Evaluating predictors of white-tailed deer (*Odocoileus virginianus*) birth-site selection along an urban-rural gradient

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ABSTRACT

Birth-site selection by parous white-tailed deer (*Odocoileus virginianus*) may affect neonate survival, but factors influencing selection in urbanized areas are poorly understood. Our objectives were to describe deer birth sites in Durham and Orange counties, North Carolina, evaluate landscape features as predictors of selection, and assess whether selection for these predictors varied along an urban-rural gradient. We captured and monitored 95 adult female white-tailed deer from 2022 to 2024. Out of those 95 individuals, we identified birth sites for 61 female deer and determined 5 available sites within each female's fawn-rearing area, derived from global positioning system (GPS) locations 6-weeks prior to and after parturition (12-week range). We assessed the influence of tree canopy cover, impervious surface, normalized difference vegetation index (NDVI), distances to roads, buildings, and forest edges, and an urbanization index (i.e., position on the urbanization gradient) on birth-site selection. We developed 3 generalized linear mixed models (GLMMs) – a null model, a model with all covariates, and a model incorporating covariate-urbanization index interactions – and ranked them using Akaike's Information Criterion for small sample sizes (AIC_c). The top model, which included only the covariates (i.e., no urbanization index interactions), indicated that landscape covariates affected selection similarly across the urban-rural gradient. Female deer, no matter their location on the gradient, selected birth sites with high NDVI that were closer to forest edges and roads, and farther from buildings. Percent impervious surface and tree canopy cover had no effect on selection. Our results indicate that female deer consistently select birth sites across the urban-rural gradient within or near areas that provide ample concealment cover to lower predation risk, and may also use areas in close proximity to roads as an anti-predation strategy.

KEYWORDS Birth-site selection, deer, female, North Carolina, *Odocoileus virginianus*, parturition, urban development, urban-rural gradient, urbanization, white-tailed deer.

Roughly 80% of the human population in the United States resides in urban areas, even though urban land accounts for only 3% of the nation's total land area (Nowak and Greenfield 2018, U.S. Census Bureau 2023). By 2060, urban land cover in the U.S. is projected to double, exceeding 163 million acres (Nowak and Greenfield 2018). This expansion will contribute to further loss and fragmentation of undeveloped patches, which has negatively impacted many wildlife species via the loss of genetic diversity, increased risk of disease transmission, and higher traffic-related mortality, among others (Lerman et al. 2021, Jardine 2022). However, some species are able to persist in urban areas despite substantial alterations to landscape composition and configuration driven by urbanization (Ryan and Partan 2014).

White-tailed deer (*Odocoileus virginianus*; hereafter, deer) are relatively tolerant of urbanization and its associated disturbances (Quinn et al. 2013). In fact, deer may even achieve high densities in urban areas (Urbanek and Nielsen 2013), where there is lower hunter harvest (Storm et al. 2007a, Lerman et al. 2021) and fewer non-human predators (Etter et al. 2002). Although urban landscapes may offer deer refuge (McCance et al. 2015, Potratz et al. 2019), they contain unique features such as increased human, road, and building densities (Ditchkoff et al. 2006), pronounced cover type interspersion (Nielsen et al. 2003), and reduced habitat availability, potentially limiting a deer's ability to spatially avoid predators (Magle et al. 2014). As a result, urban deer may exhibit modified behaviors differing from their rural counterparts that likely enhance their survival and reproductive success in developed landscapes (Gallo et al. 2019, Ritzel and Gallo 2020). For example, in densely populated and high-traffic areas, urban deer adjust their diel activity patterns to minimize negative interactions with humans, such as vehicular collisions (Gallo et al. 2022). Urban deer also alter their foraging behaviors to exploit supplemental food sources provided by humans, including gardens, ornamental plants, and birdfeeders (Grund et al. 2002, McCance 2018). Finally, urban deer may use areas in close proximity to features associated with increased human activity, such as roads and buildings, to serve as predation shields (Muhly et al. 2011, Kautz et al. 2022b).

Birth-site selection by female deer may be a life history trait that varies depending on a female's location along the urban-rural gradient. Neonates are vulnerable to predation, especially in the first few days following parturition (Shuman et al. 2017), and the selection of birth sites may help reduce predation risk (Watine and Giuliano 2016). Although deer birth-site selection has been studied in rural landscapes, little is known about the factors influencing urban deer birth-site selection and how they may differ from rural deer. In undeveloped landscapes, deer tend to select birth sites with greater concealment cover from predators (Duquette et al. 2014, Shuman et al. 2018, Michel et al. 2020). However, areas around concealing birth sites may lack appropriate forage, requiring adult females to balance their own dietary needs with providing adequate cover for neonates (Dion et al. 2021). The importance of this trade-off may vary across the urban-rural gradient, as increased human presence may act as a predation buffer (i.e., human-shielding) (Kautz et al. 2022b). Additionally, moderate to low levels of development may increase access to supplemental food sources near more concealing sites, such as forest edges (Jenkins and Howard 2021), allowing females to meet both cover and forage needs simultaneously, potentially resulting in modified selection behaviors.

We investigated white-tailed deer birth-site selection within 2 counties in North Carolina, USA. Our objectives were to: 1) identify and describe deer birth sites; 2) evaluate landscape features as predictors of birth-site selection; and 3) assess if selection for these predictors varied across the urban-rural gradient. We focused the analysis on 7 landscape covariates – percent canopy cover, percent impervious surface, normalized difference vegetation index (NDVI), distances to roads, buildings, and forest edges, and an urbanization index that represented the individual's location on the urbanization gradient. We assessed support for 3 alternative outcomes regarding effects of covariates and urbanization on birth-site selection: 1) landscape covariates did not affect birth-site selection; 2) landscape covariates affected selection similarly across the urbanization gradient; or 3) landscape covariates affected selection and the relationships varied across the urbanization gradient.

STUDY AREA

From 2022 to 2024, we captured and monitored female white-tailed deer in Durham and Orange counties, North Carolina, USA. Both counties are located within the Piedmont ecoregion, which has a humid subtropical climate, with mild winters, hot summers, and no distinct dry season (Peel et al. 2007). Additionally, the counties are located along the northernmost boundary of the Piedmont megaregion (Hagler 2009), which is characterized by rapid urban growth associated with the I-85 corridor (Doran and Golden 2016). The populations of Durham and Orange counties exceeded 330,000 and 150,000, respectively, with the majority of residents concentrated in urban areas (NC Department of Commerce 2022). Land cover across the primary study area was developed (42%), deciduous, evergreen, and mixed forest (40%), wetlands or open water (9%), pasture or cultivated land (8%), and less than 1% each of barren, herbaceous, and shrubland (Dewitz 2021). We captured and monitored deer on privately- and publicly-owned properties in Durham County, with only a few capture sites located in eastern Orange County.

METHODS

Capture and monitoring

We captured adult (≥ 1-year old) female white-tailed deer from January to April over 3 years (2022 - 2024) using drop nets (Wildlife Capture Services, Flagstaff, AZ, USA) and tranquilizer guns with high-frequency telemetry darts (CO_2 13-mm Rifle, DanInject, Austin, TX, USA; Model 414 RDD, Pneu-Dart, Williamsport, PA, USA; Model F1020D, Advanced Telemetry Systems, Isanti, MN, USA) from tree stands over bait. We anesthetized all captured deer using a combination of Butorphanol tartrate, Azaperone tartrate, and Medetomidine hydrochloride (BAM), in 2-cc syringes (Wedgewood Pharmacy, Swedesboro, NJ, USA). Atipamezole and Naltrexone were administered to reverse the effects of Medetomidine hydrochloride and Butorphanol tartrate, respectively (Wedgewood Pharmacy, Swedesboro, NJ, USA). We ear-tagged and collared each female with a global positioning system (GPS) transmitter (Model G5-2D; Advanced Telemetry Systems, Isanti, MN, USA) programmed to collect locations every 2 hours, providing 12 location fixes daily, with a potential measurement error of 11 m (Frair et al. 2010). Following the procedures of Kilgo et al. (2012) and Chitwood et al. (2015), we implanted each female with a vaginal implant transmitter (VIT; Model M3930U; Advanced Telemetry Systems, Isanti, MN, USA) to assist neonate capture and locate presumed birth sites. We conducted capture and handling under the authorization of the North Carolina Wildlife Resources Commission. All capture and handling protocols were approved by the North Carolina State University Institutional Animal Care and Use Committee (IACUC # 21-370).

We monitored birth events using the Advanced Telemetry Systems Neolink system and very high frequency (VHF) beacon schedules. We also conducted daily field-based checks on VIT signals to ensure no birthing events were missed. Once a VIT was expelled (i.e., the VIT detected a conditional change related to temperature, light, or broadcast absence), we received a Neolink birth alert and allowed ≥ 3 hours to pass from the time of parturition before initiating a search. The use of this relatively new and advanced technology to improve detection and location of parturition events has not been applied in urban environments. We searched for neonates starting at the location of the adult female deer moving in the direction of the expelled VIT. We collected GPS coordinates for the expelled VIT and for neonates once located.

Birth-site identification

We identified birth sites as the recorded GPS coordinates of each expelled VIT for all cases where at least 1 associated neonate was located. We calculated landscape characteristics at the birth-site location ($y = 1$) selected by a collared parous female and at 5 random locations depicting available space ($y = 0$) within the general area used by the female (hereafter "fawn-rearing" area) around the time of parturition (Wright et al. 2021). We estimated the fawn-rearing area for each parous female using a 90% minimum convex polygon (MCP) derived from all GPS locations collected over 12 weeks, from 6 weeks prior to parturition to 6 weeks after parturition (Schwede et al. 1993, Bertrand et al. 1996, Shuman et al. 2018) via the 'adehabitatHR' package (Calenge 2024) in R (R Core Team 2024).

Landscape covariates

In ArcGIS Pro 3.4 (Esri 2024), we extracted 7 spatial landscape features describing used and available birth-site locations – percent canopy cover, percent impervious surface, NDVI, distance to nearest road, distance to nearest building centroid, distance to nearest forest edge, and an urbanization index (Table 1). We used 1-m resolution Google Earth satellite imagery to digitize forest edges, defined as the transitional boundary between forest and non-forest land cover, within each fawn-rearing area as linear features (Soultan et al. 2021). We used the Near tool from the Analysis toolbox, the digitized forest edge features, and data managed by the North Carolina Department of Transportation and the North Carolina Floodplain Mapping Program to determine the Euclidean distance of each site location to the nearest forest edge, road, and building centroid, respectively (Dion et al. 2021). We mapped NDVI as a proxy for vegetation productivity (Pettorelli et al. 2011). We used the European Space Agency's Copernicus Browser to obtain Sentinel-2 L2A spectral band 8 (NIR; near-infrared) and band 4 (RED; red light) 28-m rasters for each data collection year closest to the mean annual parturition date with low cloud cover. We then used the Raster Calculator tool from the Spatial Analyst toolbox to create annual NDVI rasters using the equation: [$NDVI = (NIR - RED) / (NIR + RED)$] (Pettorelli et al. 2011). We also obtained and clipped the 2021 National Land Cover Database 30-m rasters for percent impervious surface and tree canopy cover to the study area (Dewitz 2021). We then projected the used and available site points to match each raster projection before extracting the covariate values. Finally, we used the Zonal Statistics as Table tool to obtain the mean value of percent impervious surface in all raster cells within each parous doe's fawn-rearing area. We termed this mean value the urbanization index, which served as a metric representing each individual's location on the urban-rural gradient.

Statistical analysis

We compared 3 generalized linear mixed models (GLMMs) to assess support for the alternative outcomes regarding covariate effects on birth-site selection and possible variation in relationships across the urbanization gradient – a null model, a model with covariates, and a model incorporating covariates and covariate-urbanization index interactions. In R (R Core Team 2024), we scaled all covariate values and interactions and fitted the 3 GLMMs using the 'glmmTMB' package (Brooks et al. 2017), with a binomial error distribution and logit link function to predict the relative probability of a site being selected as a birth-site. We treated individual deer-specific intercepts as random effects (Shuman et al. 2018, Muff et al. 2020). Available points were left unweighted, and the intercept variance was fixed at 1,000 prior to model fitting (Fithian and Hastie 2012, Muff et al. 2020). We assessed collinearity among predictor variables using Pearson's correlation coefficient (r), and retained all covariates as $|r|$ were < 0.70 for all correlations (Dormann et al. 2013). We also assessed multicollinearity among covariates using the variance inflation factor (VIF); we excluded no covariates because all values were < 3 (Zuur et al. 2010). Finally, we compared models using Akaike's Information Criterion for small sample sizes (AIC_c) and examined the estimates of the parameters in the top model.

RESULTS

We captured and collared 95 adult female deer from 2022 to 2024 and identified parturition events for 61 females. The analysis included 61 birth-site locations (2022 = 18; 2023 = 21; 2024 = 22) and 305 available locations (2022 = 90; 2023 = 105; 2024 = 110). The mean parturition dates were 25 May in 2022 (06 May - 20 Jun 2022) and 2023 (14 May - 20 Jun 2023), and 26 May in 2024 (05 May - 03 Jul 2024). All birth sites and randomly selected available sites were located within individual female fawn-rearing areas ranging in size from 15.64 ha to 313.77 ha (mean = 49.01; SE = 5.31) (Fig. 1).

Deer birth sites had a mean distance of 122.9 m (SD = 153.7 m) to the nearest road, 132.4 m (SD = 137.6 m) to the nearest building, and 26.7 m (SD = 36.3 m) to the nearest forest edge (Fig. 2A-C; Table 2). The mean values for NDVI, tree canopy cover, and impervious surface at birth sites were 0.8 (SD = 0.1), 73.7% (SD = 25.6%), and 4.7% (SD = 13.6%), respectively (Fig. 2D-F; Table 2). The urbanization index ranged from 0.0 (rural) to 24.3 (more urban), and the mean for all sites was 6.1 (SD = 7.5; Table 2).

The top model, with an Akaike weight of 0.63, included landscape covariates but excluded interactions with the urbanization index (Table 3). Distance to nearest road, building, forest edge, and NDVI had significant influence on birth-site selection (p-values ≤ 0.01 for all; Table 4). Female deer selected birth sites with high NDVI ($\beta = 0.89$; Fig. 3D), that were closer to roads ($\beta = -1.15$; Fig. 3A) and forest edges ($\beta = -1.06$; Fig. 3C), and farther from buildings ($\beta = 0.92$; Fig. 3B) no matter their location on the urban-rural gradient. Percent impervious surface and tree canopy cover were not significant predictors of selection. The second-best model, which included landscape covariates and their interactions with the urbanization index, had an Akaike weight of 0.37 (Table 3). Although no interactions were significant at $\alpha = 0.05$, the interaction with canopy cover suggested a potential relationship ($\beta = 0.81$; p-value = 0.06), which indicated that urban deer selected birth sites with greater canopy cover relative to rural deer.

DISCUSSION

We evaluated the relationship between female white-tailed deer birth-site selection and specific landscape features across an urban-rural gradient in a highly populated region of North Carolina. The most supported model indicated that landscape covariates influenced selection, but the relationships between selection and specific covariates did not vary across the urbanization gradient. More specifically, female deer, regardless of their location on the gradient, selected birth sites with high NDVI that were closer to forest edges and roads and farther from buildings.

Distance to forest edge was the strongest predictor of birth-site selection, likely because vegetation was more structurally diverse along the forest edges than in the interior of the closed canopy forests that were common across the study area (Watine and Giuliano 2016). The greater sunlight penetration from the openings adjacent to the forest patches likely fostered greater woody and herbaceous understory that provided more concealment cover for neonates. Similar selection behaviors were observed in Louisiana (Hasapes and Comer 2017) and two differing ecoregions (grassland- and forest-dominated) in Missouri (Wright et al. 2021), where female deer also selected birth sites closer to wooded edges. Additionally, in the Red Hills region of

Florida and Georgia, Watine and Giuliano (2016) reported that fawn survival increased when birth sites were closer to forest edges.

Similarly, the selection of birth sites closer to roads in our study is likely due to the availability of dense understory cover along the transition between forest and adjacent roadsides (Hasapes and Comer 2017). Although similar studies in rural areas did not document a relationship between road distance and birth-site selection (Dion et al. 2021, Wright et al. 2021), Wright et al. (2021) observed that female deer used areas closer to roads before and after birth. The use of areas closer to roads around the time of parturition was likely due to roadsides offering adequate forage for the females before birth and hiding cover for neonates after birth. In addition to increased vegetative cover, selecting birth sites near roads may be an anti-predation strategy, as Kautz et al. (2022a) documented reduced carnivore (e.g., coyote, bobcat, bear) activity near roads where human presence functioned as a predation shield.

Despite selecting birth sites closer to roads, female deer avoided birth sites near buildings. Dion et al. (2021) evaluated the relationship between deer birth-site selection and distance to buildings and documented no significant relationship. However, multiple studies in both rural and suburban areas have reported that female deer tend to use areas farther (>100 m) from buildings during the fawning season (Grund et al. 2002, Storm et al. 2007b) and avoid high-density (>400 buildings/km^2) residential areas (Potapov et al. 2014). Vegetated areas near buildings, including ornamental beds, typically do not provide sufficient concealment cover (Saalfeld and Ditchkoff 2007). Therefore, deer may have selected sites farther from buildings not to distance themselves from human activity (Parsons et al. 2016), but instead to access more concealing vegetation (Potapov et al. 2014).

Female deer consistently selected birth sites in areas with high NDVI, indicating strong selection for dense green vegetation (Pettorelli et al. 2011). Although no study has evaluated the influence of NDVI on deer birth-site selection, several studies reported that deer select for sites with greater vegetation density (Shuman et al. 2018, Dion et al. 2021). The selection for greater vegetation density, especially understory (≤ 1 m) vegetation (Michel et al. 2020, Dion et al. 2021), can improve fawn survival, reducing predation risk by providing cover and inhibiting airflow (i.e., limiting olfactory cues) which diminishes detection by predators (Shuman et al. 2018). Moreover, Bonar et al. (2016) reported increased fawn survival in areas with greater spring NDVI (i.e., more dense green vegetation). Tree canopy cover was not a predictor of birth-site selection, similar to other studies (Shuman et al. 2018, Dion et al. 2021, Wright et al. 2021). However, other results of our study indicate the importance of adequate concealment cover, which typically would be greater in forest with lower canopy cover than in closed canopy forest.

Our findings contribute to a growing understanding of deer selection behaviors across urbanization gradients. While it is possible that these selection behaviors along the urban-rural gradient may enhance neonate survival, further research is needed to connect birth-site selection to neonate survival, especially in urban areas (Saalfeld and Ditchkoff 2007, Piccolo et al. 2010).

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Figures and Tables

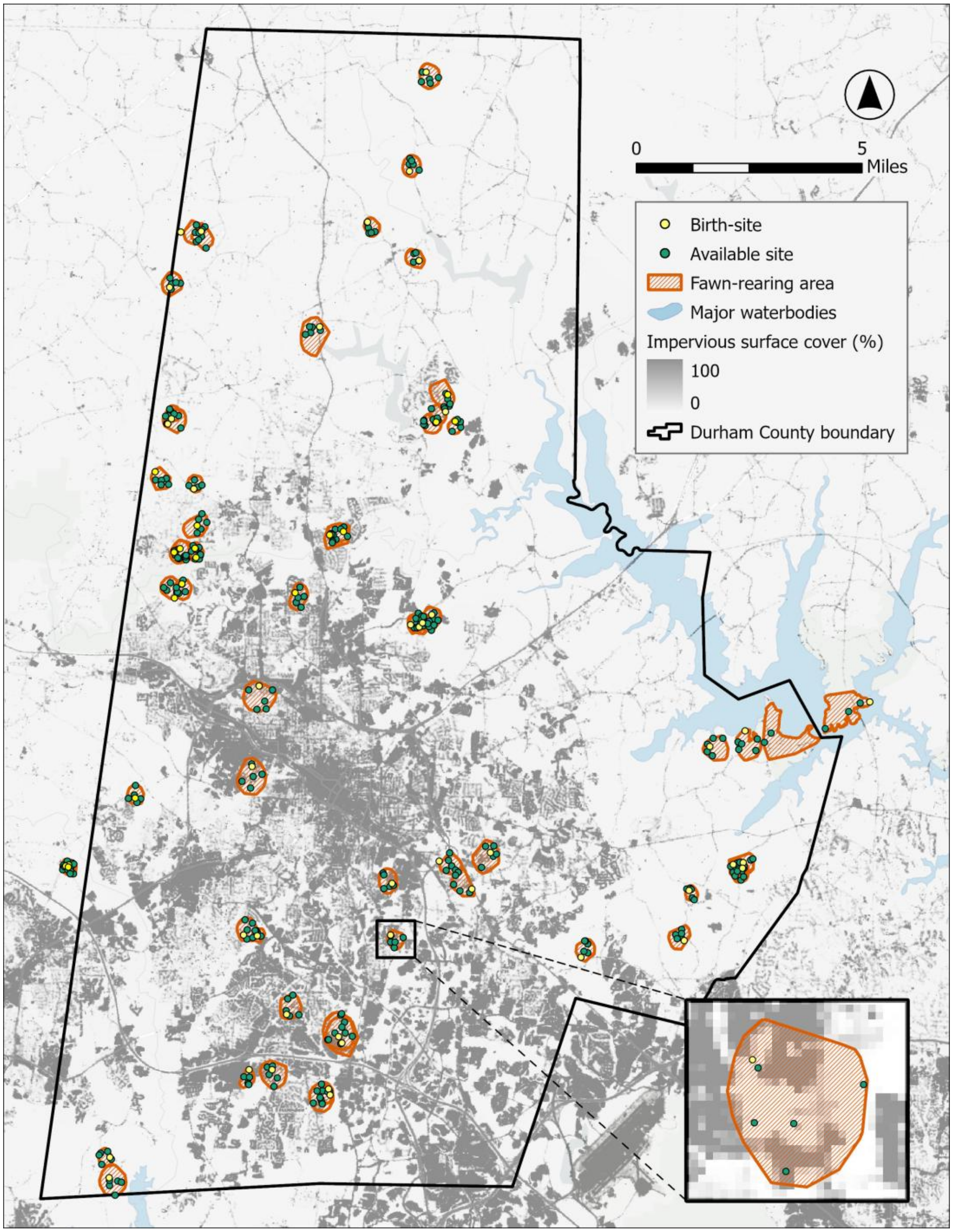

Figure 1. Female white-tailed deer birth sites, available sites, and estimated fawn-rearing areas used in the birth-site selection analysis in Durham and Orange counties, North Carolina (2022-2024). We displayed the spatial features on the National Land Cover Database 2021 impervious surface cover 30-m raster to depict sampling efforts across the urban-rural gradient. The inset displays an enlarged view of a fawn-rearing area at one of the more urban locations.

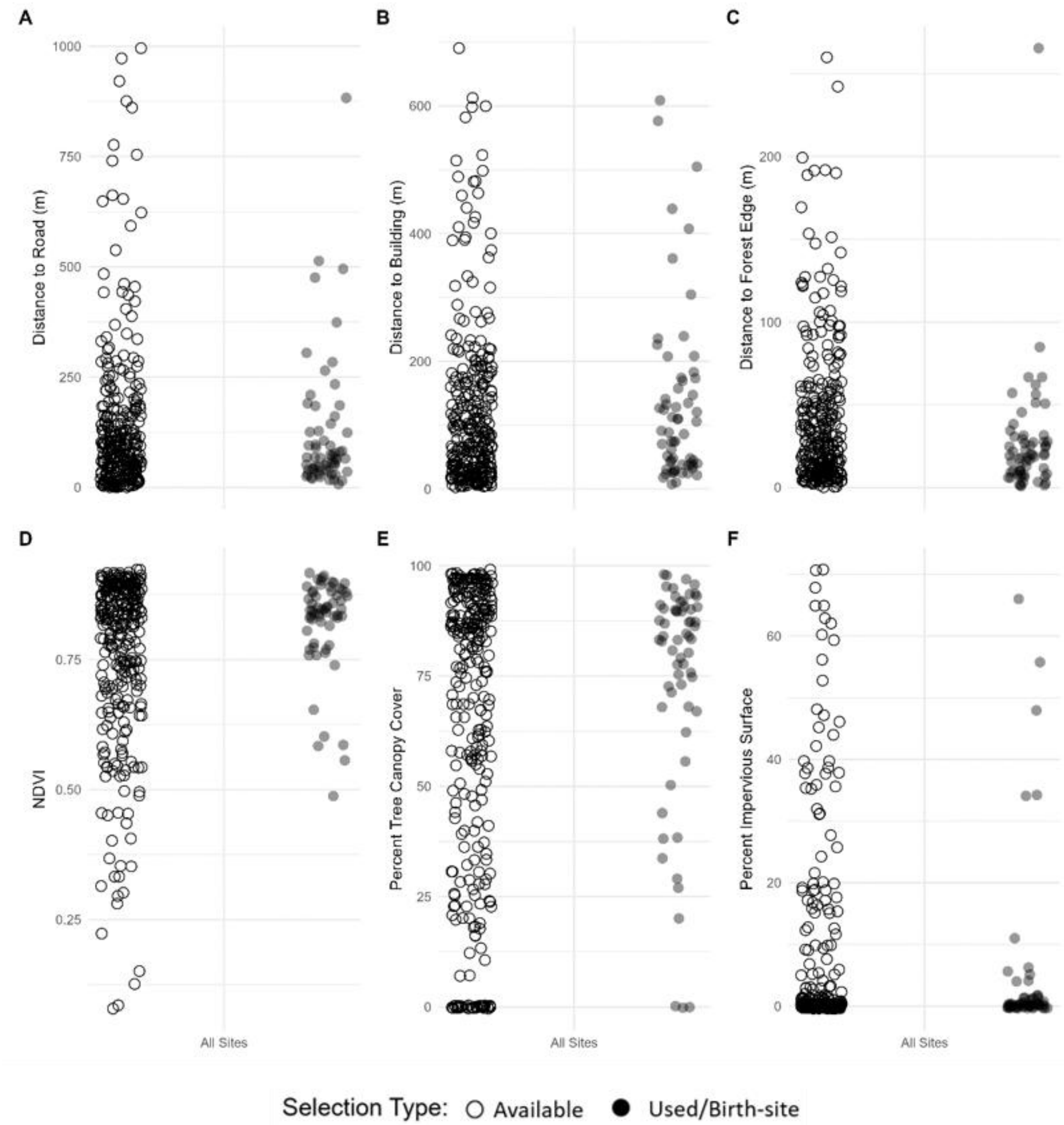

Figure 2. Covariate values for all sites available (hollow point) to and used (solid point) by female white-tailed deer in Durham and Orange counties, North Carolina (2022-2024). The covariates were distance to nearest road (A), distance to nearest building (B), distance to nearest forest edge (C), NDVI (D), percent tree canopy cover (E), and percent impervious surface (F).

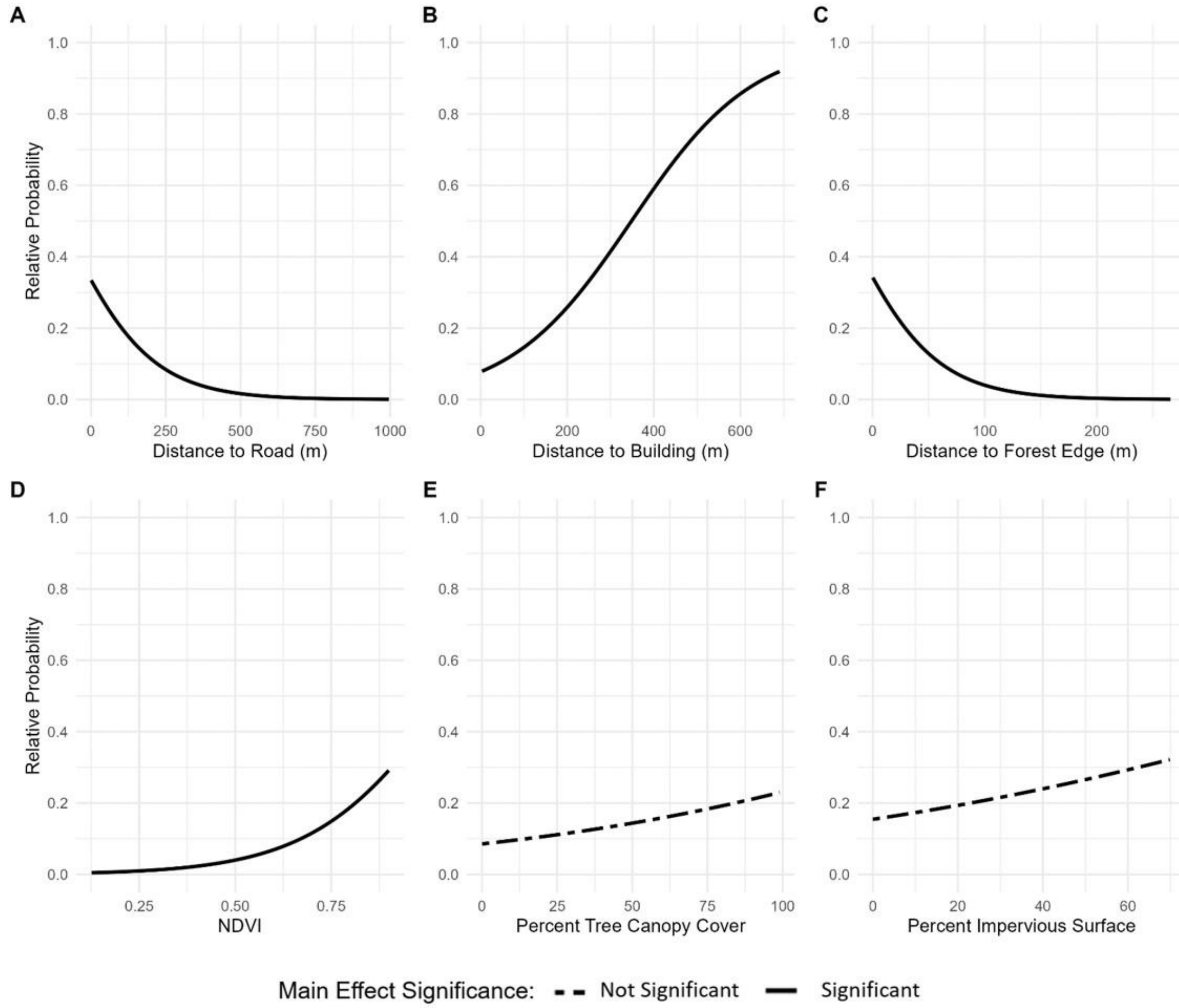

Figure 3. The relative probability of female white-tailed deer birth-site selection in relation to individual covariates in Durham and Orange counties, North Carolina (2022-2024). The covariates were distance to nearest road (A), distance to nearest building (B), distance to nearest forest edge (C), NDVI (D), percent tree canopy cover (E), and percent impervious surface (F). Solid lines represent covariates with a significant main effect, whereas dashed lines indicate non-significant main effects. We centered covariates for plotting, and back transformed x-axes to improve interpretability.

Table 1. Description of the covariates used in the white-tailed deer birth-site selection analysis in Durham and Orange counties, North Carolina (2022-2024).

Covariate	Description
Distance to Road	Site distance to nearest road (meters)
Distance to Building	Site distance to nearest building centroid (meters)
Distance to Forest Edge	Site distance to nearest forest edge (meters)
NDVI	Measure of vegetation productivity (-1 to 1)
Canopy Cover	Percent tree canopy cover (0-100%)
Impervious Surface	Percent impervious surface cover (0-100%)
Urbanization Index	Mean percent impervious surface cover within each fawn-rearing area

Table 2. Means, standard deviation (SD), and ranges for covariates at female white-tailed deer birth sites and available sites from 2022-2024 in Durham and Orange counties, North Carolina.

	Birth Sites			Available Sites		
Covariate	Mean	SD	Range	Mean	SD	Range
Distance to Road (m)	122.9	153.7	7.2 – 883.0	138.1	171.0	0.7 - 995.8
Distance to Building (m)	132.4	137.6	7.9 - 608.8	119.6	127.5	3.0 - 690.7
Distance to Forest Edge (m)	26.7	36.3	0.8 - 265.5	40.2	42.9	0.2 - 259.9
NDVI	0.8	0.1	0.5 - 0.9	0.8	0.2	0.1 - 0.9
Canopy Cover (%)	73.7	25.6	0.0 - 98.0	63.1	34.1	0.0 - 99.0
Impervious Surface (%)	4.7	13.6	0.0 - 66.0	6.9	15.2	0.0 - 71.0
Urbanization Index	6.1	7.5	0.0 - 24.3	6.1	7.5	0.0 - 24.3

Table 3. The number of parameters (*K*), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference in AIC_c value from top model (ΔAIC_c), Akaike weight (w_i), and the sum of Akaike weights for 3 models of white-tailed deer birth-site selection from 2022-2024 in Durham and Orange counties, North Carolina. Model covariates were distance to nearest road (DR; m), distance to nearest building (DB; m), distance to nearest forest edge (DE; m), normalized difference vegetation index (VI), tree canopy cover (CC; %), impervious surface cover (IP; %), and urbanization index (UI). We also included an individual deer specific intercept (1| Deer) as a random effect.

Model	K	AIC_c	ΔAIC_c	w_i	Cum. Weight
DR + DB + DE + VI + CC + IP + (1| Deer)	7	1135.48	0	0.63	0.63
DR + DB + DE + VI + CC + IP + (UI Interactions) + (1| Deer)	13	1136.54	1.06	0.37	1
Null model (1| Deer)	1	1163.45	27.96	0	1

Table 4. Top model predicting white-tailed deer birth-site selection, including the Estimate, standard error (SE), standard score (Z), P value [Pr(>|z|)], and 95% confidence interval from 2022-2024 in Durham and Orange counties, North Carolina.

	Estimate	SE	Z	Pr(>|z|)	95% CI
Intercept	0.00	128.04	0.00	1.00	(-250.95, 250.95)
Distance to Road	-1.15	0.45	-2.53	0.01	(-2.03, -0.26)
Distance to Building	0.92	0.34	2.72	0.01	(0.26, 1.58)
Distance to Forest Edge	-1.06	0.30	-3.57	0.00	(-1.65, -0.48)
NDVI	0.89	0.36	2.49	0.01	(0.19, 1.60)
Canopy Cover	0.39	0.27	1.44	0.15	(-0.14, 0.91)
Impervious Surface	0.20	0.28	0.74	0.46	(-0.34, 0.74)