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EFFECTS OF SUBURBAN ARCHERY HUNTING ON WHITE-TAILED DEER BEHAVIOR AND SURVIVAL

by

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Raena A. Kemna

Chapter 1 Abstract – Regulated hunting is the primary management tool used to limit white-tailed deer (*Odocoileus virginianus*) population growth, but safety constraints in human-dominated landscapes often restrict hunting to spatially isolated areas. Understanding how deer within an urban matrix respond to the spatial and temporal structure of hunting activities may improve outcomes for urban deer management efforts. We evaluated behavioral responses of 45 female white-tailed deer to a controlled archery hunt in northern Minnesota across a biologically relevant study period spanning five temporal phases: pre-hunt, early-hunt, mid-hunt, late-hunt, and post-hunt. We quantified space use and movement behavior during each period using 95% utilization distributions (UD), step-selection functions, and mean movement velocity. Deer were classified as hunted or unhunted based on the presence of hunted property within their 95% UD. We found no differences in space use between hunted and unhunted deer and no effects of hunting status or interactions with temporal period, although habitat use varied temporally for open and wetland cover types. Step-selection coefficients indicated consistent avoidance of forested habitat, weak avoidance of open habitat, and near-neutral selection for wetlands and anthropogenic features (roads and houses). Mean movement velocity declined throughout the study period and was consistently lower in hunted than unhunted deer. Overall, deer showed no significant differences in space use or resource selection, while movement intensity was the only behavioral difference observed between hunted and unhunted individuals. These results suggest that deer in developed areas respond differently to hunting risk than those in more rural systems, with effects primarily expressed through movement intensity rather than large-scale shifts in space use.

Chapter 2 Abstract - White-tailed deer (*Odocoileus virginianus*) are widely distributed across North America and increasingly occupy urban landscapes where abundant populations can create management challenges. Controlled archery hunting programs are commonly implemented in these areas to reduce urban deer abundance, but their ability to influence population dynamics remains uncertain. We evaluated population density, harvest data, survival rates, and cause-specific mortality of adult female deer to assess the effectiveness of a controlled archery hunt in northern Minnesota. Long-term spotlight surveys (2016–2025) indicated a stable urban deer population within the city. We captured and monitored 45 GPS-collared adult female white-tailed deer in a mosaic of hunted and unhunted urban areas in Bemidji, Minnesota, USA from 2024–2026. Annual survival was 0.63 (95% CI: 0.52–0.76) and varied with landscape context, decreasing with road density and increasing with housing density. Survival did not differ between deer in hunted versus unhunted areas. These results indicate that adult female survival was primarily influenced by anthropogenic factors not directly associated with harvest. Despite sustained harvest pressure, controlled archery hunting did not measurably reduce deer density or survival, suggesting limited population-level effects under current management conditions. Given uncertainty surrounding the level of harvest required to

influence urban deer populations, efforts to increase harvest in controlled archery programs may improve management outcomes.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

RESPONSES TO A CONTROLLED ARCHERY HUNT IN SUBURBAN WHITE-TAILED DEER: IMPLICATIONS FOR HARVEST AND MANAGEMENT

Introduction

At the interface of developed and natural habitats, many wildlife species alter movement and behavior in response to increased human activity (Lowry et al. 2013, Ritzel and Gallo 2020). White-tailed deer (*Odocoileus virginianus*; hereafter deer) are among several wildlife species that can attain high densities in urban and suburban environments, where human-altered habitats often provide abundant food resources, reduced predation risk, and refuge from hunting (Adams and Villarreal 2020). Deer population growth in urban areas is largely driven by reduced presence of large predators (e.g., black bears (*Ursus americanus*) and wolves (*Canis lupus*)) and increased availability of anthropogenic food sources and cover (e.g., bird feeders, gardens, compost) (Urbanek and Nielsen 2013, Maurer et al. 2022). Similar conditions support other urban-adapted wildlife species such as coyotes, raccoons, foxes, and Canada geese, which often reach elevated densities in human-dominated landscapes. As a result, wildlife managers commonly implement population monitoring, regulated harvest, fertility control, habitat modification, and public education to reduce human–wildlife conflict.

Increasing deer abundances can present ecological and management challenges, particularly in urban areas (Boehne et al. 2024), although high densities may also increase opportunities for wildlife viewing and regulated hunting in some settings. High suburban deer densities are associated with habitat degradation (i.e., landscape plantings, browse-lines), increased risk of deer–vehicle collisions, and heightened potential for tickborne disease transmission (DeNicola et al. 2000, DeNicola and Williams 2008, Kilpatrick et al. 2014). These impacts underscore the need for effective management strategies to mitigate ecological and social conflicts in developed areas. However, identifying safe and effective methods to reduce urban deer populations remains challenging (Ishmael et al. 1995, Kuser 1995, Kilpatrick and Walter 1997). In urban areas, management strategies including fertility control, exclusion fencing, habitat modification, and targeted removal are used to reduce deer populations, though with varying effectiveness and logistical feasibility. Hunting is a commonly used strategy to reduce overabundant deer populations, and many municipalities have implemented controlled hunts to this end (Kilpatrick et al. 2002, Rhoads et al. 2010, Simard et al. 2013). Because firearm use is often restricted in residential areas due to human safety concerns, controlled archery hunting has become a common management practice (Kilpatrick et al. 2007).

Prey species often exhibit antipredator behaviors such as vigilance, avoidance, and altered movement in response to mortality risk (Brown et al. 1999, Frid and Dill 2002). In white-tailed deer, responses to hunting pressure are well documented and vary with age, sex, season, weather, and prior exposure to hunters (Ditchkoff et al. 2001, Webb et al. 2010, Little et al. 2014, Haus et al. 2020). These responses can include changes in space use and movement behavior. For example, deer may increase use of refuge habitats, reduce movement rates, and select for denser cover in human-frequented areas, particularly where hunting is permitted (Rhoads et al. 2013; Little et al. 2014, 2016; Marantz et al. 2016). However, such responses may occur without large-scale shifts in space use, especially in systems characterized by strong site fidelity and landscape fragmentation that constrain movement (Burt 1943, Porter et al. 2004). In such environments, behavioral responses to disturbance may instead occur through localized or fine-scale adjustments within established home ranges, rather than broad spatial redistribution.

Most GPS-based studies of deer responses to hunting have been conducted in predominantly non-urban landscapes, resulting in a paucity of research in urban and suburban systems (e.g., Karns et al. 2012, Sullivan et al. 2018, Abernathy et al. 2025). Although urban deer frequently encounter humans, fragmented suburban landscapes may constrain movement and redistribution through strong site fidelity and reduced movement across anthropogenic barriers (Porter et al. 2004, Lowry et al. 2013). As a result, it remains unclear whether deer in developed environments exhibit the same spatial and habitat-selection responses to controlled hunting documented in non-urban systems, or whether responses are instead expressed primarily through fine-scale movement behavior. Understanding these patterns is critical for evaluating the effectiveness of urban deer management strategies and improving harvest outcomes in human-dominated landscapes.

Our objectives were to evaluate deer behavioral responses to controlled archery hunting in a developed landscape by examining changes in multi-scale resource use and movement velocity. We focused on adult female white-tailed deer, the primary demographic influencing population growth and recruitment. Using high-resolution, 30-minute GPS relocation data, we quantified fine-scale spatial and temporal behavioral responses to hunting disturbance. Given the generally reduced home range sizes and high site fidelity observed in urban white-tailed deer, coupled with the patchy distribution of suburban archery hunting and its restriction to a defined seasonal window, we expect limited large-scale shifts in space use or resource selection. Instead, we anticipate that any behavioral response will be expressed primarily through fine-scale adjustments in movement behavior (e.g., movement rates and habitat use within existing home ranges), rather than broad-scale spatial redistribution.

Methods

Study Area - We conducted our research within the city limits of Bemidji (47°28′N, 94°52′W; Figure 1.1), located in Beltrami County in north-central Minnesota, USA within Deer Permit Area 684. The study area encompassed 45.3 km², with a human population of 15,733 and 1,665 unique land ownership parcels (City of Bemidji GIS Hub 2018, U.S. Census Bureau 2024). Land parcels averaged 1.55 ha in size (range = 0.01–139.97 ha; City of Bemidji GIS Hub 2018). We identified 4,611 residential structures from parcel data, corresponding to a housing density of 102 houses/km². The city was located within a coniferous forest biome and was surrounded by extensive forested areas dominated by fir (*Abies* spp.), spruce (*Picea* spp.), and tamarack (*Larix laricina*) (Minnesota Department of Natural Resources 2020). From 2006 to 2020, average summer temperatures ranged from 14.1°C to 24.9°C, with mean summer precipitation of 29.11 cm. In winter, temperatures ranged from –16.4°C to –5.2°C, with mean snowfall of 118.60 cm (NOAA 2023). Land cover within the city was primarily forested (39.67%), followed by developed urban areas (26.14%) and undeveloped open space (18.76%), while wetlands (14.19%) and open water (1.24%) comprised the remaining land cover (Dewitz and U.S. Geological Survey 2021; Table 1.1).

White-tailed deer densities in Bemidji were generally stable, averaging 10.8 deer/km² (range = 9.32–12.37 deer/km²) based on annual spotlight surveys from 2016–2025 (Kemna, Chapter 2). In response to increasing deer abundance and associated human-wildlife conflicts, the Bemidji City Council established a Deer Management Committee in 2003 to oversee a controlled archery hunt within designated areas of the city. The hunt coincided with the regular Minnesota archery season, typically running from mid-September through 31 December. Hunters were permitted to harvest up to 5 deer annually, including 1 antlered deer with remaining tags restricted to antlerless harvest. In most years, hunters could harvest more antlerless deer in the city hunt than was allowable in the surrounding Deer Permit Area under state regulations.

Hunting occurred on a combination of city-owned public land and privately owned parcels. Private landowners or their designees were eligible to participate if their property was ≥0.8 ha in size. Access to designated city-owned hunting areas was determined through an application and lottery system. In 2025, city-owned public lands were closed to hunting due to storm damage, allowing only privately owned parcels to be hunted within the city that year. From 2005 to 2025, hunters removed 579 deer during the city archery hunt, including 375 adult females, 115 fawns, and 89 adult males.

Animal capture and monitoring - We captured female white-tailed deer (≥6 months old) in Bemidji, Minnesota during winters (Jan–Mar) of 2024 and 2025 using netted cage traps and drop nets (Clover 1956, Silvy 2020). We anesthetized captured deer with an intramuscular injection of xylazine (0.5 mg/kg; Conner et al. 1987, Kreeger et al. 2023). We blindfolded sedated deer to reduce stress and minimize the risk of capture myopathy. We fitted deer weighing ≥35 kg with a global positioning system (GPS) collar equipped with activity and mortality sensors that entered mortality mode after ≥8 hours of inactivity (MG5M-2D [780 g]; Advanced Telemetry Systems, Isanti, Minnesota, USA). Each individual received 2 white plastic button cattle ear tags (3 cm diameter) with black numbers displaying a unique ID and contact number for recovery (Allflex USA Incorporated, Dallas, TX, USA). We estimated age using tooth replacement and wear (Severinghaus 1949) and recorded morphological measurements, including chest girth, neck girth, total length, hind limb length, and shoulder height (Bowman et al. 1998, Haus et al. 2019). We reversed sedation using atipamezole (0.275 mg/kg; Millspaugh et al. 2004). Throughout the handling process, we monitored vital signs (body temperature, respiration, and heart rate) at 5-min intervals until the deer departed the capture site unassisted. We recorded arousal time (from injection to eye opening and head lift) and walk time (from injection to ambulation).

To evaluate changes in deer movement in response to hunting activity, we divided the study period into 5 distinct temporal periods surrounding the archery season (mid-September – 31 December 2024 and 2025): pre-hunt (14 Aug – 13 Sep), early-hunt (14 Sep – 19 Oct), mid-hunt (20 Oct – 25 Nov), late-hunt (26 Nov – 31 Dec), and post-hunt (1 Jan – 31 Jan). We selected date ranges with approximately equal durations (30–35 days) that aligned with changes in hunting pressure and deer breeding behavior (McShea et al. 2008, MNDNR 2024). We programmed collars to record a location fix every 30 min from 14 August – 31 January (2024 – 2025 and 2025 – 2026). Outside this period, collars recorded a single daily fix to monitor general movement and detect mortality. Collars continued recording location data until mortality, device failure, or the conclusion of the annual study period (31 Jan), at which point remaining collars were remotely removed and GPS data were downloaded from the devices following recovery.

Deer Spatial Response - We quantified deer spatial responses to hunting exposure using a multi-scale approach at the 2nd and 3rd order selection levels (Johnson 1980). We evaluated 2nd-order selection by analyzing whether hunting influenced landscape composition within deer space use across temporal periods. We constructed 95% utilization distributions (UDs) using Brownian bridge movement models (BBMMs; Horne et al. 2007) in the move package in R (Kranstauber et al. 2012; R Core Team 2023). For each individual, we generated a 95% UD for each temporal period to assess changes in space use over time. We used the 95% UD to define hunting exposure as it represents the broader area available to deer during the study period and allows identification of individuals whose space use includes hunt-accessible areas. Deer were classified as hunted if their 95% UD overlapped any parcel of land actively participating in the controlled archery hunt (i.e., properties verified through city harvest reports, landowner contact, and designated public and permitted private hunting parcels), whereas individuals whose 95% UD did not intersect any hunted parcels were classified as unhunted. This classification was based on whether deer space use intersected areas available for harvest rather than the proportion of the UDs overlapping hunted parcels. Overlap with huntable areas represented potential exposure to hunting activity, although realized harvest risk likely varied among individuals due to differences in space use and landscape characteristics. Previous work has demonstrated that access to hunted areas and surrounding land use can influence deer mortality risk and harvest exposure (Haus et al. 2019). We extracted covariate values within UDs, including land cover composition (proportion forested, open, developed, and wetland), road density (km of maintained road/km^2), and housing density (number of houses/km^2).

To evaluate whether hunting status and temporal period influenced the landscape composition of the seasonal 95% UDs, we fit linear mixed-effects models for each land cover variable (proportion wetland, forest, open, and developed, road density, and housing density). Hunting status (hunted vs. unhunted) and temporal period (pre, early, mid, late, post) were included as fixed effects. We included deer ID as a random intercept because some individuals contributed multiple UD estimates across periods, violating the assumption of independence among observations (i.e., non-independence of repeated measures within individuals). Mixed-effects models are commonly used in wildlife space-use studies when repeated measurements are collected from the same animals (e.g., Brown et al. 2020). We fit models using the *lmer* function in package *lme4* (Bates et al. 2015), and p-values were obtained using the *lmerTest* package (Kuznetsova et al. 2017). We assessed statistical significance at $\alpha = 0.05$. We used nonparametric bootstrapping (1,000 iterations) to estimate mean values and 95% confidence intervals for each covariate within combinations of hunting status and temporal period.

We investigated 3rd-order resource selection using step selection functions (SSF), implemented with the *amt* package (Signer et al. 2019). SSFs compare environmental characteristics of observed movement steps to randomly generated available steps conditioned on observed movement behavior. For each observed step, we generated 10 random steps based on empirical distributions of observed step lengths and turn angles (Fieberg et al. 2021). To account for movement processes while estimating habitat selection, we included movement-related covariates, including log-transformed step length and cosine-transformed turn angle, within conditional logistic regression models. Landscape covariates included forested, open, wetland, and developed cover types, as well as distance to the nearest road and house in meters. To quantify these covariates, we used 30-m resolution land cover data from the National Land Cover Database (NLCD 2019; Dewitz and U.S. Geological Survey 2021), road centerlines (Bemidji–Beltrami County GIS 2023), and building footprints (Esri 2023). We fit separate models for each temporal period (pre, early, mid, late, post). To visualize selection patterns, we extracted model coefficients and 95% confidence intervals and plotted them by covariate and temporal period.

Deer Movement - We calculated velocity (m/hr) for each observed step by dividing step length (m) by time elapsed (hr) to assess variation in deer movement. We analyzed mean movement velocity among the 5 temporal periods and between hunting status. To test differences in movement velocity, we fit linear mixed-effects models using the *lme4* package (Bates et al. 2015). Velocity values were log-transformed, and fixed-effects included temporal period (pre, early, mid, late, post), hunting status (hunted vs. unhunted), and their interaction. Deer ID was included as a random effect to account for repeated measurements of individuals over temporal periods. We tested whether period, hunting status, or their interaction significantly affected movement velocity. If interactions were significant ($\alpha = 0.05$), we conducted post-hoc pairwise comparisons of estimated marginal means using the *emmeans* package with adjustments for multiple comparisons (Lenth et al. 2019, Wijewardena et al. 2024). Model-predicted effects were visualized using the *ggplot2* package (Wickham 2016). We used $\alpha = 0.05$ as a conventional threshold for statistical inference, reflecting a 5% tolerance for Type I error rather than a biologically meaningful cutoff.

Results

We monitored 45 female white-tailed deer during the 2024–2026 study periods ($n = 17$ in 2024; $n = 28$ in 2025). After filtering, we retained 321,894 GPS locations collected from 14 August–31 January across both years, resulting in 238 seasonal UD range estimates used in subsequent analyses. Mean 95% utilization distribution size across all deer and periods was 0.515 km^2 (SE = 0.024). UD size did not differ among temporal periods ($F_{4,134.18} = 2.23$, $p = 0.069$). Mean UD estimates were lowest during the early period (0.452 km^2) and highest during the late period (0.598 km^2).

Land cover composition within 95% UDs did not differ between hunted and unhunted deer, and we did not detect any significant interactions between temporal period and hunted status for any land cover type (Figure 1.2). Temporal period significantly affected proportion of wetland ($p = 0.005$) and open habitat ($p = 0.007$) within 95% UDs, indicating seasonal shifts in use of these habitat types. We did not detect significant temporal effects for forested or developed habitat types, or road and house covariates (all $p > 0.23$).

Step selection analyses indicated broadly consistent patterns of resource selection across temporal periods and hunting treatments. Forested habitat was consistently associated with negative selection coefficients across all periods and across hunting status. Wetland selection coefficients were near zero, with limited variation across periods. Open habitat also showed consistently weak negative selection across groups. Selection for anthropogenic features (roads and houses) was weak, with coefficients centered near zero across all temporal periods. Differences between hunted and unhunted deer were generally small across covariates; however, we observed subtle habitat-specific variation. Unhunted deer showed slightly stronger avoidance of forested, wetland, and open habitats compared to hunted deer, whereas selection for roads and houses was nearly identical between groups across all temporal periods (Figure 1.3).

Mean movement velocity varied among temporal periods and between hunting treatments, with a significant interaction between temporal period and hunting status (LMM on log-transformed velocity; $p < 0.001$). Movement velocity differed across temporal periods and was lower during the mid-, late-, and post-hunt periods relative to pre- and early-hunt periods (Figure 1.4). Hunted deer exhibited lower mean movement velocities than unhunted deer across all temporal periods (39.7 vs. 51.6 m/hr, respectively; $p < 0.001$, averaged across periods). Period-specific predicted mean velocities from the mixed-effects model showed clear temporal variation in movement behavior and a consistent decline over time for both groups. Unhunted deer exhibited the highest predicted mean velocities during the pre- and early-hunt periods (58.3 and 57.0 m/hr, respectively), followed by a gradual decline through mid (57.3 m/hr), late (46.3 m/hr), and post-hunt (39.0 m/hr) periods. Hunted deer followed a similar temporal pattern but at consistently lower predicted mean velocities, ranging from 42.5 m/hr in the pre-hunt period to 35.6 m/hr in the post-hunt period. Differences between groups were greatest during the pre- and early-hunt periods and became progressively smaller later in the season.

Discussion

We found limited behavioral responses of deer to a controlled archery hunt in a developed area, with minimal changes in space use and resource selection, but detectable differences in movement velocity. Deer largely used established ranges and habitat-use patterns throughout the study period, indicating strong site fidelity. Deer in rural hunted systems more commonly exhibit temporary displacement, changes in movement, and shifts in space use during periods of elevated perceived risk (Little et al. 2014, 2016; Brown et al. 2020; Stewart et al. 2022). Previous research using lower intensity relocation data demonstrated urban and suburban deer populations generally maintain relatively small and stable home ranges despite exposure to hunting or other disturbances (Kilpatrick et al. 1999, 2002; Rhoads et al. 2013). The lack of spatial response in our study, which used fine-scale relocation data, suggests a limited ability or need for deer in more developed habitats to discern and respond to the risk associated with hunting relative to deer in more rural areas. The constrained spatial behavior observed here likely reflects structural characteristics of developed landscapes, where fragmented cover and concentrated resources reduce movement requirements and reinforce site fidelity, supporting our prediction that urban deer would exhibit limited large-scale shifts in space use and that hunting effects would be primarily expressed through movement behavior (Vogel 1989, Urbanek and Nielsen 2013, Adams and Villarreal 2020).

This lack of spatial response may also be influenced by repeated and chronic exposure to humans in developed environments, potentially contributing to altered risk perception and behavioral tolerance in urban deer populations. Deer in urban and suburban systems are frequently exposed to non-lethal human activity, including pedestrian traffic, vehicles, and domestic animals, which can reduce flight responses or alter behavioral responses to human presence (Bateman and Fleming 2012, Lowry et al. 2013, Gaynor et al. 2018). In this context, chronic exposure to human activity may contribute to partial habituation, whereby individuals exhibit reduced responsiveness to human-associated cues relative to populations in less disturbed landscapes. As deer gradually habituate to persistent human presence and disturbance, spatial avoidance and movement responses may become diminished (Hansen and Aanes 2015, Liu and Chen 2026). Consequently, controlled archery hunting may not represent a sufficiently strong disturbance to elicit spatial avoidance or displacement, consistent with management objectives focused on population regulation rather than behavioral redistribution in human-dominated landscapes.

Despite these behavioral responses to human exposure, seasonal variation in deer home range dynamics is well documented in the literature and is typically associated with energetic demands, forage availability, winter conditions, and reproduction (Nelson and Mech 1981, Kauffman et al. 2021). In contrast to non-urban hunted systems that often report expansion or redistribution of space use during harvest (Little et al. 2014, 2016; Brown et al. 2020), deer in our study maintained stable ranges across seasons, with only modest variation in size. This pattern is consistent with other suburban populations (Porter et al. 2004), where home ranges are substantially smaller than those reported in rural agricultural and forested landscapes (Lesage et al. 2000; typically, >10 km^2), compared to the mean 95% UD size observed here (~0.52 km^2). Similar patterns have been reported in urban deer systems, including studies from Minnesota, where fragmented landscapes and concentrated anthropogenic resources support reduced spatial requirements and strong site fidelity (Grund et al. 2002, Rhoads et al. 2013, Sullivan et al. 2018).

Few urban deer studies have evaluated behavioral responses to hunting at fine temporal scales using step-selection approaches. Resource-selection patterns were broadly consistent across periods and hunting treatments. Relative to habitat availability within individual home ranges, deer exhibited consistent avoidance of forested habitat, weak avoidance of open habitat, near-neutral selection for wetlands, and weak or variable responses to anthropogenic features. Importantly, hunting exposure did not meaningfully alter step-level selection. Similar muted responses have been reported in other urban and suburban systems where movement behavior is more strongly structured by landscape configuration than short-term disturbance (Ritzel and Gallo 2020, Stewart et al. 2022).

In contrast to stronger behavioral shifts commonly observed in non-urban hunted systems, urban deer in this study showed limited spatial responses to hunting, suggesting that risk effects in developed landscapes may be mediated by both landscape structure and chronic human exposure (Little et al. 2016, Brown et al. 2020, Stewart et al. 2022). Human-modified environments may function as partial refuges, where spatial heterogeneity in human activity reduces perceived predation or hunting risk while still providing access to resources (Bowman 2012, Murphy et al. 2021, Gaynor et al. 2025). However, responses to human presence and landscape modification are not uniform, as individuals must weigh the risks associated with humans against the benefits of anthropogenic resources and altered habitat conditions (Nickel et al. 2020, Suraci et al. 2021). Such tradeoffs likely generate spatially and temporally variable risk landscapes that influence behavioral decisions at multiple scales (Laundré et al. 2010, Palmer et al.

2022). Under these conditions, deer may integrate both immediate and longer-term assessments of risk while maintaining use of human-modified habitats that provide reliable resources (Droge et al. 2017, Liu and Chen 2026). Collectively, these patterns suggest that habitat selection and space use in urban deer are structured more by landscape configuration and chronic disturbance regimes than by discrete hunting events.

Although spatial and selection-based responses were limited, movement velocity patterns indicated more subtle effects of hunting exposure. Seasonal declines in movement occurred across both hunted and unhunted deer, consistent with well-documented seasonal shifts driven by forage conditions, energetic demands, winter constraints, and reduced exploratory behavior (Rhoads et al. 2013, Kauffman et al. 2021). These patterns are widely observed across both urban and non-urban populations and reflect strong environmental control of movement behavior (Lowry et al. 2013, Urbanek and Nielsen 2013, Adams and Villarreal 2020).

Despite similar seasonal trends in velocity, hunted deer consistently exhibited lower overall movement velocities than unhunted individuals; however, this pattern reflects differences in movement intensity rather than necessarily indicating changes in resource use or habitat selection. Roden-Reynolds et al. (2022) documented fine-scale variation in movement rates of suburban white-tailed deer, indicating that movement intensity in developed landscapes is highly dynamic across temporal scales. In our study, both hunted and unhunted deer exhibited gradual seasonal declines in movement velocity but maintained a consistent separation between groups across all periods. This pattern suggests that hunting effects in this urban system are expressed less as discrete behavioral shifts and more as persistent differences in movement intensity embedded within broader seasonal patterns. Similar risk-mediated reductions in movement have been reported in hunted populations and systems experiencing elevated predation risk or human disturbance (Little et al. 2014, 2016; Brown et al. 2020; Abernathy et al. 2025; Frid and Dill 2002; Gaynor et al. 2025). These findings highlight how fine-scale GPS monitoring may detect behavioral responses that are not apparent through broader home-range analyses alone.

Taken together, patterns across space use, resource selection, and movement intensity suggest that seasonal environmental processes and landscape structure influenced urban deer behavior more strongly than localized archery hunting disturbance. Across scales, deer maintained established space-use patterns and relatively consistent habitat selection, while responses to hunting were primarily expressed through movement intensity rather than spatial redistribution. This hierarchical response suggests that space use is largely constrained by landscape structure, resource selection remains stable across disturbance periods, and hunting effects emerge primarily at fine behavioral scales through movement intensity. Most previous hunting-response studies have focused on rural or non-urban systems; accordingly, our study provides evidence from a controlled urban archery context using high-resolution GPS data. In contrast to many non-urban systems, where hunting pressure produces pronounced spatial and behavioral shifts (Little et al. 2014, 2016; Brown et al. 2020), urban landscapes appear to dampen these responses due to fragmented cover, predictable anthropogenic resources, and chronic human exposure. Collectively, these conditions are likely to reduce the benefits of large-scale displacement and instead favor behavioral adjustment within established spatial frameworks.

Management Implications

Management programs relying on archery hunting in urban environments should account for potentially limited spatial and resource-selection responses among deer exposed to hunting activity. Harvest outcomes in these systems may be influenced more by structural constraints of urban hunts (e.g., tag allocation, hunter effort, access, and season structure) than by behavioral changes in deer space use or resource selection, which were minimal in this study. In residential landscapes such as our study area, restricted access to private lands, variable hunter participation, and selective harvest behavior may contribute to uneven spatial distribution of hunting pressure and reduce overall harvest efficiency. Small home ranges and abundant anthropogenic resources may further limit the proportion of the population that regularly encounters huntable parcels, resulting in reduced exposure for portions of the population despite local hunting effort. Strategies that expand access across smaller parcels, reduce the scale of safety buffers (Bowman 2012), incentivize landowner participation, or improve hunter distribution may therefore increase effective harvest coverage. Concentrating effort earlier in the season, when movement rates are comparatively higher, may also improve harvest efficiency. Overall, these findings suggest that in urban systems, the effectiveness of archery hunting is likely determined more by the spatial distribution and timing of hunting effort than by deer behavioral responses to hunting pressure.

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TABLES

Table 1.1: Land cover classes within Bemidji city limits categorized by area (km^2) and percentage (%).

Land cover Type	**Area (km^2)**	**Percent (%)**
Forest	17.97	39.7
Developed	11.84	26.1
Open	8.50	18.8
Wetland	6.43	14.2
Water	0.56	1.2

FIGURES

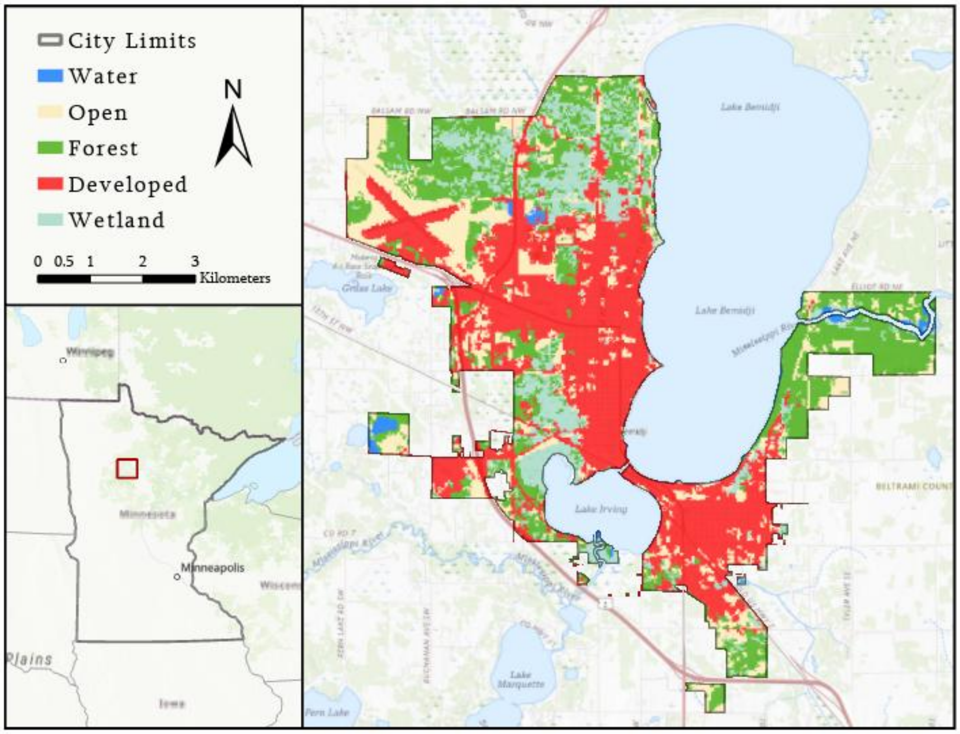

Figure 1.1: Study area in Bemidji, Minnesota, USA, showing city limits and land cover composition where GPS-collared white-tailed deer were monitored during 2024–2026.

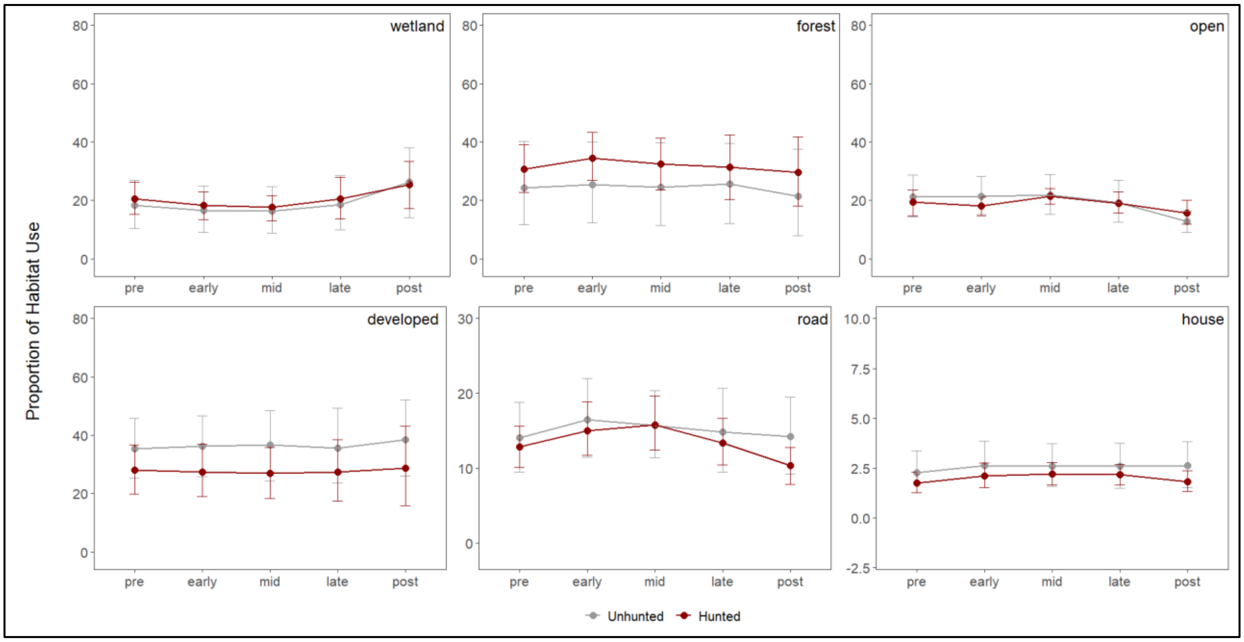

Figure 1.2: Brownian bridge movement models (BBMM) estimating proportional habitat use within 95% utilization distributions for hunted and unhunted white-tailed deer across 5 temporal periods. Proportions of wetland, forest, open, developed, road, and house habitats are shown, with error bars representing 95% confidence intervals.

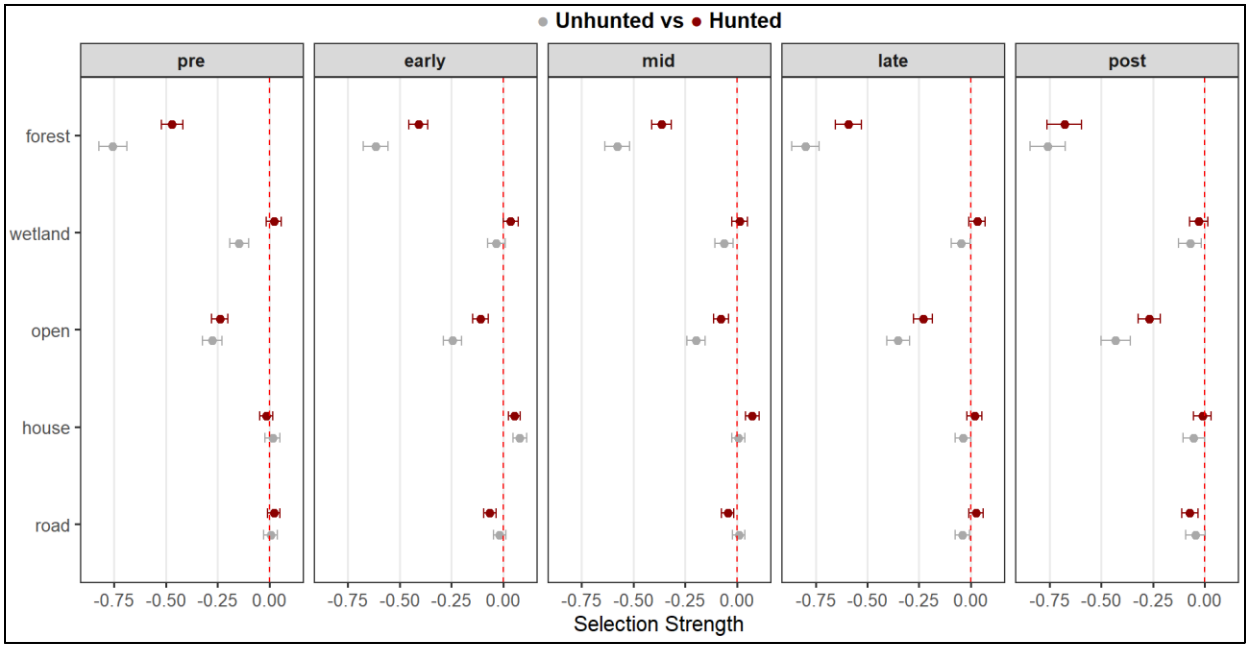

Figure 1.3: Step-selection function (SSF) coefficient estimates for white-tailed deer, comparing hunted and unhunted individuals across temporal periods (pre-, early-, mid-, late-, post-hunt). Points represent model coefficients for selection of habitat types (road, house, open, wetland, and forest) relative to availability, with error bars showing 95% confidence intervals.

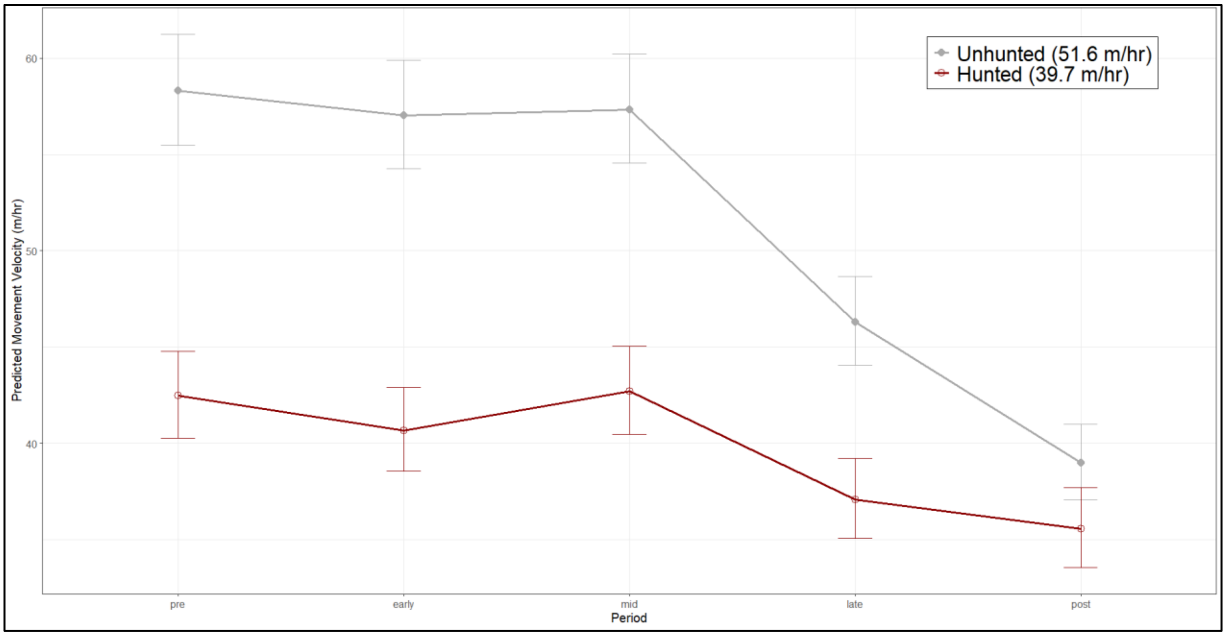

Figure 1.4: Temporal variation in predicted movement velocity (m/hr) of hunted and unhunted white-tailed deer across temporal periods. Lines represent predicted values for each group, with points showing estimates for each temporal period and error bars representing 95% confidence intervals.

FEMALE WHITE-TAILED DEER SURVIVAL DURING AND FOLLOWING A CONTROLLED CITY ARCHERY HUNT

Introduction

White-tailed deer (*Odocoileus virginianus*; hereafter deer) are highly adaptable and persist across a broad gradient of rural to highly urbanized landscapes throughout North America. Increasing urbanization in the United States has important implications for deer ecology and management, particularly as expanding urban and suburban areas generate persistent human–wildlife conflict and create conditions that may facilitate disease persistence and transmission (DeNicola et al. 2000, DeNicola and Williams 2008, Kilpatrick et al. 2014). In these systems, deer often exhibit relatively high annual survival due to reduced hunting pressure and altered predator communities, complicating population regulation and increasing the need for effective management strategies (DelGiudice et al. 2002, Brinkman et al. 2004, Storm et al. 2007).

Mortality processes differ fundamentally between rural and urban landscapes. In rural systems, adult female mortality is typically driven by regulated harvest and natural causes (Nelson and Mech 1986, Brinkman et al. 2004, Grovenburg et al. 2011). In contrast, mortality in urban environments shifts toward anthropogenic and infrastructure-related sources, primarily vehicle collisions, while harvest and predation are often reduced or spatially constrained (Hansen and Beringer 2003, Porter et al. 2004, Storm et al. 2007). In these systems, population regulation may instead occur through density-dependent changes in recruitment, age structure, or disease dynamics rather than resource limitation. Because adult females are the primary drivers of population growth, it is critical to understand how mortality structure shifts across landscapes for interpreting population dynamics (Geist 1998, McShea 2012, Haus et al. 2020). However, empirical estimates of survival and cause-specific mortality remain limited in many urban systems.

To address overabundant urban deer populations, municipalities have increasingly implemented controlled archery hunting programs, typically focused on antlerless harvest to reduce population growth (DeNicola et al. 2000, Kilpatrick et al. 2004, Hygnstrom et al. 2011). While archery harvest has successfully reduced or stabilized populations in some urban areas (McAninch 1993, Kuser 1995, Kilpatrick and Walter 1999), effectiveness varies widely due to constraints such as limited land access, restricted seasons, and variable hunter participation (Ver Steeg et al. 1995, Kilpatrick et al. 2004). These constraints create spatially heterogeneous harvest pressure across mosaics of hunted and unhunted parcels, potentially influencing both exposure to risk and vulnerability to harvest.

Controlled archery hunting and other management programs have reduced deer abundance in high-density suburban systems, including localized urban populations in the northeastern United States where densities can exceed 100 deer/mi^2 (Kilpatrick and LaBonte 2007, DeNicola et al. 2008). However, these conditions are not representative of most municipalities, where deer densities are typically lower but still sufficient to generate ecological and social concerns. Despite widespread use of controlled archery hunting in these more heterogeneous urban landscapes, its effectiveness under broadly applicable urban conditions remains uncertain, particularly in systems characterized by uneven access and variable harvest distribution. Specifically, it is unclear whether regulated hunting contributes meaningfully to adult female survival or whether mortality in urban systems is primarily driven by non-hunting anthropogenic sources. To address these questions, we evaluated annual survival and cause-specific mortality of adult female white-tailed deer in an urban landscape, compared survival between hunted and unhunted individuals during a controlled archery hunt, and quantified the influence of anthropogenic landscape features on mortality risk. We also used long-term deer density trends and harvest records to assess population status and management intensity within the study system. Based on previous studies of urban deer populations, we predicted relatively high annual survival, with vehicle collisions as the primary cause of mortality, and that anthropogenic landscape features, such as roads, would be positively associated with mortality risk.

Methods

Study Area – We conducted this study in north-central Minnesota, within the 45.3 km² city limits of Bemidji, Minnesota, USA (47°28′N, 94°52′W). The landscape was mostly flat to gently rolling, with low glacially formed hills and elevations ranging from 404 to 433 m above sea level. The region experienced strong seasonal variation, with mean summer temperatures of 22.9°C and mean winter temperatures of -12.9°C. Mean annual precipitation was 55.74 cm (NOAA 2023). Land cover within Bemidji was primarily forested (39.7%), dominated by fir (*Abies spp*.), spruce (*Picea spp.*), and tamarack (*Larix laricina*), consistent with the coniferous forest biome (Minnesota Department of Natural Resources 2020). Other land cover types included developed urban areas (26.1%), undeveloped open space (18.8%), wetlands (14.2%), and open water (1.2%; Dewitz and U.S. Geological Survey 2021). Common potential predators of white-tailed deer in and around Bemidji included coyotes (*Canis latrans*), black bears (*Ursus americanus*), and, at broader regional scales, gray wolves (*Canis lupus*), with occasional occurrence of bobcats (*Lynx rufus*) in surrounding habitats. The study area contained 1,665 unique land ownership parcels (City of Bemidji GIS Hub 2018, U.S. Census Bureau 2024), with parcel sizes averaging 1.55 ha (range = 0.01–139.97 ha; City of Bemidji GIS Hub 2018). Residential structure data identified 4,611 homes, corresponding to a housing density of 102 houses/km^2.

In response to ongoing deer-related concerns from the public, the Bemidji City Council established a Deer Management Committee in 2003 to implement and oversee a controlled archery hunt intended to limit damage to landscaping and natural areas, reduce vehicle collisions and potential disease transmission (e.g., Lyme disease), and improve overall herd health. Hunting occurred on a combination of city-owned public lands and privately owned parcels. Private landowners or their designees were eligible to participate if their property was ≥0.8 ha in size, and access to designated city-owned hunting areas was determined through an application and lottery system. Hunters were permitted to harvest up to 5 deer annually (1 antlered and 4 antlerless), with antlerless harvests not counting toward statewide bag limits. Hunting participation was reduced in 2025 due to cancellation of the city hunt (storm damage), with activity largely limited to private lands. Between 2005 and 2025, hunters removed 579 deer from the city, including 375 adult females, 115 fawns, and 89 adult males, with annual permit issuance ranging from 28 to 95 permits (Minnesota Department of Natural Resources 2026).

Density Estimates and Harvest Data - Road-based spotlight surveys were conducted between 20 Oct and 5 Nov 2016–2025 (no survey was performed in 2020). The city was divided into 3 survey routes with lengths of 20.3, 25.2, and 26.2 km, and each route was surveyed 4 times per year. Surveys began 30 min after sunset and generally followed methods described in Haus et al. (2019), with vehicles traveling <20 km/hr and observers on both passenger and driver sides searching for deer or groups of deer using 12-V spotlights. We measured perpendicular distances to individual deer or deer clusters using a laser rangefinder and recorded the initial detection location when animals moved in response to the vehicle. Deer densities were estimated using distance sampling methods implemented in R with the *Distance* package (Miller et al. 2019). For each detection, observers recorded group size, sex, and age class (adult or fawn), as well as spatial location to support post-survey demographic summaries. Harvest totals, age and sex composition, permit issuance, harvest efficiency (deer/permit), harvest intensity (deer/km^2/year), and permit density (permits/km^2/year) were summarized by year to characterize hunting pressure and harvest dynamics through time.

Animal Capture and Monitoring- We captured female (≥6 months old) white-tailed deer by Clover traps and drop nets in Bemidji, Minnesota during Jan–March of 2024 and 2025 (Clover 1956, Silvy 2020). Deer were captured at multiple locations throughout the city (Figure 2.1). We sedated captured deer with an intramuscular injection of xylazine (0.5 mg/kg; Conner et al. 1987, Kreeger et al. 2023) and reversed using atipamezole (0.275 mg/kg; Millspaugh et al. 2004). Deer weighing ≥35 kg were fitted with GPS breakaway collars equipped with 8 hour mortality sensors (MG5M-2D [780 g]; Advanced Telemetry Systems, Isanti, Minnesota, USA). Deer also received 2 plastic ear tags (3 cm diameter) that included a unique ID and contact information if recovered (Allflex USA Incorporated, Dallas, TX, USA). We recorded morphological measurements on each animal during capture (total length, hind limb length, shoulder height, chest girth; Bowman et al. 1998, Haus et al. 2019). We monitored vital signs (respiration, heart rate, and body temperature) throughout the handling process at 5-min intervals until deer left the capture site of their own volition. GPS collars were programmed to record location fixes at 30-min intervals from 14 Aug – 31 Jan, and 1 location per day the remainder of the year. Data collection continued until an animal's death, collar malfunction, or the end of the annual monitoring period (31 January 2025 or 2026), after which any remaining collars were remotely released using the collar breakoff mechanism.

Survival Analysis - We investigated all mortalities for cause, location, and estimated date of death using field evidence at the site (e.g., feces, tracks, chase sign, blood) and carcass characteristics (e.g., wounds, bite patterns; Mech et al. 1971, Cristescu et al. 2022). When we detected a mortality signal or an animal appeared stationary based on GPS data, we used the most recent GPS locations in combination with VHF telemetry to locate the carcass. We preformed field necropsies upon recovery to determine the likely cause of death. We grouped mortality causes into 3 categories; harvest (including subclassifications for legal and illegal harvest), natural causes (with subclassifications for predation and undetermined natural causes), and vehicle collisions (carcasses recovered along roadways with evidence of trauma such as fractures or subcutaneous hemorrhaging).

We estimated annual survival using Kaplan–Meier product-limit estimators (Kaplan and Meier 1958) adapted for staggered entry (Pollock et al. 1989). Time was measured in days since 1 Feb of each year (2024 and 2025). Due to staggered capture dates, all individuals were considered at risk beginning 1 February. Deer captured on or prior to this date entered the analysis on day 0, while those captured after 1 February entered the analysis using the number of days since 1 February as the entry day. Individuals were monitored until death, collar failure (loss of signal), or the end of the respective study period (31 January 2025 for individuals captured in 2024 and 31 January 2026 for individuals captured in 2025). Collar failure and study termination were treated as right-censored observations. Annual survival estimates and 95% confidence intervals were derived from Kaplan–Meier survival curves at 365 days. We evaluated the effects of landscape and anthropogenic covariates on mortality risk using Cox proportional hazards models (Cox 1972; Pollock et al. 1989). Given the limited number of mortality events, we restricted candidate models to a maximum of two covariates to maintain model stability and avoid overfitting. A total of 8 models were evaluated, including combinations of habitat covariates. Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). Relative support among models was evaluated using ΔAICc values and Akaike weights. We assessed model assumptions using Schoenfeld residuals, and parameter estimates were reported as hazard ratios with 95% confidence intervals. All analyses were conducted in program R (R Core Team 2023) using the package *survival* (Therneau 2015) and visualized with the package *survminer* (Kassambara et al. 2026).

To assess deer survival in relation to hunting activity, we defined a focal study period spanning 14 Aug–31 Jan, encompassing the entire Minnesota archery season (mid-Sep – 31 Dec 2024 and 2025). We used Cox proportional hazards models to compare survival between hunted and unhunted deer during the hunting period. Deer were classified as hunted if their 95% Brownian Bridge utilization distribution during the hunting season overlapped any parcel of land actively participating in the controlled archery hunt; individuals whose UDs did not intersect any hunted parcels were classified as unhunted. We evaluated model significance using Wald tests with an $\alpha = 0.05$ criterion and reported hazard ratios with 95% confidence intervals; effects were considered statistically significant when confidence intervals did not include 1.

Results

White-tailed deer densities in Bemidji were relatively stable, averaging 10.78 deer/km² and ranging from 9.32–12.37 deer/km² based on annual spotlight surveys from 2016–2025 (Figure 2.2), and did not exhibit a significant temporal trend across years ($\beta = 0.054$, SE = 0.138, $p = 0.706$). For the same period, a mean of 78 permits were issued annually, corresponding to a hunter density of 1.73 hunters/km²/year (Figure 2.3a). Annual harvest averaged 38 deer/year (0.83 deer/km²/year), representing approximately 7% of the estimated population annually. Harvest efficiency averaged 0.47 deer/permit. Harvest composition was dominated by adult females (61.2%), followed by adult males (20.7%) and fawns (18.1%; Figure 2.3b).

We monitored a total of 45 GPS-collared adult female white-tailed deer during 2024–2025 ($n = 17$) and 2025–2026 ($n = 28$). Annual survival was 0.63 (95% CI: 0.52–0.76), corresponding to an annual mortality rate of 37%. We documented a total of 24 mortalities during the monitoring period. Of these, 41.7% were attributed to vehicle collisions, 29.2% to natural causes, and 29.2% to hunting (Table 2.1). The annual staggered-entry Kaplan-Meier survival curve most closely aligned with a Type II curve with a relatively uniform decline in survival over time (Figure 2.4). Cox proportional hazards model selection identified anthropogenic covariates (house density and road density; Table 2.2) as the top-supported model ($\omega = 0.86$). The global model received less support (ΔAICc = 3.92, ω = 0.12), whereas the null model had minimal support (ΔAICc = 9.51, ω = 0.01). All other candidate models had substantially lower support (ΔAICc > 9.0). In the top model, mortality hazard decreased with increasing house density (β = −2.81, HR = 0.06, 95% CI: 0.01–0.31) and increased with increasing road density (β = 2.67, HR = 14.42, 95% CI: 3.13–66.40). During the hunting study period (mid-September–31 December), survival did not differ between hunted and unhunted deer (Cox proportional hazards model: β = 0.73, SE = 0.63, p = 0.24; Figure 2.5). The hazard ratio for hunted deer was elevated relative to unhunted deer (HR = 2.08, 95% CI: 0.61–7.11), although not statistically significant as the 95% confidence interval included 1.

Discussion

White-tailed deer densities in Bemidji (~11 deer/km^2) were consistent with values commonly characterized as overabundant in urban and suburban systems (DeNicola et al. 2000, Kilpatrick and LaBonte 2007, Storm et al. 2007), particularly where densities exceed levels typically considered socially or ecologically acceptable in developed landscapes. In response to these concerns, a citizen-led committee in Bemidji established a controlled archery hunt to reduce local deer abundance and address community concerns associated with high deer densities. Despite long-term implementation of controlled archery hunting in our study area, deer density remained stable throughout the study, indicating no strong directional change in abundance. This stability is consistent with density-dependent regulation in deer, where compensatory processes can buffer harvest-related mortality when populations are near carrying capacity (Caughley 1977, McCullough 1979, Bartmann et al. 1992). Stable or moderately high deer densities are commonly reported in urban and suburban systems, where management effectiveness is constrained by spatial heterogeneity in access, landownership patterns, and variable harvest intensity (Etter et al. 2002, Kilpatrick et al. 2004, Hygnstrom et al. 2011, Urbanek and Nielsen 2013b). These patterns also have implications for disease dynamics, including chronic wasting disease (CWD) and other density-dependent pathogens and parasites. The persistence of stable densities throughout the study suggests that opportunities for density-dependent pathogen transmission likely remained relatively constant, indicating that disease risk may persist in urban systems where deer populations do not exhibit strong directional change over time.

Deer densities in the Bemidji study area (~10.78 deer/km^2) were approximately twice those of the surrounding Deer Population Management Area (DPA 684; ~5.0 deer/km^2; Michel and Giudice 2024), suggesting the potential for stronger density-dependent processes within the municipality relative to the broader landscape. However, these estimates were derived from different methodologies. Bemidji densities were based on annual spotlight surveys, whereas DPA estimates are generated from Minnesota Department of Natural Resources population models, and are therefore interpreted as broadly comparable indices of relative density rather than direct point estimates. Across urban systems, deer density varies widely with development intensity, landscape configuration, and management pressure, with suburban structure identified as a key driver of local abundance (Urbanek and Nielsen 2013b). Under elevated densities, increases in anthropogenic or harvest mortality may be partially offset by compensatory survival or recruitment, limiting population-level responses to moderate harvest pressure. Population declines are generally expected when additive mortality consistently exceeds compensatory recruitment and immigration, although the specific threshold required to induce decline is context dependent and was not explicitly estimated here. In Midwestern urban systems, deer populations are often maintained through localized and spatially constrained management actions (e.g., regulated archery harvest, damage permits, and targeted removals), which are typically insufficient or too heterogeneous to drive sustained declines (DeNicola et al. 2000, Etter et al. 2002, Kilpatrick et al. 2004, Storm et al. 2007, Hygnstrom et al. 2011, DeNicola and Williams 2008, Stewart et al. 2013).

Within this management context, annual survival (0.63) aligned with values reported for urban and suburban systems dominated by anthropogenic mortality sources (DeNicola et al. 2000, Grund 2011, McShea 2012) but remained lower than estimates from less developed Midwestern systems (Brinkman et al. 2004, Grovenburg et al. 2011), indicating elevated human-associated mortality in developed landscapes. Together with stable density estimates, these patterns are consistent with a population near a management equilibrium, where harvest pressure appears sufficient to limit sustained population growth (i.e., $\lambda > 1$ or increasing density over time), but not strong enough to induce a detectable population decline. Additional reductions in abundance would likely require more intensive or spatially targeted harvest, whereas reduced hunter participation or harvest access could permit renewed population growth. Collectively, these findings suggest that controlled archery programs in moderately developed urban systems may function primarily to help stabilize deer populations rather than substantially reduce abundance.

This population-level pattern is reflected in the underlying mortality structure, where annual mortality was dominated by vehicle collisions (41.7% of deaths), indicating road networks and human activity are primary contributors to adult female mortality. The positive relationship between road density and mortality further supports roads as a key source of risk, consistent with evidence that deer–vehicle collision probability increases in more road-dense landscapes (Dusek et al. 1992, Grovenburg et al. 2011). Similar patterns have been documented in other urban and suburban deer populations where roads represent a persistent source of mortality (Etter et al. 2002, Hansen and Beringer 2003, Storm et al. 2007).

Spatial heterogeneity in development intensity may produce contrasting effects on mortality risk, as lower mortality risk in areas with higher housing density may reflect changes in movement behavior and exposure to roads. Residential development can create more predictable spatial environments characterized by consistent anthropogenic resources and human activity, which may reduce large-scale movement, thereby limiting exposure to major travel corridors where collisions are most likely. Spatial heterogeneity in human activity may also generate localized zones of reduced perceived risk, redistributing deer activity away from high-risk locations while maintaining access to anthropogenic forage resources (Kilpatrick et al. 1999, 2002; Urbanek and Nielsen 2013b; Lowry et al. 2013; Adams and Villarreal 2020). This pattern has been documented in other urban systems (Porter et al. 2004, Bowman 2012, Roden-Reynolds et al. 2022, Gaynor et al. 2025). Collectively, these patterns suggest that portions of residential landscapes may buffer deer from anthropogenic mortality through predictable human activity, constrained hunting access, and reduced large-scale movement despite high levels of development.

In addition to spatial variation in anthropogenic mortality risk across developed landscapes, hunting did not represent the dominant source of mortality, indicating that regulated archery harvest had limited influence on adult female survival. This pattern is consistent with urban and suburban deer populations where spatial constraints, fragmented land ownership, and variable hunter effort reduce harvest effectiveness (Kilpatrick and Walter 1999, Hygnstrom et al. 2011). Harvest is often spatially restricted and unevenly distributed due to safety concerns and limited access, limiting consistent population-level effects (Kilpatrick et al. 2004, Grund 2011). In this study, illegal harvest accounted for a notable proportion of hunting-related mortality (12.5%) and was higher than is generally reported in rural white-tailed deer populations, where it typically represents a small component of cause-specific mortality (Wehr et al. 2026). This suggests that in highly developed landscapes, restrictions on regulated hunting and heterogeneous access may shift a greater share of mortality into unregulated pathways, with potential implications for both population dynamics and public safety. Beyond harvest-related mortality, predation represented another source of adult female mortality. In the Bemidji area, we observed mortality associated with coyotes, gray wolves, and bobcats in portions of the study area, though their influence was likely spatially limited.

The minimal effect of hunting on adult female survival is further supported by the lack of significant differences in survival between hunted and unhunted deer. This finding is consistent with previous research showing that urban hunting systems often produce weak or variable survival responses due to spatial refuges and uneven harvest exposure (Kilpatrick et al. 2004, Storm et al. 2007). Although behavioral responses to hunting risk have been documented in deer, these responses do not always translate into detectable differences in survival outcomes (Dusek et al. 1992, Grovenburg et al. 2011). In this system, both hunted and unhunted deer were routinely exposed to anthropogenic activity across the landscape, suggesting that chronic human presence may reduce differential behavioral responses to hunting pressure.

More broadly, these survival patterns reflect multiple interacting anthropogenic mortality sources, with vehicle collisions contributing substantially to adult female mortality dynamics (Hansen and Beringer 2003, Storm et al. 2007, McShea 2012). Harvest operated within a broader anthropogenic mortality regime dominated by infrastructure-related risk, particularly roads and associated human activity (Etter et al. 2002, Grovenburg et al. 2011). Consequently, controlled archery hunting did not appear to represent a dominant source of mortality under the observed conditions of deer density, harvest intensity, and hunter access, and overall mortality patterns were more strongly associated with infrastructure-related anthropogenic sources. Notably, while many mortality sources in urban systems (e.g., vehicle collisions and other anthropogenic hazards) are not directly manageable at the population scale, harvest represents the primary mechanism through which managers can directly influence mortality rates, suggesting that additional or alternative management strategies would be required to meaningfully affect non-harvest sources of mortality in urban deer populations.

Management Implications

Municipalities attempting to manage urban white-tailed deer through controlled hunting should recognize that there is an unknown inflection point within each population where harvest mortality transitions from compensatory to additive, and that this threshold is likely influenced by baseline density, landscape context, and the relative contribution of non-harvest mortality sources. Below that rate, harvest will have negligible impact on deer populations. In systems like the city of Bemidji, achieving the desired population-level decline would likely require improved harvest efficiency through spatial access and hunter distribution, rather than solely increasing permit numbers. Non-hunting mortality, particularly vehicle collisions associated with road networks, represents a major and spatially structured source of mortality, indicating that population outcomes are also shaped by landscape configuration and infrastructure density. Incorporating road density and high-risk travel corridors into management planning can therefore help identify priority areas for targeted intervention. Harvest rates necessary to achieve additive mortality in urban systems will vary as a function of carrying capacity, non-hunting mortality, and juvenile recruitment. Because these rates are usually unknown to municipal managers, and reported rates from local populations are not always representative of broader urban systems, we recommend managers implement liberal harvest frameworks that maximize access and incorporate spatial planning tools (e.g., targeted access in high-density or high-risk areas) to promote more even hunter distribution and harvest intensity across the landscape.

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TABLES

Table 2.1: Causes of mortality for collared adult female white-tailed deer in Bemidji, Minnesota, USA, 2024–2026.

Mortality Cause (%)	n	% within cause
Hunting (29.2%)		
City hunt	4	57.1%
Illegal harvest	3	42.9%
Natural (29.2%)		
Predation	5	71.4%
Undetermined natural causes	2	28.6%
Vehicle (41.7%)	10	

Table 2.2: Summary of AICc values generated by Cox proportional hazards models evaluating annual survival of female adult white-tailed deer in Bemidji, Minnesota, 2024–2026.

Model	**K**	**AICc[a]**	**ΔAICc**	**ω[b]**
Anthropogenic (House + Road)	2	56.63	0.00	0.86
Global	4	60.55	3.92	0.12
Null	0	66.14	9.51	0.01
Road only	1	66.76	10.13	0.01
House only	1	67.86	11.23	0.00
Forest only	1	68.06	11.43	0.00
Wetland only	1	68.16	11.53	0.00
Habitat (Forest + Wetland)	2	70.13	13.50	0.00

[a]Akaike's Information Criterion corrected for small sample size.
[b]Akaike weight.

FIGURES

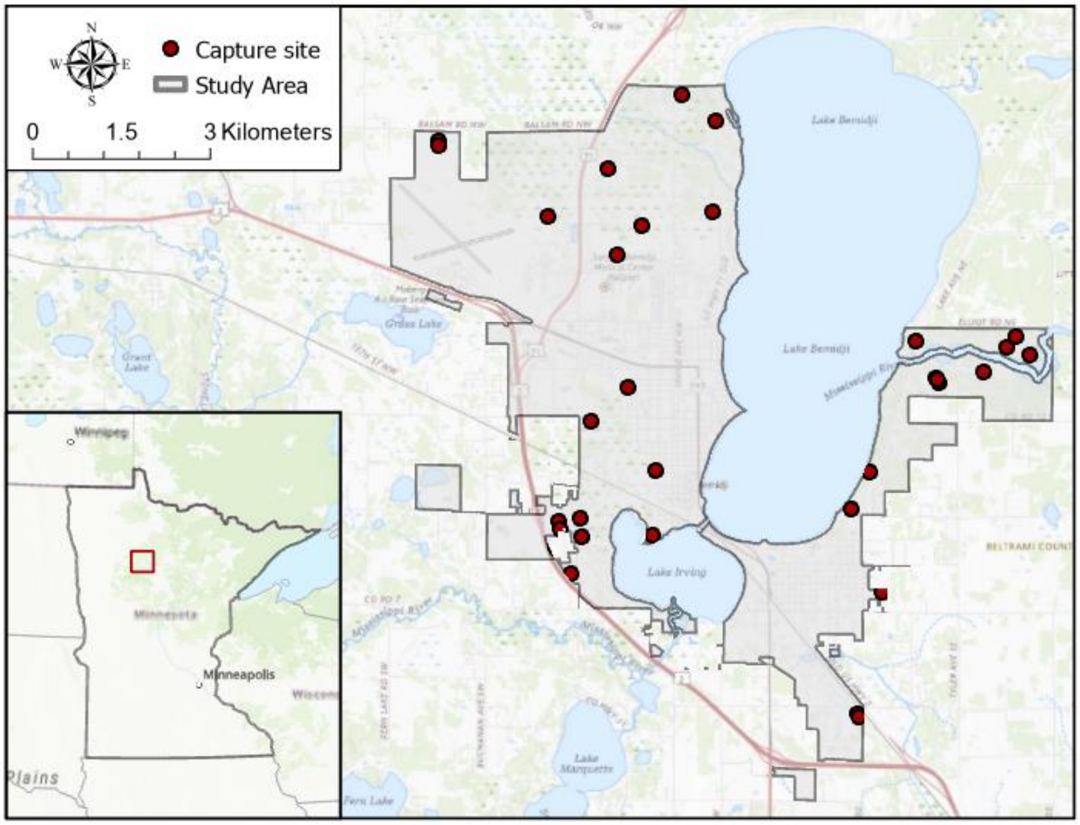

Figure 2.1: Study area in Bemidji, Minnesota, USA where GPS-collared deer were monitored during 2024–2026. Red dots represent capture locations within Bemidji City Limits.

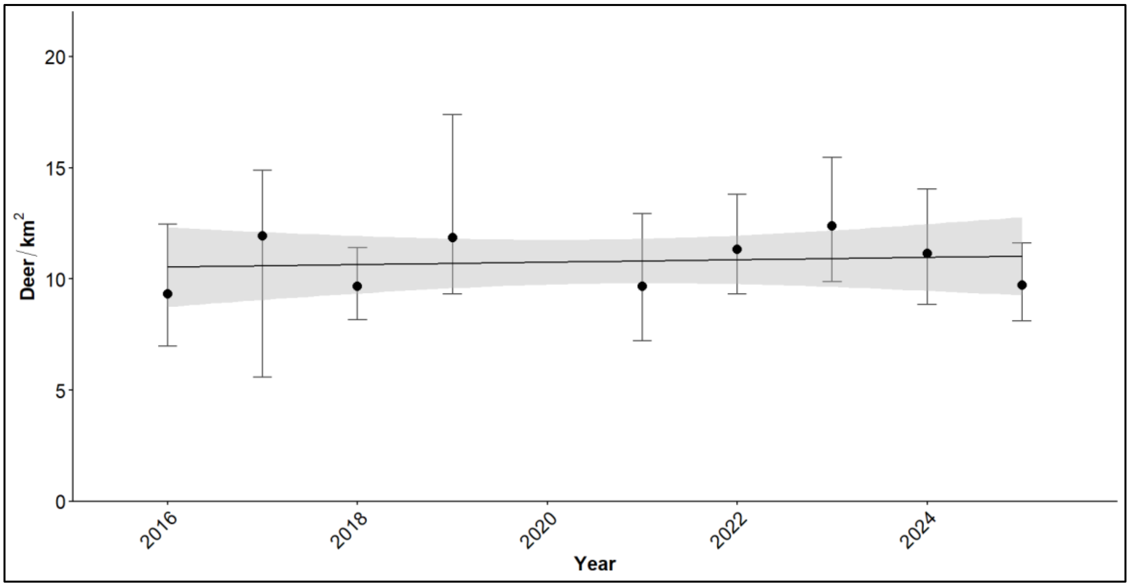

Figure 2.2: Density estimates per year and line of best fit based on annual spotlight survey data for the deer population in Bemidji, Minnesota, 2016–2025. No survey data was collected in 2020.

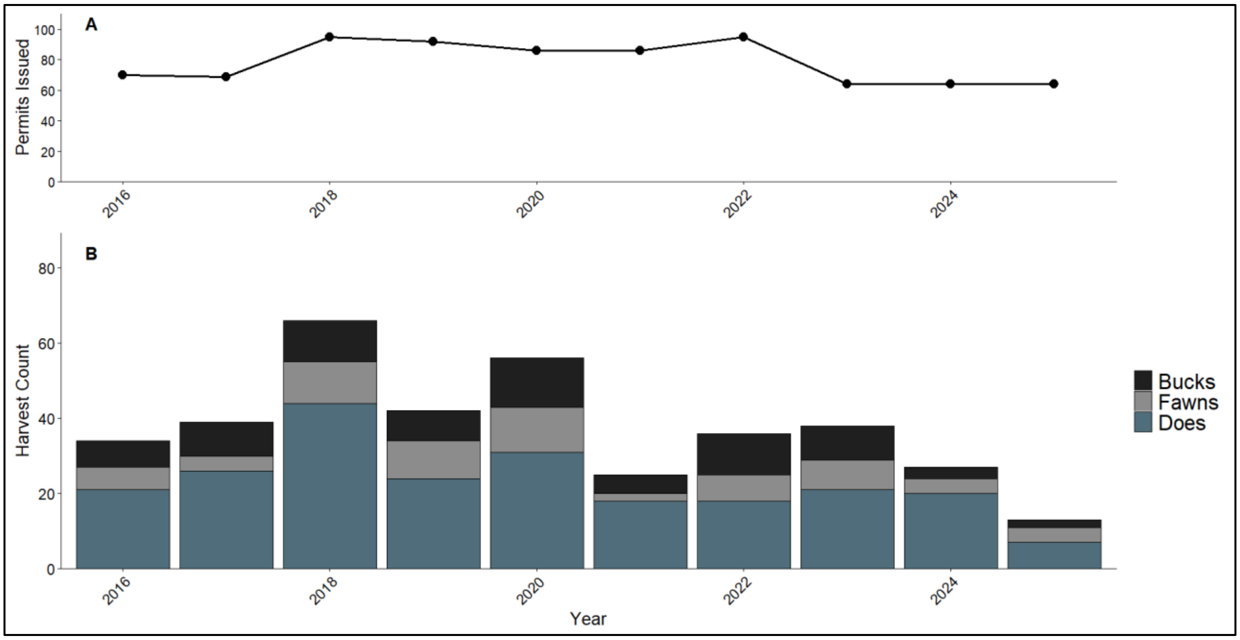

Figure 2.3: Annual harvest totals of deer by sex/age class (A) and permits issued (B) from 2016–2025 in Bemidji, Minnesota (data from Minnesota Department of Natural Resources 2026).

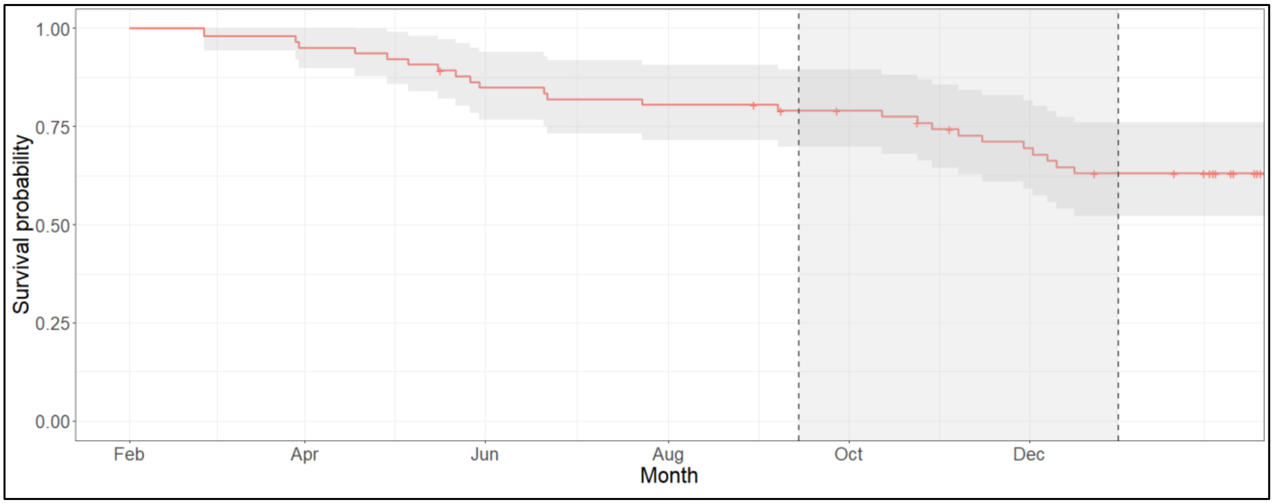

Figure 2.4: Annual staggered-entry Kaplan-Meier survival curve for adult female white-tailed deer in Bemidji, Minnesota from 2024–2026 with a 95% hazard curve. The archery hunting season (mid-Sep through 31 Dec) is within the shaded region.

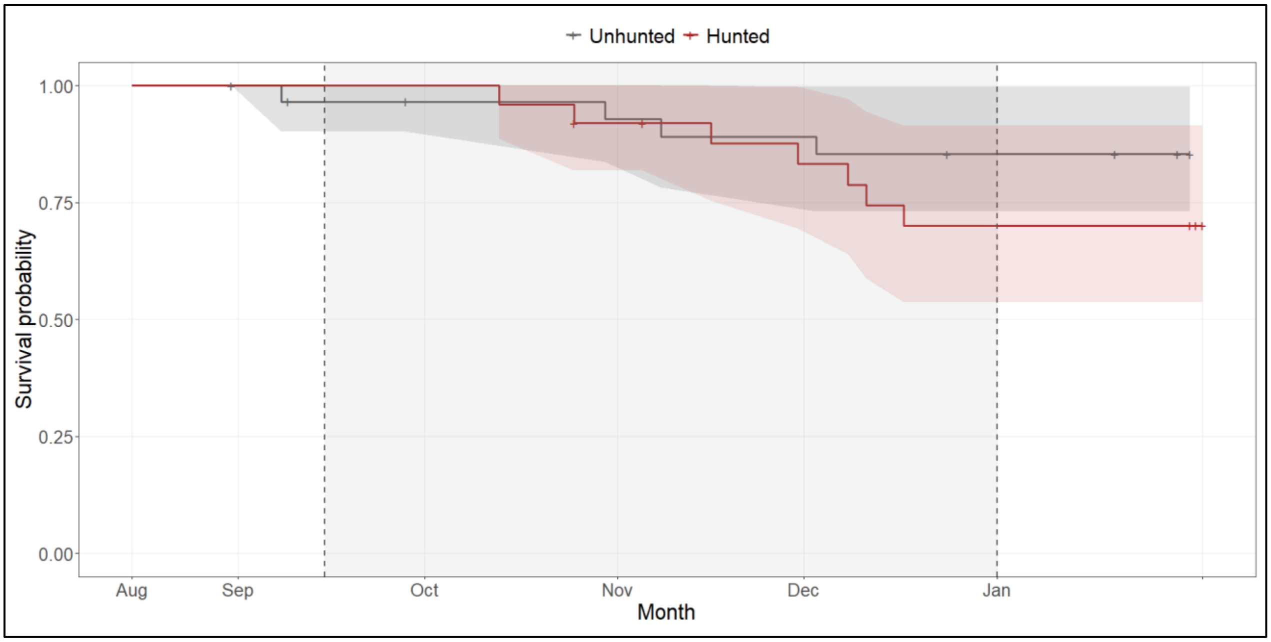

Figure 2.5: Staggered-entry Kaplan-Meier survival curves with 95% confidence intervals for female white-tailed deer whose 95% utilization distribution during the hunting season overlapped with a parcel participating in the city hunt (red) versus deer who did not overlap with a hunted parcel (grey). The archery hunting season (mid-Sep through 31 Dec) is within the shaded region.

APPENDIX A

Bemidji State University Institutional Animal Care and Use Committee (IACUC) approval of data collection protocols

1

ACADEMIC AFFAIRS
JUL 27 2023
BEMIDJI STATE UNIVERSITY

Office use only
Protocol Number___24-01__
Date Approved____7/26/2023__
Date Expires__6/30/2026__

Bemidji State University
Animal Care and Use Review Form

Type all information into this form. Explain procedures as completely as possible for an evaluation of the proposal.

I. Investigator(s) and Protocol Title

Principal Investigator:
(include position and phone #)

Dr. Jacob Haus, Assistant Professor, 218-755-4372

Co-investigators:
(include position and phone #)

Dr. Terry Kreeger, consulting veterinarian, 218-244-0248
Dr. Brian Hiller, Professor, 218-755-2212

Protocol Title:

Efficacy of suburban archery hunting to manage white-tailed deer populations

II. Type of project (check all that apply):

New project___*X*____ Renewal________

Teaching project________ Research Project________

III. Identify Species and Sources

Species	Source
White-tailed deer (Odocoileus virginianus)	*Live captured and released within Bemidji city limits.*

IV. Purpose of Proposed Use

1. State rational for use of animals and for appropriateness of species used.

Deer population within urbanized areas cause substantial socioeconomic burdens to municipalities. Overabundant deer populations result in greater rates of deer-vehicle collisions, landscape damage, and increased risk of disease transmission (e.g., Lyme Disease, CWD). Urban deer are difficult to manage as anthropogenic food sources can maintain artificially high population densities, and management practices such as firearm hunting cannot be safely conducted. Many municipalities throughout Minnesota utilize 'special city archery hunts' that allow for more liberalized harvest regulations than during regular archery seasons. The Bemidji City Council formed the Deer Management Committee in 2005 to operate special archery hunts within 3 city districts to limit negative impacts from overabundant deer populations for city residents. The hunt has removed 510 deer from within city limits since implementation, with greater rates of harvest in more recent years. Annual spotlight surveys suggest deer populations are increasing within all 3 districts, however. Deer may alter their behavior or movement in response to hunting pressure, or the number of deer harvested may simply be inadequate to prevent population growth. Special archery hunts may be able to manage urban deer populations, but more research is needed to evaluate the factors affecting their efficacy.

During the winter (January – March) of 2024 and 2025, we will live-capture a total of 40-50 adult female deer within city limits and affix individuals with GPS collars. Collars will provide information on both deer behavioral response to the city hunt as well as mortality data. Annual mortality rate of adult females is the most influential driver of deer population growth, and deer abundance is best managed by adjusting harvest rates of adult females. We will estimate the overall rate of mortality as well as mortality due to harvest inside city limits, harvest outside city limits, wounding loss, vehicle collision, and natural causes. We will track the number of special hunt permits issued, hunter effort, and spatial distribution of hunting pressure using both mandatory logs submitted by hunters at the end of the season as well as small GPS units with participating hunters.

Collars on deer will be programmed to record a GPS location fix on individual deer every 30 minutes from 1 August to 31 January each year. We will examine changes in deer behavior in response to the city hunt using resource selection functions before, during, and after the hunting season.

Most research involving urban deer management evaluates human attitudes towards deer and options for non-lethal management. Minnesota is unique in that support of regulated lethal deer management is strong among suburban residents, but there is a paucity of guidelines for effective suburban archery hunting programs. This research will develop best management practices for special city archery hunts, including the spatial distribution of hunting pressure, harvest objectives, and the necessary number of issued permits to achieve management objectives. The guidelines established during this research can be implemented to improve harvest management of the special archery hunts throughout the State.

2. Can any of the research or teaching needs described be met without the use of live animals?

No__X__Explain why animals are required.
Yes_____Explain how animals are optional.

The complexity of the processes being studied cannot be duplicated or modeled in simpler or alternative systems. When investigating a species' ecology and behavior, it is essential to observe the animals in the wild and how they respond under natural conditions.

3. List any off-campus sites where animal use/monitoring is to be conducted. If the project requires the animals to be housed at a particular site, describe how the site is compliant with the Animal Welfare Act/IACUC guidelines.

Not Applicable

V. Describe all procedures to be performed on animals and their purpose. Surgical procedures must be fully described, including post-operative care where appropriate.

1. For each distinct procedure, describe the manipulations that will be performed in the order in which they will be performed. Procedures that will be performed after the animal has been killed need not be described.

Deer Capture and Handling

We will capture 30-40 adult white-tailed deer during each winter (January–March) of 2024 and 2025 using drop nets and netted cage traps (Clover trap; Schemnitz et al. 2012). Drop nets are a 5m × 5m square net suspended by a pole at each corner. The net is secured by an electrical current powering weighted magnets attached to each pole. Deer are baited under the center of the suspended net using whole kernel corn. When a target animal moves under the net, the researcher on site presses a button on a remote controller that cuts power to the weighted magnets, which then drops the net over the top of the animal. Researchers on site quickly restrain and sedate the animal. When not active, weighted magnets can be secured to the poles using bolts to prevent the net from falling. Clover traps are passive netted cage traps approximately 1m tall × 1m wide × 2m long. On the front end of the trap is a sliding, netted door attached to a release mechanism. The release mechanism is attached to a trip wire running through the back of the trap. Deer are attracted to the back of the trap using whole kernel corn, and trip the trigger release with their head/limbs while feeding. The door slides close and traps the animal in the cage. Clover traps are secured to either a nearby tree or staked directly into the ground. Researchers check traps twice daily (early morning, late afternoon). When an animal is in a trap, a researcher will quickly enter the trap to restrain and sedate the animal. When not active, Clover traps can be locked open to prevent the door from closing and an animal from being captured.

We will sedate all captured deer using an intramuscular injection of either xylazine or medetomidine. We will place a blindfold over the eyes of each deer to minimize stress during capture. Each deer will receive 2 white plastic button cattle ear tags (3 cm diameter) with black numbers (Allflex USA Incorporated, Dallas, TX, USA) including a unique ID number and a phone number to contact researchers. We will record measurements of shoulder height, hind limb length, total length, chest girth, and estimate the age of each deer using a combination of tooth replacement and wear and body characteristics to increase accuracy of age estimates. We will affix females with a 700 g iridium GPS collar with an 8-hour mortality sensor. We will not place transmitters on any animal when it is estimated the transmitter weight will exceed 2% of the animal's total body weight (generally animals weighing <35 kg). We will reverse all deer with an intramuscular injection of tolazoline, yohimbine, or atipamezole (Kreeger et al. 1986). We will monitor all vital signs (body temperature, heart rate, and respiration) until the animal leaves the capture site under their own power. Collars will remain on the animals until their death or the completion of the study (January 2026), at which time any remaining collars can be remotely removed from the animals. The outlined methods follow the American Society of Mammalogists' guidelines for mammal care and use in research (Sikes 2016).

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

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

Sikes, R. S. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

2. Will the animals be subjected to any of the following?

Use in a previous study? Yes____ No _*X*_
Use in a future study? Yes____ No_ *X*_
Transfer to another investigator? Yes____ No_ *X*_

If yes, please specify and note that prior Committee approval is required for each of the above.

3. List any building and room outside of the BSU animal quarters where animals will be housed longer than:

12 hours___________ 24 hours_________ If none: so state *None*

VI. Describe the animal handling qualifications and training of the personnel who will be involved in this project.

Dr. Haus is a Certified Wildlife Biologist® with over 13 years of experience capturing and handling wildlife for research. He is certified through Safe-Capture International, Inc. (now 'Global Wildlife Resources, Inc.'), and regularly teaches workshops on animal capture methodology and chemical immobilization at the national conference for The Wildlife Society. He has captured and released >1,000 wild animals for research purposes, primarily white-tailed deer. Dr. Haus will be responsible for training all personnel on this project and managing all aspects of the research.

Dr. Terry Kreeger retired as the State Wildlife Veterinarian of the Wyoming Game and Fish Department. He holds a B.S. in Veterinary Science, an M.S, in Wildlife Biology, a Ph.D in Wildlife Management, and a D.V.M. degree. He is an adjunct professor at the University of Wyoming (Veterinary Sciences) and the University of Minnesota (Fisheries, Wildlife, and Conservation Biology). His research interests include wildlife capture and anesthesia, physiology and behavior, and wildlife diseases. He has captured wildlife and trained others to capture wildlife throughout North America and in Russia, Africa, and Asia. He authored the textbook 'Handbook of Wildlife Chemical Immobilization'. Dr. Kreeger will serve as a consultant on all animal capture, immobilization, and handling procedures for the project.

Dr. Brian Hiller is a professor of wildlife biology at Bemidji State University and will serve as a co-investigator on the project. He has previously managed state-funded research projects in the greater Bemidji area involving wildlife capture and monitoring.

Raena Kemna will be the graduate student responsible for coordinating field work and supervising deer capture events. She holds a B.S. in Fisheries, Wildlife, and Conservation Biology with a minor in Wildlife Care and Handling from the University of Minnesota. She has 2 years of experience capturing and collaring white-tailed deer for research while employed with the Minnesota Department of Natural Resources. Raena will be trained in all aspects of the project by Dr. Haus.

Undergraduate Field Technicians – Several Bemidji State University undergraduate students majoring in Wildlife Biology will be employed as seasonal technicians. Technicians will assist with deer capture and monitoring under the direct supervision of either Dr. Haus or the graduate student. All technicians will be trained by Dr. Haus.

VII. Assurance that analgesic, anesthetic, and tranquilizing drugs will be used where indicated and appropriate to minimize discomfort and pain to animals.

1. Check a, b, or c below and give justification below:

_____a. The procedures to be performed on animals do not involve pain or distress to the subject animals (excluding that caused by venipuncture).

__*X*__b. The procedures to be performed do involve pain, and/or anesthetic, analgesic, or tranquilizing drugs will be used throughout the entire course of the project to alleviate pain or distress including post-operative and post-procedure care. The drugs, dosages (drug amount/body weight) and routes of administration are as follows:

We will sedate captured animals using an intramuscular injection of either xylazine hydrochloride, medetomidine, or dexmedetomidine. When animal handling is complete, we will administer an intramuscular injection of a chemical antagonists for the initial drug; either tolazoline, yohimbine, or atipamezole. All injections will be placed in the hind quarter (rump) on alternating sides. Dosages are listed below.

- *3 mg/kg xylazine; antagonize with 0.2 mg/kg yohimbine or 2.0 mg/kg tolazoline or 0.3 mg/kg atipamezole*
- *0.2 mg/kg medetomidine; antagonize with 1.0 mg/kg atipamezole*
- *mg/kg dexmedetomidine; antagonize with 1.0 mg/kg atipamezole*

Several drug options are necessary due to current supply chain issues. All drugs listed are safe, effective, and commonly used to immobilize white-tailed deer for research purposes.

_____c. Pain and/or distress will be involved for subject animals but drugs will not be used because they interfere with protocol, and justification for non-use is described below.

2. Check each statement that applies to this project:

____a. Terminal (animals are killed under anesthesia without regaining consciousness).

__*X*__b. Survival (animals regain consciousness after anesthesia).

If checked, Federal law [AWA 2.31(d)] requires that aseptic technique be used. Please initial here__JMH___.

____c. Multiple survival (individual animals may undergo more than one survival surgery). If checked, provide a detailed scientific justification as required by Federal Law.

2. Where will the surgery be performed?

Animal capture and handling for this project will not involve surgery.

4. Who will perform the surgery (training of this individual should be addressed in question VI)?

Not applicable

5. What post-procedural measures will be taken to minimize discomfort and what monitoring will be done? How will post-procedural events be humanely handled?

Not applicable

6.Will paralytics be employed? Yes___ No__X__.
If yes, how will the animals be monitored to insure adequate anesthesia?

7. Where will the monitoring be performed?

Not applicable

8. Who will perform the monitoring?

Not applicable

9. Will food and/or water be withheld? Yes___ No_X-_.

If yes, what will be the duration, how often will a single animal be restricted, and what will be the duration between restrictions? Describe the monitoring that will be done to assure that adverse effects do not occur.

10. Will the animals be restrained by chairs, tethers, stanchions, metabolism cages, etc.? No___ Yes_X__

a. Method of restraint:

On occasion, captured animals may be hobbled by using a tether to secure their hind or forelimbs together near the hooves. When an animal is kicking excessively before immobilization, hobbling is used to ensure the safety of the personnel and animal.

b. Duration of restraint:

The duration of the capture event not to exceed 1 hour. Hobbles are removed prior to administration of the chemical antagonist as soon as it is safe to do so.

c. Frequency of restraint:

During live capture events, as frequently as necessary.

d. How frequently will the animal be observed during restrain?

Continuously.

e. Where restraint will occur:

At the site of capture.

11. Will hazardous agents (i.e. infectious agents, carcinogens, toxic chemicals, etc.) or radioactive material be present in the animal facility?
No _X___ Yes___
a. Identify hazardous agent or material:
b. Exposure route:
c. Exposure dose:
d. Exposure duration:
e. Will the agent be excreted? No____ Yes____
in urine___ in feces___ exhaled___
f. Describe where the animals will be housed during and after exposure:
g. Probable animal health effects

NOTE: Radioactive materials are currently not allowed on the BSU campus, but may need to be detailed if working with an off-site collaborator.

VIII. Euthanasia techniques

List by species and describe method to be used, including drug, type, dose, and route of administration:

species	method
White-tailed deer	*Penetrating captive bolt stunner applied to the cranium*

A penetrating captive bolt stunner uses blank 9mm cartridges to rapidly propel a bolt through the animal's cranium into the brain to induce sudden loss of consciousness and subsequent death. Penetrating captive bolts are described as a practical and acceptable method of euthanasia for ruminant animals (including white-tailed deer) by the American Veterinary Medical Association. The method is appropriate for this research because it is effective, safe for the operator, discreet in a suburban setting, and does not fire a projectile. Animals euthanized prior to chemical immobilization can also be disposed of without risk of contamination to the environment or scavengers. All personnel working in the field will be trained in the use of a penetrating captive bolt by Dr. Haus, however only the field supervisors will be responsible for euthanizing animals.

Euthanasia of captured animals will only be performed if, at the discretion of the supervisor in the field, an animal is injured prior to or during the capture process in a manner that would cause undue pain or distress if released into the wild. The capture methods outlined in this proposal are considered safe and effective, and euthanasia should very rarely be necessary.

IX. Claim of confidentiality

Contents of this report are available for public disclosure unless confidentiality is requested by the investigator and it is adequately shown by the investigator that the protocol discloses unpublished data or research procedures for which copyright or patent is being sought.

__*X*__ I do not claim confidentiality

______ I claim confidentiality; justification is attached

X. Assurance:

The undersigned is familiar with the AWA and the PHS Policy on Humane Care and Use of Laboratory Animals by Awardee Institutions, the NIH Guide for the Care and Use of Laboratory Animals and the University Guidelines, and agrees to abide by the Principles for the Utilization and Care of Vertebrate Animals Use in Testing, Research, and Training contained in this document. I assure that I will obtain the institutional care and use committee (ICAUC) approval prior to significant changes in the protocol. I assure that students, staff, and faculty on the project are qualified or will be trained to conduct the project in a humane and scientific manner. Any change in the care and use of animals involved in this protocol that would affect their welfare will be promptly forwarded to the ICAUC for review. Such changes will not be implemented until the Committee's approval is obtained. Animals will not be transferred between investigators without prior approval.

(Signature of Principal Investigator) 7/27/23 (Date)

XI. Approval

APPROVAL NUMBER __24-01__
DATE___7/26/2023_
EXPIRATION DATE___6/30/2026_____

APPROVAL CATEGORY: A______ (No pain or distress involved)

B___X___ (Drugs used to alleviate pain and/or distress)

C______ (No drugs used for pain and/or distress)

SPECIAL CONDITIONS: NONE_____X___ REMARKS ATTACHED________

Randy Westhoff (Approval Signature for Committee) 7/26/2023 (Date)

ACADEMIC AFFAIRS JUL 27 2023 BEMIDJI STATE UNIVERSITY