repeated analyses separately for each season and sex.

RESULTS

Capture & Collaring

We tracked 202 white-tailed deer (111 females; 91 males) for varying durations from January 2022 to January 2025. We captured 119 individuals via drop nets and 83 individuals via tranquilizer darts. After data cleaning, season- and sex-specific analyses included 188 individuals for the dormant season (106 females; 82 males) and 194 individuals for the growing season (107 females; 87 males; Table 1.1). Individual urbanness values ranged from 0.00-38.71 ($\bar{x} = 7.65$, $SD = 9.43$). Urbanness values did not exceed ~40 because deer density declined with increasing impervious surface cover (Lynn et al., 2025), resulting in limited capture opportunities in the most urbanized portions of the study area and highlighting a potential threshold of deer occupancy along the urbanization gradient.

Hidden Markov Models

Hidden Markov models identified Model 4 as the best supported across all season- and sex-specific analyses, supporting the hypothesis that urbanization affected both timing and amount of activity (Table 1.1; Fig. 1.2). Diel activity budgets varied by season, sex, and urbanness value (Fig. 1.3; S1.5). All deer were crepuscular, with the greatest activity occurring at dawn and dusk, reduced activity during the day, and moderate activity at night (Fig. 1.3).

However, as urbanization increased, females decreased activity during daylight hours and increased activity during nighttime hours (Fig. 1.3). Males in more urban areas exhibited lower activity levels throughout the diel cycle than males in less urbanized areas (Fig. 1.3). The activity differences among individuals along the urbanization gradient for both sexes were most pronounced during the dormant season (Fig. 1.3).

Integrated Step Selection

Model selection results from integrated step selection models supported Model 7 across all season- and sex-specific groups, supporting the hypothesis that deer movement and selection varied by behavioral state, landscape features, and the urbanization gradient (Table 1.3). Model 7 had complete support (AIC weight = 1.00) in all sex and season analyses (Table 1.3).

Selection for canopy cover increased as urbanization increased (Figs. 1.4 and S1.1; Table S1.6). At low urbanness values, selection for canopy cover was near zero (no selection) and sometimes negative (avoidance), but increased to strongly positive selection as urbanization increased. The change from avoidance to strong selection for canopy cover as urbanization increased was particularly evident for females in the growing season (Figs. 1.4 and S1.1; Table S1.6). The effect of behavioral state on the selection of canopy cover varied by sex and season (Fig. 1.4). Selection of canopy cover remained similar for exploratory and encamped states in the growing season for both sexes (females: difference = -0.01; $p = 0.31$; males: difference = -0.02; $p = 0.03$). However, during the dormant season, females selected for greater canopy cover in the encamped state (difference = 0.05; $p < 0.01$), whereas males exhibited the opposite pattern, selecting areas with less canopy cover in the encamped state (difference = -0.05; $p < 0.01$).

As urbanization increased, deer selected for areas farther from roads in two of the four comparisons: females-growing (estimate = 0.06; $p < 0.01$) and males-dormant (estimate = 0.11; p

< 0.01) (Figs. 1.4 and S1.1; Table S1.6). However, urbanization did not affect selection of distances to roads for females during the dormant season (estimate = 0.01; $p = 0.34$) or for males during the growing season (estimate = 0.01; $p = 0.51$). Overall, when deer were in the exploratory state, selection for distances to roads varied from avoidance to positive selection depending on sex, season, and urbanization. However, deer always avoided roads when encamped (Figs. 1.4 and S1.1; Table S1.6).

Deer avoided impervious surfaces regardless of where they were located along the urbanization gradient (Figs. 1.4 and S1.1; Table S1.6). However, deer displayed decreased avoidance for impervious surfaces as urbanization increased in all sexes and seasons, indicating deer in more urban areas exhibited less avoidance of impervious surfaces compared to deer in more rural areas (Figs. 1.4 and S1.1; Table S1.6). Additionally, individuals in the encamped state avoided impervious surfaces less than individuals in the exploratory state (Figs. 1.4 and S1.1; Table S1.6).

Deer movement, as measured by step length, remained relatively consistent across the urbanization gradient (Fig. 1.5). Parameter estimates indicated that average step lengths increased as urbanization increased (Table S1.7); however effect size differences were minimal and therefore not likely to be biologically meaningful (Fig. 1.5).

DISCUSSION

Urbanization influenced deer movement and diel activity budgets, likely reflecting behavioral adjustments to anthropogenic disturbances (e.g., traffic volume, human activity, resource availability). These findings supported our prediction that, as urbanization increased, deer would exhibit activity that minimized human interactions; however, these results did not support our other prediction that deer in more urbanized areas would exhibit shorter step lengths

than their counterparts in less urbanized areas. Our results build on an increasing number of studies demonstrating changes in wildlife diel activity budgets in response to human disturbances (e.g., white-tailed deer, Hansen et al., 2024, Péter et al., 2025; roe deer *Capreolus capreolus*, Bonnot et al., 2012; black bears *Ursus americanus*, Beckmann & Berger, 2003, Evans et al., 2019, Zeller et al., 2019, Hansen et al., 2024; marmosets *Callithrix penicillata*; Duarte et al., 2011; bobcats *Lynx rufus* and coyotes *Canis latrans*, Tigas et al., 2002). As urbanization increased, female deer exhibited reduced daytime activity and increased nighttime activity, likely to avoid periods of peak human activity (Gallo et al. 2022). The shift toward increased nighttime and reduced daytime activity in urban areas may be a strategy employed by females to reduce risk while still allowing time for resource allocation. In contrast, as urbanization increased, males reduced their activity across the entire diel cycle and did not exhibit the clear shift in activity timing observed in females. Sex-specific differences in diel activity budgets likely reflect a combination of differences in metabolic demand, reproductive roles, and risk avoidance strategies (Beier & McCullough, 1990). Nevertheless, both sexes exhibited the lowest activity during daylight hours, reflecting a shared strategy during this period of the diel cycle to potentially minimize encounters with humans and/or perceived risks (Bonnot et al., 2012; Little et al., 2016; Gallo et al., 2022; Bassing et al., 2024; Péter et al., 2025).

Results were consistent with our prediction that resource selection would vary between seasons and sexes and across the gradient, reflecting flexible strategies that support persistence in human altered landscapes. As urbanization increased, deer exhibited strong selection for areas with canopy cover, likely reflecting a reliance on forested greenways and parks for forage and shelter in fragmented, human-dominated landscapes (Grund et al., 2002). Conversely, as urbanization decreased, individuals demonstrated less selection for canopy cover, likely due to

more continuous vegetation cover across a variety of land cover types (e.g., cropland, pasture, powerline rights-of-way) that provided concealment and/or abundant forage (Coulon et al., 2008; Gregovich et al., 2024). This contrast across the urbanization gradient reflects divergent habitat-use strategies shaped by landscape context. As urbanization increases, individuals are more constrained and dependent on canopy cover, whereas in less developed areas, individuals may benefit from more diverse vegetation conditions less connected to the presence of tree canopy. State-specific differences in selection for canopy cover were most notable during the dormant season for both sexes. Encamped females showed stronger selection for canopy cover during the dormant season, potentially for shelter and concealment in colder months. In contrast, exploratory males prioritized canopy cover during the dormant season, possibly to enhance concealment during periods of increased activity, particularly during the hunting season (Bonnot et al., 2012; Sergeyev et al. 2022). Together, these sex-specific differences indicate a divergent strategy in resource selection when vegetation cover is reduced (Beier & McCullough, 1990).

As urbanization increased, sex and season specific avoidance of roads was likely connected to the species' natural history. For more urban females, increased road avoidance during the growing season may reflect efforts to seek areas of seclusion for their fawns while they are young (Leblond et al., 2013). For more urban males, increased avoidance of roads during the dormant season may reflect a need to maximize concealment (Potapov et al., 2014; Haus et al., 2020). With decreasing urbanization, many individuals exhibited weaker avoidance of roadsides and, in some cases, even selected areas closer to roads, particularly while in the exploratory state. Roadsides can serve as attractive movement corridors that offer increased forage abundance, particularly in less developed locations with lower traffic volumes where the perceived risk may be reduced (Rea, 2003; Darlington et al., 2022). In less developed settings,

lower traffic density combined with roadside forage availability likely drove selection for areas near roads, particularly during the dormant season when forage was scarce in surrounding closed-canopy forests (Darlington et al., 2022; Gregovich et al., 2024). Stewart et al. (2022) reported that females were more likely than males to use risky areas that contained food resources (e.g., roadsides), likely due to smaller body size and increased nutritional demands during gestation and lactation. Across seasons and sexes, individuals in the exploratory state were more likely to exhibit reduced avoidance to roads than those in the encamped state, indicating that deer bed in areas farther from roads to avoid chronic disturbances such as traffic noise and human interactions. Similar behavior has been observed in roe deer, marmosets, and elk (*Cervus canadensis*), which selected bedding and loafing sites farther from roads to avoid disturbances (Coulon et al., 2008; Duarte et al., 2011; Prokopenko et al., 2017).

The strength of avoidance of impervious surfaces declined as urbanization increased, which may be due to variation in both real and perceived risk associated with developed areas as well as variation in cover and resources. Consistent with previous work, deer have been shown to avoid impervious surfaces in developed landscapes (Potapov et al., 2014). Building on these findings, we observed that individuals in less urbanized areas exhibited the strongest avoidance of impervious surfaces, likely because they can minimize exposure and access resources farther from developed hotspots. The magnitude of avoidance for impervious surfaces was greater in the exploratory state than in the encamped state, which may reflect a combination of limited resource availability and heightened risk of encountering humans or vehicles while moving (Coulon et al., 2008).

CONCLUSIONS

Our findings demonstrate that animals modify when, where, and how they move to balance resource acquisition with avoidance of human disturbance, reflecting behavioral flexibility that enables persistence along urbanization gradients. These findings add to the growing body of literature showing that individuals of urban-tolerant species exhibit behaviors that enable them to persist amid human activity, often by minimizing exposure to anthropogenic disturbance (Burger & Gochfeld, 1991; Tigas et al., 2002; Bonnot et al., 2012; Gallo et al., 2022; Péter et al., 2025). By comparing individuals along an urbanization gradient and integrating behavioral state and movement into resource selection analyses, we provide a more nuanced understanding of how animals interact with human-altered landscapes. As urbanization continues to reshape landscapes globally, understanding behavioral adjustments across species can inform urban planning and wildlife management strategies aimed at reducing negative human-wildlife interactions, and supporting biodiversity in expanding urban systems.

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TABLE 1.1. Hidden Markov model comparisons for different seasonal and sex-specific groups. AIC values were calculated for five models (Null, 1, 2, 3, and 4) for each group (Female Dormant, Female Growing, Male Dormant, and Male Growing). Estimated parameter count is listed for each model under “nPars”. Delta AIC values represent the difference between each model's AIC and that of the best-fitting model (lowest AIC value) within each group. Model weights indicate the relative likelihood of each model given the data. Model 4 was the top-ranked model in all groups. Model 4 suggests variation in both time and amount of activity depending on where a deer is located along the urbanization gradient.

Group	Model	nPars	AIC	Δ AIC	Weight
Female Dormant (n = 106)					
	4	18	2203359	0	1.00
	2	10	2203780	421	0.00
	1	9	2203970	611	0.00
	3	17	2206890	3531	0.00
	Null	1	2223448	20089	0.00
Female Growing (n = 107)					
	4	18	3830463	0	1.00
	3	17	3830487	24	0.00
	2	10	3831421	958	0.00
	1	9	3831783	1320	0.00
	Null	1	3843810	13347	0.00
Male Dormant (n = 82)					
	4	18	1219734	0	0.97
	2	10	1219741	7	0.03
	3	17	1220150	416	0.00
	1	9	1220705	971	0.00
	Null	1	1229517	9783	0.00
Male Growing (n = 87)					
	4	18	2920407	0	1.00
	3	17	2920531	124	0.00
	2	19	2920759	352	0.00
	1	9	2921507	1100	0.00
	Null	1	2934124	13717	0.00

TABLE 1.2. Summary of integrated step selection models used to explore the effects of behavior, landscape features, and urbanization on deer movement (step lengths and turning angles) and selection. Behavior state distinguishes between two behavior states (exploratory, encamped). Landscape features include impervious surface, canopy cover, and distance to road rasters. Urbanization is the urbanness value of an individual. Inclusion of covariates is denoted by X. See Table S1.4 for detailed equations.

Model	Movement			Selection		
	Behavior state	Landscape features	Urbanization gradient	Behavior state	Landscape features	Urbanization gradient
1	X					
2	X	X			X	
3	X			X	X	
4	X	X		X	X	
5	X		X		X	X
6	X	X	X		X	X
7	X	X	X	X	X	X

TABLE 1.3. Integrated step selection model comparisons for different seasonal and sex-specific groups. AIC values were calculated for five models (1-7) for each group (Female Dormant, Female Growing, Male Dormant, and Male Growing). Estimated parameter count is listed for each model under “nPars”. Delta AIC values represent the difference between each model's AIC and that of the best-fitting model (lowest AIC value) within each group. Model weights indicate the relative likelihood of each model given the data. Model 7 was the top-ranked model in all groups. Model 7 suggests deer movement and selection varies by state, landscape, and location on the urbanization gradient.

Group	Model	nPars	AIC	Δ AIC	Weight
Female Dormant	7	27	380773	0	1.00
	6	24	381090	318	0.00
	4	21	381336	563	0.00
	2	18	381705	932	0.00
	5	15	381708	936	0.00
	3	12	381865	1093	0.00
	1	6	387287	6515	0.00
Female Growing	7	27	711774	0	1.00
	6	24	711863	89	0.00
	5	15	712386	612	0.00
	4	21	713197	1423	0.00
	2	18	713313	1540	0.00
	3	12	713717	1944	0.00
	1	6	720456	8682	0.00
Male Dormant	7	27	208651	0	1.00
	6	24	208747	96	0.00
	5	15	209085	434	0.00
	4	21	209154	503	0.00
	2	18	209301	650	0.00
	3	12	209418	768	0.00
	1	6	214926	6276	0.00
Male Growing	7	27	528890	0	1.00
	6	24	529059	169	0.00
	4	21	529546	657	0.00

TABLE 1.3 (continued).

5	15	529702	813	0.00
2	18	529754	864	0.00
3	12	530107	1217	0.00
1	6	537169	8279	0.00

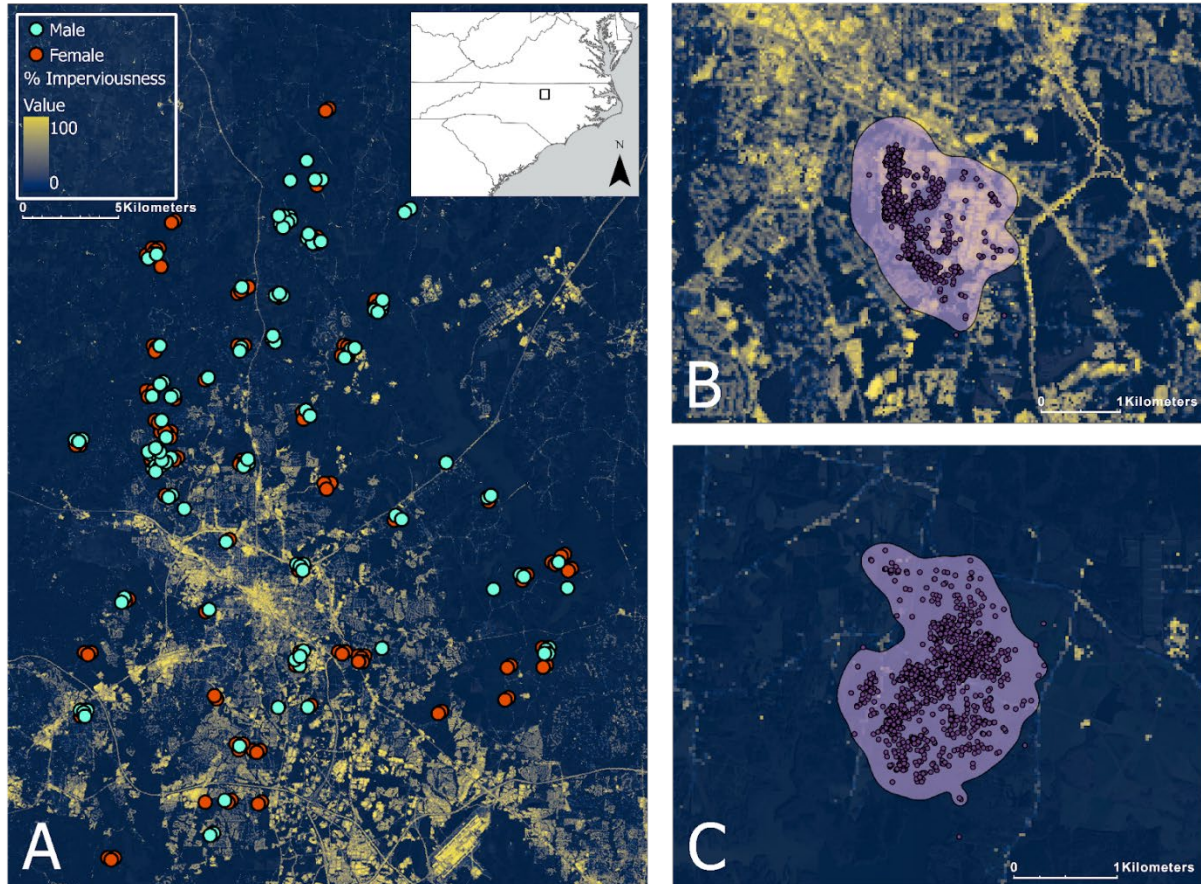


FIGURE 1.1. A) Capture locations (points) for female and male white-tailed deer overlaid on the percent impervious surface raster. The study area included Durham and Orange counties, North Carolina, USA. Urbanness values were calculated for each individual as the mean percent impervious surface in an individual's 99% autocorrelated kernel density estimated (AKDE) range distribution (purple polygon). Panels B and C show GPS locations and AKDE for B) an individual in a more urban area (urbanness value = 36.59) and (C) an individual in a more rural area (urbanness value = 0.75).

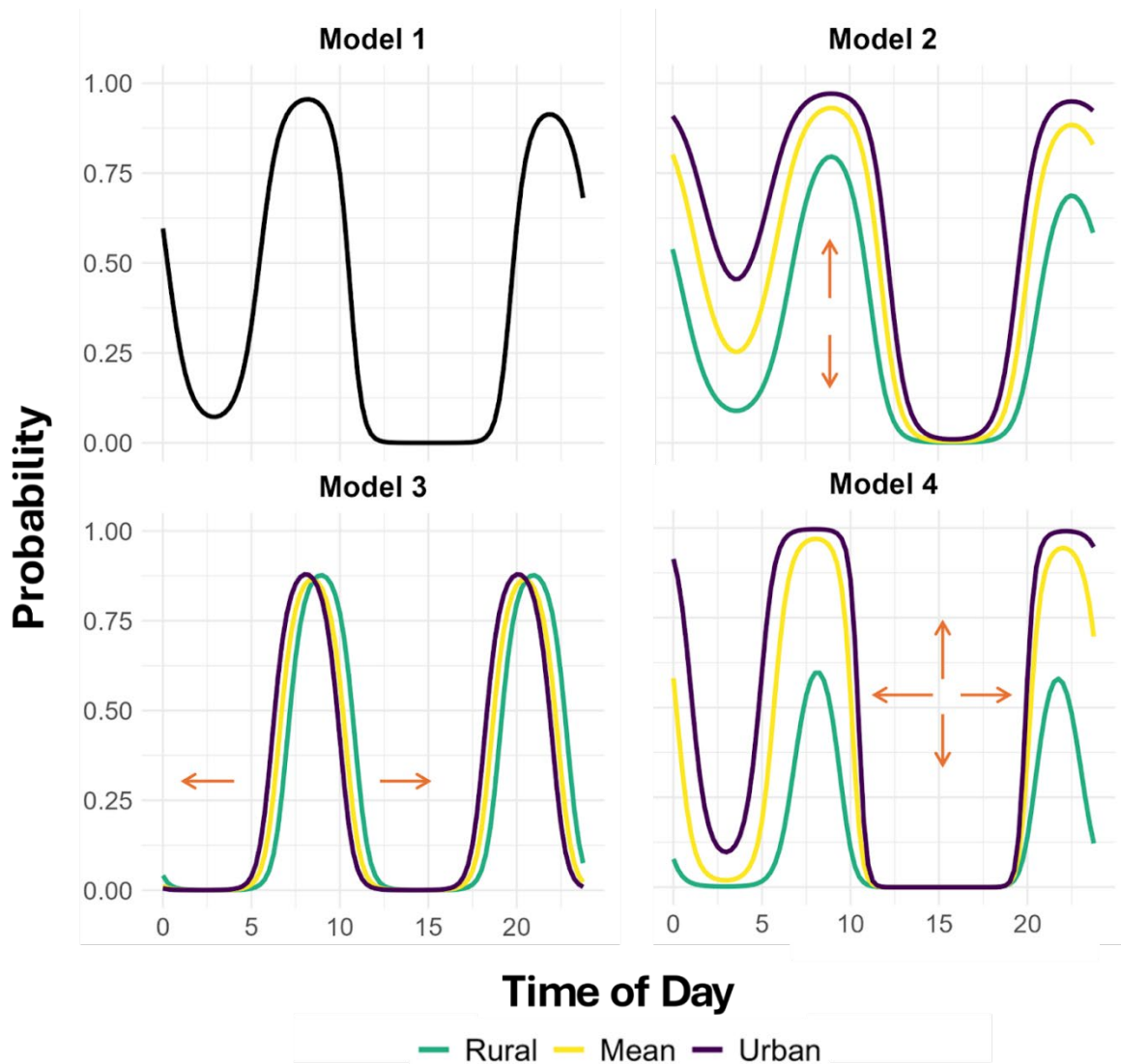


FIGURE 1.2. Visual representation of 4 a priori hypotheses on how urbanization influences deer activity, measured as the probability of being in the exploratory state. Activity patterns are shown across a 24-hour day (x-axis) and vary with levels of urbanization (represented by different lines). Hypothesized urbanization effects include: (1) no effect, (2) a change in overall activity levels, (3) a shift in activity timing, and (4) a change in both activity levels and timing.

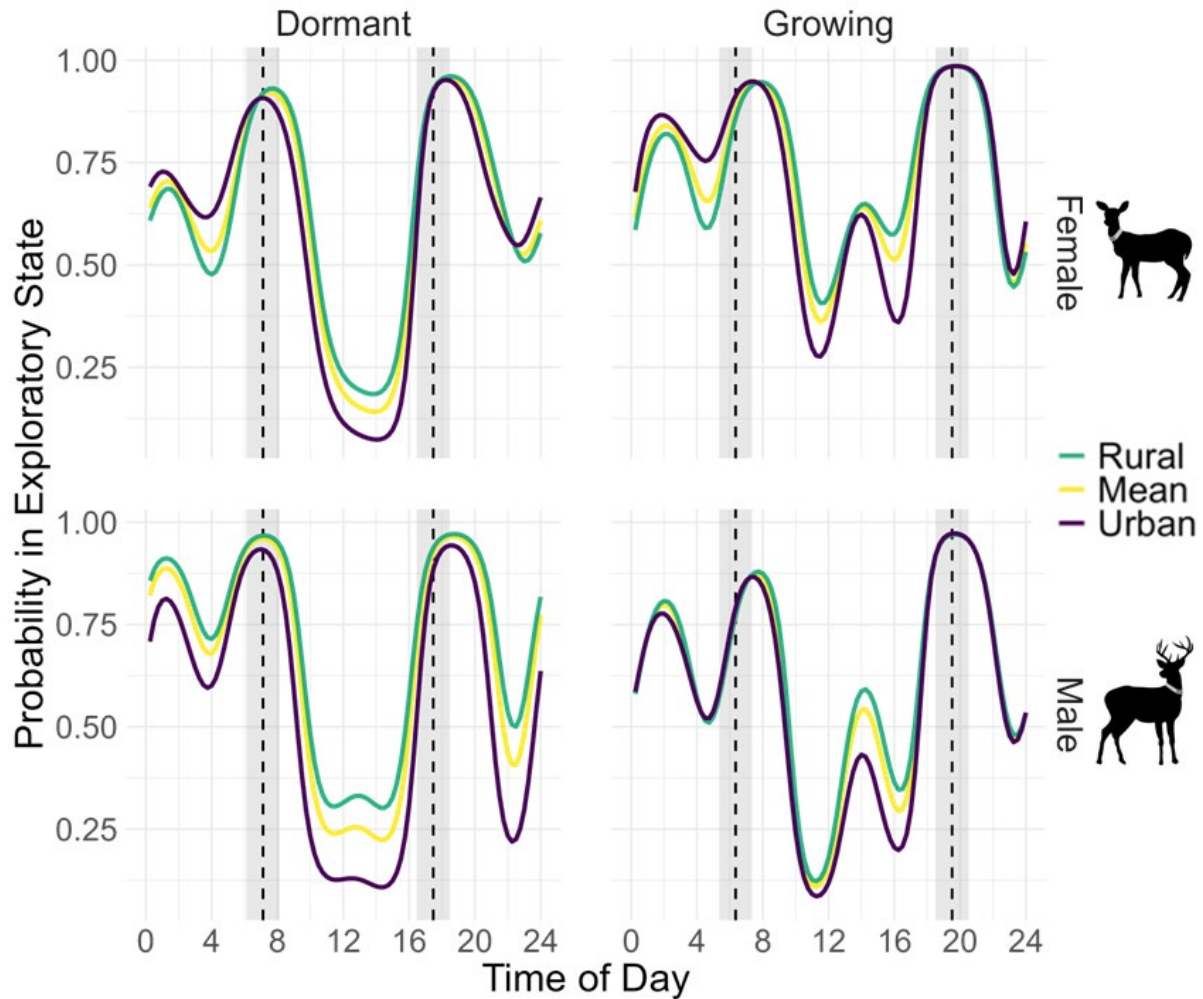


FIGURE 1.3. Stable state probability plots for each seasonal and sex-specific groups based on top hidden Markov model (Model 4) parameter estimates. Colored curves depict the probability of being in the exploratory state at the end of each 2-hour fix interval over a 24-hour period for individuals representing rural (10th percentile), average (mean), and urban (90th percentile) urbanness values. Vertical dotted lines indicate the transformed sunrise and sunset times using the average double anchoring technique to account for seasonal variation in day length. Dormant season = 07:12 (sunrise) and 17:47 (sunset); Growing season = 06:35 (sunrise) and 19:51 (sunset). Gray shaded areas include ± 1 hour of the transformed sunrise and sunset times to indicate dawn and dusk, which are key times for crepuscular animals such as deer. Each prediction curve highlights when deer are likely to be in an exploratory state throughout a 24-hour period for individuals along an urbanization gradient (differing colored lines). See Table S1.5 for transition probability estimates.

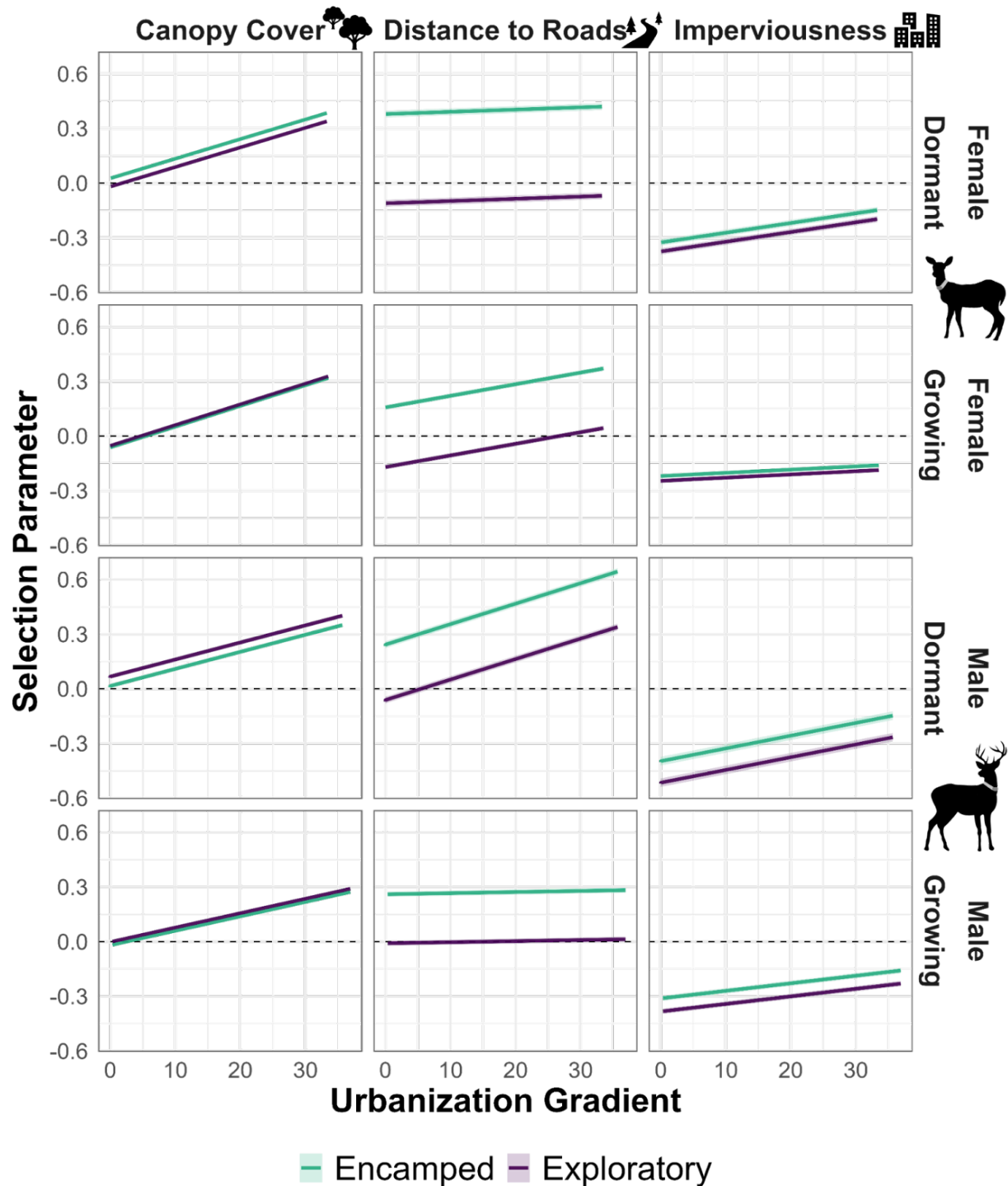


FIGURE 1.4. State based modeled selection coefficient plots for each covariate, season and sex based on the top integrated step selection function model (Model 7). The urbanization gradient (urbaness values) is plotted along the x-axis with increasing urbanization from left to right. Positive selection parameter values indicate selection for greater 1) canopy cover, 2) distance to roads, and 3) impervious surfaces (imperviousness) while negative values indicate the inverse. Dashed horizontal lines represent a neutral selection value ($\beta = 0$).

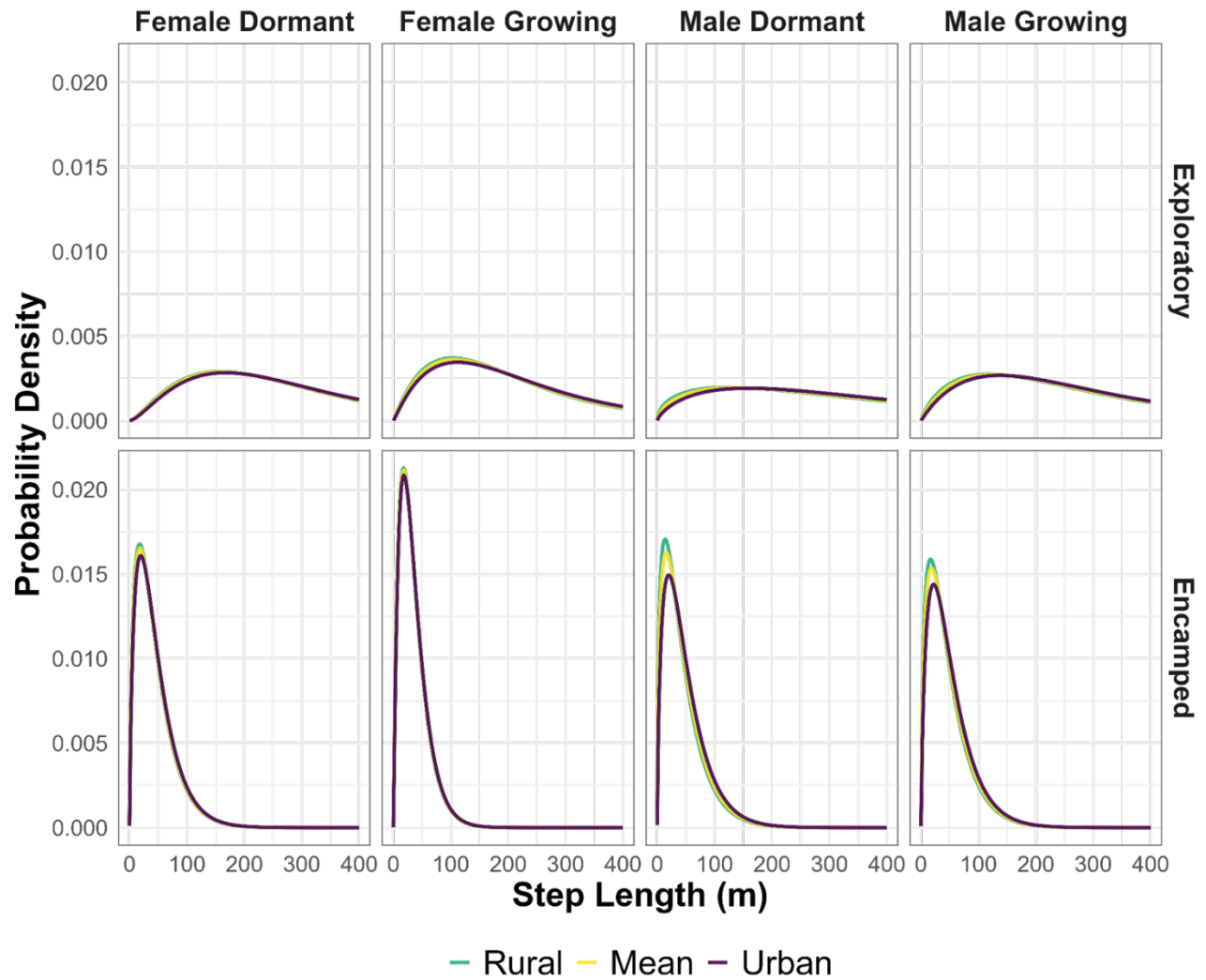


FIGURE 1.5. Estimated step length distributions (Gamma) from the top integrated step selection function model (Model 7) for each dataset. Plots display probability density for step lengths in both the exploratory (top row) and encamped (bottom row) behavioral states. Each set of curves represent predictions for areas considered more rural (10th percentile), average (mean), or urban (90th percentile) based on urbanness values. For more information regarding step mean and standard deviations by state, see Table S1.3.

CHAPTER 2: Seasonal Resource Selection by White-tailed Deer Along an Urban-Rural Gradient

ABSTRACT

Cities are rapidly expanding and changing the resources available for wildlife. Urbanization can alter wildlife resource selection, because seasonal food and cover change along urban-to-rural gradients. We investigated how seasonal resource selection of white-tailed deer (*Odocoileus virginianus*) varied across an urbanization gradient in Durham and Orange counties, North Carolina, using GPS collar data collected from 202 deer (111 females; 91 males) at 2-hour intervals throughout 2022-2025. We hypothesized that 1) deer would increasingly select for less developed landscape features, including lower impervious surface, greater canopy cover, and greater distance from roads as urbanization increased, 2) individual variation in selection would decrease with increasing urbanization, reflecting a shift from generalist selection to disproportionate selection for key features, and 3) male and female seasonal resource selection would differ due to life history constraints. Deer consistently avoided developed features, and individual variability in selection decreased with increasing urbanization. Deer across all seasons selected areas with lower impervious surfaces, which became increasingly scarce in more urbanized landscapes. Considerable individual variability in selection for distance to roads and canopy cover in more rural areas led to weak population-level selection; however, as urbanization increased selection became significantly positive and consistent across individuals reflecting a shift towards disproportionate use of greenspaces at the individual and population-level. Deer altered their selection in response to intensifying urbanization, showing stronger and more consistent selection for less developed areas as urbanization increased. The decline in individual variation as urbanization increased illustrates how urbanization can drive

homogenization of resource selection, with even generalist species converging on similar resource-use strategies in highly urbanized environments. Such convergence likely reflects a narrowing of available habitat, indicating that maintaining and connecting diverse green spaces in urban areas can support variable resource-use strategies across deer and other wildlife species that enable persistence in urbanizing environments.

INTRODUCTION

Cities are rapidly expanding, transforming landscapes through increased impervious surfaces, habitat fragmentation, and novel resource availability, thereby presenting both challenges and opportunities for wildlife (Aronson et al., 2014; Seto et al., 2012; Liu et al., 2016; Zipperer et al., 2020). In response, many species modify their resource selection to navigate altered landscapes and anthropogenic features such as roads and buildings (McKinney, 2006; Aronson et al., 2014; Larson et al., 2020). Over time, these adjustments can produce individual- and species-specific resource selection patterns that vary from rural counterparts (Caspi et al., 2022; Walters et al., 2023; Tranquillo et al., 2024; Larson & Sander, 2025). Understanding how individual- and population-level resource selection varies across a continuum of highly urbanized to suburban, exurban, and rural areas (hereafter “urbanization gradient”) is thus essential for predicting species responses to urbanization and guiding effective wildlife conservation.

Individual variation in behavioral responses can reflect a population’s ability to confront novel conditions associated with urbanization (Sol et al., 2013; Santini et al., 2019; Ritzel & Gallo, 2020; Walters et al., 2023). Wildlife often respond to novel environments by altering their use of resources (Gardiner et al., 2019; O'donnell & delBarco-Trillo, 2020; Ritzel & Gallo, 2020; Chapter 1). Resource selection can reveal how individuals meet their needs in response to spatial

(e.g., urbanization gradient) and temporal (e.g., seasonal resources) environmental heterogeneity (Boyce & McDonald, 1999). Additionally, individual-level selection is driven by intrinsic (e.g., age, sex, body condition) and extrinsic factors (e.g., urbanization, climate, predation, competition, and resource availability), often leading to different resource-use strategies among individuals of the same species (Leclerc et al., 2016; Muff et al., 2020). When individuals are aggregated at the population level, overarching trends in selection may emerge, highlighting diverse resource-use strategies and providing insight into how populations may respond to large scale factors such as urbanization. Previous research has advanced understanding of how individuals vary in their responses to environmental change, highlighting the importance of behavioral flexibility in response to novel environments (Lowry et al., 2013; Sol et al., 2013; Caspi et al., 2022; Walters et al., 2023; Chapter 1). However, the mechanisms underlying individual variation in resource selection, and the extent to which this variation enables wildlife to adjust to novel environments, remain poorly understood.

Understanding how landscape change interacts with life history stage, sex, and season to influence resource selection is key to predicting wildlife responses to urbanization. Seasonal fluctuations in biological needs, such as those related to breeding, overwinter survival, or rearing of young, alter energetic demands and drive shifts in resource use (Fretwell, 1972; Svoboda et al., 2019; Joly et al., 2025). These seasonal and demographic differences may further interact with varying levels of urban development and lead to context-dependent patterns of selection along the gradient (Chapter 1). As food and cover availability fluctuates temporally and spatially, wildlife may modify their use of features along the gradient differently, reflecting tradeoffs between resource acquisition and mortality risk (Svoboda et al., 2019; Schoenecker et al., 2023).

Research on variation in resource selection along an urbanization gradient has important conservation implications and can help managers better predict species persistence, guide efforts to maintain habitat connectivity, and reduce negative human-wildlife interactions in increasingly urban environments. Despite growing recognition of the effects urbanization has on wildlife (Aronson et al., 2014; Larson et al., 2020; Larson & Sander, 2025), research is needed to evaluate how individuals and populations respond to resources spatially across urbanization gradients and temporally among seasons (Rodewald & Shustack, 2008; Ibáñez-Álamo & Soler, 2010).

We investigated the spatial and temporal effects of urbanization on third-order resource selection (Johnson, 1980) through a multi-year study of white-tailed deer (*Odocoileus virginianus*; hereafter “deer”) along an urbanization gradient in North Carolina, USA. Deer are tolerant of a range of environmental conditions, ranging from suburbs with high human densities to sparsely populated rural areas (Grund et al., 2002), making it an ideal case study for evaluating the effects of urbanization on wildlife resource selection. Despite the vast body of literature on white-tailed deer, there is a significant gap in understanding how urbanization influences seasonal resource selection for the species, especially along a continuous rural to urban gradient. We hypothesized that individual-level seasonal resource selection would vary across the urbanization gradient, leading to population-level trends that reflect the species response to urbanization. From this hypothesis, we specifically predicted that 1) deer would select for less developed landscape features such as lower impervious surface, greater canopy cover, and greater distance from roads as urbanization increased, 2) individual variation in resource selection would decrease with increasing urbanization, reflecting a shift from generalist selection to disproportionate selection for key features, and 3) seasonal resource selection would

differ between male and female deer, driven by their differing biological requirements. This research provides new insights into the selection behaviors of wildlife in response to urban pressures, advancing our understanding of wildlife resource selection in human-altered landscapes.

METHODS

Study Area

Our study was conducted from 2022 to 2025 in the Piedmont physiographic region of central North Carolina, USA, a region experiencing rapid urbanization (Terando et al., 2014). We captured and monitored deer throughout Durham and eastern Orange counties in North Carolina, with most captured in Durham County (Fig. 2.1). The study area (approximately 77,200 ha) was characterized as a subtropical humid climate with gently rolling terrain and a mix of urban, suburban, and rural land use areas. The dominant vegetation cover was hardwood and pine forest types, including mixed hardwood-pine forest (Spooner et al., 2021). The human population of Durham County was approximately 343,628 in 2024, making it the 6th most populated county in North Carolina (U.S. Census Bureau, 2024). The central and southern portions of the study area reflected more urban areas characterized by greater levels of impervious surfaces and fragmented patches of forest. The northern part of the study area was more rural and land cover was characterized by mixed forest types, pasture, and agriculture, with low impervious surface cover (Fig. 2.1).

Capture & Collaring

We captured white-tailed deer in areas across the urbanization gradient during January-May 2022-2024 (Fig. 2.1). Deer were captured over sites baited with corn using either drop nets (Wildlife Capture Services, Flagstaff, AZ, USA) or tranquilizer dart guns with very high

frequency telemetry darts (CO2 13mm Rifle, DanInject, Austin, TX, USA; Model 414 RDD, Pneu-Dart, Williamsport, PA, USA; Model F1020D, Advanced Telemetry Systems, Isanti, MN, USA) from tree stands. We used a combination of Butorphanol tartrate, Azaperone tartrate and Medetomidine hydrochloride (BAM), in 2cc syringes/darts to immobilize deer (Wedgewood Pharmacy, Swedesboro, NJ, USA). Atipamezole and Naltrexone were used to reverse the Medetomidine hydrochloride and Butorphanol tartrate, respectively (Wedgewood Pharmacy). Female capture ceased by the end of April each year to avoid excessive stress on pregnant individuals prior to parturition. Capture methods and protocols were approved by the North Carolina State University Institutional Animal Care and Use Committee (IACUC # 21-370). Deer capture and handling was permitted by the North Carolina Wildlife Resources Commission.

We collared (Model G5-2D; 4-hr mortality delay; Advanced Telemetry Systems) and ear-tagged individual deer of varying sex and age classes across an urbanization gradient (Fig. 2.1). Collars were programmed to obtain global positioning system (GPS) locations every 2 hours, providing ~12 location fixes daily. Male collars were scheduled to drop off a year after deployment to ensure appropriate fit with neck swelling during only a single rut period after capture. Female collars were scheduled to drop off at the end of the study. Thus, several collared females included data for up to three years. To conserve collar battery, female collars were reprogrammed after the first year to take fixes every 8 hours, yielding approximately 3 location fixes per day.

Landscape Covariates

We quantified the landscape using open source geographic information system (GIS) data files (Table S2.1). Landscape covariates included percent impervious surface, percent canopy

cover, and distance to roads. The impervious surface and canopy cover data were obtained from the National Land Cover Database (Dewitz, 2023). The road data layer was created by combining data from the TIGER/Line shapefile for primary roads (U.S. Census Bureau, 2023) and the North Carolina Department of Transportation road shapefile for secondary roads (North Carolina Department of Transportation, 2024). The two datasets combined provided a comprehensive map of roads throughout the study area. We standardized all covariates (mean = 0, s.d. = 1) and verified that pairwise Pearson's correlation coefficients ($|r|$) were < 0.7 .

Seasons

We divided the year into four seasons that were meaningful to deer biology and anthropogenic influences on deer. Winter/Spring (WS) encompassed Jan 3-Apr 30 to account for rut recovery and gestation. Parturition (P) encompassed May 1-June 30 to account for the birthing season and early rearing of young fawns. Late Summer (LS) encompassed Jul 1-Sep 9 to account for the period of reduced forage quality and possible nutritional stress. Rut/Hunting (RH) encompassed Sep 10-Jan 2 to account for behavioral changes associated with the rut and the anthropogenic effect of hunting.

Data Cleaning

We censored the first two weeks of data following collar deployment for each individual to account for possible biases in movement due to capture. We removed locations recorded less than 2 minutes after the previous fix, as well as biologically implausible points with continuous speeds exceeding 1 m/s between fixes or step lengths greater than 3 km. We removed any individuals that dispersed or did not meet range residency requirements in a given season to meet the assumptions of range distribution estimation (Fleming et al., 2015). Finally, we removed a small number of locations more than 4 standard deviations from the median location to censor

location errors and brief non-representative excursions. We retained individuals with ≥ 7 days of location data for a particular season to obtain minimum effective sample sizes of ≥ 16 based on the estimated home range crossing time of deer in this study (mean = 2.4 crossings per day; Alston et al. 2023).

Urbanization Gradient

We used a continuous urbanization gradient based on impervious surface (Dewitz, 2023) to quantify where an individual lived along the rural-to-urban continuum. Specifically, we fit individual autocorrelated kernel density estimations (AKDE) using the *ctmm* package in R version 4.4.1 (Fleming & Calabrese, 2023; R Core Team, 2024) to quantify space use by each individual, then calculated the mean percent impervious surface in each individual's 99% AKDE (hereafter "urbanness value"; Figs 2.1-2.2, S2.1). All individuals were inspected to ensure range residency using semivariograms and raw data points. For individuals with multiple years of data, we combined data across years by season. This process avoids subjective classifications (e.g., urban, suburban, rural) and provides a continuous urbanness value reflecting the landscapes within an individual's seasonal range distribution (Figs 2.1-2.2).

Resource Selection

We fit resource selection functions (RSF) using the *ctmm* package in R version 4.4.1 (Fleming et al., 2015; Fleming & Calabrese, 2023; R Core Team, 2024). For each individual by season, we fit all additive combinations of the three environmental covariates and a null model and used Akaike's information criterion (AIC) to select the top model. We then used a weighted least squares regression to evaluate if selection estimates varied as a function of the urbanization gradient. We assigned weights as the precision of the individual-level selection estimate, and a value of 0 and weight of 1 was assigned when the covariate was not in an individual's top model.

Together, this approach allowed us to quantify: (1) individual-level resource selection; (2) seasonal differences in resource selection; and (3) if resource selection varied across an urbanization gradient.

RESULTS

Capture and Urbanness

We captured, collared, and monitored 202 deer (111 females; 91 males) across an urbanization gradient from January 2022 through January 2025. We captured 119 individuals via drop nets and 83 individuals via tranquilizer darts. After data cleaning, seasonal analyses included 175 individuals for Winter/Spring, 183 for Parturition, 181 for Late Summer, and 151 for Rut/Hunting (Table 2.1). The number of individuals per season varied by sex, with a range of 94-108 females and 57-78 males retained per season (Table 2.1). Seasonal urbanness values for individual deer ranged from 0 to 40, where values closer to 0 represented less urbanized areas and values closer to 40 represented more urbanized areas (Figs 2.1-2.2).

Resource Selection

Impervious Surfaces

Deer, regardless of their location on the urbanization gradient, consistently avoided impervious surfaces, and the strength of this avoidance remained fairly stable across the urbanization gradient and seasons, with the majority of selection estimates being negative or in more rural areas not included in the top model, resulting in consistent negative population-level selection (Fig. 2.3; Table S2.2). The most pronounced difference in seasonal selection between sexes occurred in Winter/Spring, with males showing stronger avoidance and females showing weaker avoidance as urbanization increased, but selection estimates remained negative across the gradient (Fig. 2.3; Table S2.2).

Canopy Cover

Deer consistently increased selection for canopy cover as urbanization increased (Fig. 2.3). At low urbanization values, mean selection for canopy cover was near 0.00 for some seasons and slightly negative for others, but displayed substantial individual-level variation (Fig. 2.3). As urbanization increased, mean selection for canopy cover increased for both sexes and in all seasons (Fig. 2.3). Although selection estimates across the gradient ranged from -1.15 to 1.17, nearly all individuals with an urbanness value >15 had positive selection estimates (i.e., selected for canopy cover) (Fig. 2.3). Seasonal means indicated that deer in less urbanized areas selected against canopy cover during the vegetation growing season (Parturition and Late Summer), but mean selection was near 0.00 during the vegetation dormant season (Winter/Spring and Rut/Hunting; Fig. 2.3). In contrast, deer in more urbanized areas maintained strong positive selection (~ 0.50 to 1.17) across all seasons (Fig. 2.3; Table S2.2). Both sexes displayed similar selection for canopy cover (Fig. 2.3).

Distance to Roads

Deer generally increased selection for areas further from roads as urbanization increased (Fig. 2.3). At low urbanization values, mean selection for distance to roads was near 0.00 with substantial individual-level variation. As urbanization increased, mean selection for distance to roads increased in six of the eight seasons-by-sex scenarios. Selection estimates across the gradient ranged from -5.22 to 5.41 (excluding one outlying estimate of 21.67), but nearly all individuals with an urbanness value >15 exhibited positive selection estimates (i.e. selecting areas further from roads) (Fig. 2.3). Selection for distance to roads was generally consistent across seasons, except for males in Late Summer and females during Parturition, which showed

no apparent selection with increasing urbanization (Fig. 2.3, Table S2.2). In general, female and male deer selected for distance to roads similarly (Fig. 2.3).

DISCUSSION

Deer modified their resource selection in response to urbanization, reflecting behavioral plasticity that facilitates persistence across the gradient. Selection for greater canopy cover and increased distances from roads became stronger and more consistent among individuals as urbanization increased. These selection patterns were consistent with our prediction that deer would select less developed landscape features in urban areas, which allows individuals to mitigate novel urban-related stressors (Ditchkoff et al., 2006; Duarte et al., 2011). In contrast, deer reduced avoidance of impervious surfaces as urbanization increased, likely because the remaining undeveloped patches were smaller and more isolated, increasing travel costs and limiting opportunities to avoid urban development. As a result, individuals may have tolerated more impervious surfaces as a way to access resources across the urban matrix. Our prediction that seasonal resource selection would differ between sexes, driven by differing biological requirements, was only partially supported, as overall trends between males and females were largely similar. Overall, results of our study align with prior research that reported that individuals in urban settings display modified behavior in response to urban stressors when compared to their rural counterparts (Ditchkoff et al., 2006; Šálek et al., 2015; Zeller et al., 2019).

Although selection for impervious surfaces remained largely consistent across seasons and among sexes, males in more urbanized settings showed stronger avoidance of impervious surfaces than females during Winter/Spring, potentially reflecting females' increased focus on resource acquisition in preparation for parturition. This finding aligns with Stewart et al. (2022),

who reported that females may be more likely than males to use riskier areas to obtain essential resources. Urban environments can alter seasonal food availability through ornamental plantings, gardens, and purposeful feeding of wildlife (e.g., bait piles, bird feeders), which may supplement resource availability, particularly during seasons when forage is limited (Ditchkoff et al., 2006; Larson et al., 2020). These anthropogenic resources may be especially attractive to females in a nutritionally costly state (e.g., pregnancy) despite the associated risks of using areas closer to human activity. Alternatively, reduced avoidance of impervious surfaces by females may reflect lower predation risk closer to human infrastructure in preparation for parturition (Conner et al., 2016; Michel et al., 2020).

Selection for canopy cover increased with urbanization, indicating that deer in more developed areas may use forest cover within urban green spaces as refuges from human activity and associated disturbances. Wildlife often frequent large residential lots, parks, and other green spaces within developed landscapes, where canopy trees and other vegetation provides critical refuge from human disturbance (Grund et al., 2002; Knopff et al. 2014; Vasquez & Wood, 2022; Fisher et al., 2024; Larson & Sander, 2025; Chapter 1). Increased selection for greater canopy cover in urban environments is often a response to elevated human disturbance and reduced availability of vegetation cover within developed areas (Duarte et al., 2011). In less urbanized settings, deer demonstrated individual variation in selection for canopy cover, particularly during the vegetation growing seasons (Parturition and Late Summer), with many individuals selecting against canopy cover. We suspect that some individuals in less urbanized settings avoided areas of high canopy cover in favor of areas with lower canopy shading and dense vegetation near the ground, which provided greater forage and cover for adults and fawns (Gregovich et al. 2024, Kroeger et al., 2020). During the dormant, leaf-off seasons (Rut/Hunting and Winter/Spring),

individuals in rural areas demonstrated an increased selection for forested areas with greater canopy cover, potentially due to the availability of mast resources like acorns or as a strategy to avoid hunters. This shift in habitat use highlights how wildlife employ flexible resource selection strategies in response to variation in environmental conditions and seasonal resource availability.

Deer navigated complex trade-offs between resource availability and mortality risk associated with roads along the urbanization gradient. As urbanization increased, deer generally avoided roads, whereas in less urbanized areas, some level of vehicle collision risk may be tolerated in exchange for access to greater forage availability in the sunlit roadsides, particularly during energetically demanding periods of the year (e.g., antler growth, late pregnancy, lactation). Trends in selection for areas farther from roads as urbanization increased were consistent across sexes and seasons with one exception, males in more urbanized areas selected for shorter distances to roads during late summer, likely tolerating road proximity to exploit nutrient-rich roadside vegetation to support antler growth. As urbanization decreased, deer displayed greater individual variability in road selection, likely due to the availability of forage in roadside environments, and reduced traffic volumes, which may reduce perceived mortality risk (Darlington et al., 2022; Gregovich et al., 2024). Variation in selection for distance from roads across the gradient highlights the dual role of anthropogenic features. As urbanization increases, roads act as barriers or mortality risks, fragmenting habitat and constraining movement (Fisher et al., 2024); in less urbanized areas, roads can function as key foraging areas with concentrated food resources (Whittington et al., 2022).

In many cases, wildlife species adjust selection behavior within urban landscapes to minimize interactions with humans (Gehrt et al., 2009; Webb et al., 2011; Knopff et al., 2014; Ellington & Gehrt, 2019; Whittington et al., 2022; Chapter 1). Such flexibility has been widely

reported as a key trait that facilitates species persistence in urban settings (Sol et al., 2013; Ritzel & Gallo, 2020; Lambert et al., 2021; Caspi et al., 2022). Our results add to this growing body of literature by demonstrating that white-tailed deer exhibit behavioral plasticity in resource selection to persist across an urbanization gradient. Deer altered their selection in response to intensifying urbanization, demonstrating stronger and more consistent selection for less developed areas as urbanization increased. Reduced individual variation with increasing urbanization can drive homogenization of resource selection, with even generalist species converging on similar resource-use strategies in urban environments. Such convergence likely reflects a reduction in habitat, and indicates that maintaining and connecting diverse green spaces in urban areas can help support variable resource-use strategies across deer and other wildlife species that enable persistence in urbanizing environments.

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TABLE 2.1. Numbers of white-tailed deer included in seasonal resource selection function analysis. Seasonal analyses used data collected during January 2022 to January 2025.

Season	Males	Females
Winter/Spring	67	108
Parturition	78	105
Late Summer	78	103
Rut/Hunting	57	94

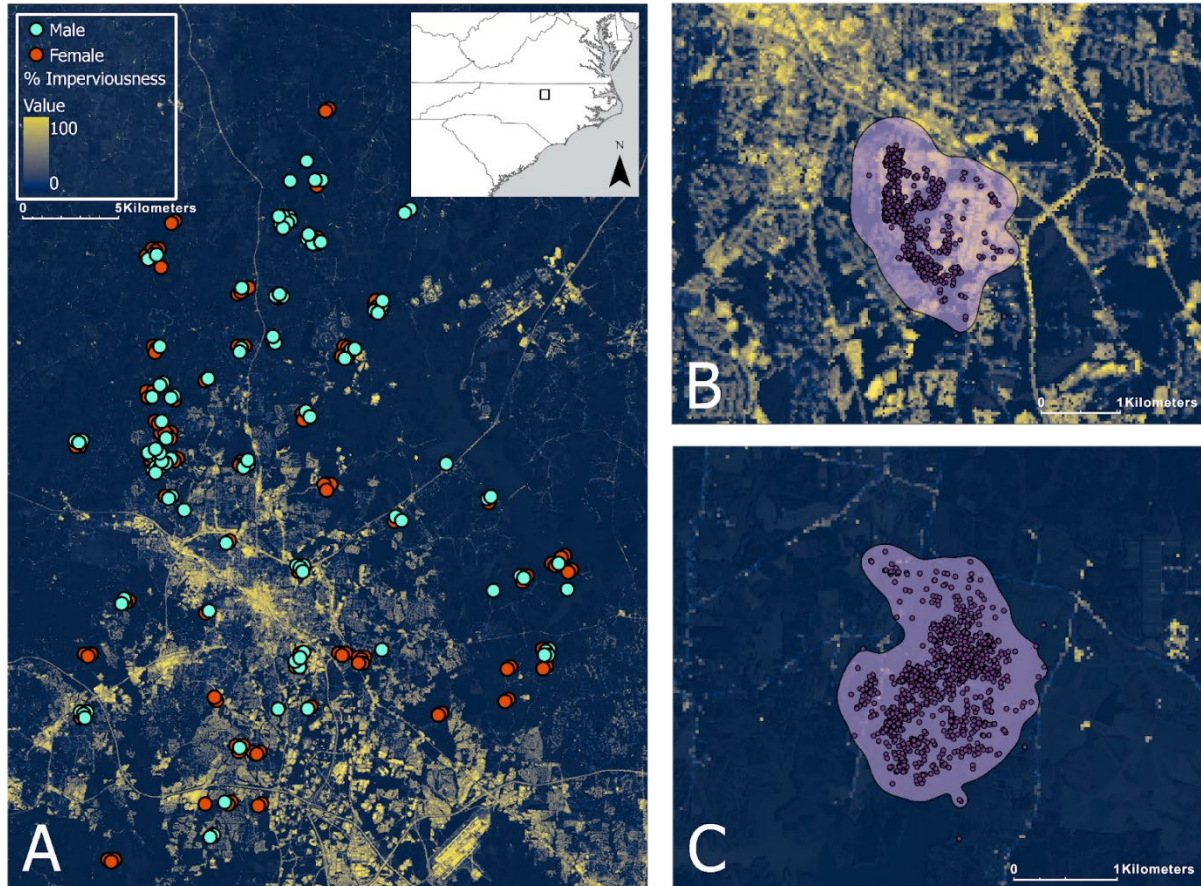


FIGURE 2.1. A) Capture locations (points) for female and male white-tailed deer overlaid on the percent impervious surface raster. The study area included Durham and Orange counties, North Carolina, USA. Urbanness values were calculated for each individual as the mean percent impervious surface in an individual's 99% autocorrelated kernel density estimated (AKDE) range distribution (purple polygon). Panels B and C show GPS locations and AKDEs for B) an individual in a more urban area (urbanness value = 36.59) and (C) an individual in a more rural area (urbanness value = 0.75).

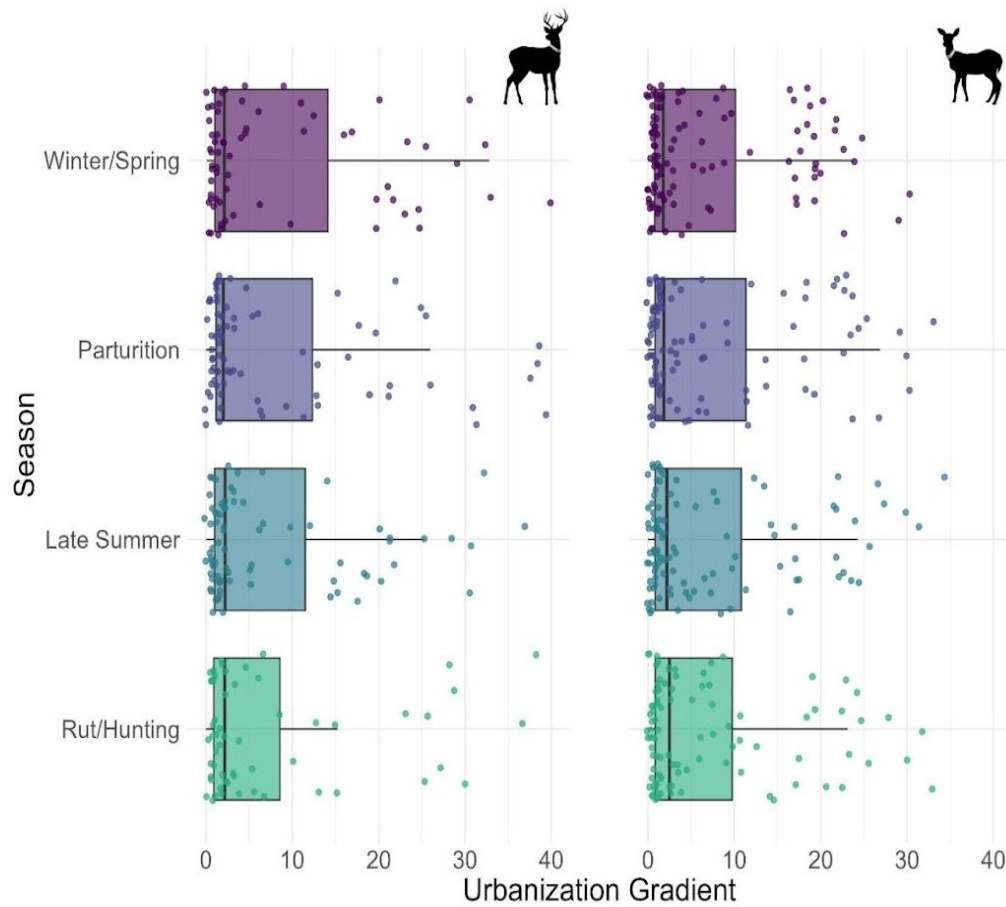


FIGURE 2.2. Urbanness values of male (left) and female (right) white-tailed deer in Durham and Orange counties, North Carolina, USA. Urbanness values were calculated as the mean impervious surface in an individual's 99% autocorrelated kernel density estimated (AKDE) range distribution for each season (See Fig. 2.1 and Methods). Higher urbanness values (urbanization gradient) correspond to more urbanized areas while lower values correspond to less urbanized areas. Box-and-whisker plots denote the median, quartiles, and 1.5 interquartile range. For additional information on AKDE size estimates by sex and season, see Fig. S2.1.

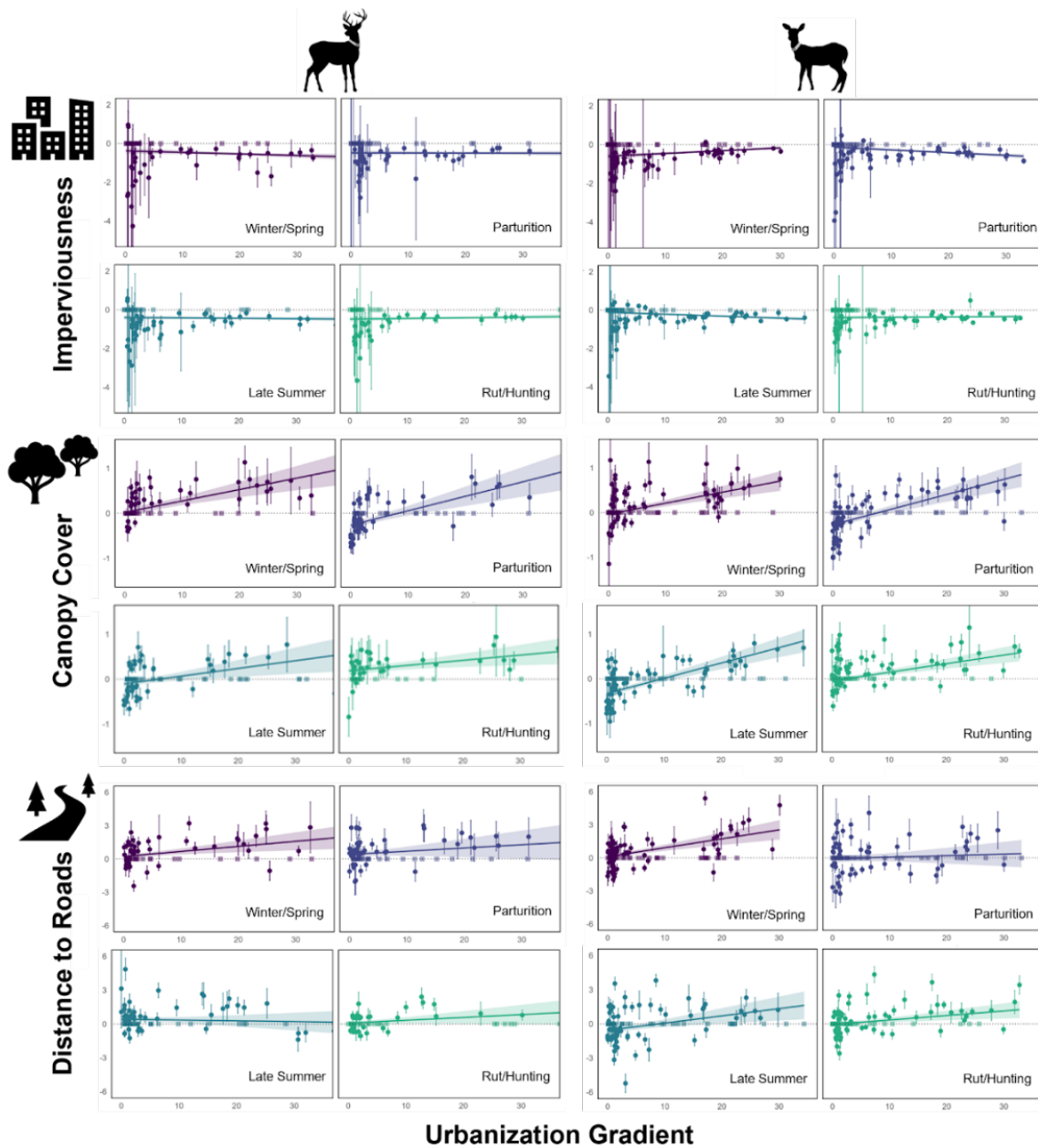


FIGURE 2.3. Seasonal resource selection estimates for male (left) and female (right) white-tailed deer along an urban-rural gradient in Durham and Orange counties, North Carolina, USA. The x-axis represents increasing urbanization (i.e., urbanness values). Solid circles represent selection estimates (95% confidence interval), while squares indicate covariates not included in an individual's top model. Solid trend lines are fitted values as a function of the urbanization gradient (95% confidence interval). For impervious surfaces (imperviousness) and canopy cover, values >0 indicate selection, while values <0 indicate avoidance. For distance to roads, positive values indicate selection for areas farther from roads.

CHAPTER 3: Influences of Urbanization on Survival and Cause-Specific Mortality of White-tailed Deer

ABSTRACT

Landscape changes associated with urbanization can influence survival by altering the relative probability of different causes of mortality. Urbanization can elevate certain risks (e.g., vehicle collisions) while reducing others (e.g., hunter harvest), creating complex patterns in survival along urbanization gradients. We analyzed data from 198 GPS-collared white-tailed deer (*Odocoileus virginianus*; 111 females, 87 males) monitored from 2022-2025 across an urbanization gradient in Durham and Orange counties, North Carolina. Using a Bayesian known-fate survival model, we estimated weekly and annual survival and cause-specific mortality in relation to urbanization, sex, age, weekly movement, dispersal events, and season (harvest and non-harvest). We predicted that: 1) annual survival would increase as urbanization increased due to reduced harvest pressure; 2) vehicle collisions would account for a greater proportion of mortality as urbanization increased; 3) increased weekly movement would negatively influence survival; and 4) weekly survival would be lower for all sex and age classes during the harvest season than in the non-harvest season. Consistent with our predictions, mortality sources significantly shifted across the gradient; however, declines in hunter harvest in more urban areas were balanced by increases in vehicle collisions, resulting in no significant differences in annual survival across the gradient. Weekly survival was lower during the harvest season than during the non-harvest season. Although weekly movement did not influence survival, yearling males had lower weekly survival during dispersal events. Adult male annual survival ranged from 0.45-0.42 along the rural-to-urban gradient, whereas adult female survival ranged from 0.77-0.81. Yearlings experienced higher proportional vehicle collision mortality than adults, with mean

annual survival ranging from 0.44-0.27 for yearling males and 0.82-0.70 for yearling females across the rural-to-urban gradient. Our findings show how urbanization alters the mechanisms driving mortality, revealing a system where substantial changes in multiple mortality sources do not lead to significant changes in survival across an urbanization gradient.

INTRODUCTION

Urbanization can reshape wildlife population dynamics by altering mortality risks, leading to complex changes in survival across urbanization gradients (McKinney 2006, Groffman et al. 2014, Rodewald and Gehrt, 2014, Blouin et al. 2019, Kautz et al. 2022). For example, increased urbanization can reduce hunter harvest, provide novel food subsidies (Duarte et al. 2015, Zepeda et al. 2025), and increase mortality from collisions with vehicles and buildings (Beckmann and Lackey 2008, Van Doren et al. 2021), whereas changes in other mortality sources such as predation may increase, decrease, or remain unaffected (Saalfeld and Ditchkoff 2007, Baker et al. 2008, Piccolo et al. 2010, Eötvös et al. 2018). Many urban-adapted species also make behavioral adjustments to mitigate mortality risks, leading to differing effects of urbanization across species, seasons, sexes, and age classes (Etter et al. 2002, Ritzel and Gallo 2020, Gallo et al. 2022, Moore et al. 2023, Moesch et al. 2024). Evaluating how altered mortality risks counterbalance or compound along urbanization gradients is thus essential for predicting population responses and guiding wildlife management in increasingly human-dominated landscapes.

White-tailed deer (*Odocoileus virginianus*; hereafter deer) populations likely respond to shifting mortality pressures across urbanization gradients as the species is highly adaptable and urban-tolerant, often reaching high population densities in moderately urbanized landscapes (DeNicola et al. 2000, Nielsen and Porter 2011, Urbanek and Nielsen 2013). Deer in urbanized

settings have increased access to novel forage (e.g., gardens, ornamental plantings) and may experience reduced pressures from predation and hunter harvest (Nielsen and Porter 2011, Urbanek and Nielsen 2013). However, urban landscapes still provide risks for deer, particularly through mortality from vehicle collisions (DeNicola and Williams 2008, Ng et al. 2008). Previous studies have documented variation in deer mortality across discrete landscape types (e.g., urban, suburban, exurban, rural; Etter et al. 2002, Harveson et al. 2007, Storm et al. 2007, Wright et al. 2020) and specific life stages (e.g., neonates; Saalfeld and Ditchkoff 2007, Piccolo et al. 2010). Yet, how multiple mortality risks shift along continuous urban-rural gradients remains poorly understood, limiting inferences about the effects of urbanization on cause-specific mortality and survival.

Our goal was to quantify deer survival and evaluate whether cause-specific mortality varies along an urbanization gradient. We estimated weekly and annual survival and cause-specific mortality of male and female yearling and adult white-tailed deer along an urbanization gradient in Durham and eastern Orange counties, North Carolina during 2022-2025. We hypothesized that survival and cause-specific mortality are shaped by interacting effects of urbanization, weekly movement, season, and demographic characteristics. We predicted that: 1) annual survival would increase with increasing urbanization due to reduced harvest pressure; 2) vehicle collisions would account for a greater proportion of mortality as urbanization increased; 3) increased weekly movement would negatively influence survival; and 4) weekly survival would be lower for all sex and age classes during the harvest season than the non-harvest season.

METHODS

Study Area

We conducted this study from 2022 to 2025 in the Piedmont physiographic region of central North Carolina, USA, a region experiencing rapid urbanization (Terando et al. 2014). We captured and monitored deer throughout Durham and eastern Orange counties in North Carolina, though a majority of deer were captured in Durham County (Figure 3.1). The study area (approximately 77,200 ha) was characterized as a subtropical humid climate with gently rolling terrain and a mix of urban, suburban, and rural land use areas. The dominant vegetation cover was hardwood and pine forest types, including mixed hardwood-pine forest (Spooner et al. 2021). The human population of Durham County was approximately 343,628 in 2024, making it the 6th most populated county in North Carolina (U.S. Census Bureau, 2024). The central and southern portions of the study area reflected more urbanized areas characterized by greater levels of impervious surfaces and fragmented patches of forest. The northern part of the study area was less urbanized, and land cover was characterized by mixed forest types, pasture, and agriculture, with low impervious surface cover (Figure 3.1).

Capture and Monitoring

We captured deer over sites baited with corn using either drop nets (Wildlife Capture Services, Flagstaff, AZ, USA) or tranquilizer dart guns with very high frequency telemetry darts (CO2 13mm Rifle, DanInject, Austin, TX, USA; Model 414 RDD, Pneu-Dart, Williamsport, PA, USA; Model F1020D, Advanced Telemetry Systems, Isanti, MN, USA) from tree stands during January-May 2022-2024. We used a combination of Butorphanol tartrate, Azaperone tartrate and Medetomidine hydrochloride (BAM), in 2cc syringes/darts to immobilize deer (Wedgewood Pharmacy, Swedesboro, NJ, USA). Atipamezole and Naltrexone were used to reverse the Medetomidine hydrochloride and Butorphanol tartrate, respectively (Wedgewood Pharmacy). Female capture ceased by the end of April each year to avoid excessive stress on late-term

pregnant individuals prior to parturition. Capture methods and protocols were approved by the North Carolina State University IACUC (IACUC # 21-370). Deer capture and handling was conducted under the authority of the North Carolina Wildlife Resources Commission.

We collared (Model G5-2D; 4-hr mortality delay; Advanced Telemetry Systems) and ear-tagged male and female deer of various classes across an urbanization gradient (Figure 3.1). Collars were programmed to obtain global positioning system (GPS) locations every 2 hours, providing ~12 location fixes daily. Male collars were scheduled to drop off a year after deployment to ensure appropriate fit with neck swelling during only a single rut period after capture. Female collars were scheduled to drop off at the end of the study. Thus, several collared females included data for >1 year. To conserve collar battery, after the first year female collars were reprogrammed to take fixes every 8 hours, providing ~3 location fixes daily.

Individual deer were assigned an age class at the time of capture (fawn, 0-12 months; yearling, 13-24; or adult, >24 months) based on approximate body weight, conformation, and dentition. We attempted to refine age classification between fawns and yearlings using tooth replacement patterns (Severinghaus 1949); however, distinction between these classes were limited due to the third milk premolar being shed during the capture season (Severinghaus 1949), thus rendering its presence or absence unreliable for assigning age. Females >1 year old were implanted with a vaginal implant transmitter (Model M3930U; Advanced Telemetry Systems) to facilitate capture of fawns for an associated study.

Fate Determination

Mortality notifications were triggered 4 hours after the collar stopped moving. Once notified, we recovered the carcass and conducted a field necropsy to determine the cause of mortality. We considered carcass location, condition, presence of subcutaneous hemorrhaging,

tracks or scat, and site specific relevant information when determining the mortality cause. At times, determining the true cause of mortality was challenging when minimal field evidence remained due to a delayed mortality notification. Thus, we specified fates as “unknown” if no soft tissue remained. If the cause of mortality was not apparent and soft tissues were present, samples were taken and submitted to the Wildlife Services Lab at the Southeastern Cooperative Wildlife Disease Study for further analysis. Fate categories included hunter harvest, vehicle collision, and other mortality causes.

Individuals were right-censored if their collar broke off, failed during deployment, or if the individual survived to the end of the study. To account for capture related bias in survival and mortality, we employed a 2-week censor period post-capture before an individual was included in analysis. Thus, analysis began the third week after capture and fates were assigned to the week an event occurred (i.e. death or censoring).

Covariates

Age and season

Our analysis included yearling and adult age classes, where we assigned May 24 as the annual transition date between age classes, corresponding to the median birthdate of neonates across all study years (Lamb et al. In Prep). Seasons were classified as harvest (17 weeks) or non-harvest (35 weeks). The harvest season encompassed 10-Sep through 02-Jan while the non-harvest season encompassed dates outside that range.

Urbanization gradient

We defined a continuous urbanization gradient based on percent impervious surface (Dewitz 2023) to describe where an individual lived along the urban-to-rural continuum (Figure 3.1). Individual ranges were estimated using autocorrelated kernel density estimations (AKDE)

implemented in the ctm package in R version 4.4.1 (Fleming et al. 2015, Fleming and Calabrese 2023, R Core Team 2024), using location data available after the censoring period. Within each individual's 99% AKDE, we calculated the mean percent impervious surface to assign a single value for each individual (hereafter urbanness value). This process avoided subjective classifications (e.g., urban, suburban, rural) and provided a continuous urbanness covariate reflecting an individual's exposure to urbanization in their range distribution. For 2 individuals that survived <3 weeks, we retained all available GPS locations as exclusion of the 2-week censoring period left insufficient points to calculate the AKDE.

Movement

We estimated weekly average hourly movement distances (hereafter movement) for each individual deer using GPS data to include as a time-varying, individual level covariate. To standardize across variable fix rates (2-8 hr), movements were calculated from paired locations 8 hr apart (± 15 min), with distances divided by the exact time between fixes. Unrealistic step lengths (>3 km) and continuous speeds (>1 m/s) were excluded, and the first 2 weeks post-capture were removed to account for capture-related movement bias. We retained all available movement data for 2 individuals that died shortly after the 2-week censor period.

Dispersal

We identified individual dispersal events and included them as a time-varying, individual-level covariate, where weeks of dispersal were coded as 1 and all other weeks as 0. Dispersal was defined as permanent emigration from a natal to adult home range, in which post-dispersal locations did not overlap pre-dispersal locations (Long et al. 2005). Transfer periods were identified using net-squared displacement for individuals exhibiting dispersal-like movement (Bunnefeld et al. 2011). The transfer period generally included the last known data

point within the natal range and the first known data point within the adult range, provided a new range was successfully established. For individuals that died shortly after leaving their natal range or prior to establishing a new range, the transfer period was defined by the last known data point within the natal range and the data point associated with mortality or collar failure.

Urbanness values were adjusted for dispersing individuals to accurately reflect their exposure along the urbanization gradient. For individuals that dispersed and successfully established a new home range, separate urbanness values were calculated for the pre- and post-dispersal ranges. For individuals that dispersed but did not successfully establish a new range, AKDEs were calculated after removing dispersal-associated locations, such that only data from resident home ranges were included, as required for AKDE estimation (Fleming et al. 2015, Fleming and Calabrese 2023). This approach ensured that urbanness values represented stable range use rather than transient dispersal movements.

Analysis

We modelled survival and cause-specific mortality for adult and yearling male and female white-tailed deer using a known-fate survival model in a Bayesian framework. Individuals entered the study at different times, so we implemented staggered entry and left-censoring to account for variation in monitoring start dates (Pollock et al. 1989). We modeled survival and cause-specific mortality on a weekly time scale, and the probability of cause-specific mortality was estimated from individuals that died. For consistency across years, we defined weeks as Sunday-Saturday starting on 23-Jan 2022. For survival, we modelled the state (alive = 1, dead = 0) of individual i in week k (z_{ik}) as a Bernoulli random variable with success probability S_{ik} , the survival probability of individual i in week k . Specifically, for the first to last week for each individual i :

$$z_{ik} \sim \text{Bernoulli}(S_{ik}).$$

We used a logit-link to model survival probability as a function of urbanness, season, sex, age, dispersal status, movement, and interaction effects of sex $\times$ season, urbanness $\times$ season, urbanness $\times$ movement, urbanness $\times$ age, and urbanness $\times$ sex. We included multiple interactions with urbanness to address our principal objectives of testing whether the urbanness effects on survival varied by season, sex, age class, dispersal status, or movement.

For individuals that died, we modelled cause of mortality (hunter harvest, vehicle collision, other mortality) as a categorical random variable with probabilities $\boldsymbol{\pi}_i$. Specifically,

$$y_i \sim \text{Categorical}(\boldsymbol{\pi}_i)$$

where y_i is the mortality cause for individual i and $\boldsymbol{\pi}_i$ is a length 3 vector for each individual describing the probability of mortality due to (1) hunter harvest, (2) vehicle collision, or (3) other mortality. We model $\boldsymbol{\pi}_i$ using multinomial logistic regression that included cause-specific parameters for the effects of urbanness, movement, sex, age, season, and an interaction of urbanness $\times$ movement. We set other mortality as the reference category. Here, π_{i1} , π_{i2} , π_{i3} denote the probability of mortality attributable to (1) hunter harvest, (2) vehicle collision, and (3) other mortality, conditional on the individual dying and $\sum \boldsymbol{\pi}_i = 1.0$. All 3 mortality sources were modelled for the harvest season, but we fixed the probability of hunter harvest to 0.0 in the non-harvest season.

We standardized all covariates (mean = 0, s.d. = 1) and verified that pairwise Pearson's correlation coefficients ($|r|$) were < 0.7 . Models were fit in JAGS (Plummer 2003) using the jagsUI package (Kellner 2024) in R (version 4.4.1, R Core Team 2024) using Markov chain Monte Carlo (MCMC) simulations to obtain posterior distributions. Each model was run for 40,000 iterations across 3 chains, with a 5,000 burn-in and a thinning rate of 10. Model

convergence was verified using trace plots and we verified $R_{hat} < 1.1$ for all parameters. Results are reported as posterior means and the 2.5% and 97.5% quantiles (95% credible intervals; hereafter 95% CI).

We derived several additional metrics as part of the model fitting process. First, we predicted the 4-fate probability simplex for each urbanness value j that consisted of (1) survival (S_j), or mortality due to (2) hunter harvest ($(1 - S_j)\pi_{1j}$), (3) vehicle collision ($(1 - S_j)\pi_{2j}$), or (4) other mortality ($(1 - S_j)\pi_{3j}$). We repeated predictions for each sex and age class in each season to display how weekly survival and cause-specific mortality varied across the urbanization gradient. Second, we derived annual survival and mortality cause probabilities for each sex and age class across urbanness values assuming 35 weeks for the non-harvest season followed by 17 weeks for the harvest season, approximating the duration of the harvest season in our study area (first Saturday in September until 2 January of the following year). Annual survival probabilities are the product of weekly survival probabilities, while cumulative mortality probabilities reflect competing risks that require an individual to survive to week k (i.e., avoid all other risks) then die due to a specific cause in week k . As with weekly probabilities, annual probabilities reflect the 4-fate probability simplex that requires individuals either (1) survive, or die due to (1) hunter harvest, (2) vehicle collision, or (3) other mortality causes within the year (i.e., probabilities sum to 1.0). On average, yearling males that successfully dispersed and established a new home range took 12.7 days (~2 weeks). Thus, we derived annual survival and cause-specific mortality probabilities for yearling males assuming 35 weeks for the non-harvest season, 15 weeks for the harvest season, and 2 weeks of the harvest season with dispersal activated. This allowed us to account for risk associated with dispersal when estimating annual survival and mortality in yearling males. Derived metrics were calculated during each MCMC

iteration to propagate uncertainty in estimates and are summarized as posterior means and 95% CI.

RESULTS

Capture and Monitoring

We monitored 202 white-tailed deer (111 females; 91 males) across an urbanization gradient for varying durations from January 2022 through May 2025 (175 weeks). We captured 119 individuals via drop nets and 83 individuals via tranquilizer darts. After data cleaning, analysis included 198 individuals (111 females; 87 males; Table 3.1). Four males were excluded from the analysis because they were collared as fawns and died before reaching the yearling age class, which was the starting point for the survival analysis. Individual urbanness values ranged from 0.00-38.71 ($\bar{x} = 7.60$, $SD = 9.37$), encompassing deer within Durham city limits to rural areas primarily north of the city of Durham (Figure 3.1). Of the 198 individuals analyzed, 88 had known mortality fates and 110 were right-censored (Table 3.1). Hunter harvest (35) and vehicle collision (33) were the dominant causes of mortality (Table 3.1; Figure S3.1, available in Supporting Information). Other mortality (20) included: depredation (individual harvested outside of regular season under a depredation permit; 1), disease (2), malnutrition (1), poaching (1), predation (3), and unknown (12). Individuals were right-censored due to collar breakoffs (57), collar failure (23), and end of the study (30; Table 3.1). Male mortality was skewed to later in the year, with most vehicle collisions and hunter harvests occurring from October to December (Figure S3.1). Female mortality, however, was more consistent throughout the year (Figure S3.1). Hunter harvests were limited to the harvest season, whereas vehicle collisions and other mortality contributed to mortality year-round (Figure S3.1).

Covariate Effects

The effects of urbanization on weekly survival differed between seasons (0.60; 95% CI 0.11 - 1.10; Figures 3.2-3.4). In the non-harvest season, weekly survival showed a non-significant decline with increasing urbanization (-0.26; 95% CI -0.92 - 0.43), whereas during the harvest season weekly survival showed a non-significant increase with increasing urbanization (0.34; 95% CI -0.43 - 1.13). In both seasons, the proportion of total mortality attributed to vehicle collisions increased with urbanization (Figures 3.2-3.4). The negative effect of urbanization on survival was stronger for males than for females, but the difference between sexes was not significant (-0.32; 95% CI -0.85 - 0.21; Figures 3.2-3.4). Similarly, the interaction between urbanization and age-class was not significant (0.17; 95% CI -0.41 - 0.74; Figure 3.2). Overall, during the non-harvest season, other mortality was low and vehicle collision mortality displayed non-significant increases with increasing urbanization. In the harvest season, increased vehicle collision mortality partially or fully offset reductions in hunter harvest mortality as urbanization increased, resulting in non-significant net changes in weekly survival across the urbanization gradient (Figures 3.2-3.4; Figures S3.2-S3.3).

Weekly survival was lower during the harvest season than during the non-harvest season (-0.68; 95% CI -1.36 - -0.01), with stronger differences for males than for females (interaction effect: -1.72; 95% CI = -2.80 - -0.70; Figures 3.2-3.4). We did not detect a difference in weekly survival between age classes; however, the proportion of total mortality attributed to vehicle collisions was significantly higher for yearlings than for adults (Figures 3.2-3.4). Mortality from other mortality causes (non-harvest, non-vehicle) remained low but was greater for males than females (Figures 3.2-3.4).

We did not detect an effect of movement distances on weekly survival (-0.02; 95% CI -0.19 - 0.16); however, there was moderate evidence that increased movement increased the

proportion of total mortality attributed to vehicle collisions and hunter harvest, compared to other mortality (reference category; Figure 3.2). The interaction of movement and urbanness on weekly survival was non-significant (0.13; 95% CI -0.08 - 0.34), but the direction of estimates indicated weekly survival may decline with greater movement in less urbanized areas and increase with greater movement in more urbanized areas. In other words, the direction of the estimate indicated that deer in rural areas experienced higher mortality with increased movement, whereas deer in urban areas experienced lower mortality with increased movement (Figures 3.2 and S3.4).

Dispersal by yearling males had a significant negative effect on weekly survival (-1.56; 95% CI -2.76 - -0.19; Figure 3.2). On the probability scale, weekly survival declined from 0.97 (0.94 - 0.99) for non-dispersing yearling males during the harvest season to 0.86 (0.66 - 0.97) for dispersing yearling males (Figure 3.5). Successful dispersal events typically lasted ~2-weeks, leading to a predicted 2-week decline in survival from 0.94 (0.88 - 0.98) to 0.75 (0.43 - 0.94) for dispersing individuals (Figure 3.5). Extrapolated to annual survival at average covariate values, a 2-week dispersal period reduced yearling male survival from 0.49 (0.24 - 0.75) to 0.40 (0.14 - 0.68; Figure 3.5).

Weekly Survival and Mortality Probabilities

Weekly survival for adult males ranged from a low of 0.96 (95% CI 0.94 - 0.97) in less urbanized areas during the harvest season to a high of 0.99 (95% CI 0.99 - 1.00) in the same areas during the non-harvest season (Figures 3.3-3.4). For yearling males, weekly survival ranged from 0.96 (95% CI 0.85 - 0.99) in more urbanized areas during the harvest season to 0.99 (95% CI 0.99 - 1.00) in less urbanized areas during the non-harvest season (Figures 3.3-3.4).

Weekly survival for adult and yearling females was ≥ 0.99 in both seasons and across the gradient (Figures 3.3-3.4).

Weekly hunter harvest probabilities were greatest for adult males in rural areas (0.03; 95% CI 0.02 - 0.05) and declined to <0.01 for adult males in urbanized areas (Figure 3.3). Weekly harvest probabilities remained <0.01 for all other sex and age classes. Weekly vehicle collision probabilities were greatest for yearling males in urbanized areas during the harvest season (0.04; 95% CI 0.01 - 0.14) and remained elevated during the non-harvest season (0.03; 95% CI 0.01 - 0.10). Adult males in urbanized areas also had high weekly vehicle collision probabilities during the harvest (0.02 95% CI 0.01 - 0.05) and non-harvest (0.02; 95% CI 0.01 - 0.05) seasons (Figures 3.3-3.4). Weekly vehicle collision probabilities were <0.01 for females, except for yearling females in the most urbanized areas during the non-harvest season (Figures 3.3-3.4). Weekly other mortality probabilities never exceeded 0.01 and were frequently <0.005 (Figures 3.3-3.4). Mean estimates with credible intervals are provided in Figures S3.2-S3.3.

Annual Survival and Mortality Probabilities

Predicted annual survival probabilities (35 weeks of non-harvest and 17 weeks of harvest) varied greatly between sexes but showed minimal variation across the urbanization gradient due to offsetting mortality causes (Figure 3.6; Figures S3.5-S3.6). For adult males, annual survival estimates ranged from 0.45 (95% CI: 0.29 - 0.61) to 0.42 (95% CI: 0.09 - 0.78) as urbanization increased (Figure 3.6, Figure S3.6). In less urbanized areas, the probability of hunter harvest was 0.36 (95% CI 0.22 - 0.51), which was the majority of total mortality (0.55; 95% CI 0.39 - 0.71). In more urbanized areas, the probability of vehicle collision was 0.54 (95% CI 0.20 - 0.88), nearly the entirety of total mortality (0.58; 95% CI 0.22 - 0.91) (Figure 3.6).

Mean annual survival of yearling males declined as urbanization increased, but the declines were not statistically significant, ranging from 0.44 (95% CI: 0.20 - 0.70) to 0.27 (95% CI 0.01 - 0.79) (Figure 3.6; Figure S3.6). For yearling males, the annual probability of vehicle collision rose sharply with urbanization, increasing from 0.28 (95% CI: 0.10 - 0.53) in less urbanized areas to 0.72 (95% CI: 0.20 - 0.99) in more urbanized areas (Figure 3.6). Hunter harvest probability for yearling males was 0.13 (95% CI 0.02 - 0.33) in the least urbanized areas (Figure 3.6).

Annual survival of adult females remained similar along the gradient; as urbanization increased, estimates ranged from 0.77 (95% CI 0.68 - 0.84) to 0.81 (95% CI 0.51 - 0.96) (Figure 3.6; Figure S3.6). In more urbanized areas, total mortality (0.19; 95% CI 0.03 - 0.49) consisted almost exclusively of vehicle collisions (0.19; 95% CI 0.03 - 0.48; Figure 3.6). In contrast, in less urbanized areas, hunter harvest (0.09; 95% CI 0.04 - 0.14) and other mortality causes (0.06; 95% CI 0.02 - 0.11) were more notable (Figure 3.6).

Mean annual survival of yearling females declined as urbanization increased, but the declines were not statistically significant, ranging from 0.82 (95% CI: 0.63 - 0.93) to 0.70 (95% CI 0.09 - 0.98) (Figure 3.6; Figure S3.6). The predominant cause of mortality for yearling females across the urbanization gradient was vehicle collision, which increased from 0.14 (95% CI: 0.05 - 0.31) in less urbanized areas to 0.30 (95% CI: 0.02 - 0.91) in more urbanized areas (Figure 3.6).

DISCUSSION

As urbanization increased, deer mortality shifted from hunter harvest to vehicle collisions but survival remained relatively constant, contrary to our prediction that survival would be highest in more urbanized settings. In less urbanized areas, hunter harvest remained a primary

cause of mortality, particularly for adult and male deer (Nelson and Mech 1986, Fuller 1990, Van Deelen et al. 1997, Brinkman et al. 2004, Wiskirchen et al. 2023), reflecting greater hunting opportunities and fewer restrictions than in urban landscapes. In contrast, in more urbanized areas, higher human and traffic densities made vehicle collisions a major source of mortality for deer year-round (Etter et al. 2002, Brinkman et al. 2004, Porter et al. 2004, Ng et al. 2008, Found and Boyce 2011), supporting our prediction that vehicle collisions replaced hunting as the primary mortality source in more urbanized areas (Hill et al. 2020). Together, these mortality sources offset one another, producing minimal net effect on overall survival along the urbanization gradient (Kautz et al. 2022). These two anthropogenic mortality sources differ in their selectivity: hunter harvest often removes more mature males, whereas vehicle collisions affect both sexes and age classes, with yearlings being especially vulnerable. Such differences can influence population dynamics even when overall survival remains stable (Hill et al. 2020).

Male survival in less urbanized landscapes remained consistent with previous studies where survival was shaped by hunter harvest, whereas survival in more urbanized areas remained similar due to offsetting mortality from increased vehicle collisions. Annual survival for adult males in less urbanized areas (~ 0.45) was comparable to previous estimates for older males in rural settings (generally 0.39–0.47; Nelson and Mech 1986, Fuller 1990, Wiskirchen et al. 2023). However, other studies have reported higher survival estimates for adult males across various age classes (0.50–0.63; Bowman et al. 2007), with hunter harvest being the dominant source of mortality across all studies. Yearling male survival in less urbanized areas (~ 0.44) was consistent with previous estimates for yearling males in rural environments (0.41–0.46; Nelson and Mech 1986, Fuller 1990), yet considerably lower than estimates reported by Bowman et al. (2007; 0.82), due to selective harvest criteria that restricted the harvest of <2.5 -year-old males to

evaluate the effectiveness of the Quality Deer Management paradigm (Bowman et al. 2007). In more urbanized areas, we showed that annual survival for adult (0.42) and yearling (0.27) males was much lower than previously estimated in suburban Chicago (0.83; Etter et al. 2002). Vehicle collision mortality was substantially higher in our study (>0.50 in urban areas) than reported by Etter et al. (2002; 0.17), which may reflect differences in sampling deer in suburban-urban landscapes (herein) versus urban forest preserves (Etter et al. 2002). In summary, increased urbanization did not lead to higher male annual survival as we predicted even though urban greenspaces, parks, and other protected areas provided refuge from hunter harvest.

In contrast to our predictions and prior studies (Etter et al. 2002), female survival remained consistent across the urbanization gradient, highlighting that female deer face low risk from hunter harvest and that urban environments are not effective refuges from vehicle collision risk. In less urbanized areas, adult and yearling female survival was 0.77 and 0.82, respectively, consistent with previous studies reporting values between 0.68 and 0.89 (Nelson and Mech 1986, Van Deelen et al. 1997, Brinkman et al. 2004, Kilgo et al. 2016; Haus et al. 2020, Wiskirchen et al. 2023), and indicating that female survival may remain relatively similar across less urbanized landscapes. In more urbanized areas in our study, annual survival was 0.81 for adult females and 0.70 for yearling females, both within the range previously reported for females in urban environments (0.62-0.89; Etter et al. 2002, Porter et al. 2004). Previous studies have demonstrated that adult female white-tailed deer exhibit relatively low variation in survival across space and time (Patterson et al. 2002, Chitwood et al. 2015). Consistent with these findings, our results indicate that adult female survival remained stable along the urbanization gradient, likely reflecting behavioral and spatial-use strategies that minimize exposure to vehicle collisions. Additionally, sex-specific harvest bias favoring males may further buffer female

survival, especially in less urbanized landscapes where hunting is common (Van Deelen et al. 1997). Survival across the gradient was lower during the harvest season than during the non-harvest season for males (Van Deelen et al. 1997) and adult females, supporting our prediction that survival would be lower during the harvest season than during the non-harvest season. The proportion of total mortality attributed to vehicle collisions was significantly higher for yearlings than adults, indicating greater vulnerability of younger individuals that may be less experienced or less adept at avoiding vehicles than older deer (Kautz et al. 2022). Demographic differences in survival may arise from variation in movement and dispersal tendencies that increase exposure to mortality risks in yearlings, particularly vehicle collisions in urban areas (Zollner and Lima 2005, Shaw et al. 2014, Kautz et al. 2022, Chapter 1).

Dispersal exerts a greater effect on yearling male survival than changes in movement patterns within a home range, highlighting the elevated risks when leaving familiar areas. Yearling males that dispersed experienced significantly lower survival than their non-dispersing counterparts (Zollner and Lima 2005, Shaw et al. 2014), whereas weekly movement did not influence survival of any sex or age class. Although recent studies have demonstrated that dispersal in white-tailed deer may not be inherently risky (Haus et al. 2019, Long et al. 2021), dispersal is generally associated with elevated mortality risk, especially where individuals traverse unfamiliar landscapes with greater road density and human presence (Peterson et al. 2017). Contrary to our prediction that increased movement would reduce survival, weekly movement did not directly influence weekly survival. It is possible that behavioral adjustments, such as shifts in activity timing, mitigated mortality risk for deer in urbanized areas despite increased movement (Gallo et al. 2022; Chapter 1). Although not a significant relationship, deer in less urbanized areas experienced higher mortality with increased movement and deer in more

urbanized areas experienced lower mortality with increased movement. These contrasting relationships likely reflect differences in how deer encounter risk with movement depending on location along the gradient. For instance, in less urbanized areas, greater movement may increase exposure to hunters, particularly when individuals cross property boundaries during the harvest season. In contrast, in more urbanized areas, increased movement may help deer navigate fragmented habitat patches by using disjunct green spaces and taking circuitous routes to avoid highly trafficked roads.

The effects of urbanization on survival reflect how human land use can shape population dynamics and highlight the balance deer and other wildlife must often strike between accessing resources and avoiding risks in urban systems (Hill et al. 2020). Understanding the dynamics associated with survival and causes of mortality is critical for anticipating how continued urban expansion will influence populations of deer and other wildlife. Deer management in urban settings remains a challenge as firearm restrictions, smaller land parcels, and public safety concerns limit the use of hunting as a management tool (Kilpatrick et al. 2010, Ford et al. 2025). Alternative management strategies are often limited in feasibility, effectiveness, and/or public acceptance (Desrochers et al. 2025), ultimately leaving vehicle collisions as a primary driver of deer mortality in these areas (Bissonette et al. 2008, Ng et al. 2008, Found and Boyce 2011).

CONSERVATION IMPLICATIONS

Managing white-tailed deer across urbanization gradients presents a challenge as mortality sources shift from hunter harvest in less urbanized areas to vehicle collisions in more urbanized landscapes. Although this transition in mortality sources across the gradient was expected, the nearly complete offset between hunting and vehicle related mortality, resulting in no net change in overall survival, highlights the importance of accounting for the urbanization

gradient in management planning. The relatively stable adult and yearling survival across the gradient indicates that other vital rates (e.g., reproduction, neonate survival) may play an influential role in shaping deer densities in urbanized landscapes, and quantifying those relationships will be important to predicting population-level responses to urbanization. Management efforts to reduce deer-vehicle collisions (e.g., wildlife underpasses, lowered speed limits) will benefit from accounting for the increased vulnerability of yearling males during dispersal and the increased risk for all individuals in urbanized areas where reduced habitat connectivity may heighten collision risk. Overall, integrating how multiple mortality sources shift with urbanization into management strategy development will improve the effectiveness and adaptability of deer population management in urbanizing regions.

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Table 3.1. Summary of monitored individuals and fates during the study. Counts are separated by sex and age class at the time of fate. Primary causes of mortality include hunter harvest, vehicle collision, and other mortality. The other mortality category includes depredation, disease, malnutrition, poaching, predation, and unknown causes. Depredation represents an individual harvested outside of harvest season under a depredation permit. Disease and malnutrition designations were determined by the Southeastern Cooperative Wildlife Disease Study, who conducted detailed post-necropsy analyses in uncertain cases. Poaching refers to an adult male harvested illegally outside of the harvest season. Unknown cases represent collared individuals whose cause of death could not be determined. Right-censored individuals include those whose collars broke off as programmed (Breakoff), collars that failed prematurely (Collar Failure), and individuals still collared at the end of the study when monitoring ceased (End of Study). All right-censored individuals were alive at the time monitoring ended and thus had no confirmed mortality.

Fate	Male		Female		Total
	Adult	Yearling	Adult	Yearling	
Hunter Harvest	22	2	11	0	35
Vehicle Collision	7	11	14	1	33
Other:					
Depredation	0	0	1	0	1
Disease	0	0	2	0	2
Malnutrition	0	0	1	0	1
Poaching	1	0	0	0	1
Predation	0	1	2	0	3
Unknown	6	1	5	0	12
Right Censored:					
Breakoff	20	8	29	0	57
Collar Failure	4	4	13	2	23
End of Study	0	0	30	0	30
Total	60	27	108	3	198

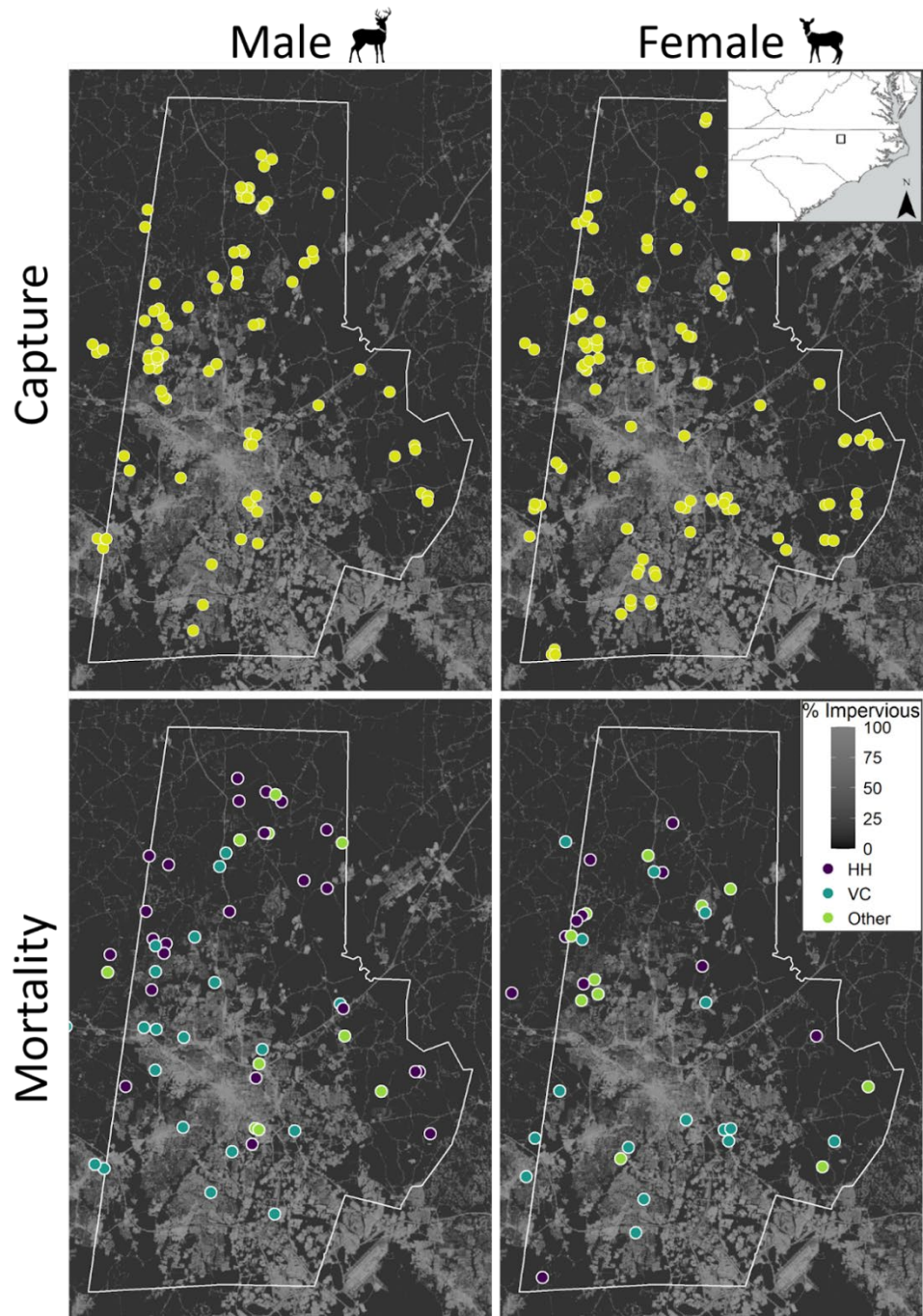


Figure 3.1. Capture (top) and mortality (bottom) locations of male and female white-tailed deer overlaid on a percent impervious surface raster to illustrate the urbanization gradient. Mortality causes are color-coded as hunter harvest (HH, purple), vehicle collision (VC, blue), and other (green). The study area is Durham County, North Carolina, USA.

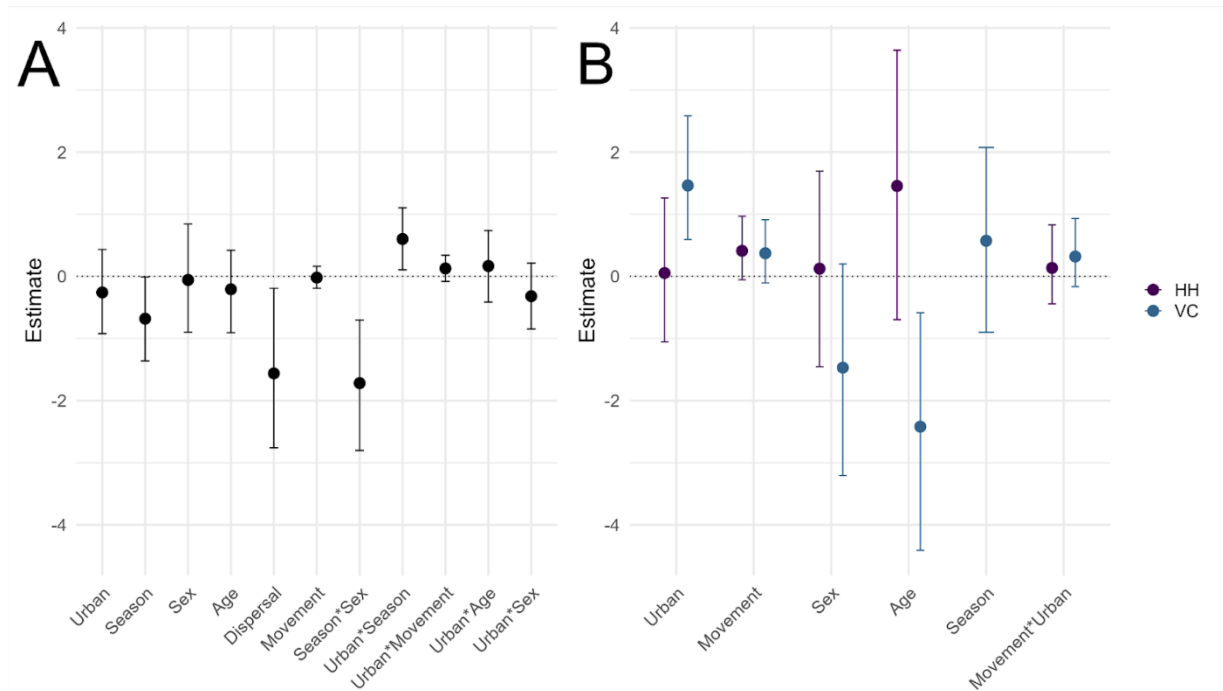


Figure 3.2. Parameter estimates for (A) survival and (B) cause-specific mortality. The reference category for cause-specific mortality was set to “other” mortality, with estimates shown for hunter harvest (HH) and vehicle collision (VC).

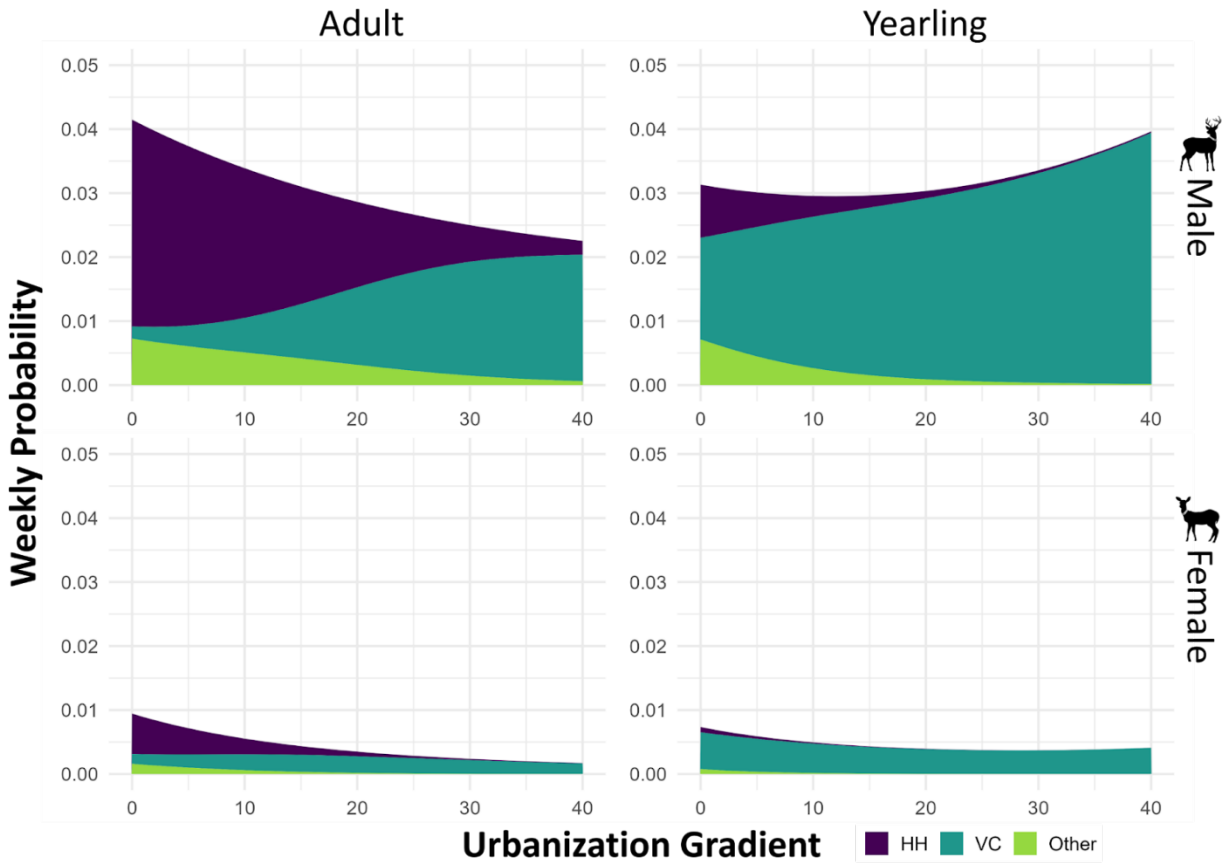


Figure 3.3. Weekly cause-specific mortality probabilities for adult and yearling male and female white-tailed deer during the harvest season. Different colors represent distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations. Figures that include credible intervals are provided in Appendix C Figure S3.2.

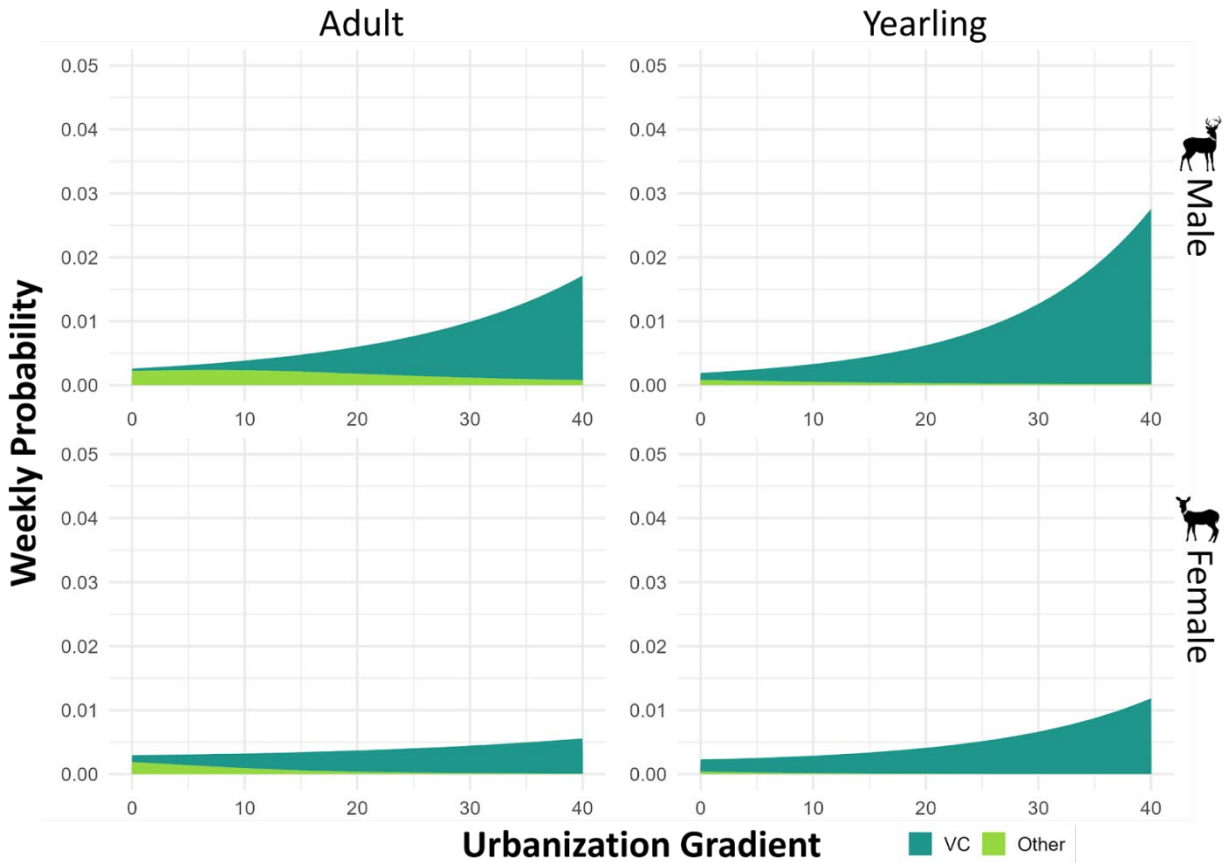


Figure 3.4. Weekly cause-specific mortality probabilities for adult and yearling male and female white-tailed deer during the non-harvest season. Different colors represent distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations. Figures that include credible intervals are provided in Appendix C Figure S3.3.

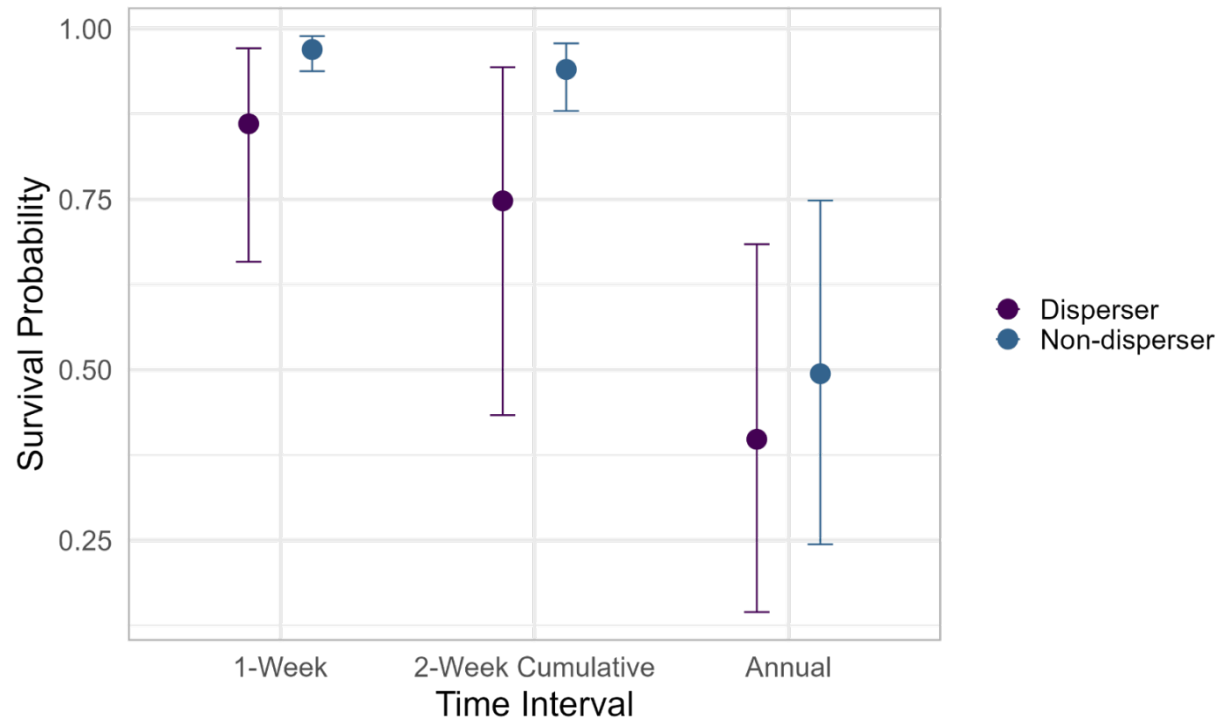


Figure 3.5. Survival probability for yearling males that dispersed (purple) and did not disperse (blue) at 1-week, 2-week cumulative, and annual time intervals. Estimates represent individuals at the mean urbanization gradient value ($\sim 7.6\%$ impervious surface within the home range). All dispersing individuals in this study were yearling males with most dispersing in the fall ($n = 13$) and a few dispersing in the spring ($n = 3$).

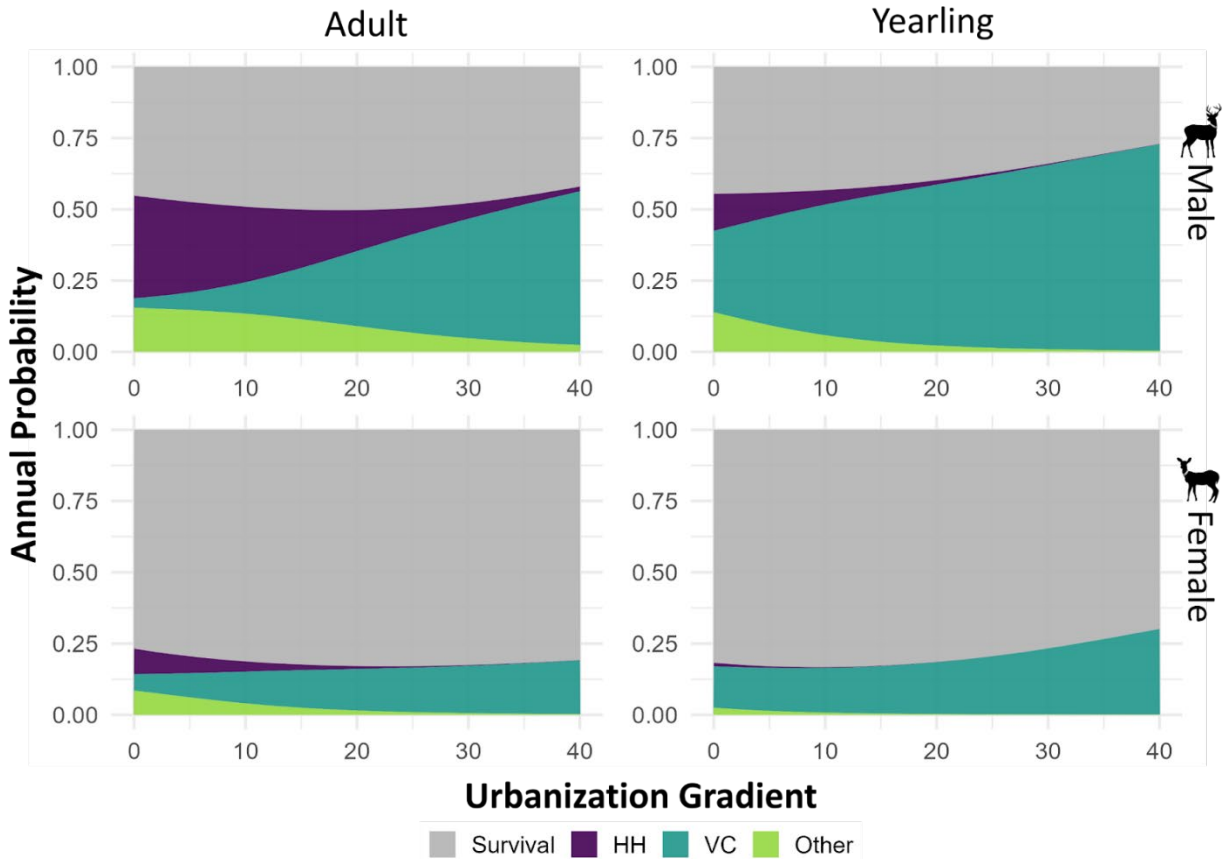


Figure 3.6. Annual survival and cause-specific mortality probabilities for adult and yearling male and female white-tailed deer. Different colors represent survival and distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations. Figures that include credible intervals are provided in Appendix C Figure S3.5 and S3.6.

APPENDICES

Appendix A: Chapter 1 Supplemental Tables and Figures.

Appendix B: Chapter 2 Supplemental Tables and Figures.

Appendix C: Chapter 3 Supplemental Tables and Figures.

Appendix A

TABLES

Supplement 1.1: Description of covariates.

Supplement 1.2: A priori HMM models, equations, and associated hypotheses

Supplement 1.3: State-dependent step and angle concentration parameters from 2-state HMMs for each seasonal and sex-specific groups.

Supplement 1.4: A priori iSSF models, equations, and associated hypotheses.

Supplement 1.5: Regression coefficients for transition probabilities for state 1 (exploratory) and state 2 (encamped) for each seasonal and sex-specific groups.

Supplement 1.6: Regression coefficient estimates for each seasonal and sex-specific group derived from the top integrated step selection model (7).

Supplement 1.7: Initial state distributions from 2-state HMMs for each seasonal and sex-specific groups.

FIGURES

Supplement 1.1: Plotted coefficient estimates from the top iSSF model (Model 7) for each seasonal and sex-specific groups.

TABLE S1.1. Description and source of landscape covariates.

Variable Name	Description	Source
% Impervious Surface	Raster file; 30 m pixel resolution; range: 0-100%	National Land Cover Database, 2021
% Canopy Cover	Raster file; 30 m pixel resolution; range: 0-100%	National Land Cover Database, 2021
Distance to Roads	Vector files; primary & secondary roadways	United States Census Bureau, TIGER/Line, 2023 & North Carolina Department of Transportation, 2024

TABLE S1.2. A priori HMM models, equations, and associated hypotheses. The variable “URBAN” is a continuous variable representing the urbanness value of an individual that captures the spatial effect of the urbanization gradient. It is calculated as the mean impervious surface value of an individual’s range distribution. Harmonic sine and cosine terms (st, ct, s2t, c2t, s3t, c3t, s4t, c4t) model cyclic patterns in activity over a 24-hour period. First order harmonics (st, ct) capture basic diel rhythms while higher order harmonics (2-4) allow for more complicated patterns with multimodal activity peaks.

Model	Equation	Hypothesis
Null	~ 1	Activity is the same for all individuals no matter what.
1	$\sim st + ct + s2t + c2t + s3t + c3t + s4t + c4t$	Activity varies by time of day and is similar for all individuals along the gradient.
2	$\sim URBAN + st + ct + s2t + c2t + s3t + c3t + s4t + c4t$	Activity varies by time of day and proportion of time in exploratory state varies by location on gradient.
3	$\sim st + ct + s2t + c2t + s3t + c3t + s4t + c4t + st:URBAN + ct:URBAN + s2t:URBAN + c2t:URBAN + s3t:URBAN + c3t:URBAN + s4t:URBAN + c4t:URBAN$	Activity levels are the same however, the timing of activity varies by location on the gradient.
4	$\sim URBAN + st + ct + s2t + c2t + s3t + c3t + s4t + c4t + st:URBAN + ct:URBAN + s2t:URBAN + c2t:URBAN + s3t:URBAN + c3t:URBAN + s4t:URBAN + c4t:URBAN$	How much and when individuals are active varies by location on the gradient.

TABLE S1.3. State-dependent step (Gamma distribution) and angle concentration (Von Mises distribution) parameters from 2-state HMMs for each seasonal and sex-specific groups.

Group	State	Step Mean (m)	Step SD	Turn Angle Concentration
Female Dormant	Exploratory	254.64	185.28	0.006
	Encamped	50.91	42.89	0.001
Female Growing	Exploratory	199.92	150.41	0.002
	Encamped	43.29	33.04	0.006
Male Dormant	Exploratory	357.86	304.98	0.010
	Encamped	49.59	42.00	0.002
Male Growing	Exploratory	254.92	211.22	0.024
	Encamped	54.57	45.61	0.001

TABLE S1.4. A priori iSSF models, equations, and associated hypotheses. The variable “URBAN” is a continuous variable representing the urbanness value of an individual that captures the spatial effect of the urbanization gradient. It is calculated as the mean impervious surface value of an individual’s range distribution. The “state” variable distinguishes between the two behavior states (exploratory, encamped). Movement parameters include step length (sl), log transformed step length (log_sl), and cosine of turning angle (cos_ta). Landscape covariates include impervious surface (IS_*), canopy cover (CC_*), and distance to road (DTR_*), each measured either at the start (*_S) of each step (reflecting movement decisions) or at the end (*_E) of each step (reflecting resource selection).

Model	Equation	Hypothesis
1	~ state:(cos_ta + sl + log_sl)	Deer movement varies solely by state; there are no effects of landscape, state, or the gradient on selection.
2	~ state:(cos_ta + sl + log_sl) + IS_S:(cos_ta + sl + log_sl) + CC_S:(cos_ta + sl + log_sl) + DTR_S:(cos_ta + sl + log_sl) + IS_E + CC_E + DTR_E	Deer movement varies by state and landscape; selection is solely influenced by landscape; relationships do not vary by location on the gradient.
3	~ state:(cos_ta + sl + log_sl) + IS_E + CC_E + DTR_E + state:(IS_E + CC_E + DTR_E)	Deer movement varies by state; selection varies by state and landscape; relationships do not vary by location on the gradient.
4	~ state:(cos_ta + sl + log_sl) + IS_S:(cos_ta + sl + log_sl) + CC_S:(cos_ta + sl + log_sl) + DTR_S:(cos_ta + sl + log_sl) + IS_E + CC_E + DTR_E + state:(IS_E + CC_E + DTR_E)	Deer movement and selection varies by state and landscape; but relationships do not vary by location on the gradient.
5	~ state:(cos_ta + sl + log_sl) + URBAN:(cos_ta + sl + log_sl) + IS_E + CC_E + DTR_E + URBAN:(IS_E + CC_E + DTR_E)	Deer movement varies by state and location on the gradient; selection varies by landscape and location on the gradient.
6	~ state:(cos_ta + sl + log_sl) + URBAN:(cos_ta + sl + log_sl) + IS_S:(cos_ta + sl + log_sl) + CC_S:(cos_ta + sl + log_sl) + DTR_S:(cos_ta + sl + log_sl) + IS_E + CC_E + DTR_E + URBAN:(IS_E + CC_E + DTR_E)	Deer movement varies by state, landscape, and location on the gradient; while selection varies by landscape and location on the gradient and does not vary by state.
7	~ state:(cos_ta + sl + log_sl) + URBAN:(cos_ta + sl + log_sl) + IS_S:(cos_ta + sl + log_sl) + CC_S:(cos_ta + sl + log_sl) + DTR_S:(cos_ta + sl + log_sl) + IS_E + CC_E + DTR_E + URBAN:(IS_E + CC_E + DTR_E) + state:(IS_E + CC_E + DTR_E)	Deer movement and selection varies by state, landscape, and location on the gradient.

TABLE S1.5. Regression coefficients for transition probabilities for state 1 (exploratory) and state 2 (encamped) for each seasonal and sex-specific groups. The variable “URBAN” is a continuous variable representing the urbanness value of an individual that captures the spatial effect of the urbanization gradient. It is calculated as the mean impervious surface value of an individual’s range distribution. Harmonic sine and cosine terms (st, ct, s2t, c2t, s3t, c3t, s4t, c4t) model cyclic patterns in activity over a 24-hour period. First order harmonics (st, ct) capture basic diel rhythms while higher order harmonics (2-4) allow for more complicated patterns with multimodal activity peaks.

Female Dormant	Covariate	Estimate	SE	95% CI	Estimate	SE	95% CI
		(1→2)			(2→1)		
	Intercept	-0.82	0.04	[-0.89, -0.75]	0.44	0.04	[0.36, 0.52]
	URBAN	0.09	0.02	[0.04, 0.13]	-0.06	0.04	[-0.14, 0.02]
	st	0.27	0.03	[0.21, 0.33]	-0.63	0.05	[-0.74, -0.52]
	ct	-0.35	0.03	[-0.40, -0.29]	0.82	0.03	[0.77, 0.87]
	s2t	-0.84	0.03	[-0.90, -0.78]	0.39	0.03	[0.33, 0.45]
	c2t	1.19	0.03	[1.14, 1.25]	-1.61	0.05	[-1.71, -1.52]
	s3t	0.54	0.02	[0.49, 0.58]	0.24	0.04	[0.16, 0.31]
	c3t	-0.64	0.03	[-0.69, -0.58]	0.49	0.03	[0.43, 0.55]
	s4t	0.37	0.03	[0.32, 0.42]	-0.28	0.03	[-0.35, -0.22]
	c4t	-0.17	0.02	[-0.21, -0.12]	0.55	0.04	[0.48, 0.62]
	URBAN:st	0.01	0.03	[-0.06, 0.07]	0.05	0.06	[-0.07, 0.17]
	URBAN:ct	-0.05	0.03	[-0.12, 0.01]	0.47	0.03	[0.41, 0.54]
	URBAN:s2t	-0.11	0.03	[-0.18, -0.05]	0.03	0.03	[-0.03, 0.09]
	URBAN:c2t	-0.08	0.03	[-0.13, -0.02]	0.09	0.05	[-0.02, 0.20]
	URBAN:s3t	0.04	0.03	[-0.01, 0.09]	0.06	0.05	[-0.03, 0.15]
	URBAN:c3t	0.06	0.03	[0.01, 0.12]	0.04	0.04	[-0.03, 0.11]
	URBAN:s4t	0.05	0.03	[0.00, 0.11]	0.02	0.04	[-0.06, 0.10]
	URBAN:c4t	0.13	0.02	[0.08, 0.17]	0.01	0.05	[-0.08, 0.11]

Female Growing	Covariate	Estimate	SE	95% CI	Estimate	SE	95% CI
		(1→2)			(2→1)		
	Intercept	-1.78	0.06	[-1.90, -1.66]	0.23	0.05	[0.13, 0.34]
	URBAN	-0.01	0.02	[-0.05, 0.03]	0.02	0.04	[-0.06, 0.10]
	st	0.57	0.04	[0.49, 0.66]	0.27	0.09	[0.10, 0.44]

TABLE S1.5 (continued).

ct	-0.21	0.02 [-0.24, -0.17]	0.45	0.04	[0.38, 0.53]
s2t	-0.38	0.03 [-0.43, -0.33]	0.30	0.06	[0.19, 0.41]
c2t	1.09	0.04 [1.01, 1.17]	-0.69	0.05	[-0.79, -0.60]
s3t	-0.15	0.02 [-0.20, -0.11]	0.07	0.03	[0.00, 0.14]
c3t	-0.10	0.02 [-0.15, -0.06]	0.32	0.08	[0.16, 0.48]
s4t	0.13	0.03 [0.08, 0.19]	-0.04	0.04	[-0.12, 0.05]
c4t	-0.73	0.02 [-0.77, -0.68]	1.00	0.06	[0.88, 1.12]
URBAN:st	0.09	0.03 [0.02, 0.15]	0.09	0.06	[-0.03, 0.21]
URBAN:ct	-0.16	0.02 [-0.19, -0.12]	0.31	0.05	[0.22, 0.41]
URBAN:s2t	-0.04	0.02 [-0.08, 0.01]	0.07	0.06	[-0.05, 0.19]
URBAN:c2t	-0.04	0.03 [-0.10, 0.02]	0.07	0.06	[-0.04, 0.18]
URBAN:s3t	0.05	0.02 [0.01, 0.10]	0.23	0.06	[0.12, 0.35]
URBAN:c3t	0.14	0.02 [0.09, 0.19]	0.02	0.07	[-0.11, 0.15]
URBAN:s4t	0.10	0.02 [0.05, 0.14]	0.10	0.04	[0.01, 0.18]
URBAN:c4t	0.01	0.02 [-0.03, 0.05]	0.14	0.05	[0.03, 0.24]

Male Dormant	Covariate	Estimate SE 95% CI			Estimate SE 95% CI		
		(1→2)			(2→1)		
	Intercept	-1.58	0.06	[-1.70, -1.47]	-0.11	0.07	[-0.26, 0.03]
	URBAN	0.23	0.03	[0.16, 0.29]	-0.41	0.04	[-0.48, -0.33]
	st	0.31	0.05	[0.22, 0.40]	-0.15	0.11	[-0.37, 0.06]
	ct	-0.80	0.04	[-0.88, -0.71]	0.55	0.07	[0.42, 0.68]
	s2t	-0.69	0.04	[-0.77, -0.60]	0.93	0.10	[0.74, 1.13]
	c2t	0.92	0.05	[0.82, 1.01]	-0.86	0.08	[-1.02, -0.69]
	s3t	0.51	0.04	[0.44, 0.58]	0.20	0.05	[0.10, 0.31]
	c3t	-0.33	0.04	[-0.41, -0.25]	0.61	0.08	[0.45, 0.76]
	s4t	0.53	0.04	[0.44, 0.61]	-0.66	0.06	[-0.79, -0.54]
	c4t	-0.30	0.04	[-0.37, -0.23]	0.47	0.06	[0.36, 0.59]
	URBAN:st	0.00	0.05	[-0.09, 0.09]	0.09	0.06	[-0.03, 0.22]
	URBAN:ct	-0.01	0.04	[-0.09, 0.07]	0.12	0.04	[0.04, 0.20]
	URBAN:s2t	0.02	0.05	[-0.07, 0.11]	0.10	0.06	[-0.02, 0.21]

TABLE S1.5 (continued).

URBAN:c2t	0.01	0.04 [-0.07, 0.09]	0.09	0.05	[-0.01, 0.18]
URBAN:s3t	0.02	0.04 [-0.05, 0.09]	0.01	0.04	[-0.07, 0.09]
URBAN:c3t	0.02	0.04 [-0.07, 0.10]	0.02	0.05	[-0.08, 0.11]
URBAN:s4t	0.02	0.04 [-0.06, 0.10]	0.03	0.04	[-0.05, 0.12]
URBAN:c4t	0.09	0.04 [0.02, 0.17]	-0.01	0.05	[-0.11, 0.08]

Male Growing Covariate	Estimate	SE	95% CI	Estimate	SE	95% CI
	(1→2)			(2→1)		
Intercept	-1.28	0.05	[-1.37, -1.18]	-0.26	0.04	[-0.34, -0.17]
URBAN	0.08	0.03	[0.01, 0.14]	-0.07	0.03	[-0.13, -0.01]
st	0.66	0.05	[0.57, 0.76]	-0.24	0.04	[-0.32, -0.16]
ct	-0.21	0.02	[-0.26, -0.16]	0.94	0.04	[0.87, 1.01]
s2t	-0.46	0.03	[-0.53, -0.40]	0.15	0.05	[0.06, 0.25]
c2t	0.78	0.05	[0.69, 0.87]	-0.77	0.03	[-0.83, -0.71]
s3t	-0.13	0.03	[-0.19, -0.07]	0.05	0.03	[-0.00, 0.11]
c3t	-0.16	0.04	[-0.24, -0.09]	-0.26	0.04	[-0.34, -0.18]
s4t	0.16	0.03	[0.10, 0.23]	-0.02	0.03	[-0.08, 0.04]
c4t	-0.68	0.03	[-0.73, -0.63]	1.15	0.06	[1.04, 1.26]
URBAN:st	0.08	0.06	[-0.03, 0.19]	0.06	0.05	[-0.03, 0.15]
URBAN:ct	-0.04	0.03	[-0.09, 0.01]	0.16	0.04	[0.09, 0.23]
URBAN:s2t	-0.02	0.04	[-0.10, 0.06]	0.01	0.04	[-0.07, 0.09]
URBAN:c2t	0.04	0.05	[-0.06, 0.14]	-0.02	0.04	[-0.09, 0.05]
URBAN:s3t	0.00	0.03	[-0.07, 0.07]	0.04	0.03	[-0.01, 0.10]
URBAN:c3t	0.08	0.05	[-0.01, 0.17]	0.09	0.04	[0.01, 0.17]
URBAN:s4t	0.10	0.04	[0.02, 0.17]	0.03	0.03	[-0.03, 0.08]
URBAN:c4t	0.00	0.03	[-0.05, 0.06]	0.01	0.04	[-0.07, 0.09]

TABLE S1.6. Regression coefficient estimates for each seasonal and sex-specific group derived from the top integrated step selection model (7). *Covariate abbreviations listed at bottom of table.

Female Dormant	Variable	Estimate	SE	Z	P Value
	IS_E	-0.33	0.01	-37.48	< 0.01
	CC_E	0.06	0.00	13.25	< 0.01
	DTR_E	-0.10	0.01	-10.58	< 0.01
	EXPLOR: COS TA	-0.13	0.01	-22.62	< 0.01
	ENCAMP: COS TA	-0.28	0.01	-37.63	< 0.01
	EXPLOR: SL	0.00	0.00	-70.32	< 0.01
	ENCAMP: SL	-0.03	0.00	-119.90	< 0.01
	EXPLOR: LOG SL	1.54	0.01	122.97	< 0.01
	ENCAMP: LOG SL	0.74	0.01	68.43	< 0.01
	COS TA: URBAN	0.00	0.01	0.69	0.49
	SL: URBAN	0.00	0.00	0.52	0.60
	LOG SL: URBAN	0.03	0.01	4.87	< 0.01
	COS TA: IS_S	-0.01	0.01	-2.00	0.05
	SL: IS_S	0.00	0.00	3.12	< 0.01
	LOG SL: IS_S	-0.06	0.01	-9.09	< 0.01
	COS TA: CC_S	0.05	0.00	9.68	< 0.01
	SL: CC_S	0.00	0.00	6.94	< 0.01
	LOG SL: CC_S	-0.01	0.01	-1.09	0.27
	COS TA: DTR_S	0.02	0.00	3.42	< 0.01
	SL: DTR_S	0.00	0.00	11.13	< 0.01
	LOG SL: DTR_S	-0.01	0.01	-1.05	0.29
	IS_E: URBAN	0.05	0.01	9.57	< 0.01
	CC_E: URBAN	0.10	0.00	22.24	< 0.01
	DTR_E: URBAN	0.01	0.01	0.96	0.34
	IS_E: ENCAMP	0.05	0.01	4.14	< 0.01
	CC_E: ENCAMP	0.05	0.01	4.80	< 0.01
	DTR_E: ENCAMP	0.49	0.03	16.97	< 0.01

TABLE S1.6 (continued).

Female Growing	Variable	Estimate	SE	Z	P Value
	IS_E	-0.23	0.01	-39.91	< 0.01
	CC_E	0.03	0.00	10.11	< 0.01
	DTR_E	-0.12	0.01	-17.45	< 0.01
	EXPLOR: COS TA	-0.40	0.00	-105.87	< 0.01
	ENCAMP: COS TA	-0.41	0.01	-53.96	< 0.01
	EXPLOR: SL	0.00	0.00	-70.64	< 0.01
	ENCAMP: SL	-0.05	0.00	-120.94	< 0.01
	EXPLOR: LOG SL	0.89	0.01	130.00	< 0.01
	ENCAMP: LOG SL	0.87	0.01	64.29	< 0.01
	COS TA: URBAN	0.02	0.00	5.96	< 0.01
	SL: URBAN	0.00	0.00	6.95	< 0.01
	LOG SL: URBAN	0.01	0.01	2.03	0.04
	COS TA: IS_S	-0.03	0.00	-6.76	< 0.01
	SL: IS_S	0.00	0.00	8.13	< 0.01
	LOG SL: IS_S	-0.05	0.01	-9.47	< 0.01
	COS TA: CC_S	0.04	0.00	11.68	< 0.01
	SL: CC_S	0.00	0.00	2.36	0.02
	LOG SL: CC_S	0.02	0.01	4.06	< 0.01
	COS TA: DTR_S	0.02	0.00	4.82	< 0.01
	SL: DTR_S	0.00	0.00	4.73	< 0.01
	LOG SL: DTR_S	-0.01	0.01	-2.23	0.03
	IS_E: URBAN	0.02	0.00	4.48	< 0.01
	CC_E: URBAN	0.11	0.00	32.27	< 0.01
	DTR_E: URBAN	0.06	0.01	7.08	< 0.01
	IS_E: ENCAMP	0.03	0.01	2.40	0.02
	CC_E: ENCAMP	-0.01	0.01	-1.01	0.31
	DTR_E: ENCAMP	0.33	0.03	9.69	< 0.01

TABLE S1.6 (continued).

Male Dormant	Variable	Estimate	SE	Z	P Value
	IS_E	-0.46	0.01	-38.64	< 0.01
	CC_E	0.14	0.01	22.11	< 0.01
	DTR_E	0.03	0.01	2.68	0.01
	EXPLOR: COS TA	-0.07	0.01	-9.88	< 0.01
	ENCAMP: COS TA	-0.27	0.01	-22.49	< 0.01
	EXPLOR: SL	0.00	0.00	-32.26	< 0.01
	ENCAMP: SL	-0.03	0.00	-76.89	< 0.01
	EXPLOR: LOG SL	0.75	0.01	77.68	< 0.01
	ENCAMP: LOG SL	0.72	0.02	44.95	< 0.01
	COS TA: URBAN	0.03	0.01	3.97	< 0.01
	SL: URBAN	0.00	0.00	-7.07	< 0.01
	LOG SL: URBAN	0.10	0.01	13.18	< 0.01
	COS TA: IS_S	-0.02	0.01	-3.28	< 0.01
	SL: IS_S	0.00	0.00	5.82	< 0.01
	LOG SL: IS_S	-0.04	0.01	-5.45	< 0.01
	COS TA: CC_S	0.02	0.01	3.18	< 0.01
	SL: CC_S	0.00	0.00	-1.70	0.09
	LOG SL: CC_S	0.06	0.01	8.26	< 0.01
	COS TA: DTR_S	0.03	0.01	4.23	< 0.01
	SL: DTR_S	0.00	0.00	-1.12	0.26
	LOG SL: DTR_S	0.05	0.01	6.71	< 0.01
	IS_E: URBAN	0.07	0.01	7.91	< 0.01
	CC_E: URBAN	0.09	0.01	14.00	< 0.01
	DTR_E: URBAN	0.11	0.01	9.88	< 0.01
	IS_E: ENCAMP	0.12	0.02	5.76	< 0.01
	CC_E: ENCAMP	-0.05	0.02	-3.22	< 0.01
	DTR_E: ENCAMP	0.30	0.04	7.75	< 0.01

TABLE S1.6 (continued).

Male Growing	Variable	Estimate	SE	Z	P Value
	IS_E	-0.35	0.01	-45.92	< 0.01
	CC_E	0.06	0.00	13.97	< 0.01
	DTR_E	0.00	0.01	-0.60	0.55
	EXPLOR: COS TA	-0.04	0.00	-8.70	< 0.01
	ENCAMP: COS TA	-0.27	0.01	-41.18	< 0.01
	EXPLOR: SL	0.00	0.00	-48.79	< 0.01
	ENCAMP: SL	-0.03	0.00	-131.87	< 0.01
	EXPLOR: LOG SL	0.92	0.01	119.42	< 0.01
	ENCAMP: LOG SL	0.69	0.01	74.28	< 0.01
	COS TA: URBAN	0.00	0.00	0.87	0.38
	SL: URBAN	0.00	0.00	-5.99	< 0.01
	LOG SL: URBAN	0.08	0.01	15.63	< 0.01
	COS TA: IS_S	-0.03	0.00	-7.05	< 0.01
	SL: IS_S	0.00	0.00	2.56	0.01
	LOG SL: IS_S	-0.04	0.01	-7.40	< 0.01
	COS TA: CC_S	0.01	0.00	3.52	< 0.01
	SL: CC_S	0.00	0.00	1.56	0.12
	LOG SL: CC_S	0.04	0.00	8.74	< 0.01
	COS TA: DTR_S	0.02	0.00	4.00	< 0.01
	SL: DTR_S	0.00	0.00	4.63	< 0.01
	LOG SL: DTR_S	0.02	0.00	3.36	< 0.01
	IS_E: URBAN	0.04	0.00	8.85	< 0.01
	CC_E: URBAN	0.07	0.00	18.57	< 0.01
	DTR_E: URBAN	0.01	0.01	0.65	0.51
	IS_E: ENCAMP	0.07	0.01	6.96	< 0.01
	CC_E: ENCAMP	-0.02	0.01	-2.24	0.03
	DTR_E: ENCAMP	0.27	0.02	11.71	< 0.01

*Covariate abbreviations:

TABLE S1.6 (continued).

CC: Canopy Cover

DTR: Distance to Roads

IS: Impervious surface

URBAN: Urbanness value

SL: Step length

LOG SL: Log-transformed step length

COS TA: Cosine of turning angle

EXPLOR: Exploratory state

ENCAMP: Encamped state

TABLE S1.7. Initial state distributions from 2-state HMMs for each seasonal and sex-specific groups.

Group	Exploratory	Encamped
Female Dormant	0.54	0.46
Female Growing	0.78	0.22
Male Dormant	0.52	0.48
Male Growing	0.51	0.49

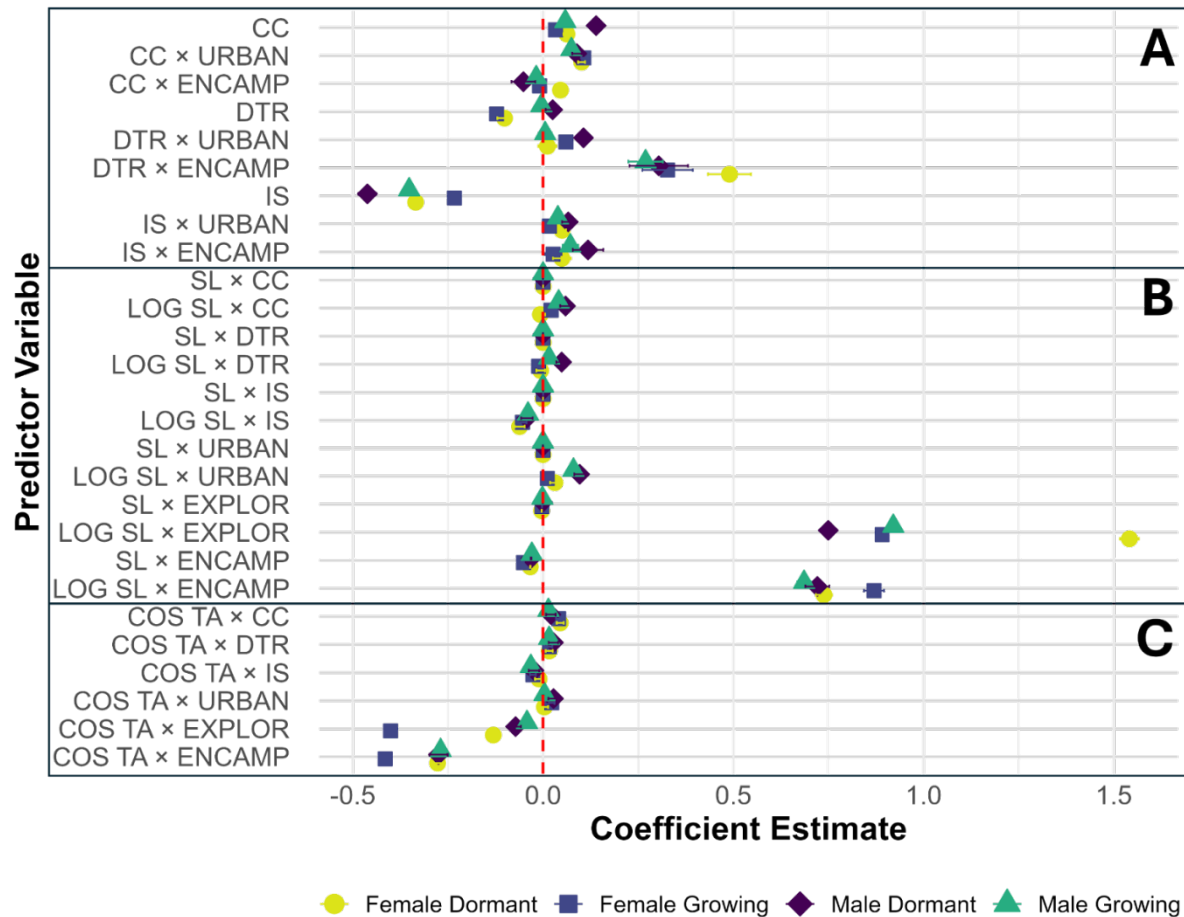


FIGURE S1.1. Coefficient estimates ($\pm$ SE) from the top iSSF model (Model 7) for each seasonal and sex-specific groups. Points represent parameter estimates for a specific covariate/interaction. Shape and color denote group identity. Interaction terms (x) indicate state/covariate specific effects. The vertical red dashed line indicates a null effect ($\beta = 0$). Positive coefficients indicate an increase in selection while negative coefficients indicate a decrease. Coefficient estimates are segmented out by A) selection processes, B) step length and C) turning angle concentration parameters.

Covariate abbreviations:

CC: Canopy Cover

DTR: Distance to Roads

IS: Impervious Surface

URBAN: Urbanness value

SL: Step length

LOG SL: Log-transformed step length

COS TA: Cosine of turning angle

EXPLOR: Exploratory state

ENCAMP: Encamped state

Appendix B

TABLES

Supplement 2.1: Description and source of landscape covariates.

Supplement 2.2: Generalized linear model (GLM) slope estimates and 95% confidence intervals for each seasonal resource selection plot (Fig 2.3).

FIGURES

Supplement 2.1: Seasonal home range size (95% auto-correlated kernel density estimator [AKDE]) for males and females included in analysis.

TABLE S2.1. Description and source of landscape covariates.

Variable Name	Description	Source
% Impervious Surface	Raster file; 30 m pixel resolution; range: 0-100%	National Land Cover Database, 2021
% Canopy Cover	Raster file; 30 m pixel resolution; range: 0-100%	National Land Cover Database, 2021
Distance to Roads	Vector files; primary & secondary roadways	United States Census Bureau, TIGER/Line, 2023 & North Carolina Department of Transportation, 2024

TABLE S2.2. Generalized linear model (GLM) slope estimates and 95% confidence intervals for each seasonal resource selection plot (Fig 2.3). GLM trend lines were calculated using weighted least squares regression (see Methods).

Sex	Season	Covariate	Estimate (95% CI)
M	Winter/Spring	Impervious Surface	-0.008 (-0.015, -0.001)
F	Winter/Spring	Impervious Surface	0.014 (0.008, 0.021)
M	Parturition	Impervious Surface	-0.001 (-0.006, 0.005)
F	Parturition	Impervious Surface	-0.014 (-0.020, -0.008)
M	Late Summer	Impervious Surface	-0.002 (-0.007, 0.003)
F	Late Summer	Impervious Surface	-0.010 (-0.015, -0.005)
M	Rut/Hunting	Impervious Surface	0.003 (-0.002, 0.009)
F	Rut/Hunting	Impervious Surface	0.002 (-0.004, 0.007)
M	Winter/Spring	Canopy Cover	0.025 (0.015, 0.036)
F	Winter/Spring	Canopy Cover	0.025 (0.016, 0.033)
M	Parturition	Canopy Cover	0.032 (0.020, 0.044)
F	Parturition	Canopy Cover	0.034 (0.024, 0.043)
M	Late Summer	Canopy Cover	0.017 (0.006, 0.028)
F	Late Summer	Canopy Cover	0.034 (0.026, 0.042)
M	Rut/Hunting	Canopy Cover	0.012 (0.003, 0.020)
F	Rut/Hunting	Canopy Cover	0.019 (0.012, 0.026)
M	Winter/Spring	Distance to Roads	0.046 (0.016, 0.075)
F	Winter/Spring	Distance to Roads	0.081 (0.048, 0.113)
M	Parturition	Distance to Roads	0.029 (-0.016, 0.074)
F	Parturition	Distance to Roads	0.014 (-0.028, 0.056)
M	Late Summer	Distance to Roads	-0.007 (-0.036, 0.022)
F	Late Summer	Distance to Roads	0.064 (0.025, 0.103)
M	Rut/Hunting	Distance to Roads	0.025 (-0.006, 0.056)

TABLE S2.2 (continued).

F	Rut/Hunting	Distance to Roads	0.040 (0.014, 0.065)
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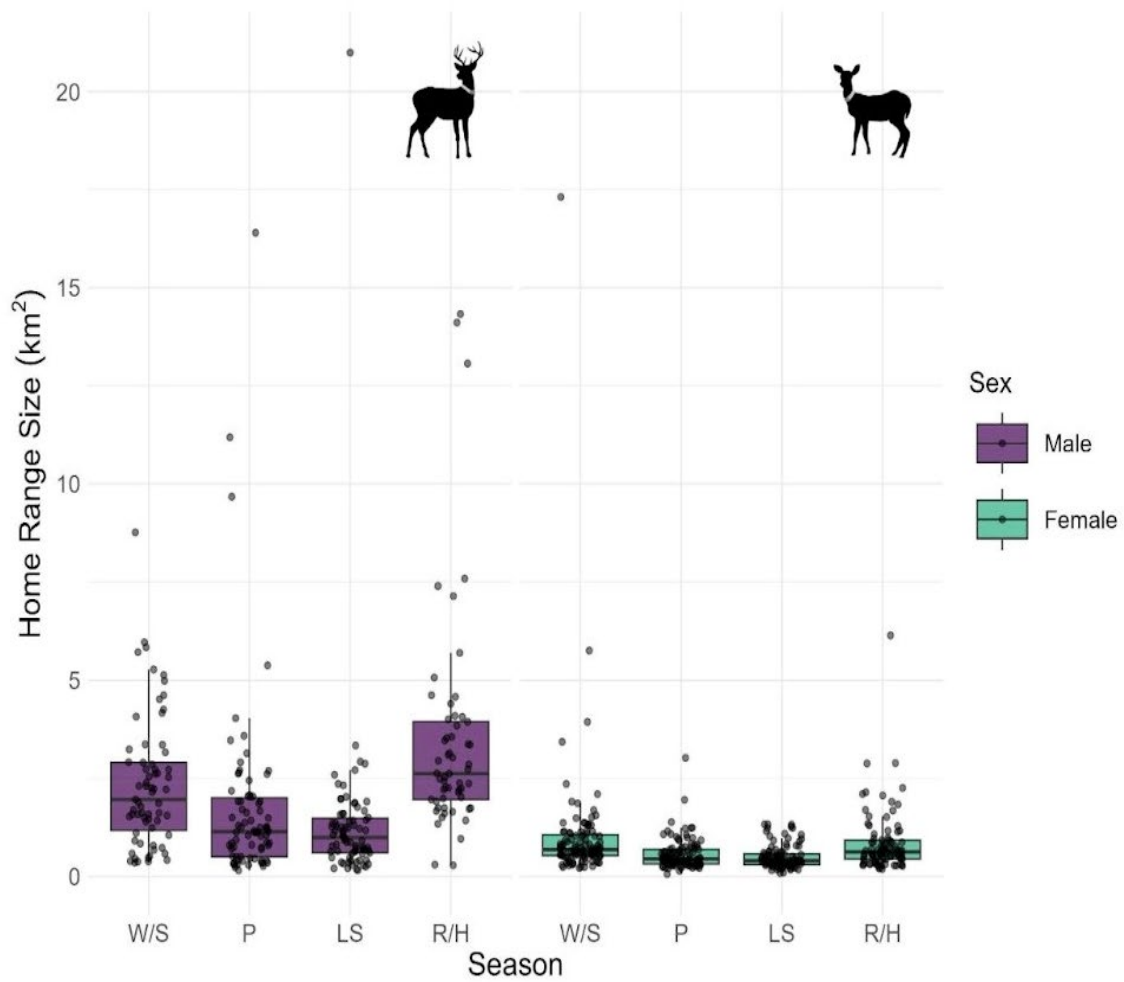


FIGURE S2.1. Seasonal home range size (95% auto-correlated kernel density estimator [AKDE]) for males (left) and females (right) included in analysis.

Appendix C

FIGURES

Supplement 3.1: Monthly number of mortalities for male and female white-tailed deer with confirmed causes of death across the study period.

Supplement 3.2: Weekly cause-specific mortality probabilities with credible intervals for adult and yearling male and female white-tailed deer during the harvest season.

Supplement 3.3: Weekly cause-specific mortality probabilities with credible intervals for adult and yearling male and female white-tailed deer during the non-harvest season.

Supplement 3.4: Weekly survival as a function of average weekly distance traveled for adult males during the harvest season.

Supplement 3.5: Annual cause-specific mortality probabilities with credible intervals for adult and yearling male and female white-tailed deer.

Supplement 3.6: Annual survival probabilities with credible intervals for adult and yearling male and female white-tailed deer.

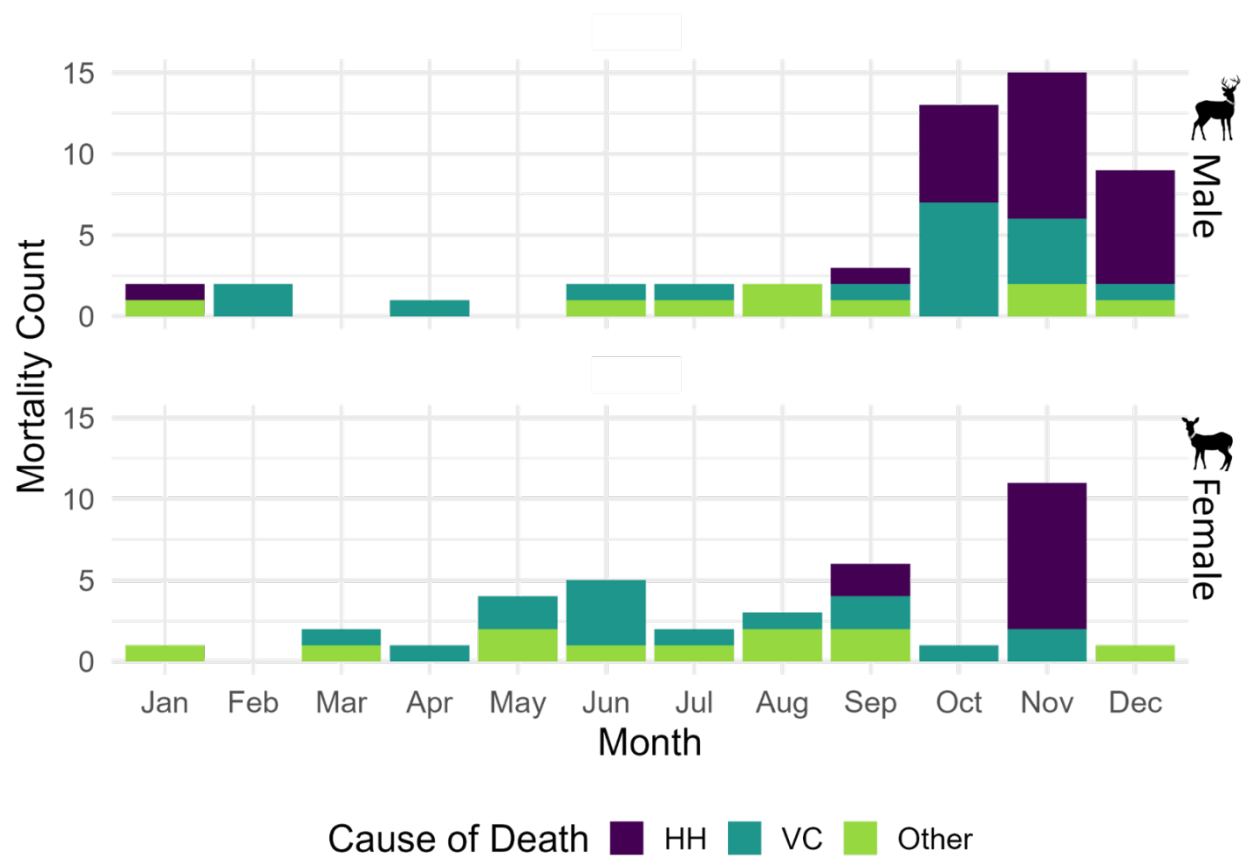


Figure S3.1. Monthly number of mortalities for male and female white-tailed deer with confirmed causes of death across the study period. Colors indicate different mortality causes. Harvest season in the study area spans September through early January.

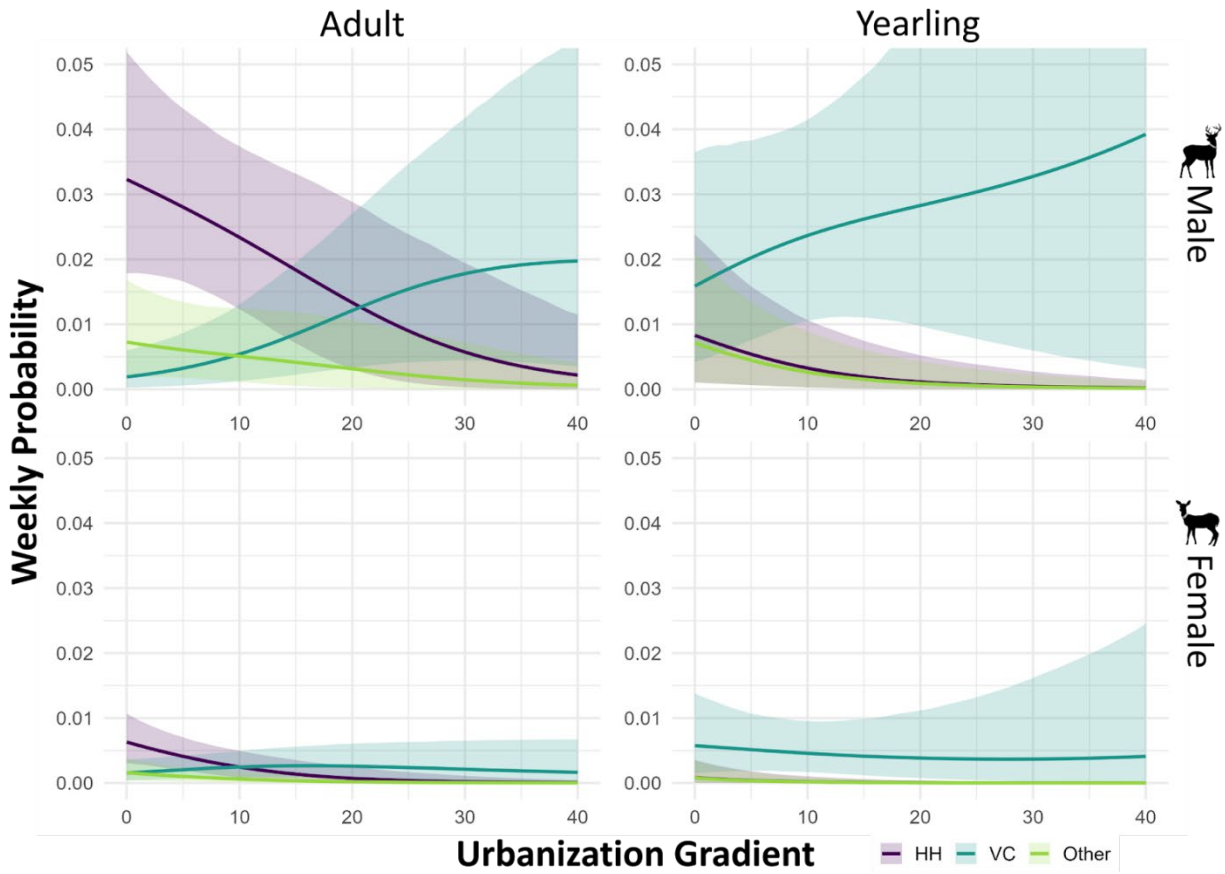


Figure S3.2. Weekly cause-specific mortality probabilities with credible intervals for adult and yearling male and female white-tailed deer during the harvest season. Different colors represent distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations.

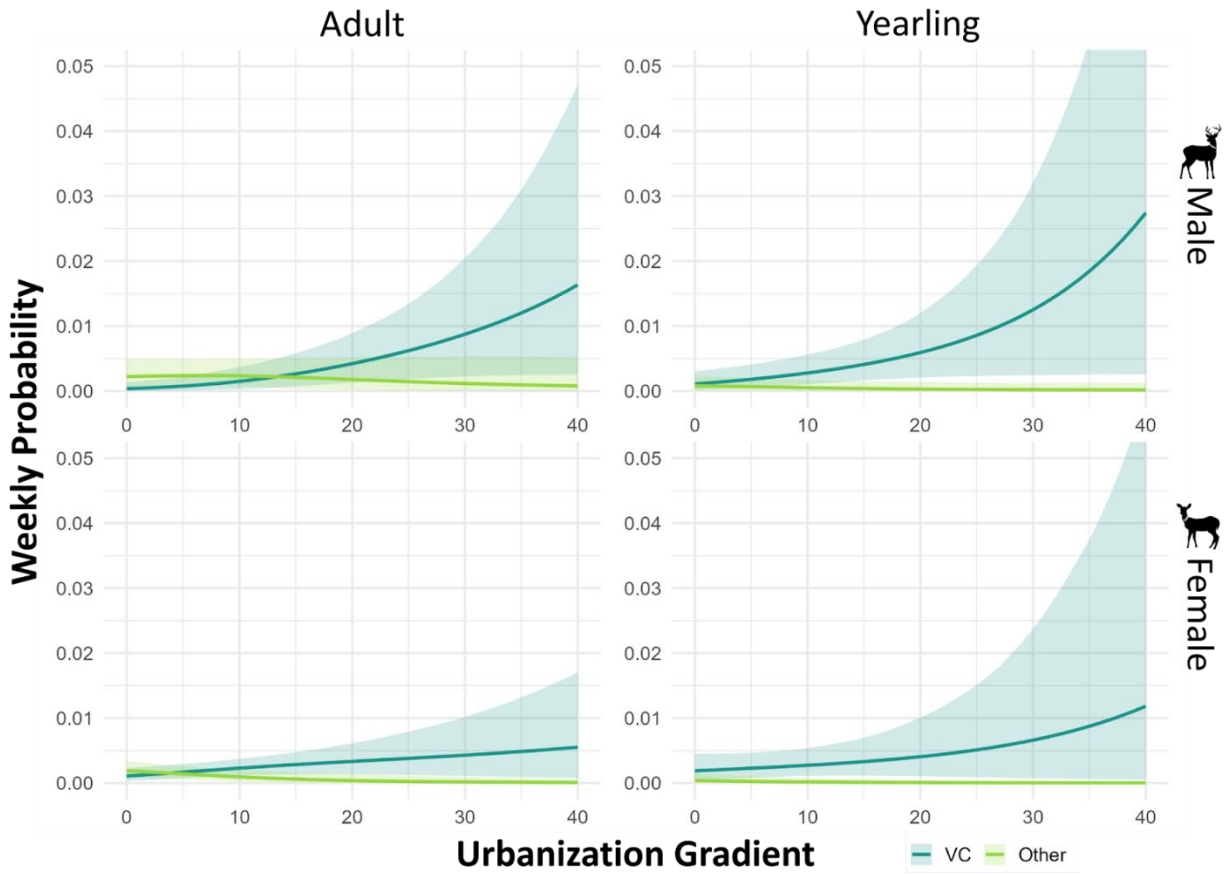


Figure S3.3. Weekly cause-specific mortality probabilities with credible intervals for adult and yearling male and female white-tailed deer during the non-harvest season. Different colors represent distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations.

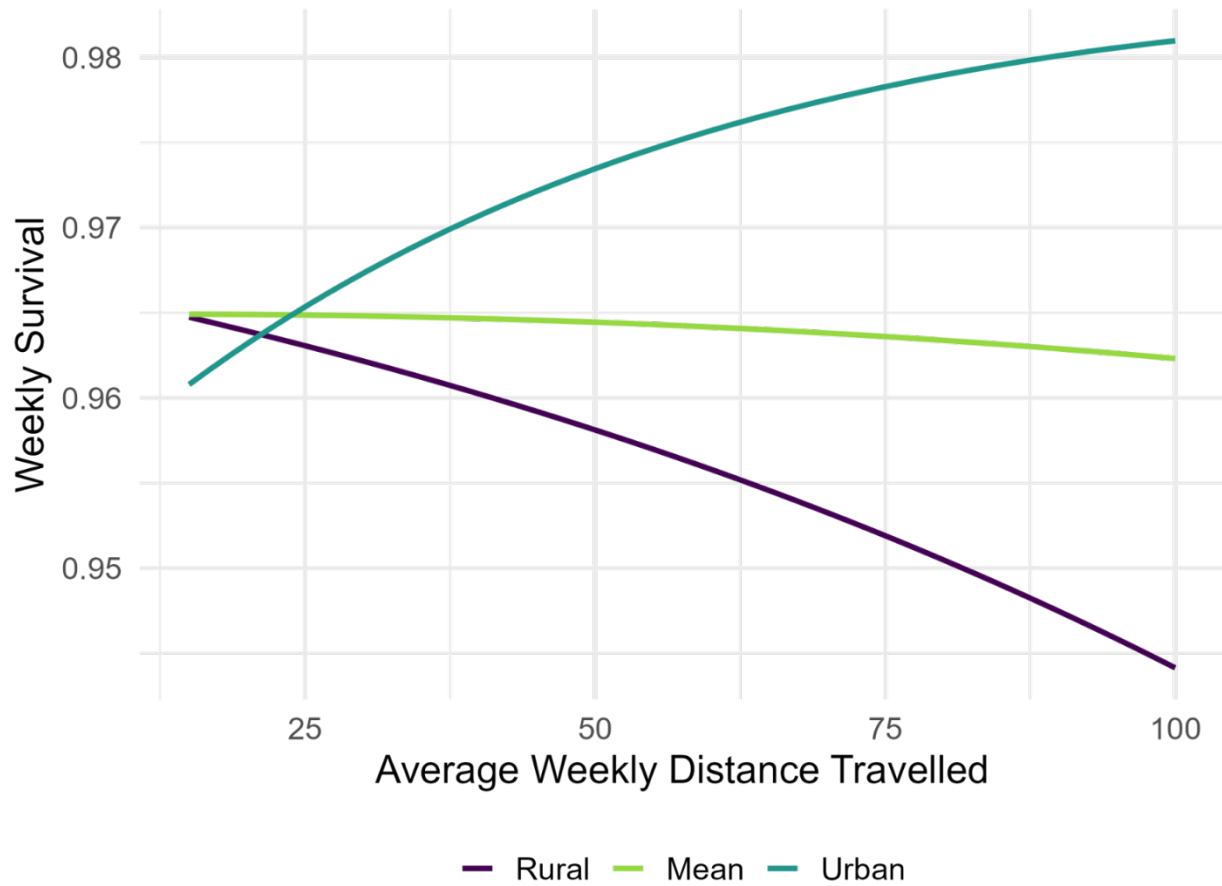


Figure S3.4. Weekly survival as a function of average weekly distance traveled for adult males during the harvest season. Rural, Mean, and Urban represents predictions to the 10th percentile (0.5), mean (7.6), and 90th percentiles (22.5) of urbanness values for study individuals, respectively.

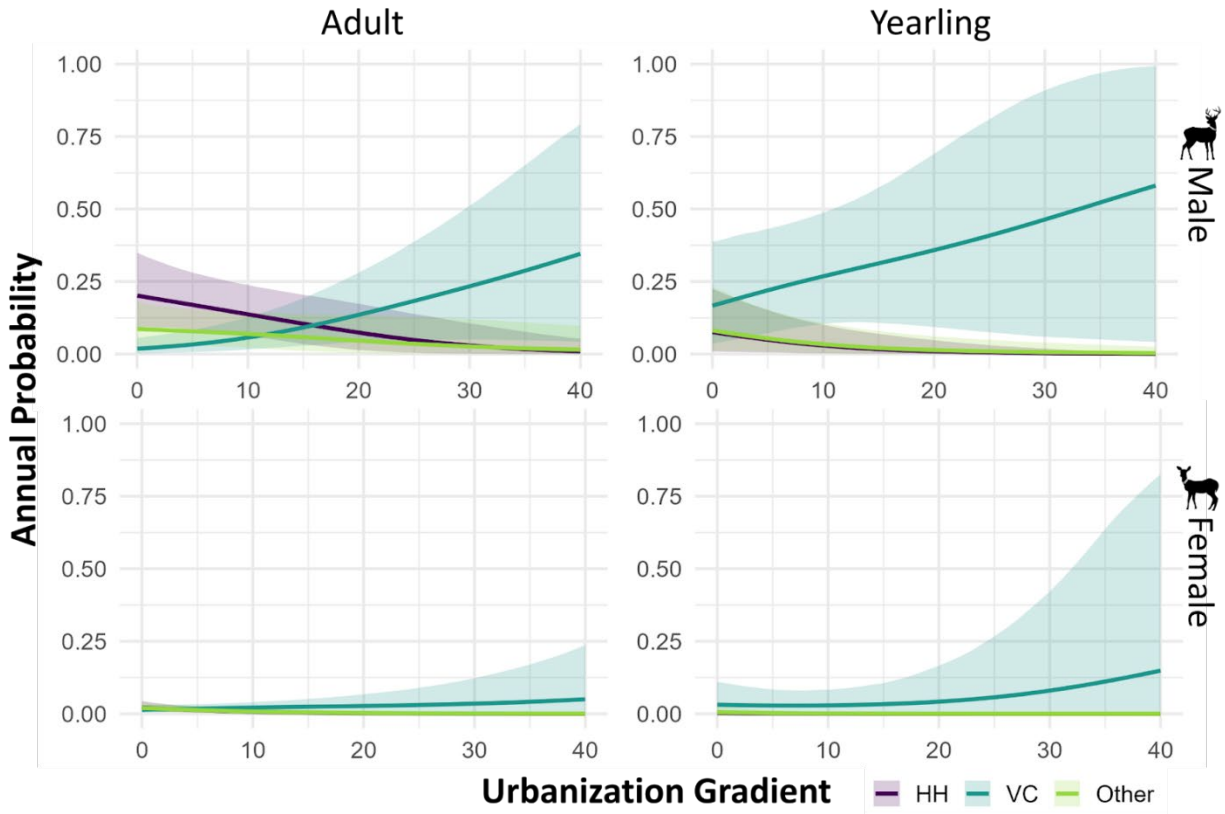


Figure S3.5. Annual cause-specific mortality probabilities with credible intervals for adult and yearling male and female white-tailed deer. Different colors represent survival and distinct causes of mortality, and probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations.

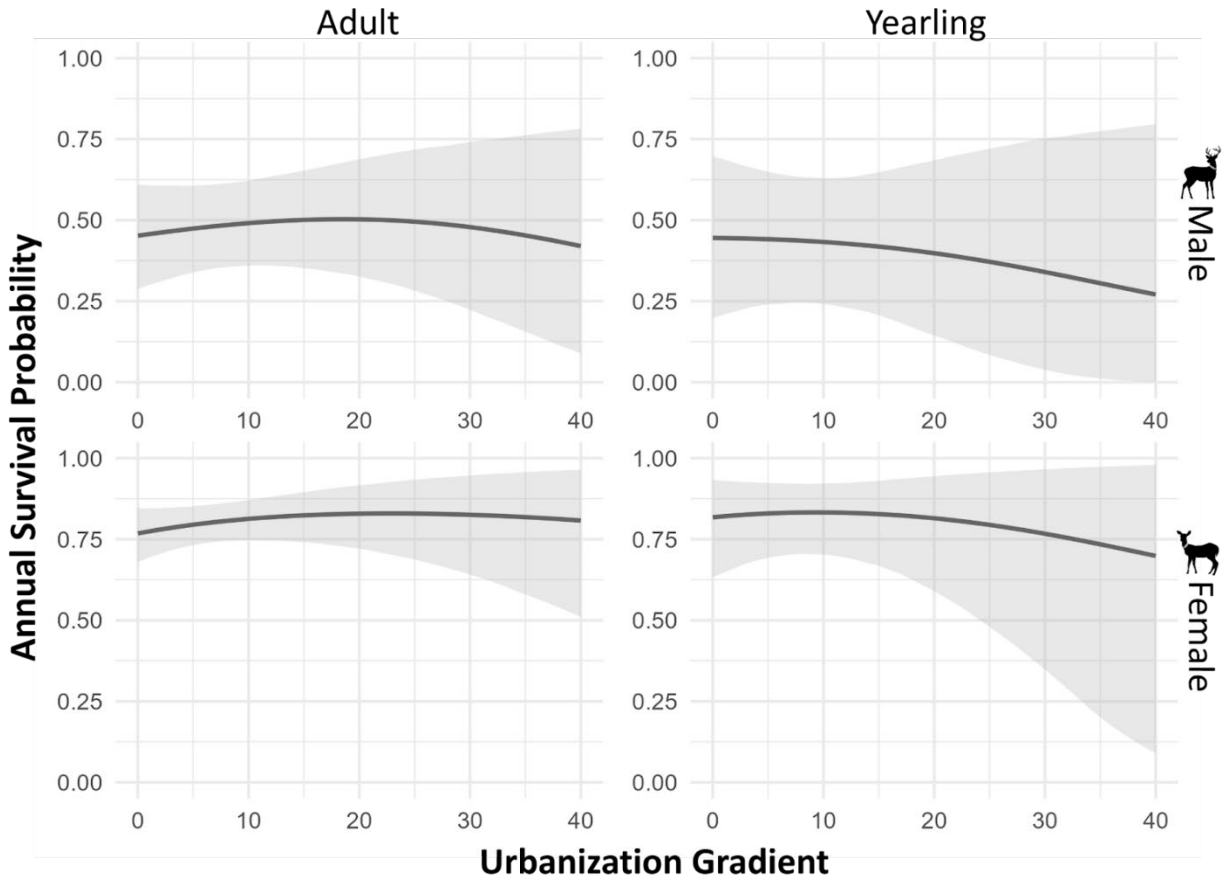


Figure S3.6. Annual survival probabilities with credible intervals for adult and yearling male and female white-tailed deer. Probabilities are shown along the urbanization gradient, with values near zero representing more rural locations and values near 40 representing more urban locations.