ABSTRACT

LAMB, JARED. What the Future Entails for White-tailed Deer: Harvest Susceptibility and Population Growth Across an Urbanization Gradient. (Under the direction of Dr. Nathan Hostetter and Dr. Christopher Moorman).

Urbanization alters landscapes in novel ways that can lead to changes in wildlife population dynamics. White-tailed deer (*Odocoileus virginianus*; hereafter deer) is an urban tolerant species that persist across a range of rural, exurban, and suburban landscapes. Understanding how urbanization affects deer population dynamics (e.g., survival, reproduction, population growth), especially harvest as the primary tool for deer population management, is therefore critical to predict how deer will respond to increasingly human dominated landscapes and to evaluate management strategies across urbanization gradients. To address these challenges, I monitored collared deer across an urbanization gradient within Durham and Orange counties, North Carolina from 2022-2025 to: 1) evaluate the effects of urbanization on deer survival and cause-specific mortality during the hunting season (chapter 1); 2) quantify how deer reproduction varied across the urbanization gradient (chapter 2); and 3) synthesize stage-specific survival and reproduction results across multiple complementary studies to identify how urbanization alters deer population growth rates (chapter 2). Overall, 111 females, 91 males, and 112 neonates were available for individual analyses of survival and reproduction of white-tailed deer across the urbanization gradient. In chapter 1, I identified that harvest probability significantly declined as urbanization increased, but females and yearling males maintained relatively constant survival as non-harvest mortality offset reductions in harvest. In chapter 2, I documented that expected litter size significantly increased with urbanization, likely due to varying food availability across the continuum. Overall, dynamic deer vital rates contributed to a non-linear relationship between population growth rate and urbanization. Population growth rate peaked in suburban areas ($\lambda =$

1.01) and declined into more rural ($\lambda = 0.96$) and urban ($\lambda = 0.90$) areas, driven by reductions in litter size in rural areas and reduced neonate survival in urban areas. My results support previous literature that documented lower deer harvest in urban areas and reveal how changes in mortality risk and reproduction alter deer population growth across an urbanization gradient. Further, my results underscore the complex deer population dynamics in urbanizing landscapes, and how changes in deer mortality, reproduction, and population growth create unique deer population management considerations across an urbanization gradient.

What the Future Entails for White-tailed Deer: Harvest Susceptibility and Population Growth Across an Urbanization Gradient.

by
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DEDICATION

I dedicate this work to my mother and father. Mom, your unconditional love and support makes it easy to do hard things, and I know you will always be there to fall back on. Dad, your love and admiration for nature, in which you've passed down to me, has led me to live a pretty cool life doing some pretty cool things.

BIOGRAPHY

Jared grew up in China Grove, North Carolina, where he was raised by a hunting and fishing family. Jared attended North Carolina State University and received his bachelor's degree in Fisheries, Wildlife, and Conservation Biology where the program, professors, and friends he made poured fuel on the fire that was his love for the outdoors. After graduating in December of 2020, Jared was hired as a lead technician for an elk capture project in the Gila National Forest of New Mexico. After his time in New Mexico darting elk, chasing elk calves, and running into mountain lions, he was led back home and hired as a lead technician on the urban deer research project with his alma mater, where after a year and a half he was elevated to a master's research assistant.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Harvest probability of white-tailed deer (*Odocoileus virginianus*) across an urbanization gradient

ABSTRACT

Hunter harvest is an important tool to manage wildlife populations, but urbanization can shift land use and socio-demographics in ways that reduce an individual animal's risk of harvest (hereafter harvest probability). Although white-tailed deer (*Odocoileus virginianus*; hereafter deer) occur across urbanization gradients, the effects of urbanization on deer harvest probability remains poorly understood. We evaluated deer survival and cause-specific mortality during the hunting season across an urbanization gradient. Specifically, we evaluated how individual-level (sex, age) and urban-related covariates (impervious surface cover and huntable lands) affected deer fate (harvested, non-harvest mortality, survived). From 2022-2024, we monitored 70 male and 95 female deer during the hunting season in the Piedmont physiographic region of North Carolina. The top model included covariates for percent impervious surface cover in the individual's range distribution (i.e., urbanness value), sex, and age. Harvest probability declined as urbanness value increased. However, females and yearling males maintained relatively constant survival probability because probability of non-harvest mortality increased as urbanization increased. In contrast, adult male survival probability during the hunting season substantially increased as urbanness value increased, as probability of non-harvest mortalities did not offset the reduction in harvest probability. Our results support previous literature that indicates lower harvest probability in urban areas. However, we further demonstrated that shifts in mortality sources, which vary by sex and age, can sometimes offset reduced harvest but lead to other management challenges (i.e., increased vehicle collisions). These results underscore the complex ecological and social dynamics in urbanizing landscapes and the need to account for changes in all mortality sources when evaluating management actions along urbanization gradients.

Keywords: white-tailed deer, *Odocoileus virginianus*, urbanization, urbanization gradient, harvest, hunting

INTRODUCTION

Urbanization changes landscapes in ways that influence wildlife survival and causes of mortality (Ditchkoff et al. 2006). Survival can be reduced by elevated risks of some mortality causes in urban areas, including from wildlife-vehicle collisions, disease, and exposure to contaminants (Riley et al. 2004, 2014, Barbosa et al. 2020, Blais et al. 2024). Conversely, for some species, survival may increase in urban areas as primary causes of mortality are reduced (e.g., reduced hunting in urban areas; Ditchkoff et al. 2006, Phillips et al. 2018, Brouwer et al. 2024). As such, urbanization can lead to a variety of outcomes for wildlife species, ranging from exclusion to overabundance, creating a need to evaluate how multiple mortality risks interact across urbanization gradients (DeStefano and DeGraaf 2003, Fischer et al. 2015).

Hunting is commonly used to manage wildlife populations, but may be challenged in urbanizing areas due to complex socio-ecological processes. Urbanization can reduce the social acceptance of hunting through changing political and management perspectives (Manfredo and Zinn 1996, Patterson et al. 2003, Vajas et al. 2023, Desrochers et al. 2025). Furthermore, municipal regulations can restrict hunting and weapon discharge, which limits hunting access within urban areas (Harden et al. 2005, Bowman 2012). Even in areas where hunting is legally allowed, access is predominantly dependent on private landowner decisions that further complicate the application of hunting as a management tool (Daley et al. 2004, Golden et al. 2013, Burke et al. 2019*a*). Urbanization results in landscape fragmentation that reduces parcel size (parcelization; Peterson et al. 2013), which reduces hunter access (Poudyal et al. 2008, Campa III et al. 2011, Lovely et al. 2013). Additionally, roads, buildings, and other forms of urban infrastructure, all forms of impervious surface, may affect hunting (McKinney 2002, Hansen et al. 2005). For example, the probability a property is hunted (hereafter huntable lands) declines as road density and housing density increases and parcel size decreases (Burke et al. 2019*b*). Thus, the distribution of huntable lands and impervious surfaces may influence the extent to which urbanization affects harvest and other causes of mortality.

Changes in white-tailed deer (*Odocoileus virginianus*; hereafter deer) harvest risk (hereafter harvest probability) along an urbanization gradient remain poorly understood, but improved insights are essential for effectively managing deer populations in urbanizing landscapes. Hunter harvest remains the predominant method to manage deer populations, but reduced hunter harvest in urban areas may lead to deer overabundance and associated nuisance issues (Warren 1997, Brown et al. 2000, Adams and Hamilton 2011, Burke et al. 2019*b*, Wiskirchen et al. 2023). Although previous studies have documented lower harvest of deer in urban areas, little is known about how harvest probability varies along continuous urbanization gradients or whether observed patterns are driven by direct effects of urbanization, reductions in huntable lands, or a combination of these factors (Etter et al. 2002, Storm et al. 2007*a*, Stewart 2011). Simultaneously, it is also important to assess changes in non-harvest mortality, as reductions in harvest may increase survival and population growth or be offset by other mortality sources, such as vehicle collisions that introduce additional management challenges (Etter et al. 2002, Hussain et al. 2007).

We conducted a 3-year study to estimate probabilities of harvest and non-harvest mortality of deer during the hunting season across an urbanization gradient in Durham and eastern Orange counties, North Carolina. Our objectives were to 1) identify key predictors of deer fates during the hunting season, and 2) evaluate how harvest and non-harvest mortality may compound or offset one another across an urbanization gradient. We quantified the individual's location on the urbanization gradient using the percentage of impervious surface cover (urbanness value) and its exposure to hunting using huntable lands (huntable lands value) within its range distribution. We hypothesized that individual deer harvest probability would decline as urbanization increased because of increased proximity to urban development and changes in social and regulatory factors that reduce hunter access. To test this, we compared models that evaluated whether urbanness value, huntable lands value, or both best predicted deer fates during the hunting season. Additionally, we included sex and age to examine how demographic factors interact with urbanization in shaping harvest probability and deer fates during the hunting season.

STUDY AREA

We captured and monitored white-tailed deer across Durham County and eastern Orange County, North Carolina from 2022-2024 (Figure 1.1). A majority (90%) of monitored individuals were in Durham County, and individuals monitored in Orange County were near the Durham County border. Durham County was approximately 772 km2 and located in the Piedmont physiographic province of central North Carolina (North Carolina Geological Survey 2004). Durham County represented a strong urbanization gradient, from the city of Durham, which has approximately 280,000 residents and over 85% of the county’s human population (US Census Bureau 2020), to rural areas primarily in the northern portion of the county (Figure 1.1). In general, urban and suburban land cover was prominent in the southern and southeastern regions of the county, whereas perimeter suburban areas to the north and northwest transitioned into exurban communities, forest, and row crop agriculture (Figure 1.1). The deer hunting season was from the first Saturday in September until 2 January of the following year. Hunting was permitted within the city limits of Durham under 2 conditions: 1) only archery equipment could be used at least 76.2 m from any dwelling, and 2) the hunter had to have landowner access to at least 2.0 ha, either as a single parcel or multiple adjoining parcels.

METHODS

Capture and monitoring

We captured male and female deer using drop nets (Wildlife Capture Services, Flagstaff, AZ, USA) and dart projectors (Model JM Standard, Dan-Inject, Austin, Texas, USA) from January to May in 2022 – 2024. We immobilized each deer with a 2-cc intramuscular injection of BAM (butorphanol 27.3 mg/ml, azaperone 9.1mg/ml, medetomidine 10.9mg/ml) (Wedgewood, Swedesboro, NJ, USA). We assigned individuals to 1 of 3 initial age classes (fawn: 7–11 months, yearling: 1.5–1.9 years, and adult: ≥2 years) based on tooth replacement and wear characteristics (Severinghaus 1949), supplemented by estimated weight derived from chest girth measurements with comparison to local deer weights and ages (North Carolina Wildlife Resources Commission 2006–2025; unpublished data). We equipped captured deer with a global positioning system (GPS) collar (Model G5-2D, Advanced Telemetry Systems, Isanti, MN, USA) and a yellow ear tag with a unique identification number. Collars collected GPS fixes every 2 hours and contained a mortality beacon that activated if the collar remained inactive for > 4 hours. At the conclusion of each workup, we antagonized BAM with a 4.0-cc injection of atipamezole (25 mg/ml) and a 0.5-cc injection of naltrexone HCl (50 mg/ml) (Wedgewood, Swedesboro, NJ, USA). Furthermore, we notified the public that it was allowable to harvest tagged deer through press releases distributed by the North Carolina Wildlife Resources Commission, a website detectable by search engines, and engagement with landowners where tagged deer were located.

We monitored each individual remotely via satellite GPS for the first hunting season after its initial capture. To avoid resampling biases, we censored individuals after their first hunting season. Additionally, we advanced the age class of captured fawns (captured at 7-11 months old) and yearlings (captured at 1.6-1.9 years old) to reflect the age during the hunting season following capture. We excluded individuals less than 1 year old during the hunting season (captured as neonates), because we did not document hunter harvest of individuals in this age class. We classified the fates of individuals that were alive at the start of the hunting season into 3 categories: survived, harvested, and non-harvest mortality during the hunting season. We assigned the fate as "survived" if the individual remained alive at the conclusion of its first hunting season and the GPS collar remained functional. We censored individuals from analysis if GPS points ceased to transmit and the VHF signal was lost after multiple exhaustive searches during the hunting season. In the event of mortality, we determined the cause of death via field necropsies. We assigned "harvest" when mortality was reported by the hunter or if we observed evidence of hunting related mortality during a legal hunting season at the mortality site (i.e., projectile wound), and we recorded the harvest weapon type (firearm or archery) when possible. We assigned "non-harvest mortality" if the cause of death was non-hunting related, including deer-vehicle collisions and unknown causes of mortality. We assigned the cause of death as unknown if the mortality signal was delayed and the carcass was fully consumed from scavenging with little evidence to discern the cause of death.

Urbanization and huntable lands

To quantify where individuals lived on the urbanization gradient (hereafter urbanness value), we calculated a range distribution for each individual using a 99% autocorrelated kernel density estimate and then averaged the percent impervious surface of all 30- × 30-m grid cells with centroids in an individual's range distribution (Fleming et al. 2015). We used GPS locations from 1 July to 7 September to represent a pre-hunting season range distribution. Additionally, we used the huntable lands model developed by Burke et al. (2019b), which we modified for local regulations by including parcels within city limits, to estimate the probability a parcel was hunted. This model assigned each parcel in the study area a huntable probability based on the parcel size, housing density, and road density (Figure 1.1). Using the huntable probabilities, we derived the area-weighted average of parcel-specific huntable probabilities within each individual's range distribution (henceforth "huntable lands value"). Thus, each deer had individual-level covariates for sex, age, urbanness value within its range distribution, and huntable lands value within its range distribution. We used pre-hunting season locations to minimize potential biases in range distribution estimation for individuals harvested early in the hunting season and to eliminate complications of computing range distributions for non-range resident individuals, such as dispersing yearling males. Although deer ranges typically expand during hunting seasons (DeYoung and Miller 2011), we verified there was a negligible difference in urbanness and huntable lands values derived from range distributions using locations collected pre-hunting season compared to those collected during the hunting season.

Statistical Analysis

We used a multinomial logistic regression to model 3 fates during the hunting season (0 = survived; 1 = harvest; 2 = non-harvest mortality) and developed 4 models that reflected our *a priori* hypotheses. These candidate models were: 1) sex + age; 2) sex + age + urbanness value; 3) sex + age + huntable lands value; 4) sex + age + urbanness value + huntable lands value. We used baseline categories of adult and female for age and sex covariates, respectively. Additionally, we standardized urbanness values for analyses (mean = 0, standard deviation = 1) and ensured urbanness values and huntable lands values were not correlated (|r| < 0.7). We ranked all candidate models based on Akaike's Information Criterion corrected for small sample size (AICc; Anderson and Burnham 2002). We reported covariate effects as statistically significant when the 95% confidence intervals of the parameter estimate did not include 0. For multinomial models with three categories, parameter estimates are expressed relative to a reference category, in this case survival. For example, the model including urbanness value estimates two slope parameters describing the effects of urbanness value on harvest and non-harvest mortality relative to survival. Given the number of parameters, sample sizes, and study objectives, we limited models to additive effects, though we recognize that sex- and age-specific interactions (i.e., 2- or 3-way interactions) may be important and warrant future investigation. To aid interpretation, we presented parameter estimates and predicted probabilities from the top model.

To display the spatial variation in harvest probability, we used the top model to predict probabilities of survival, harvest, and non-harvest mortality across Durham County. Specifically, we used the NLCD 30-x30-m raster grid and smoothed covariates at a 1-km2 area to reflect the approximate range distribution area for female deer in our study. We conducted model analysis and predictions in R (R Core Team 2024), using the nnet package (Venables and Ripley 2002) and the effects package (Fox 2003).

RESULTS

We collared 174 deer from 2022-2024 that survived to the beginning of the following hunting season. Of surviving deer, we censored 9 individuals where collars malfunctioned during the hunting season, resulting in 165 deer for analyses (70 males - 50 adults, 20 yearlings captured as fawns; 95 females - 91 adults, 4 yearlings). In total, 112 deer (32 male, 80 female) survived until the end of the hunting season, 33 deer were harvested (24 male, 9 female; 19 firearm, 13 archery, 1 unknown weapon type), and 20 deer died of non-harvest mortality causes (14 male, 6 female; 14 deer-vehicle collisions, 6 unknown; Figure 1.2; Table 1.1). Urbanness values of individual deer ranged from 0 (rural) to 36 (urban); however, 31 of 33 harvested individuals had urbanness values < 7 (Figure 1.2). Conversely, huntable lands values for individual deer ranged from 0 to 99, and harvest occurred across the entire range of huntable lands values (Figure 1.2).

The top model included sex, age, and urbanness value as predictors of fate, and all other candidate models were non-competitive (ΔAICc > 2; Table 1.2). Given the lack of competing models, we summarized results from the top model. Males had higher probability of harvest (2.29; 95% CI = 1.35, 3.23) and non-harvest mortality (1.57, 95% CI = 0.44, 2.71; Figures. 1.2, 1.4, 1.5; Appendix 1.1). Age was a significant predictor of harvest (-1.80, 95% CI = -3.43, -0.18), with yearlings having a lower probability of harvest than adults, but age was not related to the probability of non-harvest mortality (Figures 1.4, 1.5; Appendix 1.1). Harvest probability decreased as urbanness value increased (-0.84, 95% CI = -1.52, -0.16), but the positive effect of urbanness value on non-harvest mortality was not significant (0.09, 95% CI = -0.36, 0.54; Figure 1.3; Appendix 1.1).

Harvest probability decreased as urbanness value increased, especially for adult males, with harvest probability declining from 0.57 to 0.05 as urbanness values increased (Figures 1.4, 1.5). Harvest probability was similar for yearling males and adult females and declined from ~0.15 to <0.01 as urbanness values increased, whereas yearling female harvest probability was < 0.03 regardless of location on the gradient (Figure 1.4). The non-significant increase in non-harvest mortality as urbanness value increased was driven by increased deer-vehicle collisions in more urban areas (Figure 1.2). Increases in non-harvest mortality during the hunting season did not offset the reduction in harvest in adult deer, resulting in adult male survival probability increasing from 0.32 to 0.65 as urbanness values increased (Figure 1.4, 1.5). For adult females, survival probability during the hunting season increased from 0.80 to 0.91 as urbanness values increased (Figure 1.4, 1.5). Yearling males and females maintained a relatively constant survival probability across urbanness values, as harvest probability was lower (yearling females) or offset by increased non-harvest mortality (yearling males; Figure 1.4) in more urban areas.

Impervious surface cover within our study area did not follow a predictable pattern along a continuous urban-to-rural gradient (Figure 1.1). Instead, fragmented parcels of undeveloped land cover created a complex spatial patchwork of harvest probabilities across the landscape (Figure 1.5). Notably, parcels with low urbanness values (0-5) occurred within the urban and suburban matrix (i.e., within city limits, close proximity to city center), resulting in a wide range of adult male harvest probability (0.00 to > 0.40) in some of the more developed areas (Figure 1.5). More specifically, individual deer within the more developed portions of the study area varied in harvest probability because of the range of impervious surface cover within their range distributions (Figures 1.1, 1.5).

DISCUSSION

Our results support previous literature indicating that white-tailed deer harvest probability declines as urbanization increases (Hansen and Beringer 2003, Harden et al. 2005, Storm et al. 2007*a*, Kilpatrick et al. 2011). By examining the complete set of fates across the hunting season (harvest, non-harvest, survive), we identified that probability of non-harvest partially or completely offset reductions in harvest probability for females and yearling males as urbanization increased. Adult male survival, however, increased as urbanization increased due to non-harvest probability not fully offsetting reduced harvest probability. Our results demonstrate the complexity of wildlife management across urbanization gradients, which involves multifaceted socio-ecological processes related to hunter access, state and municipal regulations, shifts in the causes of mortality, and altered deer behavior (Etter et al. 2002, Hansen and Beringer 2003, Storm et al. 2007*a*, Burke et al. 2019*a*, Desrochers et al. 2025).

The decline in deer harvest probability as urbanization increases may involve multiple socio-ecological processes related to hunter access and decisions, and deer behavior (Hansen and Beringer 2003, Harden et al. 2005, Storm et al. 2007*b*). For example, deer in urban areas may reduce overall activity or become more active at night in areas of high human activity, further minimizing harvest risk where hunting can occur (Péter et al. 2025). Furthermore, deer may select areas that do not allow hunting and serve as refugia during the hunting season in response to hunting pressure (Lovely et al. 2013, Rhoads et al. 2013, Little et al. 2014, 2016, Marantz et al. 2016). Hunting refugia are common in urban areas, due in part to regulations that limit weapon discharge within a certain distance from buildings, thus reducing the proportion of land that is available to hunt (Etter et al. 2002, Harden et al. 2005, Storm et al. 2007*a*, Bowman 2012). Hunting was allowed within the city limits of our study area but was restricted to archery equipment and > 76.2 m from any dwellings. Additionally, hunter access can be limited in more urban areas due to individual landowner decisions to restrict hunting on their property, and some hunters may be less willing to harvest deer in more urban landscapes (Stedman et al. 2008, Burke et al. 2019*a*, Desrochers et al. 2025). Together, these processes likely cause reduced harvest probability in more urban areas, and future research that disentangles the contributions of these factors is essential to guide targeted management actions in urbanizing landscapes to maintain harvest as a viable management tool.

Although complex changes in land cover and human social dynamics across urbanization gradients make it difficult to model relationships between urbanization and wildlife demographics, the simplified urbanization gradient derived from impervious surface cover captured much of the variation in harvest locations. More specifically, 31 of 33 deer harvests occurred in urbanness values ranging from 0-7, despite collared deer having urbanness values of 0-35. Impervious surface cover reflects various components of urban development, including roads, buildings, parking lots, and other non-permeable surfaces, but impervious surface cover may also serve as a proxy for socio-demographic shifts associated with urbanization, such as changing attitudes and emotions toward hunting and hunter access (Jagnow et al. 2006, Campa III et al. 2011, Golden et al. 2013, Burke et al. 2019*a*, Desrochers et al. 2025). Somewhat surprisingly, urbanness values outperformed the huntable lands values in predicting deer harvest outcomes. The huntable lands model from which we derived the huntable lands values places heavy emphasis on parcel size, and tends to assign low huntability to small parcels regardless of their location along the urbanization gradient. However, we observed multiple harvests on smaller parcels (< 2 ha), resulting in harvest regularly occurring in areas with low huntable lands values (0–25). This may be a result of the additional legal parameters required to hunt in urban areas outweighing the effects of parcel size in the huntable lands model. Although a range of metrics can be used to quantify urbanization (e.g., impervious surface, road density, housing density, census districts; Brown et al. 2005, McKinney 2008, Seress et al. 2014), we showed that impervious surface cover effectively captured spatial variation in harvest probability and proved to be a relevant predictor at the scale of individual deer. However, it is important to consider the diversity of regulations and legal status of hunting in different municipalities when predicting urban harvest probabilities. Additional research that investigates how regulations across various municipalities affect harvest probability may provide insight into which regulations may best promote harvest.

Hunting season survival probability reflected offsets between harvest and non-harvest mortality, as well as how these fates varied across the urbanization gradient (Hansen and Beringer 2003). For adult males, survival during the hunting season increased with greater levels of urbanization, driven by sharp reductions in harvest probability as urbanization increased. In contrast, yearling males experienced a high rate of non-harvest mortalities, primarily from deer-vehicle collisions, which outweighed harvest mortality and resulted in minimal effects of urbanization on survival. For yearling males, the risk of deer-vehicle collisions generally increases during the hunting season as individuals also disperse from their natal ranges during this time of year (Nelson 1993, McCoy et al. 2005). Conversely, although adult males expand their space use and activity during the breeding period, dispersal events are rare and likely resulted in fewer deer-vehicle collisions than for yearling males (DeYoung and Miller 2011, Simoneaux et al. 2016). Increased activity by adult males during the rut and hunter desire to harvest mature individuals likely drove the overall greater harvest probability of adult males relative to yearling males and females (Decker and Connelly 1989, Heberlein and Kuentzel 2002, Simoneaux et al. 2016). Further, hunter activity in urban areas may be driven by hunter desire to harvest older age class males that persist where hunter pressure is low (Heberlein and Kuentzel 2002), which was supported by our observation that harvested individuals with the highest urbanness values were adult males.

Lower adult female harvest probability in urban areas could be a result of hunter decisions, which has potential effects on the overlying population dynamics (Bhandari et al. 2006, Desrochers et al. 2025). Urban hunters may adhere to rational choice theory when choosing whether to hunt, and if so, which age class to harvest (Coleman 1990). Depending on hunter motivation, the risk of harvesting deer in urban areas (i.e., risk of public disapproval), especially females (i.e., smaller, no antlers), may not outweigh the benefits, whereas adult male harvest may be worth the risk for some hunters (Decker and Connelly 1989, Bhandari et al. 2006). Future research that investigates hunter attitude and motivations of harvesting male or female deer in urban areas can provide insight on the complexities of these effects on harvest outcomes. Furthermore, reduced female harvest probability and higher survival as urbanization increases may lead to increased deer populations. Adult females are the most influential demographic on populations due to high reproductive potential (Gaillard et al. 1998, 2000), and future research evaluating how current harvest probabilities of adult females influences population trajectories will greatly inform adaptive harvest management strategies in urbanizing landscapes.

MANAGEMENT IMPLICATIONS

Urbanization introduces complex challenges to managing white-tailed deer populations. Although decreasing hunter harvest is offset by increasing vehicle collisions as urbanization increases, using deer-vehicle collisions to manage urban deer populations is not a viable strategy. However, strategies to reduce deer-vehicle collisions (e.g., road underpasses, roadside fencing, reduced speed limits) could indirectly increase deer densities in urban areas if the challenges of low hunter harvest remain unaddressed. Managers will therefore benefit from simultaneously evaluating strategies that address both low hunter harvest and high risk of deer vehicle collisions. For example, managers may be able to leverage hunter desire to harvest adult males, indicated by higher harvest probabilities, to incentivize increased female harvest in urban and suburban areas where hunting already occurs. Our study further demonstrated that the challenges of reduced harvest do not solely arise in urban areas but likely occur along a continuum of urbanization. Even moderate levels of urbanization can lead to reduced harvest and increased vehicle collision risk. Consequently, management of hunter harvest and vehicle collision risk will benefit from comprehensive approaches across the urbanization gradient rather than based solely on an urban-rural dichotomy.

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TABLES

Table 1.1 Fates of white-tailed deer during the hunting season in Durham and Orange counties, North Carolina, USA (2022-2024). Counts are separated by year, fate, and sex. The number of deer with active collars at the start of the hunting season is denoted by "Available".

Year	Fate[a]	Male		Female	
		Adult	Yearling	Adult	Yearling
2022	Available	19	7	32	2
	Survived	7	5	26	2
	Harvested	10	1	4	0
	Non-harvest Mortality	2	1	2	0
2023	Available	15	9	31	2
	Survived	9	4	26	2
	Harvested	5	1	3	0
	Non-harvest Mortality	1	4	2	0
2024	Available	16	4	28	0
	Survived	5	2	24	0
	Harvested	7	0	2	0
	Non-harvest Mortality	4	2	2	0
Total	Available	50	20	91	4
	Survived	21	11	76	4
	Harvested	22	2	9	0
	Non-harvest Mortality	7	7	6	0

[a] Non-harvest mortality includes vehicle collision and unknown mortalities.

Table 1.2 Model selection results from multinomial logistic regression predicting the fate of individuals during the hunting season in Durham and Orange Counties, North Carolina, USA (2022-2024). The table includes model description, number of parameters (*K*), Akaike Information Criterion score corrected for small sample sizes (AICc), the relative difference to the top model (ΔAICc), and Akaike weight (w_i).

Model	*K*	AICc	ΔAICc	w_i
Sex + Age + Urbanness Value	8	247.57	0.00	0.79
Sex + Age + Urbanness Value + Huntable Lands Value	10	251.39	3.82	0.12
Sex + Age + Huntable Lands Value	8	253.42	5.85	0.05
Sex + Age	6	253.86	6.28	0.05

FIGURES

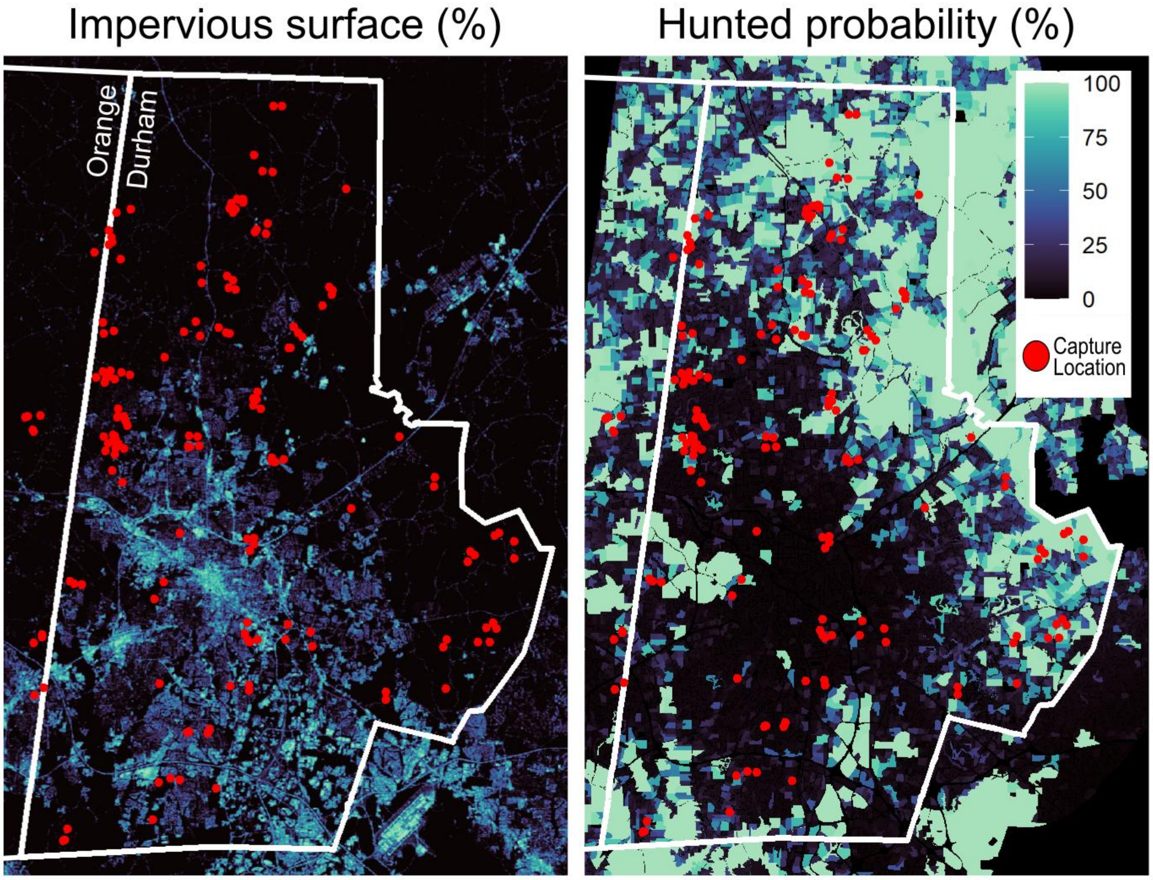

Figure 1.1 Map of white-tailed deer capture locations (red) with impervious surface (left) and huntable lands value probability (right) in Durham and Orange counties, North Carolina, USA (2022-2024). Impervious surface values are from the National Land Cover Database, while huntable lands values are based on Burke et al. (2019b) and adapted for local regulations.

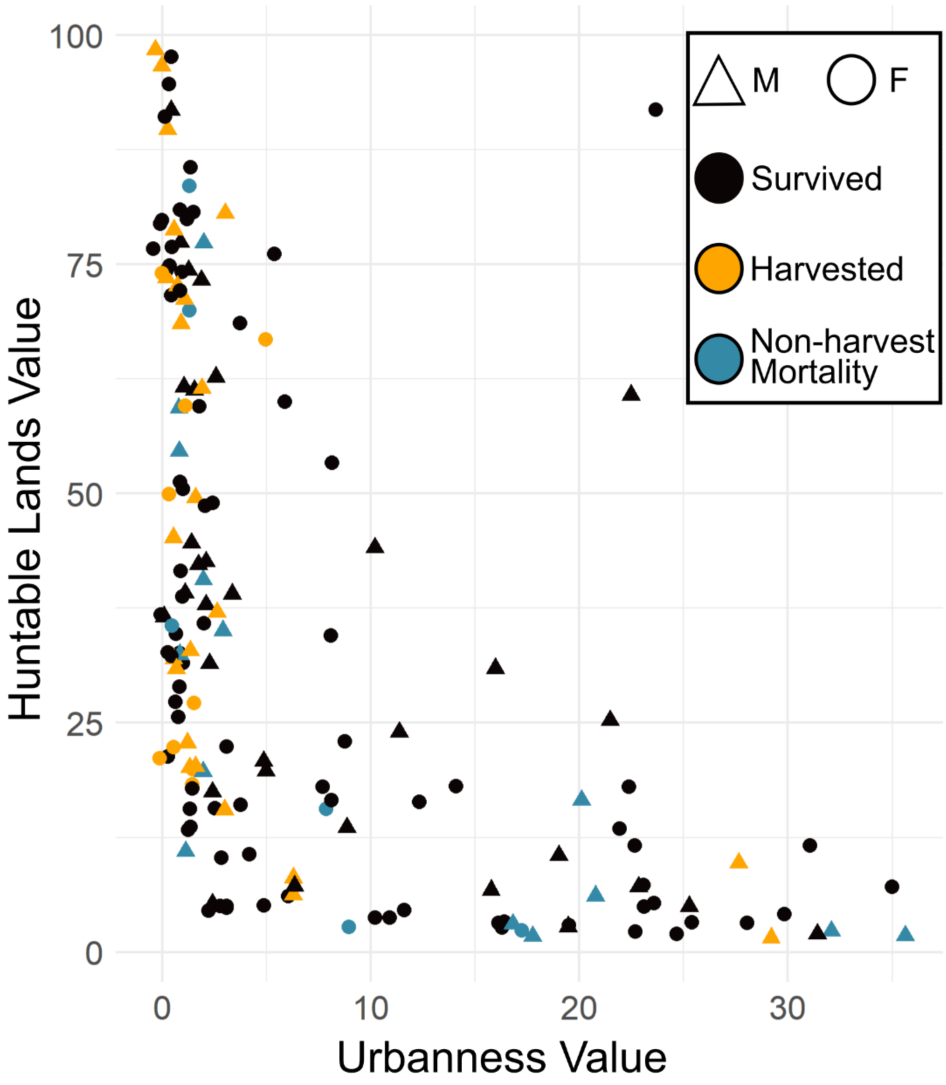

Figure 1.2 Fates during the hunting season of monitored white-tailed deer in Durham and Orange counties, North Carolina, USA (2022-2024). The x-axis denotes the individual's location across the urbanization gradient (urbanness value), and the y-axis denotes the area-weighted huntable lands probabilities (huntable lands value) found within the individual's range distribution. Color denotes fate (black = survived; orange = harvested, blue = non-harvest mortality). Shape denotes the sex (triangle = male; circle = female).

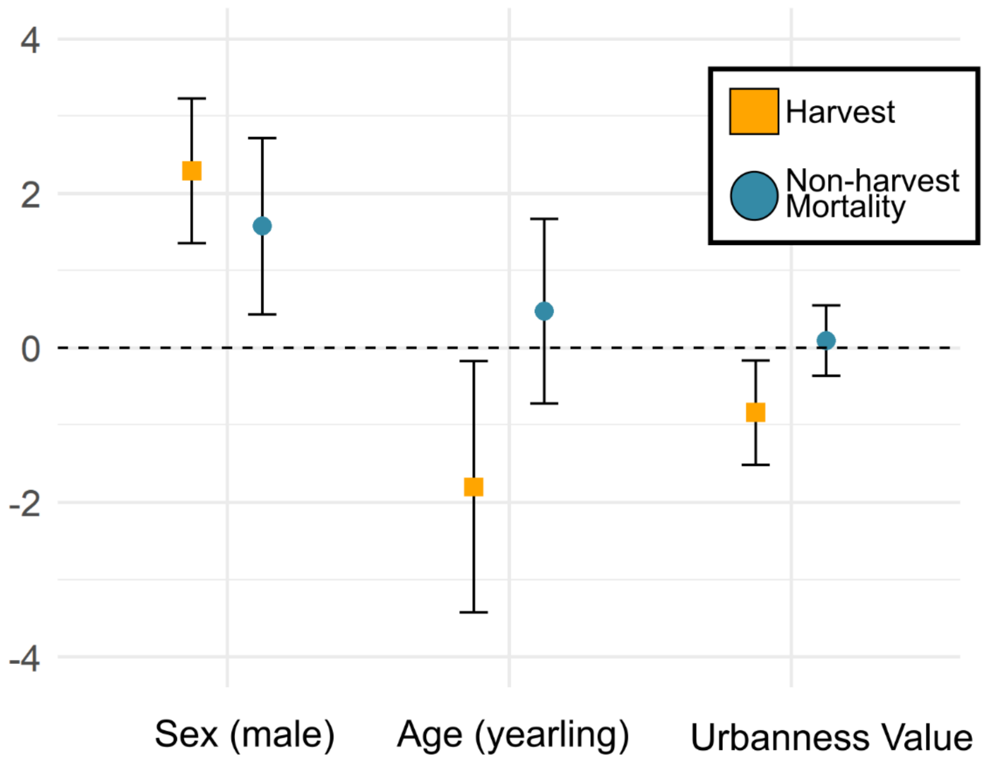

Figure 1.3 Covariate effects from the top candidate model (Fate ~ Sex + Age + Urbanness Value) for white-tailed deer fates (harvest = orange; non-harvest mortality = blue) in Durham and Orange counties, North Carolina, USA (2022-2024). Values > 0 denote an increased likelihood of the represented fate.

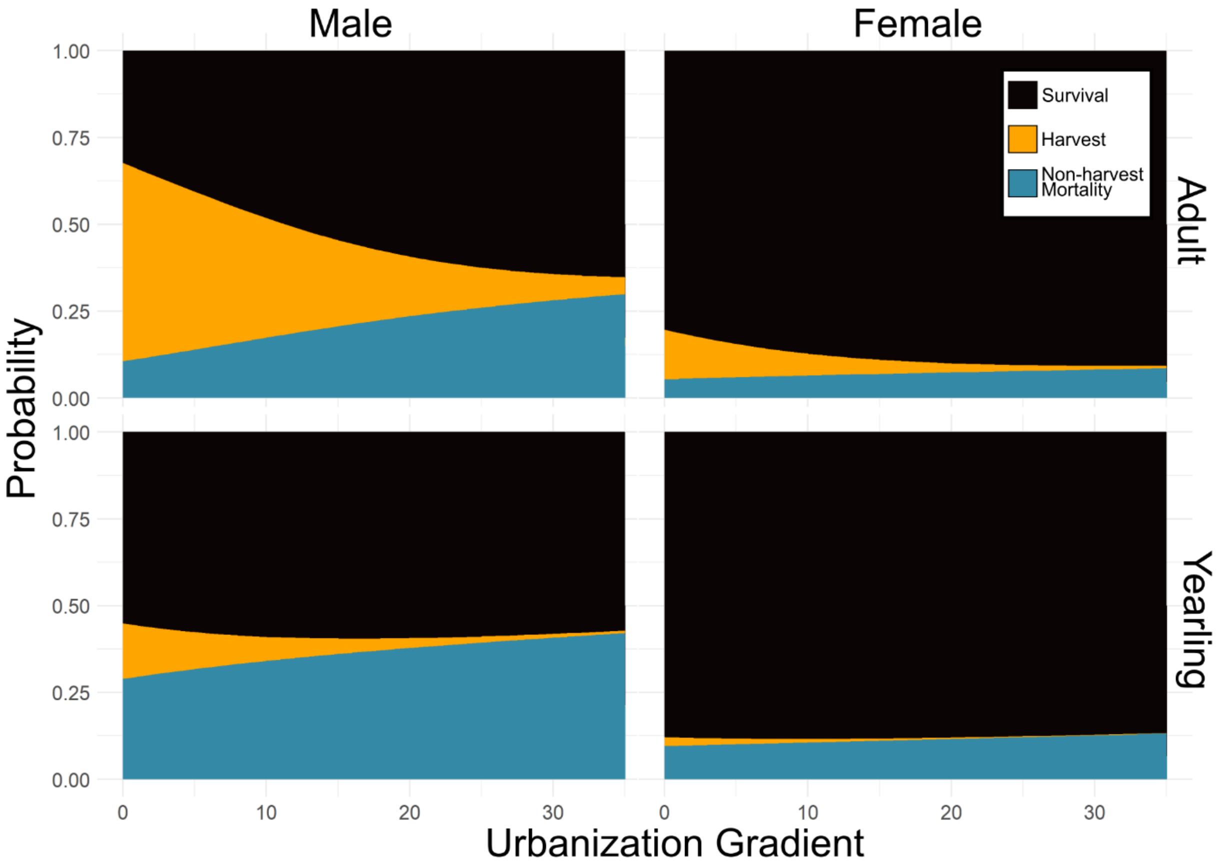

Figure 1.4 Probabilities of white-tailed deer fates as a function of the urbanization gradient (x-axis) in Durham and Orange counties, North Carolina, USA (2022-2024). Probabilities of each fate (survival = black; harvest = orange; non-harvest mortality = blue), where the heights describe the set of probabilities at the given urbanness value. Columns denote sex (left = male; right = female), and rows denote age (top = adult, bottom = yearling).

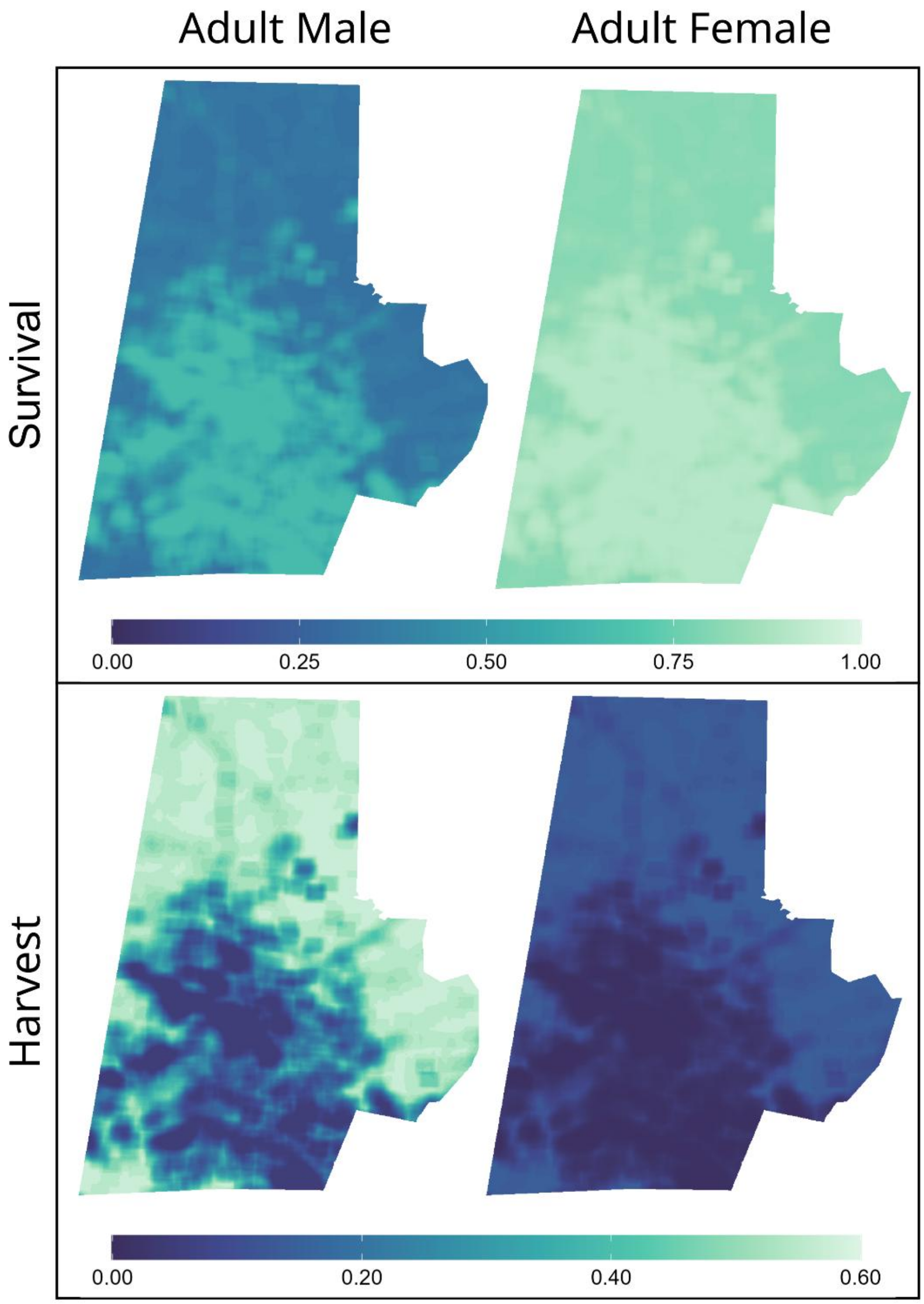

Figure 1.5 Map of predicted probabilities for white-tailed deer survival (top) and harvest (bottom) across Durham County, North Carolina, USA (2022-2024). Column denotes sex (left = male; right = female). Row denotes fate (top = survived; bottom = harvest). Legend and assigned color values vary by row.

APPENDIX

Appendix 1.1 Covariate effects and 95% confidence intervals from the top model (Fate ~ Sex + Age + urbanness value) for white-tailed deer harvest and non-harvest mortality in Durham County, North Carolina, USA (2022-2024). Values > 0 denote an increased likelihood of the represented fate.

	Harvest		Non-harvest mortality	
Covariate	Coefficient	Confidence interval	Coefficient	Confidence interval
Intercept	-1.72	(-2.46, -0.99)	-2.69	-3.61, -1.77
Sex (male)	2.29	(1.35, 3.23)	1.57	0.44, 2.71
Age (yearling)	-1.80	(-3.43, -0.18)	0.47	-0.72, 1.67
Urbanness value	-0.09	(-0.16, -0.02)	0.01	-0.04, 0.06

CHAPTER 2

Suburban landscapes maximize white-tailed deer (*Odocoileus virginianus*) population growth as vital rates change along an urbanization gradient

ABSTRACT

Survival and reproduction for wildlife species that persist in urbanizing areas may differ from the demographic rates of populations in adjacent rural landscapes. Although white-tailed deer (*Odocoileus virginianus*; hereafter deer) tolerate relatively high levels of urban land cover, the population dynamics of deer across a continuous urbanization gradient remain poorly understood. From 2022-2025, we conducted several complementary studies that investigated survival of neonate, yearling, and adult deer across an urbanization gradient in Durham and Orange counties, North Carolina. To contribute to this body of work, and provide a holistic view of deer population dynamics across an urbanization gradient, we: 1) quantified deer reproduction across the gradient, 2) synthesized previously reported survival estimates, and 3) projected population growth rates to investigate changes across an urbanization gradient. Expected litter size significantly increased with urbanization, and dynamic vital rates contributed to a non-linear relationship between population growth rate and urbanization. Population growth rate peaked in suburban areas ($\lambda = 1.01$) and declined into more rural ($\lambda = 0.96$) and urban ($\lambda = 0.89$) areas driven primarily by reductions in litter size in rural areas and reduced neonate survival in urban areas. Our results provide insight on ecological mechanisms behind deer population growth across urbanization gradients and reveal the varying contributions of vital rates to deer population growth in urbanizing landscapes.

Keywords: white-tailed deer, *Odocoileus virginianus*, urbanization gradient, population growth, survival, fecundity, projection matrix

INTRODUCTION

Urbanization alters resource distribution and mortality risk for wildlife, which can lead to changes in survival and reproduction across the urban-to-rural continuum (Ditchkoff et al. 2006, Rodewald and Gehrt 2014, Albaladejo-Robles et al. 2023, Pharr et al. 2023). Urbanization fragments habitat, often forcing individuals to move more frequently or over longer distances to obtain food and cover, which can increase exposure to mortality risks (e.g., predators, vehicles) and reduce energy available for reproduction (Bateman and Fleming 2012, Moran et al. 2021, Vanek et al. 2023). Concurrently, urbanization may suppress predator communities and provide supplemental food (e.g., gardens, ornamental plants), potentially enhancing survival and reproduction for some species (Lowry et al. 2013, Eötvös et al. 2018, Hansen et al. 2020). Despite the importance of these contrasting effects, our understanding of how survival and reproduction vary along continuous urbanization gradients remains limited. Even less is known about how interacting demographic processes, such as trade-offs between survival and fecundity, may amplify or counteract to generate non-linear patterns of population growth across urbanization gradients.

Life-history traits shape how wildlife populations are influenced by urbanization. Species that successfully exploit urban environments often exhibit fast life histories characterized by higher reproductive output, lower adult survival, and earlier maturation (Bateman and Fleming 2012, Lowry et al. 2013, Sol et al. 2013). However, for species that persist across urbanization gradients, relatively little is known about how stage-specific vital rates vary with urbanization, or how changes in vital rates interact to influence population growth. For example, white-tailed deer (*Odocoileus virginianus*) is an ungulate that occurs across urbanization gradients and can reach high densities in suburban landscapes (Bowman

2011, McAninch 1995, Urbanek and Nielsen 2013). Life-history theory predicts that ungulate population growth is most sensitive to adult female survival, but reproduction and neonate survival are typically more variable and among the first demographic rates to respond to environmental stressors (Gaillard et al. 1998, 2000). Disentangling how urbanization alters stage-specific vital rates (reproduction and survival) and how those changes compound or counteract to affect population growth across an urbanization gradient is therefore critical for predicting wildlife responses to urbanization and evaluating management strategies aimed at enhancing or reducing populations in urbanizing landscapes.

White-tailed deer (hereafter deer) exhibit variable densities and population dynamics across rural-to-urban areas, providing opportunities to investigate how urbanization alters vital rates and the drivers of population growth (Etter et al. 2002; Saalfeld and Ditchkoff 2007; Storm et al. 2007). Hunter harvest remains the primary cause of mortality for adult deer in rural areas; however, reduced hunter harvest in urban landscapes may be offset by higher risks of deer vehicle collisions (Chapter 1, Storm et al. 2007). Moreover, the types and distribution of foods for deer differ along urbanization gradients, which could influence the condition of reproductively mature females in a manner that alters reproduction across the urbanization gradient (Doenier et al. 1997, Readyhough et al. 2025). Finally, neonate survival and causes of mortality may vary due to changes in predator densities, the quantity and quality of hiding cover, and exposure to vehicle collisions as naive neonates become more mobile (Riley et al. 2003, Randa and Yunger 2006, Kays et al. 2008, Piccolo et al. 2010, Lamb et al. in-prep). Although an increasing number of studies have examined how specific demographic rates vary between rural and urban environments (Etter et al. 2002, Saalfeld and Ditchkoff 2007, Storm et al. 2007), little is known about how vital rates vary across a continuous urbanization gradient (Carver-McGinn

2025, Lamb et al. in-prep), how changes in multiple demographic rates contribute to changes in population growth, and which vital rates drive changes in population growth across urbanization gradients.

Accurate estimates of deer population growth rates across an urbanization gradient require information on multiple vital rates, which is largely lacking in the current literature. To address this information gap, we conducted a comprehensive study of deer demographics across an urbanization gradient in Durham County, North Carolina during 2022-2025. Our objectives were to quantify survival and reproduction by stage class (neonate, yearling, and adult) across a continuous urbanization gradient, then herein, evaluate how changes in vital rates affect population growth across the gradient. To accomplish these objectives, we: (1) quantified changes in deer reproductive rates across an urbanization gradient, then (2) synthesized previously reported neonate, yearling, and adult survival estimates from complementary studies (Carver-McGinn 2025, Lamb et al. in-prep) and used a population projection matrix and life table response experiment to evaluate how population growth rates (λ), stable stage distributions, vital rate elasticities, and the contributions of each vital rate to changes in population growth varied across an urbanization gradient. Our research employed a novel approach to quantify spatially dynamic deer population growth rates across a continuous urbanization gradient, and combined results across multiple studies to reveal the vital rates driving dynamic changes in deer populations across rural to urban landscapes.

STUDY AREA

We investigated deer demographics across Durham County, North Carolina. Durham County was approximately 772 km^2 and located in the Piedmont physiographic province of central North Carolina (Figure 2.1; North Carolina Geological Survey 2004). Durham County represented a strong urbanization gradient, from the city of Durham, which has approximately 280,000 residents and over 85% of the county's human population (US Census Bureau 2020), to rural areas primarily in the northern region (Figure 2.1). In general, urban and suburban land cover was prominent in the southern region of the county, whereas perimeter suburban areas to the north transitioned into exurban communities, forest, and row crop agriculture (Figure 2.1). Although Durham County was the focus of the project, deer capture and monitoring efforts spanned Durham County and eastern Orange County during 2022-2024. A majority (90%) of monitored individuals were in Durham County, and individuals monitored in Orange County were near the Durham County border.

METHODS

Reproduction

We captured yearling (>1.5-year-old) and adult (≥ 2.5-year old) female deer using drop nets (Wildlife Capture Services, Flagstaff, AZ, USA) and dart projectors (Model JM Standard, Dan-Inject, Austin, Texas, USA) from January to May in 2022 – 2024. We immobilized each deer with a 2-cc intramuscular injection of BAM (butorphanol 27.3 mg/ml, azaperone 9.1mg/ml, medetomidine 10.9mg/ml) (Wedgewood, Swedesboro, NJ, USA). We assigned female age as yearling or adult based on tooth eruption and wear characteristics (Severinghaus 1949), supplemented by estimated weight derived from chest girth measurements with comparison to local deer weights and ages (North Carolina Wildlife Resources Commission 2006–2025; unpublished data). We equipped captured females with a global positioning system (GPS) collar (Model G5-2D, Advanced Telemetry Systems, Isanti, MN, USA) and a vaginal implant transmitter (VIT; Model M3930U, Advanced Telemetry Systems, Isanti, MN, USA) with light and temperature signals, which triggered a birth notification when expelled from the female.

VITs had a precise event transmitter (PET) that emitted a sequence to mark the occurrence of a temperature alert, and thus the time of the birth event. At the conclusion of each workup, we antagonized BAM with a 4.0-cc injection of atipamezole (25 mg/ml) and a 0.5-cc injection of naltrexone HCl (50 mg/ml) (Wedgewood, Swedesboro, NJ, USA). We initiated searches for neonates 4 hours after receiving a birth notification from the VIT to allow for grooming and bonding. We tracked into the collared adult female, then to the VIT to search for neonates, aided by handheld forward-looking infrared units (FLIR Scion OTM, Teledyne FLIR, Wilsonville, OR, USA; (Haskell et al. 2007, Kilgo et al. 2012). Once at least 1 neonate was located, we recorded sex, mass, and location of the neonate. We continued to search for siblings if none were in the immediate area before evacuating the area to limit disturbance of bonding time with the dam.

Live birth probability — We estimated the probability a female that survived to the birthing period gave birth to at least one live neonate. Specifically, for females that survived to the birthing period we defined $y_i = 1$ if collared female i had at least one live neonate, and $y_i = 0$ if female i had no live neonates (fully stillborn litter or retained the VIT throughout the birthing period). We modeled the probability of producing offspring (θ) as

$$y_i \sim Bernoulli(\theta)$$

Litter size. — We estimated the expected litter size (1 or 2 neonates) for females that survived to the birthing period and produced at least one neonate, and if expected litter size varied as a function of dam age (yearling versus adult) and location on the urbanization gradient. We included litter size counts in the analysis if they were: 1) observed ≤ 24 hours from birth indicated by the VIT, and 2) alive and viable. We excluded neonate counts >24 hours after birth to avoid underestimating litter size. We followed methods in Chapter 1 and Carver-McGinn et al.

(2025) to quantify the urbanization gradient. Specifically, we calculated a range distribution for each dam using a 99% autocorrelated kernel density estimate from GPS locations collected from 1 May to 30 June of the monitored birth year (Fleming et al. 2015). Then, we derived the mean percent impervious surface from the 2021 National Land Cover Database impervious surfaces raster (Dewitz 2023) within the range distribution to describe the location of the female and the associated litter on the urbanization gradient (henceforth “urbanness value”). Because we only observed litter sizes of 1 or 2, we modeled the probability a female had twins by defining $n_i = 1$ if female i had 2 neonates and $n_i = 0$ if female i had 1 neonate. We modeled this binary outcome as a function of the female’s age and urbanness value, specifically,

$$n_i \sim Bernoulli(p_i)$$

$$logit(p_i) = \beta_0 + \beta_1 \times Urbanness_i + \beta_2 \times age_i.$$

Here, p_i is the probability female i had twins, $Urbanness_i$ and age_i are the urbanness value and age (yearling = 0, adult = 1) for female i, respectively, β_0 is the logit-scale intercept, and β_1 and β_2 describe the effects of urbanness and age, respectively. We then derived the expected litter size (l_i) as $p_i + 1$ and the expected reproductive output of a female as $\theta \times l_i$.

We assumed females within the first year of life (i.e., fawns) had a litter size of 0 while recognizing that such births occur, and statewide data indicates that the average fetus count of this stage class was 0.17 (NCWRC; Unpublished data). Although we observed anecdotal evidence of 1 tagged female of this stage class giving birth to 1 non-viable neonate (genetic deformity), we maintained the assumption that the litter size of deer within the first year of life was 0, because of the precedent set by previous studies and the inability to effectively monitor reproduction via VITs at this age (Gaillard et al. 2000, Chitwood et al. 2015, Peters et al. 2020, Clevinger et al. 2023, Edge et al. 2023).

Implementation. — We fit the models in a Bayesian framework using JAGS (Plummer 2003) and the jagsUI package (Kellner 2024) in R (version 4.4.1, R Core Team 2024). We ran models for 15,000 iterations across 3 chains, with a 5,000 burn-in and a thinning rate of 2. We verified convergence using Gelman-Rubin diagnostic values ($R < 1.1$) and report results as posterior medians and the 2.5% and 97.5% quantiles (95% credible intervals; hereafter 95% CrI).

Projection Matrix

Vital rates – Survival and fecundity were derived based on data from complementary studies in Durham County (Table 2.1). Specifically, female neonate survival estimates were obtained from Lamb et al. (in-prep), which estimated 0–52-week survival using 135 collared neonates across the urbanization gradient during 2022-2025 (Table 2.1). Similarly, yearling and adult female survival estimates were obtained from Carver-McGinn et al. (2025), which used 111 collared yearlings and adults to estimate female survival across the urbanization gradient in Durham County during 2022-2025 (Table 2.1).

Projection – We investigated the effects of urbanization on deer demographics using a female only, post-birth census projection matrix (A) with annual time steps (Figure 2.2). The matrix included 3 stage classes: neonate (immediately after birth; $i = 1$), yearling (1-year old; $i = 2$), and adult (≥ 2-years old; $i = 3$; Figure 2.2). We evaluated the effects of urbanization by simulating the projection matrix across a range of urbanness values ($j=0, 1, 2, \ldots J=40$), where the component vital rates reflected estimates for that urbanness value. We defined transitions as a function of survival for stage class i at urbanness value j (S_{ij}) and recruitment as a function of fecundity for stage class i at urbanness value j (F_{ij}; Figure 2.2)

$$A_j = \begin{array}{c|ccc|} & 1 & 2 & 3 \\ \hline 1 & 0 & F_{2j} & F_{3j} \\ 2 & S_{1j} & 0 & 0 \\ 3 & 0 & S_{2j} & S_{3j} \\ \hline \end{array}$$

We defined fecundity in the post-birth census projection model as the product of: 1) female survival probability (S_{ij}), 2) the probability of giving birth to at least one neonate conditional on survival (θ), and 3) expected litter size (l_{ij}). Specifically:

$$F_{ij}=(S_{ij}\times\theta\times l_{ij})/2$$

where we divided the expected rate by 2 to reflect an equal sex ratio at birth. Values for the probability of giving birth to at least one neonate conditional on survival and expected litter size were derived from the methods described above (Methods - Reproduction; Table 2.1).

We incorporated uncertainty in the component vital rates by simulating the projection matrix for 10,500 iterations at each urbanness value. During each iteration, we populated the matrix by drawing a random value from the posterior distribution of each component's vital rate at the selected urbanness value (j). We then calculated the expected population growth rate (λ), stable stage distribution (*SSD*), and stage class specific elasticity values (e) at each urbanness value. We then used a life table response experiment (LTRE) to quantify the contribution of each vital rate to changes in population growth across the urbanization gradient (Caswell 1989). For the LTRE, we set urbanness value of 15 as the reference value because it had the highest population growth rate. For each urbanness value, the contribution (c_j) of a given vital rate represents its influences on the difference in population growth rate between the selected urbanness value and the reference. Here, a small contribution indicates that the vital rate either varies little across the gradient or that population growth is relatively insensitive to changes in that vital rate, whereas positive and negative contributions indicate positive and negative effects on changes in population growth, respectively. Importantly, our matrix model and LTRE approaches do not provide a single estimate across the study area, but quantify how population growth rates, stable stage distributions, elasticities of component vital rates, and contributions of component vital rates to changes in population growth rate vary across the urbanization gradient. We summarized results using the median, 25th and 75th quantiles (50% CI), and 2.5th and 97.5th quantiles (95% CI) for each urbanness value.

We made several assumptions to align with previous literature and reflect the available information: 1) density independence, 2) geographic closure, 3) no male limitations, 4) homogeneity for each stage, and 5) no reproductive senescence (Chitwood et al. 2015, Peters et al. 2020, Clevinger et al. 2023, Edge et al. 2023). We calculated population growth rates, stable stage distributions, and elasticities using the popbio package (Stubben and Milligan 2007) in R (version 4.4.1, (R Core Team 2024). To display the spatial variation in population growth rate, we predicted values across Durham County using the NLCD 30-x30-m impervious surface raster smoothed at a 1-km^2 area to approximate the urbanness values used across all studies (Carver-McGinn 2025, Lamb et al. in-prep; Table 2.1).

RESULTS

Reproduction

Live birth probability — We captured and implanted VITs in 99 females (88 adults, 11 yearlings) and included 66 individuals that met criteria for analyzing the probability of live birth. We censored 33 females from this analysis because of premature VIT expulsion (9), death before birthing period (5), VIT malfunction (2), or instances of neonates never being located (17). We captured a live neonate from 63 females, 2 females gave birth to fully still born litters, and 1 female was not pregnant and retained the VIT until 17 August when the VIT battery died. Thus, the probability of a female giving birth to at least 1 live neonate (θ) was 0.95 (95% CrI = 0.88, 0.98).

Litter size. — We included 48 females (41 adults, 7 yearlings) that met the criteria to derive the expected litter size (Figure 3). We censored 18 females from this analysis because of stillborn litters (2), non-pregnancy (1), and litters located > 24 hours after the VIT expulsion (15). We were not able to locate some neonates within 24 hours after VIT expulsion because it often took an extended amount of time to acquire property owner permission to access birth sites. In addition, the delay of emailed VIT notifications occasionally exceeded 24 hours after the time of expulsion as indicated by the PET sequence. Expected litter size significantly increased as urbanness values increased (0.14; 95% CrI = 0.05, 0.24), with the estimated litter size ranging from ~1.20 at the lowest urbanness values to ~2.00 at the highest urbanness values for each age class (Figure 2.3; Appendix 2.1). Estimated adult litter size was larger than yearlings, but the difference was not significant (0.74; 95% CrI = -1.16, 2.81; Figure 3; Appendix 2.1).

Projection Matrix

Vital rates – Vital rates varied considerably across the urbanization gradient with median adult survival and fecundity increasing with urbanization, whereas neonate and yearling survival declined (Figure 2.4). Changes in adult survival across the gradient were relatively small, with a non-significant increase from 0.77 (95% CrI = 0.68, 0.85) to 0.83 (95% CrI = 0.51, 0.96; Appendix 2.2), whereas yearling survival had a non-significant decrease from 0.83 (95% CrI = 0.64, 0.93) to 0.76 (95% CrI = 0.09, 0.98; Appendix 2.3) as urbanization increased (Carver-McGinn 2025; Figure 2.4). Neonate survival decreased from 0.41 (95% CrI = 0.25, 0.57) to 0.07 (95% CrI = 0.00, 0.28) as urbanization increased (Lamb et al. in-prep; Fig 4; Appendix 2.4). Adult fecundity increased from 0.43 (95% CrI = 0.37, 0.50) to 0.78 (95% CrI = 0.47, 0.91;

Appendix 2.5) and yearling fecundity increased from 0.44 (95% CrI = 0.33, 0.59) to 0.70 (95% CrI = 0.08, 0.92; Appendix 2.6) as urbanization increased (Figure 2.4).

Projection – Dynamic vital rates resulted in population growth rate peaking at urbanness value 15 and declining as areas became more rural or urban (Figure 2.5). Population growth rate was 0.96 in the most rural areas (95% CrI = 0.85, 1.06; $j = 0$), increased to 1.01 in suburban landscapes (95% CrI = 0.90, 1.12; $j = 15$), and then declined to 0.89 at the highest level of urbanization where deer were monitored (95% CrI = 0.56, 1.09; $j = 40$; Figure 2.5). Median population growth rates were >1 across urbanness values ranging from 8 to 22, which generally reflected the rural-suburban interface in our study area (Figures 2.1, 2.5). Conversely, median population growth rates were <1 at more rural and urban ends of the continuum (j = 0-8; 24-40), but 95% CrI's always included 1.0 (Figure 2.5). The proportion of the population that were yearlings declined, driven by increased adult survival and decreased neonate survival as urbanization increased (Figure 2.6).

Adult survival retained the highest elasticity value across the gradient, ranging from 0.53 (95% CrI = 0.43, 0.65) to 0.84 (95% CrI = 0.53, 0.99) as urbanization increased (Figure 2.6). However, changes in adult and yearling fecundity (0.42 - 0.78; 0.42 - 0.71) and neonate survival (0.41 - 0.07) were substantially larger than changes in adult survival (0.77 - 0.83) across the gradient (Figure 2.4). Relative to the peak in population growth rate at urbanness value 15, declining population growth rates as urbanization decreased were driven by negative contributions from declining adult fecundity ($c_0 = -0.05$), adult survival ($c_0 = -0.02$), and yearling fecundity ($c_0 = -0.01$), which offset the positive contribution of increased neonate survival ($c_0 = 0.04$; Figure 2.7). As urbanization increased relative to the peak at urbanness value 15, declining population growth rates (λ) were driven by negative contributions from declining neonate survival (c_{40} = -0.14) and yearling survival (c_{40} = -0.01), which offset positive contributions of increasing adult fecundity (c_{40} = 0.02) and adult survival (c_{40} = 0.01; Figure 2.7).

DISCUSSION

Our results demonstrate non-linear deer population growth across a continuous urbanization gradient, driven by the cumulative effects of multiple vital rates. Consistent with previous reports of high deer densities in suburban landscapes, population growth peaked at low to moderate levels of urbanization (Etter et al. 2002, Urbanek and Nielsen 2013). Importantly, the peak in population growth was not explained by the maximization of a single vital rate, but rather by a combination of increasing litter size, declining neonate survival, and small changes in adult survival as urbanization increased from the most rural areas. Although adult survival had the highest elasticity, high variability in more plastic rates such as litter size and neonate survival ultimately drove changes in population dynamics, consistent with previous studies of deer (Robinson et al. 2014, Chitwood et al. 2015) and long-standing theories on the demographic drivers of ungulate population growth (Gaillard et al. 1998, 2000). Specifically, declines in neonate survival contributed to reduced population growth in the most urban areas, whereas declines in litter size reduced population growth in rural landscapes. Our results highlight the importance of evaluating changes in multiple vital rates to understand how urbanization alters deer fitness and underscore the need to consider interactions among vital rates and urbanization to develop effective management strategies across urbanized landscapes.

Mechanisms underlying the positive relationship between litter size and urbanization remain uncertain but likely involve differences of food availability across the urbanization gradient. Body condition is a well-documented driver of litter size in ungulates (Cook et al. 2004, DelGiudice et al. 2007, Johnstone-Yellin et al. 2009, Readyhough et al. 2025) and spatiotemporal variation in food resources across the urbanization gradient may drive changes in litter size (Kilpatrick and Spohr 2000, Hansen et al. 2020). Feeding deer year-round is common in urban and suburban areas, and year-round availability of supplemental food resources can improve female condition and in-utero productivity (Doenier et al. 1997, Hansen et al. 2020, Ozoga and Verme 1982, Thompson et al. 2008). Further, the female nutritional condition during the breeding and post breeding periods have high influences on litter size productivity of females (Verme 1969). Thus, lack of timely access to supplemental food during the late fall, combined with cumulative effects of year round nutritional stress may decrease litter size. However, we did not investigate nutritional condition of mothers across the urbanization gradient, and deer fecundity is shaped by complex relationships between deer social dynamics, physiological condition, and environmental factors (Corlatti et al. 2018, DelGuiudice et al. 2007, Gaillard et al. 2000, Miller et al. 1997). Future studies linking maternal nutritional condition, and the effects of supplemental food variability across continuous urbanization gradients will be critical for identifying the commonality of our findings and mechanisms driving increased litter size in urban environments.

Litter counts collected post-parturition can underestimate true litter size due to early predation, neonate mobility, and imperfect detection by researchers (Haskell et al. 2007, Kilgo et al. 2012). We minimized these risks by conducting thorough searches and restricting analyses to litters located within 24 hours of parturition. Even with these precautions, mean litter size estimates in more rural areas (~1.2) were lower than most observed rates reported in literature (~1.3 - 1.8; Chitwood et al. 2015, Ditchkoff et al. 2011, Peters et al. 2020, Clevinger et al. 2023, Edge et al 2023). Although potential bias in litter size estimates could affect growth rate estimates, underestimation should not alter the relationship with the urbanization gradient unless bias varied systematically with urbanization. In our study, locating all neonates was often more difficult in urban areas because searches required access to multiple small parcels. Litter counts in more rural areas typically occurred within 10 hours of parturition (mean = 5 hours), whereas those in more urban areas occurred 10–24 hours after parturition (mean = 16 hours), reducing the likelihood that early predation or neonate movement led to underestimation in rural areas (Haskell et al. 2007). Nonetheless, we cannot rule out all potential sources of bias, and future studies that validate these findings and examine mechanisms underlying variation in litter size will improve understanding of factors driving deer population growth across urbanization gradients.

Population growth rate declined at the most rural end of the urbanization gradient primarily through declining fecundity and a non-significant decline in adult survival, supporting hypotheses that deer gain some fitness benefit from low levels of urbanization (Porter et al. 2004, Urbanek and Nielsen 2013). In this study, adult female deer were susceptible to multiple mortality causes in more rural areas, including hunter harvest, vehicle collisions, and other mortalities (e.g., malnutrition, disease) that culminated in a non-significant decline in annual survival as urbanization declined (Carver-McGinn 2025). Although adult survival showed a non-significant decrease, the substantial reduction in expected litter size drove lower population growth in more rural areas. Declines in reproductive output can have strong consequences for population growth as the number of offspring produced sets the upper limit on recruitment into the population (Stearns 1998). In species with relatively low reproductive rates, modest reductions in litter size or neonate survival can substantially depress population growth (Gaillard et al. 1998, 2000). Urbanization may amplify these effects by altering food resources in suburban areas, which in turn improve body condition and increase reproductive success compared to the most rural areas (Ditchkoff et al. 2006, Rodewald and Gehrt 2014, Potratz et al. 2019). Thus, declines in reproductive output emerged as a key demographic mechanism driving changes in population growth at the most rural end of the urbanization gradient.

Decreasing neonate survival overwhelmed the increase in litter size in more urban areas which drove the decline in population growth rate. Neonate survival declined in more urban areas due to cumulative mortality risks throughout the first year of life, including elevated predation risk in the first 16 weeks and increased vehicle collisions from weeks 17 to 52 (Lamb et al. in-prep). First-year survival is often more variable than survival in later life stages and may differ across urbanization gradients, making it a likely driver of deer population dynamics in urbanizing landscapes (Riley et al. 2003, Saalfeld and Ditchkoff 2007, Piccolo et al. 2010, Lamb et al. in-prep). The reduction in neonate survival as urbanization increased also shifted stable stage distributions, producing increasingly bimodal age structures in urban areas dominated by neonates and adults with few yearlings. The lack of recruitment into the yearling stage class ultimately limited population growth and drove declines in highly urban areas, where growth rates dropped to 0.89 and reflected our observations of very low to no deer in these most urban areas. Caution is warranted when interpreting estimates at very high urbanness values (>30), where sample sizes were limited due to low deer densities and thus required extrapolation of some vital rates (e.g., litter size). Overall, our results indicate that while deer benefit from low to moderate levels of urbanization, high levels impose demographic constraints that limit population viability, reflecting a hormetic response to urbanization.

Variation in vital rates led to peak population growth at low to moderate urbanization, and illustrates how a species' response to urbanization is shaped through tradeoffs among survival, reproduction, and recruitment (Albaladejo-Robles et al. 2023). In more rural areas, lower fecundity and reduced adult survival constrained growth, whereas neonate survival limited population growth in more urban areas. At urbanness levels that encompassed suburban landscapes, these constraints offset one another, creating demographic conditions that maximized population growth. The peak in population growth rate supports and elucidates the possible mechanisms driving deer abundance in suburban areas (McShea et al. 1997, Urbanek and Nielsen 2013). Deer that inhabit the suburban-rural interface may benefit from the proximity and advantages present in both suburban and rural areas (DeNicola et al. 2000, Etter et al. 2002, Storm et al. 2007). For example, deer may select rural areas with better neonate hiding cover and less traffic density (Grund et al. 2002, Potapov et al. 2014), but also exploit suburban-associated resources such as supplemental foods and refugia from hunting (DeNicola et al. 2000, Kilpatrick and Spohr 2000, Lovely et al. 2013, Little et al. 2014, Marantz et al. 2016). Together, these conditions can maximize individual fitness and population growth, leading to high deer densities in suburban environments.

Our results quantifying the effects of urbanization on deer vital rates and population growth provide a framework for predicting population responses to future land use change and management actions. Although minimal variation in highly elastic vital rates is a well-known characteristic of ungulate life histories (e.g., adult female survival; Gaillard et al. 1998, 2000), we further demonstrated that this stability likely persists across urbanization gradients. Here, yearling and adult female survival remained relatively consistent due to offsetting mortality sources (declines in hunter harvest balanced by increases in vehicle collisions as urbanization increased; Carver-McGinn 2025; Chapter 1), whereas changes in population growth were driven by variation in the more variable demographic rates of litter size and neonate survival. Evaluating vital rates and population growth along a continuous urbanization gradient thus provides insights into wildlife responses across the gradient and possible indicators for changes as landscapes urbanize. For example, increased litter size combined with persistence of the yearling stage class may signal areas of increasing deer density and human-wildlife interactions at rural-suburban interfaces. Conversely, an aging population or reduced recruitment of neonates into the yearling stage class may indicate urbanized landscapes where deer populations are beginning to decline. Finally, regardless of the location on the urbanization gradient, changes in adult survival remain the greatest proportional contributor to changes in population growth (i.e., highest elasticity). Overall, our ability to identify how vital rates shift with urbanization allows managers to better predict population trajectories and assess the likely effectiveness of management strategies aimed at different vital rates (e.g., lethal or non-lethal) in increasingly human-dominated environments.

MANAGEMENT IMPLICATIONS

Our results indicate that management actions focused on altering adult survival will provide the greatest proportional changes in population growth, although variations in fecundity and its contribution to population growth rate reveal opportunities for supplemental strategies to alter population growth. To increase deer populations in rural areas, managers should combine reduced female harvest with efforts to improve female condition and thus fecundity. However, deer management objectives commonly seek to reduce densities where hunter harvest is low and negative-deer human interactions are high, especially in urbanizing landscapes where deer-vehicle collisions are the dominant source of mortality. To lower deer densities in urban landscapes, we recommend promoting hunter harvest and limiting human subsidized supplemental feed to reduce fecundity.

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TABLES

Table 2.1. White-tailed deer vital rates across an urbanization gradient in Durham and Orange counties, North Carolina, USA 2022-2025. Range estimates are posterior medians from the lowest urbanness values (*j*=0) to the highest (*j*=40) with 95% credible intervals. Parameter estimate sources are provided in footnotes.

Rate	Range $j = 0 - 40$	95% Credible Interval
(θ) - Live birth[1]	0.95	(0.88, 0.98)
(S_1) - Neonate Survival[2]	0.41 – 0.07	(0.25, 0.57) – (0.00, 0.28)
(S_2) Yearling Survival[3]	0.83 – 0.79	(0.64, 0.93) – (0.11, 0.97)
(S_3) Adult Survival[3]	0.76 – 0.84	(0.68, 0.84) – (0.51, 0.97)
(l_2) Yearling Litter Size[1]	1.11 – 1.97	(1.01, 1.48) – (1.70, 2.00)
(l_3) Adult Litter Size[1]	1.16 –1.98	(1.07, 1.30) – (1.80, 2.00)
(F_2) Yearling Fecundity[1,3]	0.44 – 0.73	(0.33, 0.60) – (0.11, 0.92)
(F_3) Adult Fecundity[1,3]	0.43 – 0.79	(0.37, 0.49) – (0.47, 0.91)

[1] Current study

[2] Lamb et al. (in-prep)

[3] Carver-McGinn et al. (2025)

FIGURES

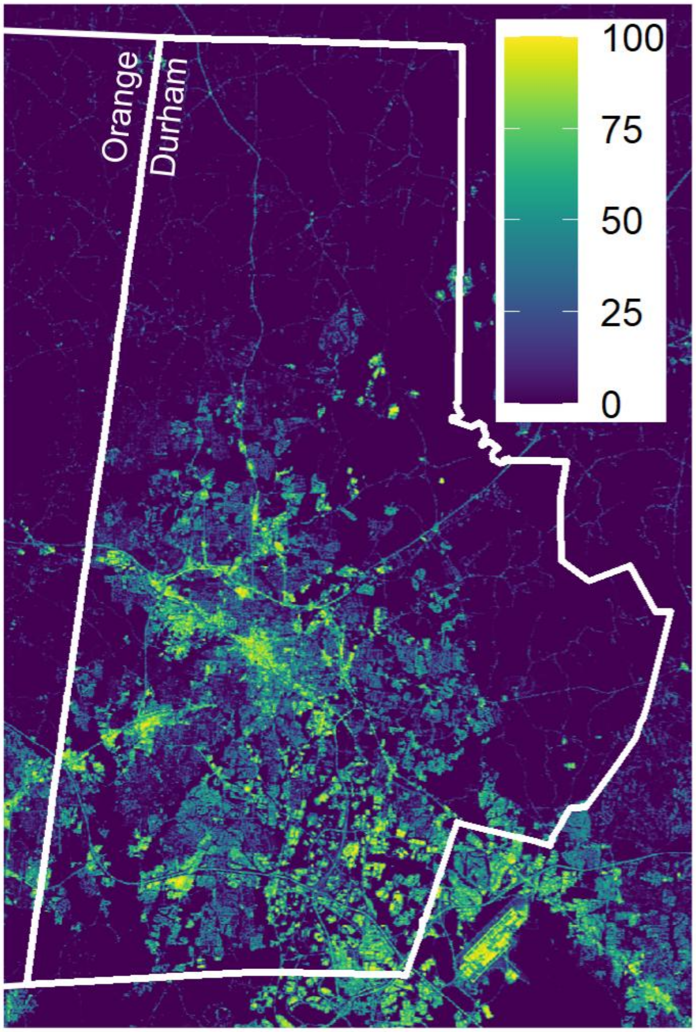


Figure 2.1. Map of the percent impervious surface cover within the study area in Durham and Orange counties, North Carolina, USA (2022-2024). Percent impervious surface cover was obtained from the National Land Cover Database.

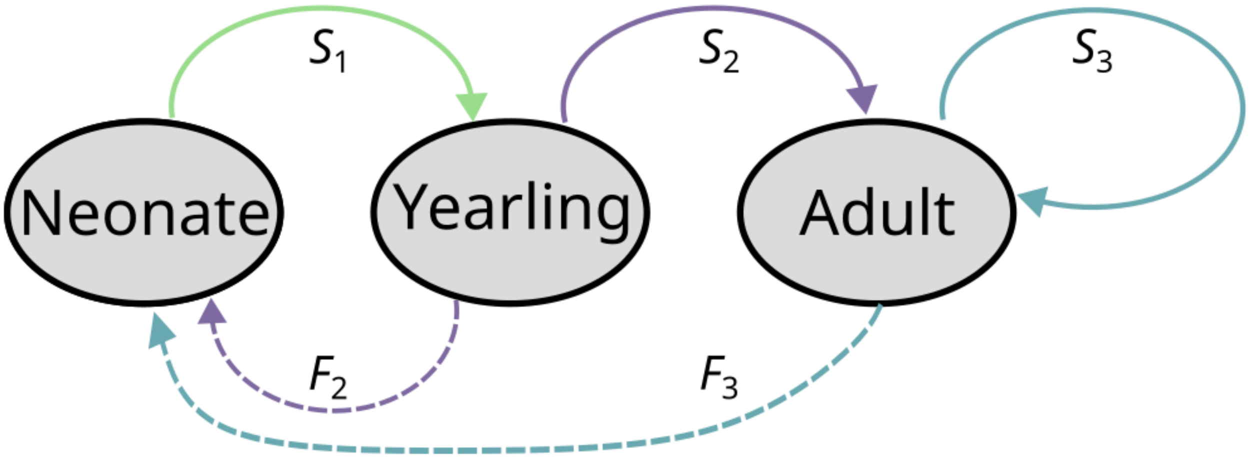


Figure 2.2. Post-breeding census life stage model for neonate (i=1, green), yearling (i=2, purple) and adult (i=3; blue) white-tailed deer with survival (S; solid), and fecundity (F; dashed) represented between each stage.

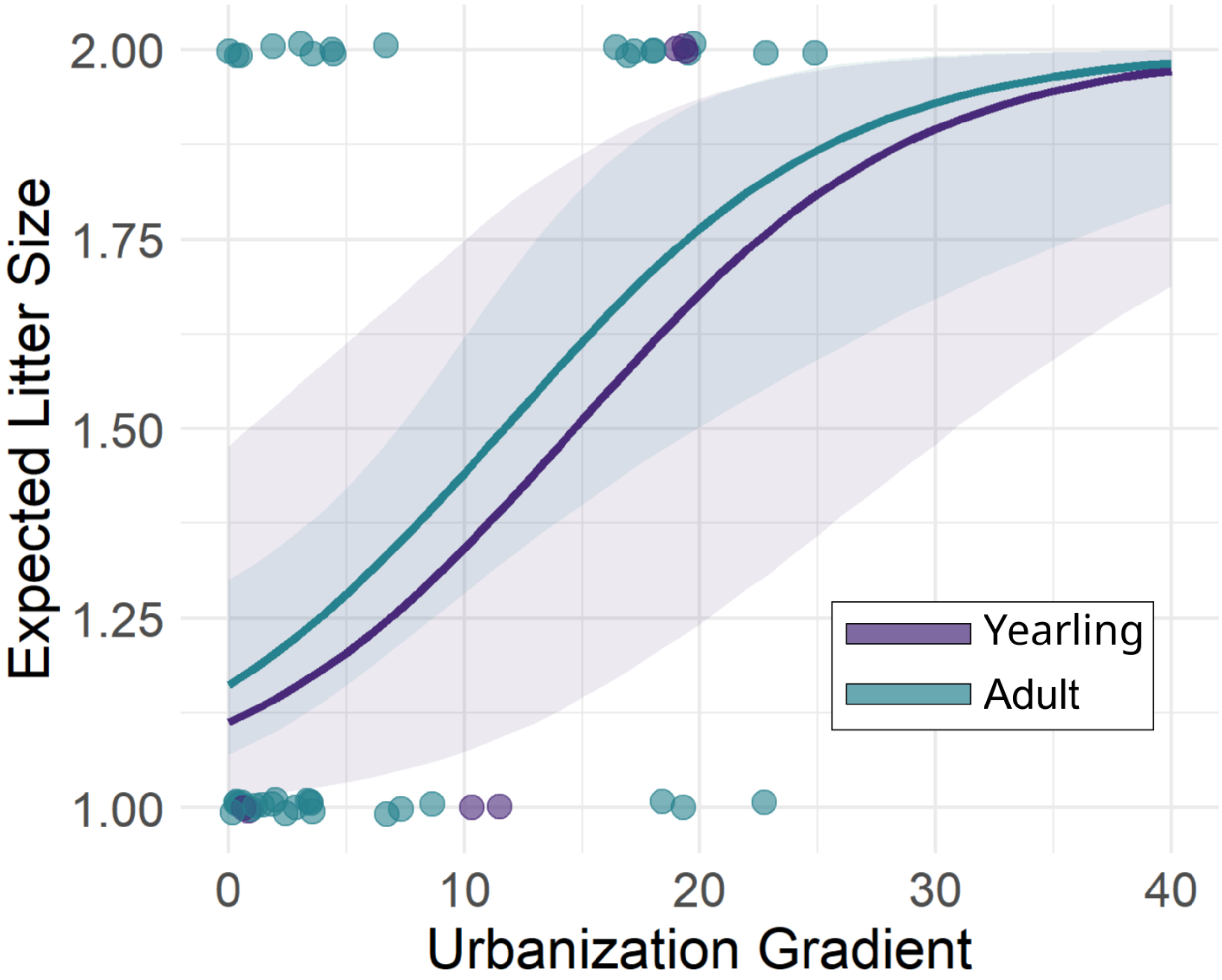


Figure 2.3. Expected litter size (l_i; y-axis) of yearling (purple) and adult (blue) white-tailed deer across the urbanization gradient (x-axis) documented in Durham and Orange counties, North Carolina, USA, 2022-2024. Lines are posterior medians, and shaded areas represent the 95% credible interval. Observed litter size of each female and the corresponding location on the urbanization gradient are represented by circles.

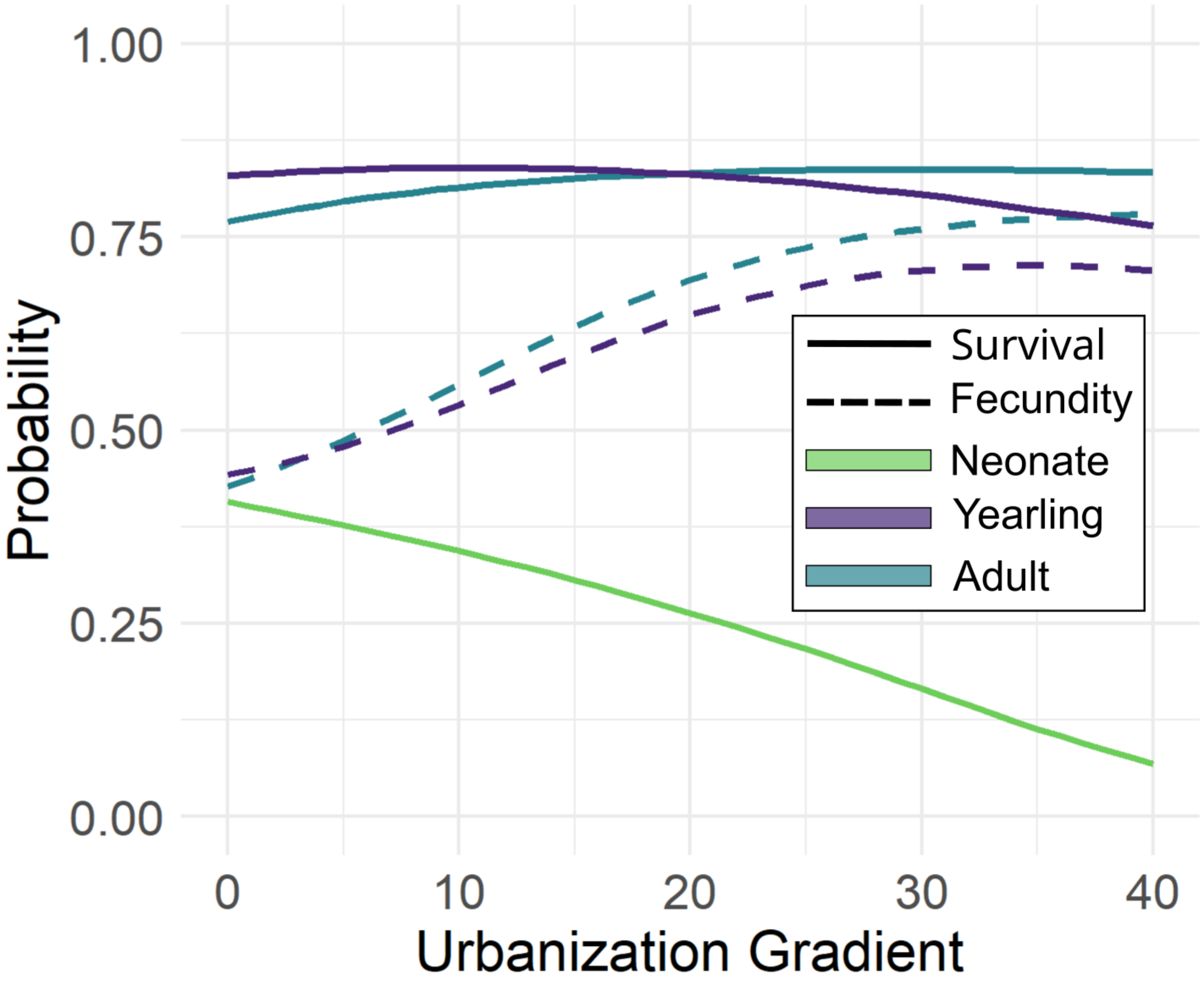


Figure 2.4. Predicted survival probabilities (solid) and fecundity rates (dashed) of white-tailed deer across the urbanization gradient in Durham and Orange counties, North Carolina, USA, 2022-2025. Adult (blue) and yearling (purple) survival probabilities are reported in Carver et al. (2025), and neonate (green) survival is reported in Lamb et al. (in-prep).

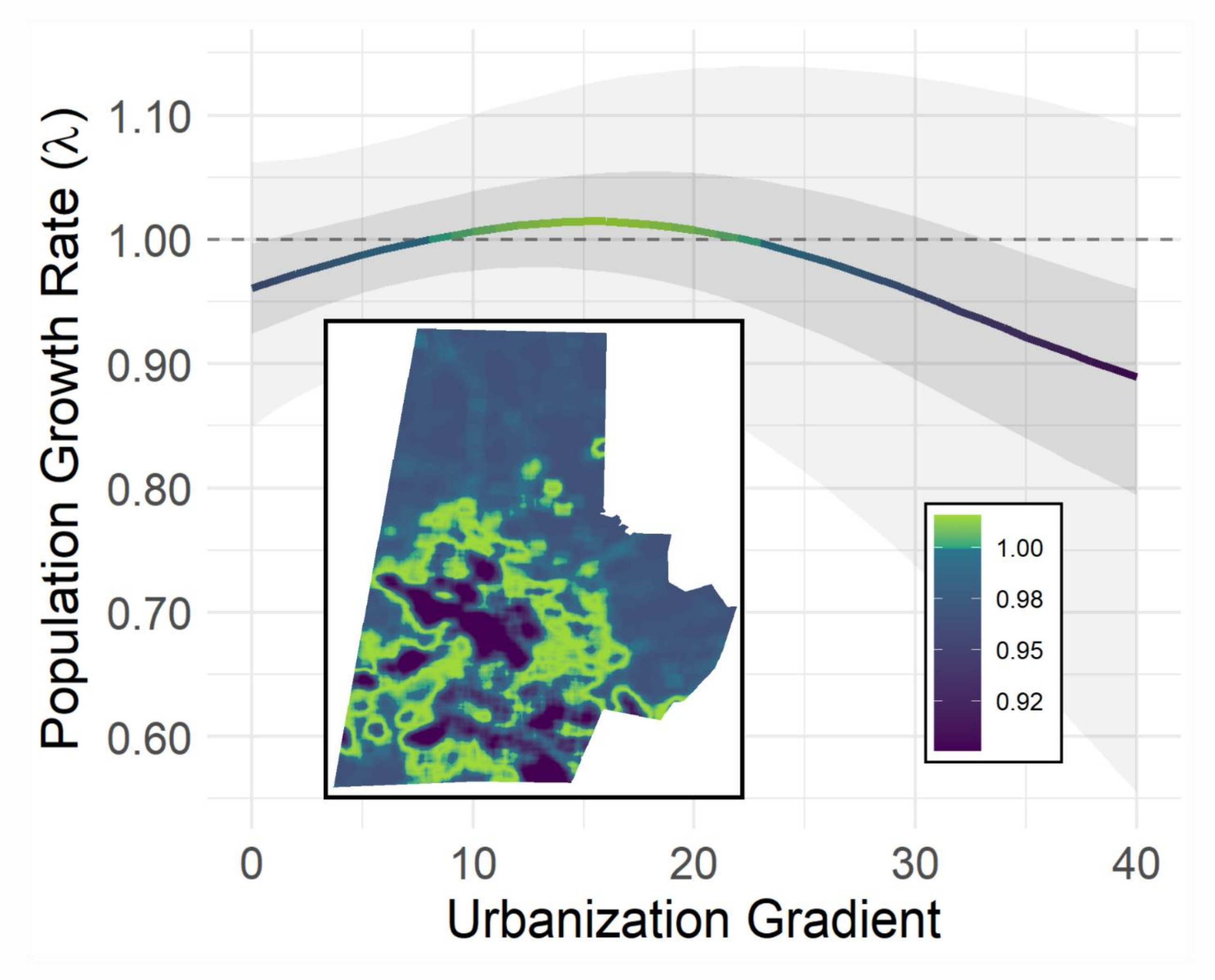


Figure 2.5. Predicted population growth rate (λ) of white-tailed deer across the urbanization gradient in Durham County, North Carolina, USA, during 2022-2025. Estimates are posterior medians with 50% (dark grey) and 95% (light grey) credible intervals. Population growth rates > 1 are shown on a green gradient and those < 1 are shown on a blue gradient.

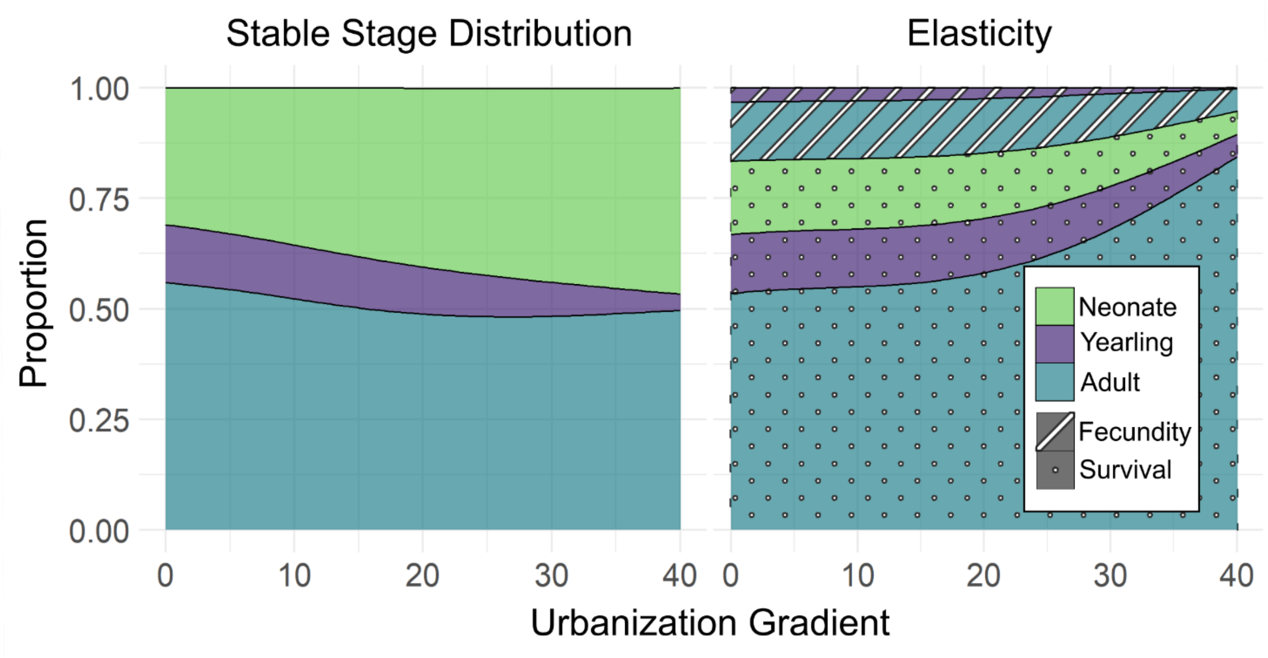


Figure 2.6. (Left) Stable stage distribution of neonate (green; top), yearling (purple; middle), and adult (blue; bottom) white-tailed deer across the urbanization gradient in Durham and Orange counties, North Carolina, USA, 2022-2025. (Right) Vital rate elasticity for fecundity (striped) and survival (dotted) of neonate (green), yearling (purple), and adult (blue) white-tailed deer across the urbanization gradient in Durham and Orange counties, North Carolina, USA, 2022-2025. Values are posterior medians.

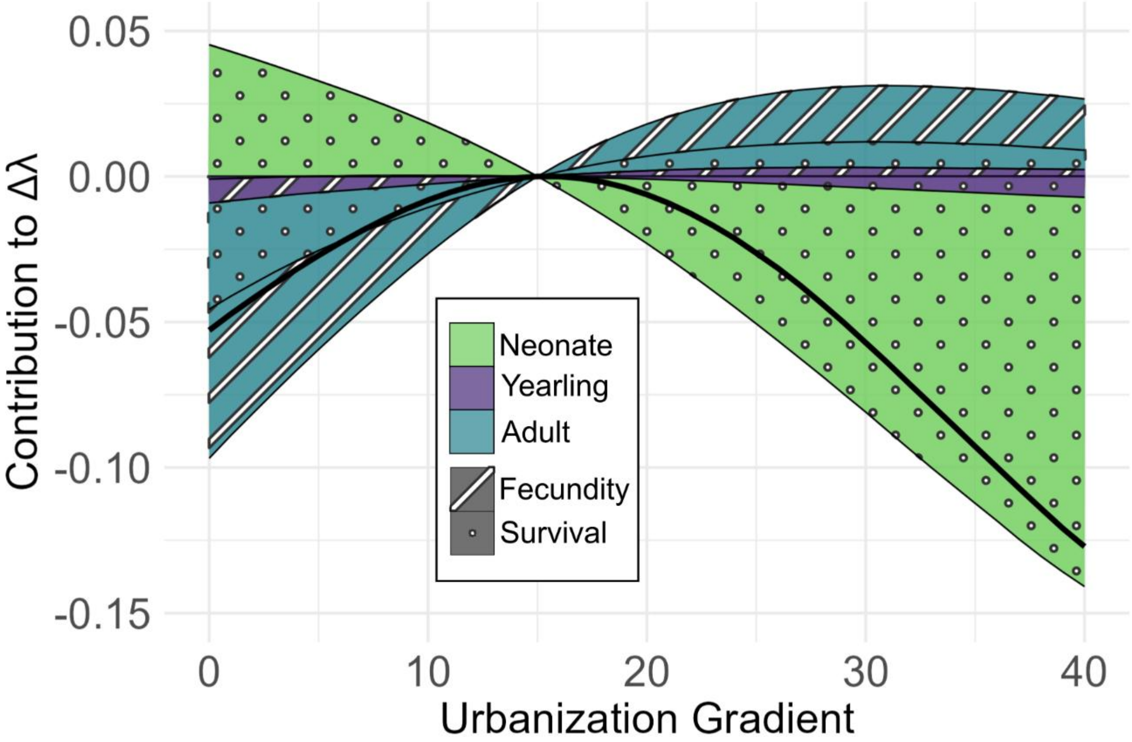
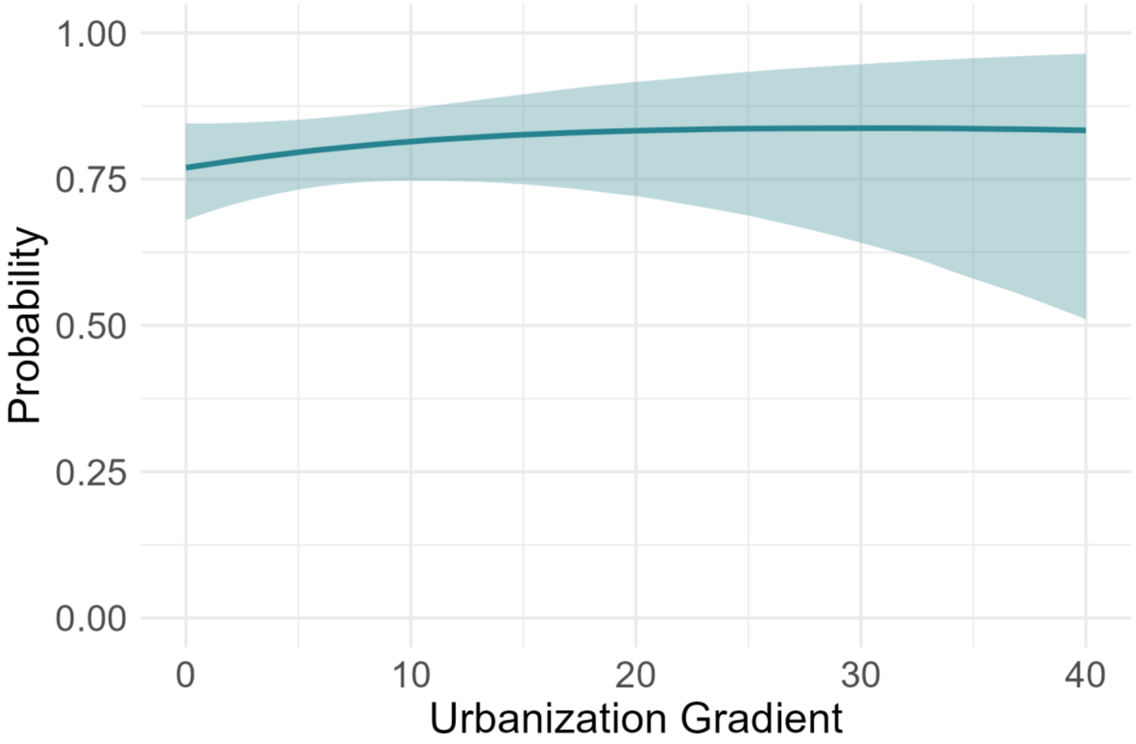


Figure 2.7. Contributions of component vital rates (fecundity = striped; survival = dotted) of white-tailed deer (neonate = green; yearling = purple, adult = blue) to changes in population growth rate ($\Delta\lambda$; solid black line) across the urbanization gradient in Durham and Orange counties, North Carolina, USA, 2022-2025. We set the reference location at urbanness value 15, where population growth rate was the highest.

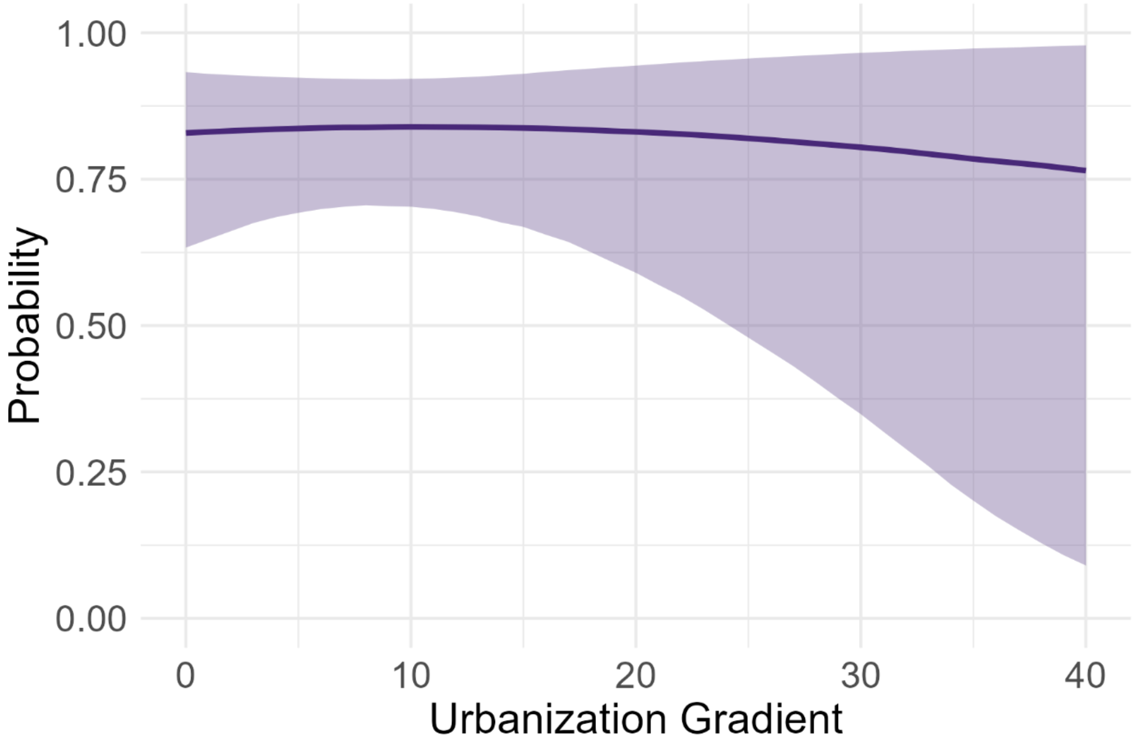
APPENDICES

Appendix 2.1. Reproductive parameter estimates for white-tailed deer across an urbanization gradient in Durham and Orange counties, North Carolina, USA 2022-2025. Parameters include the probability of live birth (θ) and logit-scale estimates for the probability of birthing two (instead of one) neonate (p_i), including the intercept and effects of the urbanization gradient (Urbanness value) and adult versus yearling stage class (Stage class). Values are posterior medians and 95% credible intervals.

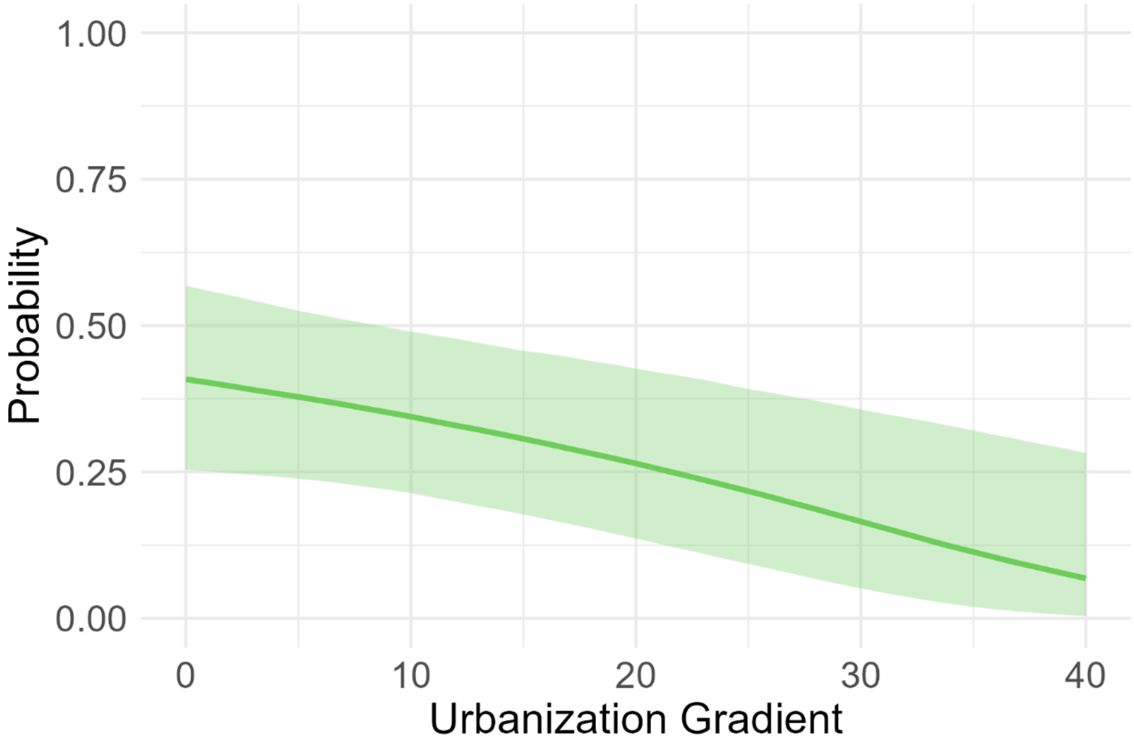
Parameter	Median (95% CrI)
Live Birth	0.95 (0.88, 0.98)
Intercept	-1.99 (-4.31, -0.03)
Urbanness value	0.14 (0.05, 0.24)
Stage class (adult)	0.74 (-1.16, 2.81)



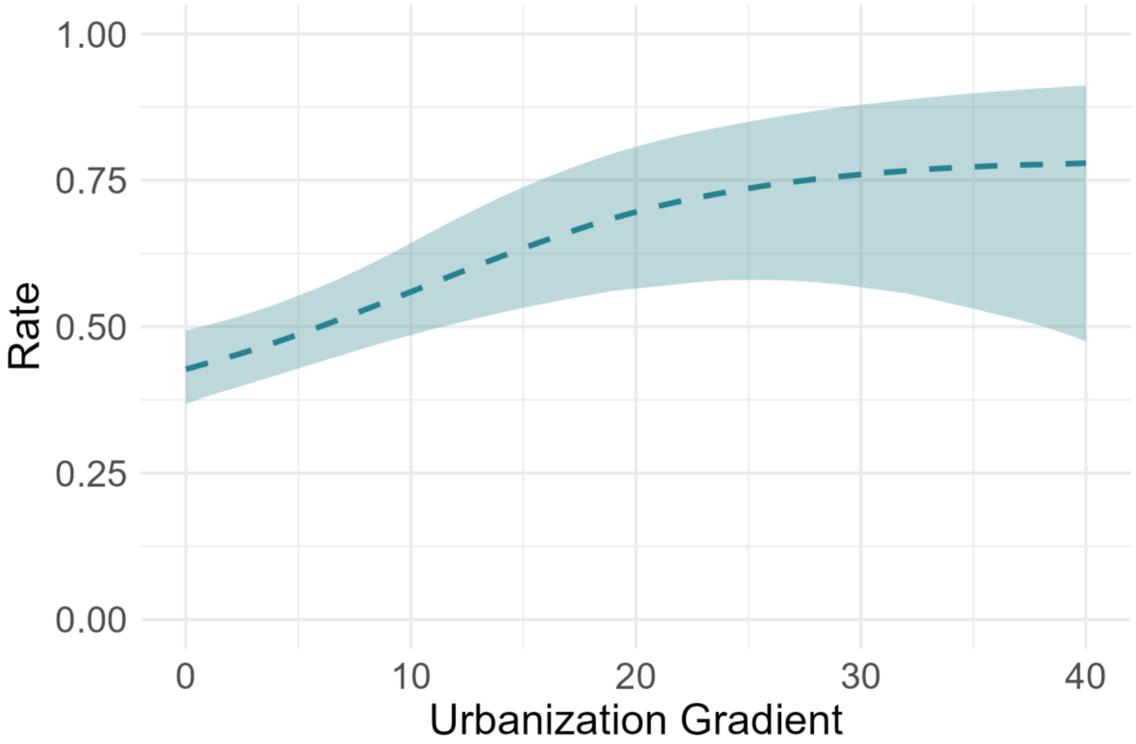
Appendix 2.2. Predicted adult survival (S_3) of white-tailed deer across the urbanization gradient in Durham County, North Carolina, USA, during 2022-2025. Line is the posterior median, and shaded area represents the 95% credible interval.



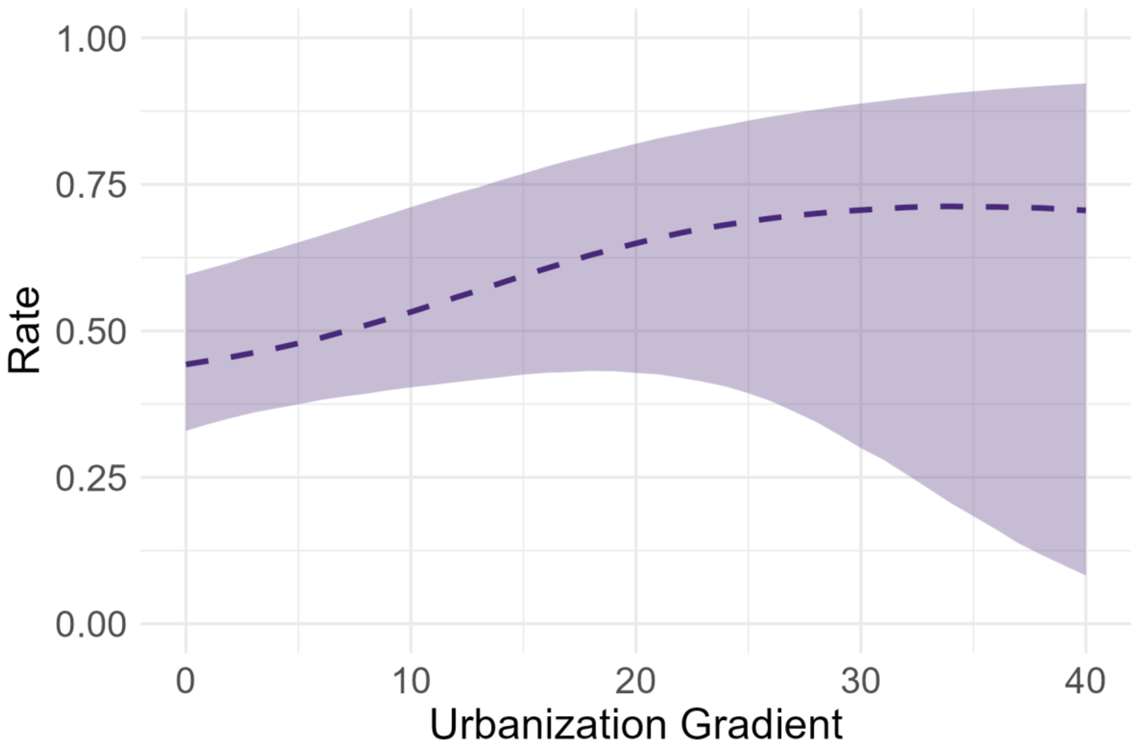
Appendix 2.3. Predicted yearling survival (S_2) of white-tailed deer across the urbanization gradient in Durham County, North Carolina, USA, during 2022-2025. Line is the posterior median, and shaded area represents the 95% credible interval.



Appendix 2.4. Predicted neonate survival (S_1) of white-tailed deer across the urbanization gradient in Durham County, North Carolina, USA, during 2022-2025. Line is the posterior median, and shaded area represents the 95% credible interval.



Appendix 2.5. Predicted adult fecundity (F_3) of white-tailed deer across the urbanization gradient in Durham County, North Carolina, USA, during 2022-2025. Line is the posterior median, and shaded area represents the 95% credible interval.



Appendix 2.6. Predicted yearling fecundity (*F_2*) of white-tailed deer across the urbanization gradient in Durham County, North Carolina, USA, during 2022-2025. Line is the posterior median, and shaded area represents the 95% credible interval.