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Effects of Fertility Control on the Movement Ecology of White-Tailed Deer

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LIST OF SYMBOLS AND ABBREVIATIONS

AKDE	Autocorrelated kernel density estimate
BAM	Butorphanol, azaperone, medetomidine
CI	Credible interval
CTSD	Continuous-time speed and distance
CTSP	Continuous-time stochastic process
DVC(s)	Deer-vehicle collision(s)
ESS	Effective sample size
GAM(s)	Generalized additive model(s)
GPS	Global positioning system
HGAM(s)	Hierarchical generalized additive model(s)
HGAMLS	Hierarchical generalized additive model for location and scale
HR	Home range
NYC	New York City
OUF	Ornstein-Uhlenbeck-Foraging
REML	Restricted maximum likelihood
RSPP	Rockefeller State Park Preserve
SI	Staten Island
SI units	International system of units
SLD	Straight-line displacement
VeDBA	Vectorial dynamic body acceleration
WVCs	Wildlife-vehicle collisions

ABSTRACT

This doctoral thesis explores the effects of fertility control on the movement ecology of white-tailed deer (*Odocoileus virginianus* Zimmermann). Deer populations may become abundant in human-dominated landscapes, taking advantage of anthropogenic resources and the lack of natural predators. This abundance poses increasing ecological, economic, and social challenges globally. As human activities expand, conflicts between deer populations and human interests intensify, manifesting in issues such as deer-vehicle collisions (DVCs), the spread of tick-borne illnesses, and habitat degradation. While traditional population control methods, such as controlled hunting, have proven effective, they are often impractical in suburban and urban settings. Non-lethal fertility control methods, including vasectomy, ovariectomy, and immunocontraceptive vaccines, present alternative solutions that may circumvent the need for lethal management. However, these methods induce physiological changes that may alter movement behavior. This thesis aims to bridge the knowledge gap concerning how fertility control interventions impact the movement behavior of white-tailed deer.

Chapter 2 lays the groundwork by addressing a critical methodological issue often overlooked in studies of ecological movement responses — specifically, the relationship between mean speeds and diffusion rates using continuous-time speed and distance estimation techniques. Accurate modeling of an animal's speed and distance traveled can be critical for interpreting behavior, yet ecological data often are too coarse, or the location error is too great to resolve these measures. Diffusion rates, in contrast, can be estimated using continuous-time models at even coarser sampling intervals. To examine this relationship, a regression analysis was conducted to estimate the correlation between mean speed and diffusion rate, accounting for uncertainties in both variables. Results indicated a

strong, sublinear correlation between mean speed and diffusion rate, with a 1% increase in diffusion rate in my focal species predicting a 0.40% increase in mean speed (99% CI: 0.38–0.42%). Sampling intervals were progressively coarsened to assess the robustness of these estimates, and simulations were run using known true values to further evaluate the relationships. Across all sampling intervals, diffusion rates consistently remained substantially more accurate and precise than mean speed estimates, even when speed estimation was not possible. These findings establish diffusion rates as a more reliable and robust metric for linking movement to behavior across a wider range of datasets, thereby providing a foundation for the subsequent analyses of fertility control effects on deer movement in Chapters 3 and 4.

Chapter 3 evaluates the effects of a large-scale vasectomy program on the movement behavior and activity of free-ranging white-tailed deer. This study leverages an existing fertility control program implemented on Staten Island, New York, USA, where vasectomies were performed on over 97% of antlered males, resulting in a dramatic reduction in fawning (approximately 95%). This intervention effectively left most female deer unbred, leading to multiple estrous cycles throughout the breeding season. Concerns have been raised that the additional estrus periods may extend breeding activity, potentially leading to decreased body condition and increased incidence of DVCs. To investigate these potential consequences, biologging devices were deployed on a total of 158 deer, across two sites: the treatment site on Staten Island and a control site at Rockefeller State Park Preserve in Pleasantville, NY, USA. The dataset included global positioning system (GPS) and accelerometry data from 84 females and 40 males. Advanced analytical methods, including continuous-time movement models and Hierarchical Generalized Additive Models (HGAMs), were applied to assess deviations in space use, movement patterns, and activity levels between treated and untreated groups. The results indicate that, contrary to initial concerns, the vasectomy program did not induce behavioral or social changes likely to negatively affect population health or safety during the study period.

Chapter 4 investigates the effects of ovariectomy, an alternative fertility control method, on female white-tailed deer movement behavior. Ovariectomy induces anestrus, thereby preventing treated females from entering estrus, and eliminating estrous cycles and associated behaviors. Concerns have been raised that the absence of reproductive behavior could lead to altered movement patterns that might negatively impact body condition or increase the likelihood of DVCs. This chapter employs a treatment-control design using IoT-based telemetry data from 20 free-ranging female deer who were part of a management program in South Euclid, Ohio, USA. Ten individuals had undergone ovariectomy, while the remaining ten served as untreated controls. To assess the impact of ovariectomy on movement ecology, a 7-day moving window approach was applied to analyze diffusion rates, home-range size, and excursivity. Consistent with the findings from Chapter 3, the analysis revealed no significant differences in movement behavior between the treated and control groups, suggesting that ovariectomy does not introduce behavioral risks that would exacerbate management concerns.

The findings from this thesis provide substantial evidence that fertility control methods, specifically vasectomy and ovariectomy, do not induce significant changes in the movement behavior of white-tailed deer at the time scales investigated. These results support the viability of non-lethal fertility control as a management strategy for addressing abundant deer populations in urban and suburban environments. By ensuring that such methods do not lead to unintended behavioral consequences, this work contributes to the development of new approaches to wildlife management in human-dominated landscapes.

CHAPTER 1. INTRODUCTION AND METHODOLOGICAL APPROACHES

Wildlife populations have become increasingly abundant in human-modified landscapes, posing complex ecological, economic, and social challenges (Garrott et al., 1993; DeStefano & DeGraaf, 2003; Gortázar, 2006). This global phenomenon is more evident in large generalist mammals, such as ungulates, omnivores, and mesopredators, that have successfully adapted to anthropic or semi-anthropic environments (Garrott et al., 1993; DeStefano & DeGraaf, 2003; Gortázar, 2006). Anthropogenic factors such as land-use changes, predator extirpation, supplementary food availability (e.g., landscaping plants, agricultural fields, refuse), and shifting human-wildlife interactions have contributed to these changes (Distefano, 2005; Carpio et al., 2020). In many regions, natural predators have been extirpated or remain at very low densities, removing a key check on herbivore populations (DeStefano & DeGraaf, 2003; Carpio et al., 2020). At the same time, human-altered landscapes provide abundant food and refuge. Ornamental plantings, gardens, irrigated lawns, and agricultural crops serve as year-round food sources, while parks and greenbelts offer ample cover (DeStefano & DeGraaf, 2003). Human hunting pressure is often limited or absent in suburban settings due to firearm restrictions and local ordinances, allowing ungulates and other wildlife to survive at much higher rates (DeStefano & DeGraaf, 2003). This combination of few predators, plentiful year-round forage, protective cover, and minimal hunting creates ideal conditions for certain species' local populations to exceed their habitat's social and ecological capacity.

1.1 Wildlife abundance in anthropogenic environments

Traditionally, wildlife abundance has been defined in terms of populations reaching or exceeding the ecological carrying capacity of their habitat (Caughley, 1981). However, in human-dominated landscapes, an abundant population is often defined by social carrying capacity – or impact on human communities, infrastructure, and ecosystem function rather than solely on resource limitations (Caughley, 1981; Côté et al., 2004). Abundant populations of large herbivores can exert significant pressure on ecosystems. Excessive browsing and grazing alter plant community composition, reduce biodiversity, and hinder forest regeneration (Swihart & Conover, 1988; Tilghman, 1989; Côté et al., 2004). These cascading effects can reduce habitat quality for other wildlife species and disrupt trophic interactions. By selectively feeding on palatable herbs, shrubs, and tree seedlings, dense deer herds reduce plant diversity and hinder forest regeneration (Côté et al., 2004). Ecological effects include the decline of understory-nesting birds and other wildlife dependent on intact vegetation structures (Côté et al., 2004). In many forests, sustained heavy browsing creates "browse lines" of missing foliage and shifts the plant community toward less preferred or invasive species, changes that may persist for decades (Côté et al., 2004).

Beyond ecological impacts, there are significant economic and social costs to having too many large herbivores in close proximity to people. Wildlife-vehicle collisions are a well-documented hazard in suburban areas, causing human injuries, fatalities, and costly property damage (Conover et al., 1995; Bissonette et al., 2008; Huijser et al., 2009). In the United States, such collisions collectively result in hundreds of millions of dollars in damage annually (Conover et al., 1995; Bissonette et al., 2008). For instance, over a five-year period in Utah, ~13,000 deer-vehicle collisions (DVCs) incurred an estimated 45 million USD in total costs (including vehicle repair, medical expenses, and lost wildlife value; Bissonette et al., 2008). Increased wildlife densities elevate the frequency of vehicle collisions, structural damage to residential and agricultural areas, and interactions that raise public safety risks (Conover et al., 1995; DeNicola & Williams, 2008; Bissonette et al., 2008).

High ungulate densities also facilitate the transmission of diseases (Kilpatrick et al., 2014; Telford, 2017). While tick ecology is complex, deer are known to be a primary host for adult blacklegged ticks (*Ixodes scapularis)*, which transmit Lyme disease to humans; studies show human Lyme cases are positively correlated with local deer abundance (Garnett et al., 2011; Kilpatrick et al., 2014). Likewise, dense herds can amplify the risks of chronic wasting disease (CWD) spread among cervids, a management concern wherever CWD occurs (Jennelle et al., 2014). Beyond these measurable impacts, public tolerance for wildlife quickly erodes when animals are seen causing accidents, agricultural losses, and neighborhood damage. In some communities, wildlife that was once appreciated as a part of nature has become regarded as pests due to eating landscaping, devouring gardens, and even "threatening human health and safety" at high densities (DeStefano & DeGraaf, 2003; Côté et al., 2004).

1.2 White-tailed deer ecology

Historical population trends and recovery in the United States

White-tailed deer (*Odocoileus Virginianus* Zimmerman; hereafter deer) were once one of the most abundant large mammals in North America, but by the late 19th and early 20th centuries, unregulated market hunting and widespread deforestation led to drastic population declines (Halls, 1984). Historical records suggest that deer populations plummeted to an estimated 300,000 individuals nationwide by the early 1900s—a nearly 99% reduction from pre-colonial levels (McCabe & McCabe, 1984; VerCauteren, 2003). This decline was more severe in the eastern United States, where deforestation for farming and logging added to hunting pressures, leaving only small, isolated groups of deer in pockets of forested habitat (Halls, 1984; Ellingwood & Caturano, 1988).

In response to this steep decline, concerted conservation efforts were initiated in the early 20th century to help the deer population rebound. Establishing hunting regulations, protective legislation such as the Lacey Act of 1900, and creating state wildlife agencies helped curb further losses (Leopold et al., 1947; Halls, 1984). By the mid-20th century, extensive restocking programs were launched, reintroducing deer to areas where they had been extirpated (Halls, 1984). At the same time, large-scale land-use changes, including the forest regrowth on abandoned farmlands, created new habitats that supported population recovery (Alverson et al., 1988). These combined efforts led to rapid and widespread population expansion. As an example, on the George Reserve in Michigan, the species' remarkable reproductive capacity was demonstrated, where a population of only six individuals introduced in 1928 increased to 162 within five years, and a later reintroduction of ten deer expanded to 212 in the same timeframe (McCullough, 1979). This exponential growth capacity, improved habitat conditions, and regulated harvest facilitated the deer's return to landscapes across North America. Today, populations have rebounded to historic or even supra-historic densities, with estimates exceeding 30 million individuals in the U.S. alone (VerCauteren, 2003).

Habitat and feeding ecology

Deer are generalist herbivores with a highly adaptable diet and habitat preference (Hewitt, 2011, pp 188-189). They occupy diverse environments across North America – from forests and woodlots to fields, swamps, and semi-urban areas – and especially favor habitats with a mix of cover and open foraging areas (Hewitt, 2011, pp 12-33; Nugent et al., 2011; Urbanek & Nielsen, 2013). Deer are primarily browsers, feeding on the leaves, twigs, and buds of woody plants, but they also graze on herbs and grasses and readily consume hard and soft mast (acorns, nuts, fruits) when available (Fulbright & Ortega-Santos, 2013). This flexibility allows them to exploit whatever foods each season offers: in spring and summer, they focus on tender greens, forbs, and agricultural crops; in autumn, they feed on acorns, corn, and other high-energy foods to build fat reserves; and in winter they subsist on woody browse like saplings and shrubs once other food is scarce (Hewitt, 2011, pp 80-89; Fulbright & Ortega-Santos, 2013). Their multi-chambered ruminant stomach enables them to digest a wide variety of vegetation and to switch diets with the seasons by adjusting their gut microbes (Hewitt, 2011, pp 80-89; Fulbright & Ortega-Santos, 2013). Notably, the items deer prefer are most abundant in disturbed or edge habitats rather than deep mature forests, so deer densities tend to be highest in "edge" environments where forests meet fields or suburban development (Hewitt, 2011, pp 602-603; Laurent et al., 2021). These edge-rich suburban landscapes provide both the cover and the nutrition deer need, underpinning their success in human-altered areas (Hewitt, 2011, pp 602-603; Curtis, 2020).

Predator avoidance behavior

Deer have evolved highly effective anti-predator behaviors shaped by natural selection in response to predation pressure from large carnivores, including wolves (*Canis lupus*), cougars (*Puma concolor*), and bobcats (*Lynx rufus*) (Lingle & Wilson, 2001; Hewitt, 2011, pp 148-149). These behaviors persist even in regions where predators have been extirpated, influencing movement patterns, habitat selection, and vigilance levels (Laundré et al., 2001; Cherry et al., 2015). Deer possess acute olfactory, auditory, and visual senses that aid the detection of predators at a distance (Hewitt, 2011, pp 63-64). They rely heavily on their sense of smell to detect predators and human activity and also have exceptional hearing, with large swiveling pinnae that enhance their ability to sound sources (Hewitt, 2011, pp 64-65). Their vision is specialized for low-light conditions, enabling them to detect movement and silhouettes at dawn and dusk—when many predators are most active (Jacobs et al., 1994).

Upon detecting a threat, deer will often freeze to avoid visual detection, but if the threat approaches, they alert other deer with a loud snort and startle the predator (Hirth & McCullough, 1977; Stankowich & Coss, 2006). Once a deer decides to flee, it initiates a bounding escape run to gain distance quickly from a threat. The characteristic tail flagging behavior—raising the white underside of the tail—is thought to serve multiple functions, including signaling danger to other deer, confusing predators, or deterring pursuit (Caro, 1995). Group living provides an additional anti-predator advantage with the many-eyes effect, where individuals scan for threats while others feed (Lima, 1995). If one deer detects danger, it will warn others, prompting an immediate flight response (Hirth & McCullough, 1977).

Deer select habitats that optimize food availability and safety, frequently favoring areas with dense escape cover (Kie et al., 1999). This trade-off is evident in crepuscular activity patterns, where deer feed in more open areas during low-light periods while remaining near forested refugia for rapid escape (Kunkel & Pletscher, 2001). Studies indicate that deer adjust their movement patterns and space use in response to predator risk, increasing vigilance and modifying habitat use in areas with high carnivore activity, even when food resources are abundant (Creel et al., 2005; Gulsby et al., 2018).

Newborn fawns rely on crypsis and immobility rather than fleeing (Lent, 1974). Their reddish-brown coat with white spots camouflages them among sun-dappled vegetation (Estes, 1972, p 178), and during their first weeks of life, fawns lie still and emit minimal scent to avoid detection (Ozoga et al., 1982). Mothers hide fawns separately and return briefly to nurse, reducing the risk of attracting predators (Lent, 1974).

Breeding behavior and strategies

Deer exhibit a polygynous mating system in which a single male may breed with multiple females during the breeding season (DeYoung et al., 2009). Typically, the breeding season occurs in the fall, with a distinct peak between October and November in temperate regions of North America (Verme, 1965; Hewitt, 2011, pp 330-331). Exact timing can be variable and depends on latitude and environmental conditions (Verme, 1965; Hewitt, 2011, pp 330-331). Males and females exhibit distinct reproductive behaviors during this period, with males increasing movement and competition for access to receptive females, while females undergo a short, highly synchronized estrus period (Hirth, 1977; Webb et al., 2010).

Male deer experience a steep increase in testosterone levels during the breeding season that triggers various behaviors, including increased roaming activity that can lead to increased levels of DVC in suburban environments (Bubenik et al., 1982; Gomes et al., 2021). Males do not form harems but instead adopt a roving mate-search strategy, moving extensively to locate receptive females (Webb et al., 2010; Foley et al., 2015). Studies using GPS telemetry have documented that males expand their home range size and increase movement activity and daily movement distances during the breeding season, often making excursions beyond their typical home range to seek receptive females (Webb et al., 2010; Karns et al., 2012; Foley et al., 2015; Airst et al., 2020). This movement strategy is necessary because females in estrus are scattered across the landscape, and each female is only receptive for a short window (Knox et al., 1988; Hölzenbein & Schwede, 1989; DeYoung et al., 2009). The risk of this strategy in suburban and urban environments is an increase in DVCs and other human-wildlife interactions (Allen & McCullough, 1976; Sudharsan et al., 2006; McShea et al., 2008; Muller et al., 2014).

During the breeding season, competition among males for estrus females is intense. Males engage in ritualized displays, scent-marking, and fighting to establish breeding rights (Hewitt, 2011, pp 330-332). Studies show a positive correlation between body mass, antler size and reproductive success, indicating that mature, larger-bodied males tend to sire the majority of offspring (DeYoung et al., 2009). However, despite this known hierarchy, subordinate males often adopt alternative mating tactics and can increase their reproductive success (DeYoung et al. 2009). Males typically remain with estrus females for 24-48 hours, keeping them from other competing males until copulation occurs (Hewitt, 2011, p 332). After mating, the male will search for other receptive females, potentially breeding with multiple females in a single breeding season (DeYoung et al., 2009). Genetic studies have confirmed that a single female's litter (usually 1–2 fawns) may have multiple sires if she mates with more than one male during her estrus period (DeYoung et al., 2002).

Female deer typically reach sexual maturity at around 1.5 years and undergo seasonal estrous cycles, breeding annually in autumn (Verme, 1965; Hewitt, 2011, p 332). Unlike males, who remain reproductively active throughout the breeding season, females enter estrus for only ~24-48 hours (Knox et al., 1988; McShea et al., 1997). If a female is not bred during her initial estrus period, she will return to estrus approximately every 28 days until conception occurs or the breeding season ends (Knox et al., 1988; McShea et al., 1997). In populations with skewed sex ratios or low densities, some females may remain unbred and undergo multiple estrous cycles. This can result in an extended breeding season that continues into late winter (Verme & Ozoga, 1981) and can impact population dynamics and management, as prolonged breeding seasons can delay fawn births and impact juvenile survival rates (Verme, 1965).

During the breeding season, female movement patterns are less pronounced than those of males. Some studies suggest that females may increase their home range size or movement rates in the breeding period, thus facilitating encounters with males, particularly in environments with low densities or skewed sex ratios (Ozoga & Verme, 1975; McShea et al., 1997; D'Angelo et al., 2005; Hernandez et al., 2006; Kolodzinski et al., 2010; Webb et al., 2010; Sullivan et al., 2017). Ozoga & Verme (1975) noted increased activity in penned females around the estrus period. When encountering a male, a female's response will depend on her reproductive status. If she is not yet receptive, she may evade or actively rebuff the male – this can lead to chase behaviors frequently seen during the breeding season (Hewitt, 2011, p 332). However, as estrus progresses, the female becomes increasingly tolerant (Hewitt, 2011, p 332). Once a female allows copulation, she does not form a lasting bond with the male. Instead, after mating, she separates and resumes normal movement patterns, with gestation lasting approximately 200 days until fawning in late spring (Verme, 1965).

Deer breeding behavior is characterized by sexual dimorphism in movement and reproductive strategies. Males engage in highly mobile, competitive mate-searching, while females exhibit brief but synchronized estrous cycles, which determine the timing and success of conception. The resulting polygynous structure influences population genetics, dispersal patterns, and reproductive timing, all of which have important implications for wildlife management.

Seasonal variations in movement patterns are largely shaped by reproductive cycles. In females, late gestation and parturition are when the most significant shift occurs. This period is when females isolate from social groups and select secluded, vegetated fawning sites for concealment and predator avoidance (Ozoga et al., 1982; Kie & Bowyer, 1999). High-quality sites also offer nearby resources, enabling females to minimize movement while meeting nutritional needs (Ozoga & Verme, 1986). Home range size contracts markedly prior to parturition, with females confining activity to a small core area (D'Angelo et al., 2005; Webb et al., 2010; Wright et al., 2021). This strategy supports fawn survival by limiting detection (Grovenburg et al., 2010). As fawns gain mobility, maternal ranges expand, and fawns begin accompanying their mothers (Bertrand et al., 1996; D’Angelo et al., 2005; Wright et al., 2021). By late summer, movement returns to pre-fawning levels, and females shift their behavior again as the breeding season nears (D’Angelo et al. 2005).

Male movement is most variable during the breeding season, with elevated testosterone driving long-range excursions and increased activity (Webb et al., 2010; Karns et al., 2012; Foley et al., 2015). Males often leave established home ranges to locate females in estrus, with 63% in one study making excursions (Karns et al., 2012). Within core ranges, daily travel distances also increase as males revisit areas with known females (Foley et al., 2015). These energetically costly behaviors contribute to post-breeding season weight loss and subsequent reduction in movement as males recover (Hewitt, 2011, pp 56-57; Foley et al., 2015; Karns et al., 2012).

Social structure and dispersal

Deer exhibit a matrilineal social structure, with female family groups forming the core social unit outside the breeding season (Hawkins & Klimstra, 1970). These groups typically include an adult doe, her fawns, and often yearling females, with multiple generations sometimes forming stable, kin-based networks within traditional home ranges (Hirth, 1977). Dominance hierarchies exist within female groups but are generally non-aggressive, except around parturition, when maternal females may defend fawning areas (Ozoga et al., 1982). Matrilineal groups may form larger aggregations in winter, particularly in northern regions where food and cover are limited, before dispersing in spring (Hawkins & Klimstra, 1970; Porter et al., 1991).

Male deer are more transient, forming non-territorial bachelor groups in late winter composed of similarly aged individuals (Hawkins & Klimstra, 1970; Hewitt, 2011, pp 311-314). These groups persist through summer and offer benefits such as predator avoidance and social learning (Hewitt, 2011, pp 311-314), though dominance hierarchies are subtly maintained. As testosterone rises in early autumn, bachelor groups dissolve, and males become solitary and antagonistic in pursuit of mates (Webb et al., 2010; Foley et al., 2015). During the rut, dominant males exclude subordinates from females in estrus (DeYoung et al., 2009), and some may reform small groups post-breeding, while others remain solitary (Hewitt, 2011, pp 311-314).

Juvenile dispersal is a key component of population dynamics, especially among males. Young males typically disperse between 6 months and 1.5 years of age, often in spring or early fall (Nixon et al., 2007). Dispersal distances vary widely; in the Mid-Atlantic, 44–68% of yearling males dispersed, averaging 4–10 km, with some exceeding 100 km (Hewitt, 2011, pp 152-153). In contrast, females' dispersal rates are more variable, with 70–90% remaining within or near their mother's range (Hawkins & Klimstra, 1970; Nixon et al., 2007). Dominance influences access to resources and reproductive success in both sexes: dominant females outcompete younger individuals for food and fawning sites (Ozoga et al., 1982), while dominant males control mating access during the breeding season (DeYoung et al., 2011).

Ecological success in suburban landscapes

Although initially a species associated with rural and forested landscapes, deer have successfully adapted to suburban and urban environments, where populations persist at high densities in many regions (DeNicola et al., 2000; Kilpatrick & LaBonte, 2003). Several ecological and anthropogenic factors have facilitated this expansion. The widespread reduction of natural predators, particularly the extirpation of wolves (*Canis lupus*) and cougars (*Puma concolor*), has eliminated top-down pressure that historically helped regulate deer numbers (Ripple & Beschta, 2005). In addition, suburban and exurban development has created edge-rich landscapes composed of fragmented forests, manicured lawns, and gardens, which provide year-round food resources and protective cover (Swihart et al., 1995). Additionally, hunting restrictions in suburban areas due to firearm discharge regulations, limited hunter access, or social opposition reduce human-mediated mortality (Kilpatrick et al., 2007; Williams et al., 2013), and allow deer populations to grow largely unchecked.

Suburban deer populations frequently reach densities that exceed 103–258 individuals per square kilometer, well above densities observed in natural landscapes (McShea et al., 1997; DeNicola et al., 2008). High-density deer populations contribute to DVCs, which result in significant economic costs and safety concerns, with over 1 million DVCs occurring annually in the United States (Huijser et al., 2009). Further, heavy browsing pressure by deer is known to alter native plant communities, reduce forest regeneration, and contribute to biodiversity declines, as seen in studies where increased deer densities correlate with reductions in understory vegetation and bird populations (Côté et al., 2004). Additionally, deer serve as a primary host for blacklegged ticks (*Ixodes scapularis*), which are vectors of Lyme disease and other tick-borne pathogens, exacerbating public health concerns in high-deer-density areas (Kilpatrick et al., 2014; VanAcker et al., 2019). Given the ecological and societal challenges associated with high suburban deer densities, managing populations in these areas remains a priority for wildlife agencies and local governments.

1.3 Managing abundant wildlife and fertility control

Managing abundant wildlife in suburban and urban settings

Managing abundant wildlife in suburban and urban settings is challenging (Decker & Chase, 1997). Traditionally, population control has relied on lethal removal—typically recreational hunting or culling by trained sharpshooters—to reduce numbers (DeNicola et al., 2000; Nugent et al., 2011). While effective in many contexts, lethal control is often impractical or socially contentious in suburban and urban settings due to legal restrictions, public opposition, logistical constraints, and ethical concerns (Loker et al., 1999; Valente et al., 2019; Desrochers et al., 2025). Safety concerns and local regulations often prohibit the discharge of firearms near homes and roads, limiting hunting opportunities (DeNicola et al., 2000). Equally significant is public opposition: suburban residents are frequently uncomfortable with or actively opposed to lethally removing wildlife in their neighborhoods (Desrochers et al., 2025). As a result, wildlife agencies must balance biological needs with public values. In many cases, lethal methods alone are not feasible or socially acceptable in suburban environments (DeNicola et al., 2000). This has spurred interest in non-lethal management tools that can curb population growth and are perceived to be humane (Fagerstone et al., 2010; Asa & Moresco, 2019).

Approaches such as trap-and-relocate, exclosures around gardens, repellents, and road-crossing structures have all been attempted, with mixed success (DeNicola et al., 2000; Beringer et al., 2002; Duka & Masters, 2005; Fagerstone et al., 2010; Wright et al., 2020). Among non-lethal options, fertility control has gained particular attention as a potential long-term solution for urban wildlife problems (Fagerstone et al., 2010; Massei et al., 2014). The promise of fertility control is the ability to gradually reduce birth rates without removing or killing animals, thereby lowering population density over time in a way that might be more palatable to the public (Gray & Cameron, 2010; Fagerstone et al., 2010; Asa & Moresco, 2019). Before committing to such programs, however, assessing their practicality and effects is crucial – both intended and unintended.

The role of fertility control in wildlife management

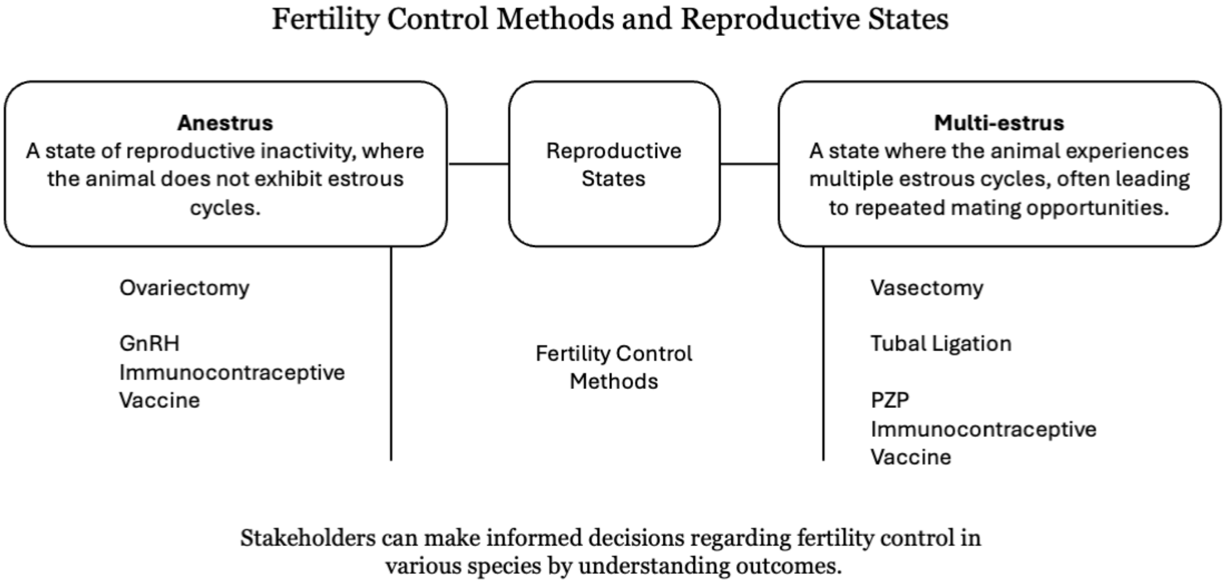
Fertility control aims to reduce reproductive rates and, over time, stabilize or decrease population size. Public support for this approach has been documented in managing suburban populations of deer (*Odocoileus spp.*), wild boar (*Sus scrofa*), and mesocarnivores such as badgers

(*Taxidea taxus*) (Kilpatrick et al., 2007; Massei et al., 2008; Kontsiotis et al., 2020). Fertility control methods include various techniques to reduce reproduction in wildlife populations. These methods fall into two broad categories: surgical sterilization and non-surgical contraception (Asa & Moresco, 2019). Surgical approaches involve physically altering or removing reproductive organs to permanently prevent breeding (Fagerstone et al., 2010; Asa & Moresco, 2019). Common surgical methods include ovariectomy (removal of ovaries) or tubal ligation in females and vasectomy or castration in males (Asa & Moresco, 2019). Such procedures effectively and permanently eliminate an animal's ability to reproduce. For example, ovariectomy of females ensures no future pregnancies, and male vasectomy stops sperm transport while allowing the male to continue mating behavior and supports typical male traits like antler growth. Surgical sterilization has the advantage of being one-time and permanent, but it requires capturing each animal and performing anesthesia and surgery (Boulanger et al., 2012; DeNicola & DeNicola, 2021; NYCDPR, 2024). This makes it logistically demanding and expensive to implement at large scales (Evans et al., 2016).

Non-surgical methods, by contrast, cause temporary infertility without invasive surgery (Asa & Moresco, 2019). The most widely used are immunocontraceptive vaccines that stimulate an animal's immune system to interfere with reproduction (Massei & Cowan, 2014; Asa & Moresco, 2019). Two vaccines have been particularly prominent in ungulate management: those targeting the porcine zona pellucida (PZP), which prevent fertilization by inducing antibodies against egg proteins, and those targeting gonadotropin-releasing hormone (GnRH, e.g. the GonaCon vaccine), which suppress reproductive hormone levels (Asa & Moresco, 2019; Massei, 2023). PZP and GnRH vaccines have been successfully used to reduce fertility in wild ungulates, including deer, horses, and wild boar (Massei, 2023). Other non-surgical options include synthetic hormonal implants or contraceptive bait that prevent ovulation or implantation, and experimental methods like intrauterine devices in animals (Hampton et al., 2015). Non-surgical approaches avoid the risks of surgery and can sometimes be delivered remotely (e.g., darting an animal with a vaccine). However, most contraceptives induce only temporary infertility and require booster doses or re-treatment after a certain period (often 1–5 years) to maintain effectiveness (DeNicola et al., 2000; Gray & Cameron, 2010; Asa & Moresco, 2019). In practice, this means managers must re-capture or re-dart a large portion of the population periodically, which is labor-intensive and can become more difficult over time as animals become more wary (Evans et al., 2016). Each fertility control method comes with trade-offs in terms of cost, duration of effect, and feasibility, and these factors often determine which approach (if any) is suitable for a given situation (Gray & Cameron, 2010; Hampton et al., 2015; Asa & Moresco, 2019; Massei, 2023).

Behavioral and physiological effects of fertility control

Although fertility control is designed to limit reproduction, its behavioral and physiological effects may extend beyond sterility (Fig. 1). Because many contraceptive techniques alter an animal's hormonal state or breeding cycle, they may inadvertently influence behavior, movement, and energetics (Gray & Cameron, 2010; Hampton et al., 2015). For example, immunocontraceptive vaccines like PZP or GnRH can disrupt normal reproductive hormones. Female ungulates treated with PZP continue to cycle in and out of estrus when they would otherwise become pregnant, potentially leading to an extended breeding season with repeated mating attempts (McShea et al., 1997; Gray & Cameron, 2010; Hampton et al., 2015; Massei, 2023). Surgical sterilization methods that leave the gonads intact (such as tubal ligation in females or vasectomy in males) have a similar effect – the animals remain hormonally active but never achieve a pregnancy, causing females to undergo extra estrous cycles and potentially causing breeding behaviors in males and females to continue beyond the usual timeframe (Gilman et al., 2010; Gray & Cameron, 2010; Hampton et al., 2015). This prolonged reproductive behavior may increase energy expenditure as animals spend more time and effort on mating pursuits. Skinner (2007) documented that female deer whose pregnancies were prevented via tubal ligation showed higher rates of DVCs, and non-maternal movement was suggested as a possible cause (Gilman et al., 2010).



Fertility Control Methods and Reproductive States

Stakeholders can make informed decisions regarding fertility control in various species by understanding outcomes.

Figure 1 — Conceptual framework illustrating how different fertility control methods influence reproductive states in wildlife. Methods that induce anestrus (e.g., ovariectomy, GnRH immunocontraceptives) eliminate estrous cycling, while others (e.g., vasectomy, PZP) allow continued hormonal cycling and may lead to a multi-estrus state. Understanding these distinctions helps stakeholders anticipate and manage behavioral and ecological outcomes of fertility control programs.

Likewise, males treated with a GnRH-based contraceptive (which lowers testosterone) showed markedly reduced breeding behavior – treated male deer attempted to mate far less frequently with females than untreated males (Miller et al., 2000). Such changes could alter social dynamics (for instance, reduced fighting among GnRH-treated males or continued harassment of unbred females by multiple males). Apart from breeding behavior, fertility control might influence movements and foraging patterns. If a female does not become pregnant or raise offspring, she may range more widely (because she has no fawns to nurse or hide), or she might need to compensate for hormonal changes by adjusting food intake (Gilman et al., 2010). On the other hand, animals spared from the costs of gestation and lactation could potentially be in better nutritional condition and allocate more time to feeding or resting (Miller et al., 2001). The net effect on activity budgets (how animals divide their time between behaviors like feeding, resting, traveling) is not immediately obvious and could depend on the type of fertility control. For instance, a deer treated with PZP might spend more time moving (searching for mates) during the breeding season. In contrast, a female deer sterilized via ovariectomy might be more sedentary if relieved from reproductive efforts. The key point is that fertility control is not biologically neutral – it can alter hormone levels and behavior, which in turn may affect movement patterns, social interactions, and energetics of the animals (Gray & Cameron, 2010; Hampton et al., 2015; Massei, 2023). Such unintended effects merit careful study because they could influence how effective and desirable a fertility control program is. If treated animals roam farther and increase their chances of vehicle collisions, for example, that would be a serious unintended consequence. Conversely, if contracepted animals maintain normal behavior aside from not reproducing, that would support fertility control as a minimally disruptive management tool.

Efficiency and effectiveness of fertility control programs

Logistical, financial, and biological factors typically impact the feasibility of fertility control programs. Large-scale implementation requires sustained efforts to capture, treat, and monitor individuals over multiple years, often with specialized permitting and veterinary involvement (Boulanger et al., 2012; Evans et al., 2016). Treatment coverage must reach a high proportion of the population to meaningfully reduce birth rates, which is difficult in open populations with high immigration rates (Boulanger et al., 2012; DeNicola & DeNicola, 2021). On the positive side, populations have been successfully controlled through high treatment coverage (Gray & Cameron, 2010; Rutberg et al., 2013; DeNicola & DeNicola, 2021; NYCDPR, 2024). DeNicola & DeNicola (2021) documented an average population reduction of ~45% (29%-56%) after four years of successive treatment with ovariectomy at six suburban study sites with a treatment rate of >90%. This demonstrates that fertility control can yield a meaningful reduction in ungulate numbers if a high enough proportion of animals are treated, and new births are virtually eliminated. Another case involved immunocontraception of wild horses on Assateague Island: with consistent PZP vaccine treatment of most mares, the horse population growth was halted and eventually reversed, preventing further overpopulation (Kirkpatrick & Turner, 2008). However, such successes generally occurred in situations with little to no immigration of fertile animals and where managers achieved very high (80%+) treatment rates in the population (DeNicola & DeNicola, 2021). These conditions are challenging to meet in more open systems. Many suburban deer populations are not closed – animals can disperse into the area from surrounding lands, "replacing" those rendered infertile. If fertile outsiders immigrate faster than treated animals die off, the population may not decline despite contraception efforts (Boulanger et al., 2012). The importance of high treatment coverage is evident in a review by Boulanger et al. (2012): "if much less than about 80% of adult females are treated, deer populations typically continue to grow or only stabilize at best."

Achieving such coverage is labor-intensive and costly because it requires capturing or darting almost every breeding female or male, depending on the treatment type. Consequently, several well-intentioned fertility control programs in suburban communities have struggled. A notable example comes from a six-year study at Cornell University, where researchers sterilized dozens of female deer on campus using tubal ligation and ovariectomy. The deer population did not decrease because large numbers of male deer immigrated (perhaps due to females in estrus or hunting pressure nearby), and a few remaining fertile females could still sustain the herd (Boulanger & Curtis, 2016). A 38% and 79% decrease in total adult females and fawns visible in camera traps was noted. Similarly, trials of the GonaCon GnRH vaccine in free-ranging deer showed reduced fawning by treated females but failed to shrink the overall population without complementary lethal removal, again due to incomplete coverage (Walker et al., 2021). This herd was previously managed using culling (it was stopped due to unpopularity with citizens), and individuals were difficult to capture for treatment as they were wary (Walker et al., 2021).

Beyond biological efficacy, managers have faced practical challenges in the field. Capturing wary wild deer for treatment can be difficult in wooded residential areas, and some individuals inevitably evade treatment (Evans et al., 2016; Walker et al., 2021). Each surgical sterilization can cost hundreds to over a thousand dollars per animal when factoring in staffing, veterinary work, and equipment (Boulanger et al., 2012; Evans et al., 2016). In sterilization programs, animals require only a one-time treatment, meaning the highest costs are incurred in the initial years when the majority of captures and procedures occur. As treatment coverage increases and fewer new individuals require sterilization, operational costs decline significantly, making long-term program maintenance more affordable (DeNicola & DeNicola, 2021; NYCDPR, 2024; Briggs, 2025). A notable case study demonstrating the long-term feasibility and cost-effectiveness of surgical sterilization as a fertility control strategy comes from Clifton, Ohio, USA (Briggs, 2025). In this community-led program, the initial phase was carried out by wildlife biologists, who conducted a high-volume capture effort to sterilize a substantial portion of the local deer population (Briggs, 2025). Over time, program responsibilities transitioned to a team of trained volunteer veterinarians and capture specialists, significantly reducing operational costs while maintaining effectiveness. In Year 1, 41 female deer were sterilized for 40,000 USD, covering equipment, personnel, and procedural training (Briggs, 2025). By Year 9, only five additional females required treatment, and annual expenses had dropped to 6,000 USD (Briggs, 2025). Over this period, the deer population declined from 99 to 58 per square mile, highlighting the potential for sustained, community-led fertility control programs to achieve population reductions at a lower long-term cost (Briggs, 2025).

Immunocontraception via darting is somewhat less expensive per animal but requires repeat treatments; maintaining a long-term program can rival or exceed lethal control on a per-animal basis (Walker et al., 2021). Additionally, community stakeholders sometimes grow impatient with the gradual results of fertility control – unlike a cull, which can immediately remove animals, contraception works by attrition over the years (DeNicola & DeNicola, 2021; Walker et al., 2021). In summary, fertility control for ungulates shows promise in specific scenarios (small populations, good access, naive deer with strong community support) and has demonstrated some successful outcomes in reducing population growth. However, many programs have encountered logistical, financial, or biological hurdles that tempered their success (Gray & Cameron, 2010; Boulanger & Curtis, 2016; DeNicola & DeNicola, 2021; Walker et al., 2021). Fertility control must be applied intensively and persistently, and even then, its effectiveness hinges on limiting immigration and treating a large proportion of animals (Massei, 2023). These challenges underscore why ongoing research is critical – both to improve fertility control methods (e.g., developing longer-lasting contraceptives) and to understand how animals respond when fertility is suppressed using various methods (Gray & Cameron, 2010; Massei, 2023).

Fertility control in suburban deer

Fertility control can alter deer behavior, with different outcomes depending on the method used. Ovariectomized females do not enter estrus (creating permanent anestrus), which may eliminate seasonal spikes in movement and reduce interactions with males during the breeding season. In contrast, vasectomized males maintain normal reproductive behaviors, and populations with high numbers of sterile males may have instances of delayed conception among females (where the few remaining untreated males breed), leading to a prolonged breeding season and late-season fawn births (Curtis, 2020). A prolonged breeding season resulting from extra estrous cycling in vasectomy-treated populations may result in elevated energy expenditure and increased deer-vehicle collision risk, although empirical evidence remains limited (Curtis, 2020).

The feasibility of fertility control programs depends on funding, regulatory approval, and long-term commitment (Boulanger et al., 2012). Surgical sterilization programs for deer typically cost 500–1,500 USD per individual, while immunocontraceptive programs range from 300–800 USD per deer per year due to recurring booster requirements (Boulanger et al., 2012; Evans et al., 2016). Capture methods, such as remote darting or baiting stations, require extensive labor and expertise, particularly in suburban environments where property access is a challenge (Curtis 2021). Regulatory approval is another factor, as fertility control for deer requires state-level permits, and the use of immunocontraceptives is often restricted to research or experimental applications (Miller et al., 2013).

Success depends on high treatment coverage, low immigration rates, and long-term monitoring to make fertility control a viable part of an integrated management strategy. While it presents challenges in cost and implementation, fertility control remains a socially acceptable tool for managing localized deer populations, particularly in communities where lethal methods are not an option (DeNicola & DeNicola, 2021; NYCDPR, 2024).

1.4 Biologging technologies for monitoring wildlife behavior

Understanding animal movement is fundamental to evaluating how fertility control influences behavior, space use, and broader ecological dynamics. Advances in sensor technologies, such as global positioning system (GPS) trackers with integrated accelerometers and improved analytical methods, allow for the robust examination of animal movements and activity at finer temporal scales, which can inform management decisions (Cagnacci et al., 2010; Brown et al., 2013). The current collective understanding regarding the behavioral implications of fertility control is based on captive wildlife and coarse movement data (VHF relocation or direct observation), and acceleration data were not available (Massei et al., 2008; Gray & Cameron, 2010; Duncan et al., 2017). A remaining challenge is retrieving these data from free-ranging animals in a cost-effective way. The Internet-of-Things (IoT) revolution has had a considerable impact: new low-power communication networks (Sigfox, LoRaWAN, etc.) allow inexpensive, lightweight collars to transmit data to base stations or the cloud with minimal battery use (Wild et al., 2023).

Accelerometry and activity monitoring

Another advancement in biologging has been the integration of triaxial accelerometers in collars to record animal activity at fine scales (Brown et al., 2013; Dentinger et al., 2022). Accelerometers measure acceleration along three orthogonal axes (surge, sway, heave), capturing movements like running, walking, resting, and even head or limb motions (Brown et al., 2013;

Gurule et al., 2022). Metrics that serve as proxies for activity level can be derived by separating dynamic body acceleration (from the animal's movements) from static acceleration (gravity) (Brown et al., 2013). One widely used measure is Overall Dynamic Body Acceleration (ODBA), defined as the sum of absolute dynamic acceleration on each axis (Brown et al., 2013). A closely related metric is Vectorial Dynamic Body Acceleration (VeDBA), which uses the vector sum (Euclidean norm) of dynamic acceleration:

$$\text{VeDBA} = \sqrt{ax^2 + ay^2 + az^2}$$

where *ax, ay, and az* are the dynamic accelerations along each axis (Qasem et al., 2012). VeDBA is rotationally invariant and tends to be more robust than ODBA because it avoids over-counting acceleration due to gravity or collar orientation (Qasem et al., 2012; Martin et al., 2022). Accelerometry thus provides a way to quantify behaviors (e.g., resting vs. moving) and infer energy use at temporal scales much finer than GPS fixes alone.

1.5 Methods and metrics used to analyze wildlife behavior

High-resolution biologging data (GPS and accelerometry sensors) were analyzed using models that account for irregular sampling and individual variation to quantify wildlife movement and activity patterns. The following methods emphasize why each approach was chosen and the insights they provide.

Continuous-Time Movement Modeling (ctmm)

Continuous-time movement modeling (implemented via the ctmm R package) was the foundation for deriving space-use metrics (Calabrese et al., 2016). Unlike traditional discrete-time analyses, ctmm treats animal trajectories as continuous-time stochastic processes, which is ideal for irregularly-timed, autocorrelated GPS data with measurement error (Calabrese et al., 2016). This approach separates the animal's movement behavior from the sampling schedule, yielding inferences that do not depend on fix interval or timing (Noonan et al., 2019). Adopting ctmm ensured estimated movement metrics were rigorously estimated, sampling-independent, considered measurement error, and included confidence intervals following the recommendations of Calabrese et al. (2016)

Movement Metrics

Several movement metrics used in Chapter 3 and Chapter 4 were derived using the GPS data and ctmm-fitted models to characterize space use and mobility. Each metric is defined briefly below, along with its rationale:

- 7-day home range: The short-term home range area was computed over a moving 7-day window using AKDE (Autocorrelated Kernel Density Estimation). This metric represents the area an animal occupies in a given week, capturing changes in space use that would not be visible in a single overall home range. A 7-day interval balances temporal resolution of biological processes (24-48 hr estrus windows in females, peak breeding season in males) with enough data for reliable estimation. By estimating weekly AKDE home ranges, it is possible to detect expansions or contractions of range and consider why space use changes over time. The AKDE method was chosen because it accounts for autocorrelation and provides more accurate home range estimates than traditional methods (Calabrese et al., 2016).

- Daily diffusion: Daily diffusion measures the rate at which an animal's positional uncertainty (or area explored) increases per unit time. In continuous-time movement models, diffusion rate corresponds to the movement intensity or velocity of area spread (with units of area per day) (DeNicola, Chapter 2). It effectively captures how mobile an animal is on a daily basis. Ctmm-generated diffusion rate can act as a proxy for ctmm-generated speed when data are coarse or irregular. Further, these ctmm-generated metrics are more resistant to change as data quality degrades, unlike straight-line displacement derived distance traveled (Noonan, 2019, DeNicola, Chapter 2). A higher diffusion rate indicates the animal rapidly covers a new area (high daily mobility), whereas a lower rate indicates localized, restricted movement. This metric reveals changes in movement activity while avoiding biases introduced by GPS fix interval.

- Excursivity: Excursivity quantifies the extent of an animal's forays beyond its core range. Using the AKDE home range distribution from the full telemetry, the quantile of each location is evaluated (e.g., the 95% AKDE contour), and the daily mean AKDE quantile is calculated. A value near 0 indicates that the individual remained in high-use areas that day, whereas a value near 1 indicates that the individual spent more time in "peripheral" areas. Excursivity is defined as the tendency to reach outer range quantiles or beyond – effectively measuring how often and how far an individual ventures to the periphery of its home range. For example, a high excursivity day might mean the animal spent significant time near or outside its 95% range boundary, indicating a long-distance excursion or exploratory movement. This metric was included to identify ecologically important movements (such as scouting trips or dispersal events) that would be masked by average home range size. By basing it on AKDE quantiles, the measure is ensured to be relative to the animal's typical range and informed by autocorrelated space-use patterns. This proportion was modeled with appropriate methods (e.g., beta distribution) to account for its 0–1 bounded nature.

- Speed/distance traveled: Although Speed/distance traveled are conceptually intuitive indicators of animal movement (Noonan et al., 2019), they were not used as primary metrics due to inherent limitations in datasets with coarse or irregular sampling. Even when derived from continuous-time movement models (e.g., via ctmm), these estimates are sensitive to sampling resolution and require sufficient temporal density to support estimation (Noonan et al., 2019). Distance traveled in ctmm is only defined when the selected movement model includes velocity autocorrelation—such as the Ornstein-Uhlenbeck Foraging (OUF) or Integrated Ornstein-Uhlenbeck (IOU) models (Noonan et al., 2019). When data were too sparse, simpler models like Ornstein-Uhlenbeck (OU) or IID were favored, in which case speed is undefined. Because of these challenges, daily diffusion was explored as a proxy for movement rate (DeNicola, Chapter 2).

Activity Metrics

In addition to spatial movement, accelerometers provided insight into activity levels. Data were collected at 32 Hz and processed into 2-second Vectorial Dynamic Body Acceleration (VeDBA) averages. The natural log of VeDBA was calculated to facilitate clustering and reduce skew. To account for variation across devices, individuals, and collar placement, behavioral states were defined separately for each animal by identifying local minima in the distribution of log mean VeDBA values (Minasandra et al., 2023). Values near zero VeDBA (log mean VeDBA = $-\infty$) were classified as a no-activity state. This process resulted in four activity states: no, low (e.g., resting or bedding), medium (e.g., foraging), or high activity (e.g., traveling or active foraging). Each 2-second interval was then assigned one of three states based on these thresholds. Two daily activity metrics were then derived from the animal's behavioral state classifications (Minasandra et al., 2023). These metrics were used in Chapter 3 to summarize daily activity patterns:

- Percent Time in Low/No Activity State: This is the percentage of each day the animal spent in a low-activity or inactive state (e.g., resting, stationary behavior). Based on accelerometer-derived behavior states, periods of low movement (such as bedding or stationary foraging) were identified, and the proportion of time in this state or the no activity state was calculated per day. This metric acts as a daily inactivity budget, indicating how sedentary or restful the animal was. It is ecologically informative because changes in this percentage can reflect seasonal energy conservation (e.g., more resting in winter), reproductive status (e.g., parturition), or health. By focusing on a proportion of time, it standardizes for day length or sampling duration and allows comparison across individuals and seasons. This proportion was modeled with appropriate methods (e.g., beta distribution) to account for its 0–1 bounded nature.

- Behavioral State Transitions: This metric counts how many times per day the animal switches between no-activity, low-activity, medium-activity, and high-activity states. The number of daily transitions reflects the changes in activity bouts: for instance, an individual with many short foraging bursts and frequent resting will have a high transition count, whereas one with prolonged active periods and long rests will have fewer transitions. This measure can indicate behavioral strategies or responses to disturbance (frequent start-stop may imply intermittent disturbances or sporadic foraging). Changes in daily routine complexity were modeled using the count of transitions (using a count-based GAM, e.g., negative binomial). Together with the percentage of low activity, the transitions metric helps reveal how much time is spent resting vs. moving and how activity bouts are structured throughout the day.

Modeling Temporal Patterns with Hierarchical GAMs

To analyze how these movement and activity metrics changed over time (e.g., across seasons and between groups), hierarchical generalized additive models (HGAMs) were applied. HGAMs were chosen for their ability to flexibly model non-linear trends within groups (such as seasonal cycles; Wood et al., 2017; Pedersen et al., 2019). Each movement and activity metric was modeled as a smooth function of time (for example, day-of-year to capture seasonal variation). The hierarchical structure accounts for the grouped or nested structure (repeated measures within individuals, sexes, and sites) and allows variation within and across groups. This means that while an overall smooth curve describes the seasonal pattern of a metric, each animal can have its own intercept or slight differences in shape – improving fit and avoiding pseudoreplication by not treating all data as independent (Pedersen et al., 2019).

For metrics with specific distributional characteristics, appropriate generalized models were used. Continuous, positive-valued responses like diffusion rate, distance traveled, or home range area were modeled as a Gamma distribution. Proportion data were modeled with a Beta distribution (via a logit link for the mean) to handle their 0–1 range properly. Count data (behavioral transitions) were modeled with a negative binomial distribution to accommodate count nature. In some cases, a location-scale GAM (HGAMLS; Rigby & Stasinopoulos, 2005) was employed – this extends the model to allow the scale (variance) of the response to change over time or by group, not just the mean. For example, if the variability in a metric increased during certain seasons, the model could capture that by modeling the dispersion parameter as a function of time.

The use of HGAMs offers several advantages. First, it handles seasonal trends smoothly: for instance, diffusion rates or home range sizes might rise and fall cyclically through the year, which a smooth term can capture (peaking in one season and dipping in another) without prescribing a fixed sinusoidal form. Second, including random smooths per individual (in some cases by year) addresses individual variation: each animal might have a different baseline level of movement or activity and possibly a slightly different timing or magnitude of seasonal change. The hierarchical model structure ensures that these differences are accounted for, avoiding bias in the population-level trend and properly quantifying among-individual variation. Finally, modeling all individuals together increases statistical power to detect patterns (each animal contributes to the estimation of the smooth trend), ensuring that any detected pattern is common across individuals.

A Bayesian statistical framework was used for inference to quantify uncertainty and interpret treatment effects probabilistically. While models were fit using frequentist methods (e.g., REML for GAMs), posterior distributions of fitted values were examined to estimate 95% credible intervals. This approach allows intuitive probabilistic statements (e.g., the probability that treated animals had lower diffusion rates; given the data and model, there is a 95% probability that the true value lies within the interval) and better accommodates hierarchical data structures with small sample sizes. Bayesian inference also enables the propagation of uncertainty across model stages—for instance, from estimated diffusion rates to temporal trends—yielding more transparent and interpretable results for ecological decision-making.

Justification of approach

This suite of methods and metrics was chosen to address common data challenges and understand differences in movement and activity between two groups. The continuous-time modeling approach (ctmm) is crucial for handling irregular GPS data, avoiding biases from autocorrelation, and enabling the estimation of measures with confidence intervals (Calabrese et al., 2016). The analysis integrates spatial and behavioral dimensions of movement by using activity state information, giving a more complete picture of activity and movement patterns. The application of hierarchical GAMs then links these metrics to temporal dynamics (e.g., seasonal changes), while accounting for individual and group differences in behavior. This combined approach provides a robust framework for analyzing this wildlife telemetry dataset.

1.6 Aim and research objectives

This research aims to evaluate how fertility control influences seasonal deer movement behavior and activity patterns. GPS tracking and accelerometry was used to assess whether vasectomy-induced estrous cycling or ovariectomy-induced anestrus altered behavioral patterns. Hierarchical generalized additive models (HGAMs) were used to account for individual variation and temporal trends while providing insights into the behavioral impacts of fertility control on these suburban deer populations. As each of the following chapters represents a manuscript that reflects my work with several important collaborators, the word "we" is used throughout Chapters 2, 3, and 4 of this thesis.

The core methodological contribution of this thesis, detailed in Chapter 2, addresses a common challenge in movement ecology: accurately estimating animal movement metrics from spatial data (Noonan et al., 2019). This manuscript (Manuscript 1) introduces ctmm-generated diffusion as a proxy for ctmm-generated speed and establishes its utility for analyzing ecological movement data as a more available, consistent, and robust metric (Calabrese et al., 2016). Researchers often use speed and distance traveled (calculated by summing straight-line displacements between sampled locations) to interpret animal behavior and energy expenditure (Noonan et al. 2019). However, these estimates can be biased or unreliable, especially when the data are collected at coarse intervals or contain location errors (Noonan et al., 2019). Further, if data is sparse or irregular, CTSD estimation (using ctmm in R; Calabrese et al., 2016) may not provide a speed estimate, or if it does provide an estimate, the estimate may be unreliable. In response to these limitations, Chapter 2 examines the relationship between ctmm-generated speed and diffusion and predicts that diffusion would be a more reliable measure of movement activity, particularly with increasingly coarse telemetry data.

The study detailed in Chapter 3 of this thesis examines the impact of vasectomy-induced estrous cycling on male and female deer behavior in a suburban context. This manuscript (Manuscript 2) draws on data from Staten Island, New York, USA, where over 97% of antlered males were treated with a vasectomy (NYCDPR, 2024). The study evaluates whether the multi-estrous cycles induced in females by failed conception affect movement patterns and activity levels. Movement behavior and activity in individuals at the vasectomy site was compared to individuals at an untreated control site at Rockefeller State Park Preserve in Pleasantville, NY, USA, which was similar in habitat composition and anthropization. Both males ($n = 52$) and females ($n = 106$) were monitored during two seasons using GPS and triaxial accelerometry data to understand the effect of vasectomy-induced extra estrus periods on movement and activity patterns. In this context, the extra estrus periods caused by the vasectomy program were predicted to have no impact on the large-scale movement of males and females, no impact on the fine-scale movement of males, and a limited impact on the fine-scale movement of females around these extra estrus periods (Table 1).

The study detailed in Chapter 4 of this thesis explores the impact of ovariectomy-induced anestrus on the movement behavior of female deer in a suburban context. By comparing treated and untreated individuals in South Euclid, Ohio, USA, this manuscript (Manuscript 3) investigates whether the absence of estrous cycles altered movement patterns during critical periods such as breeding, parturition, and post-parturition. GPS data was used to examine whether the absence of these reproductive cycles altered space use patterns over time. Biologging devices with GPS were deployed on treated (*n = 10*) and untreated (*n = 10*) females in South Euclid, Ohio, USA, where an ovariectomy program (Boulanger & Ellingwood, 2024) was implemented. Treated females were predicted to show more consistent movement throughout the year. In contrast, untreated females were expected to respond to the hormonal cues surrounding estrus and parturition, varying their movement accordingly (Table 2).

Table 1 — Summary of study design and related hypotheses, predictions, data, consequences, and methods used in assessing vasectomy impacts on breeding-related movement behavior and activity in free-ranging white-tailed deer. This study occurred at a treatment site in Staten Island, NY, USA (SI) and a control site in Rockefeller State Park Preserve, Pleasantville, NY, USA (RSPP) between 2021 and 2023.

Hypothesis	Prediction (Control-RSPP)	Prediction (Treatment- SI)	Data Source and Measure	Consequence	Method
Male white-tailed deer increase exploratory behavior in response to elevated testosterone levels.	Male white-tailed deer at the control site will show peak home range, distance traveled, diffusion, and excursivity from late October to December. These measures will decrease as testosterone levels drop in early January.	No expected differences with respect to Control	1 GPS fix/hour; 7-day home range, daily distance traveled, daily diffusion, daily excursivity	Increased deer-vehicle collisions, decreased body condition	Measures derived via ctmm package in R with 7-day moving window/3-day slide; Modeled with HGAMLS
Female white-tailed deer show increases in exploratory behavior in response to estrus periods.	Female white-tailed deer at the control site will show increases in home range, distance traveled, diffusion, and excursivity in November - December during a	There are no expected differences with respect to Control despite extra-estrus, as these changes might not be noticeable in the modeled data.	1 GPS fix/hour; 7-day home range, daily distance traveled, daily diffusion, daily excursivity	Increased deer-vehicle collisions, decreased body condition	Measures derived via ctmm package in R with 7-day moving window/3-day slide; Modeled with HGAMLS

	window around their estrus period. Due to the short duration of estrus, these changes may not be noticeable in the modeled data.				
Male white-tailed deer become more active in response to elevated testosterone levels.	Male white-tailed deer at the control site will show peak activity from late October to December. These measures will decrease as testosterone levels drop in early January.	No expected differences with respect to Control	32 Hz tri-axial accelerometry; # of activity state transitions/day; proportion of time/day spent in no/low activity state	Increased deer-vehicle collisions, decreased body condition	Derived measures using 2-s window log (VeDBA); states identified via clustering with GMM; modeled with HGAM
Female white-tailed deer show increases in activity in response to estrus periods.	Female white-tailed deer at the control site will increase activity in November - December during a window around their estrus period. Due to the short duration of estrus, these changes may not be noticeable in the modeled data.	Female white-tailed deer at the treatment site will increase in activity from November - March during a window around their estrus periods (extra-estrus).	32 Hz tri-axial accelerometry; # of activity state transitions/day; proportion of time/day spent in no/low activity state	Increased deer-vehicle collisions, decreased body condition	Derived measures using 2-s window of log (VeDBA); states identified via clustering with GMM; modeled with HGAM

Table 2 — Summary of study design and related hypotheses, predictions, data, consequences, and methods used in assessing ovariectomy impacts on breeding and parturition-related movement behavior and activity in free-ranging white-tailed deer. This study took place in South Euclid, OH, USA, between 2023 and 2024.

Hypothesis	Prediction (Control)	Prediction (Treatment)	Data Source and Measure	Consequence	Method
Female white-tailed deer show increased exploratory behavior in response to estrus periods and decreased activity in response to parturition and post-parturition periods.	Untreated female white-tailed deer will show increases in home range, diffusion, and excursivity in November - December during a window around their estrus period and decrease home range, diffusion, and excursivity in May - July during parturition and post-parturition.	Female deer treated with ovariectomy will maintain consistent space use throughout the November - December breeding season and the May—July parturition and post parturition period.	1 GPS fix/hour; 7-day home range, daily diffusion, daily excursivity	Increased deer-vehicle collisions, decreased body condition	Measures derived via ctmm package in R with 7-day moving window/3-day slide; Modeled with HGAM

CHAPTER 2. ARE YOUR DATA TOO COARSE FOR SPEED ESTIMATION? DIFFUSION RATES AS AN ALTERNATIVE MEASURE OF ANIMAL MOVEMENT

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Abstract

1. Estimates of speed and distance traveled are routine in ecological research to provide a link between behavior and energetics. Conventional straight-line displacement (SLD) methods return severely and differentially biased estimates with no ability to evaluate the accuracy of the estimate. Recent methodological advances have improved our ability to estimate these parameters using continuous-time speed and distance (CTSD) estimation. However, even with CTSD estimation, many datasets are too coarse, or the location error is too great to reliably measure speed or distance traveled.
2. To address these limitations, we investigated the relationship between CTSD-estimated mean speed and diffusion rate, where diffusion rate is defined as the variance in displacements per time interval. We calculated CTSD mean speed and diffusion rate estimates using telemetry data (i.e., trajectory data) from over 100 white-tailed deer and simulated telemetry data generated from a known movement model. We examined the relationship between the two measures in both datasets and the effect of sampling frequency on the effective sample size and the estimation of the two parameters.
3. We found that mean speed and diffusion rate were strongly and nonlinearly correlated, with a 1% increase in diffusion rate predicting a 0.40% increase in mean speed (99% CI: 0.38–0.42%) for our focal species. Diffusion rate estimates remained substantially more accurate and precise than speed across sampling interval regimes, even when speed estimation was not possible.
4. *Synthesis and applications:* Our findings demonstrate that diffusion rate outperforms mean speed as a measure of movement activity under marginal data conditions. Diffusion rate is a reliable measure of movement activity and can link behavior to energetics across a wider

range of datasets while maintaining accuracy even when data quality is low. By using speed and diffusion together, researchers can rely on more robust insights into space use across a range of ecological contexts.

Keywords: animal movement, animal tracking, continuous-time, ctmm, diffusion rate, distance traveled, GPS, speed

Introduction

Animal movement is a fundamental and rapid dynamic response to environmental or physiological stimuli (Nathan et al., 2008), driven by energetic requirements, reproductive needs, competitor and predator avoidance, habitat fragmentation, and other processes operating at various spatial and temporal scales (Carbone et al., 2005; Nathan et al., 2008; Schlägel et al., 2020; Van Moorter et al., 2016). Measures of how much and how fast animals move are central to optimal foraging theory (Brown et al., 1999) and the marginal value theorem (Charnov, 1976), as both frameworks emphasize the trade-off between energetic costs and resource acquisition. Movement serves as the bridge between these costs and benefits, with distance and speed influencing the time and energy required to locate, access, and consume resources. The marginal value theorem predicts that animals should leave a foraging patch once resource intake falls below the environment's average intake rate — a decision shaped by movement speed and distance. Similarly, optimal foraging theory suggests that animals adjust movement patterns to balance exploration for new resources with exploitation of known patches. As a result, estimates of distance traveled and speed are widely used in ecological research as proxies for the energetic costs of movement, providing a tangible link between theory, behavior, and energetic efficiency (Garland, 1983; Wilson et al., 2008).

Often, distance traveled is estimated using the linear distance between consecutive locations, referred to as straight-line displacement (SLD), and speed is estimated by dividing an SLD by the time elapsed between the corresponding pair of locations. This form of estimation is straightforward to calculate, but it results in biased estimates of both distance traveled and speed (Noonan et al., 2019; Rowcliffe et al., 2012; Sennhenn-Reulen et al., 2017). SLD-derived estimates fail to account for the inherently tortuous and non-linear nature of many animal trajectories (Nathan et al., 2022; Fig. 2a in Noonan et al., 2019), resulting in a substantial underestimation of the true distance traveled and speed (Noonan et al., 2019). This underestimation occurs because an animal's movement trajectory is a latent variable: it is not possible to know exactly the true single steps building up the movement path. While one can approximate that using sequences of telemetry-based locations (e.g., GPS locations, Nathan et al. 2008; henceforth "telemetries"), such data only provide partial information on where and how the animal moved (Fleming et al., 2016). Thus, SLD underestimates speed and distance traveled, particularly when animals exhibit complex behaviors, such as foraging or social interactions, at a timescale that is finer than the sampling interval of the locations. This is exacerbated by coarse sampling and data thinning, which is regularly used to homogenize sampling interval (Rowcliffe et al., 2012). Conversely, fine-scale sampling mitigates this underestimation but can also result in an overestimation driven by telemetry measurement error (Fig. 2b Noonan et al., 2019; Rowcliffe et al., 2012). Finally, although the SLD method can be modified to account for these measurement error biases (Johnson et al., 2011), fine-scale sampling introduces autocorrelation structures that cannot be accounted for using SLD methods (Noonan et al., 2019). Additionally, applying conventional SLD methods will return speed and distance traveled estimates without confidence intervals or uncertainty estimates (Noonan et al., 2019).

Continuous-time speed and distance (CTSD) estimation is an alternative to SLD-based estimation that corrects the issues mentioned above. It is based on continuous-time stochastic movement models (Fleming et al., 2014; Gurarie et al., 2009) that leverage the autocorrelation in the data to inform both tortuosity and measurement error simultaneously (Fleming et al., 2014, 2016; Noonan et al., 2019). By accounting for the non-independence between locations, CTSD estimation produces estimates of effective sample size (ESS) for movement parameters, including speed, home-range crossing time, and home-range size. ESS is a measure of the number of independent samples for each parameter estimate and ensures that parameter estimates and confidence intervals reflect the true informational content of the data and avoid biases caused by unmodeled autocorrelation (Fleming & Calabrese, 2017). Recent applications of CTSD estimation have demonstrated its ability to accurately reconstruct movement behaviors and allow ecologists to understand behavioral processes at fine ecological timescales (Nathan et al., 2022; Noonan et al., 2019; Thompson et al., 2021). However, CTSD estimation only provides accurate estimates when the data are sufficiently fine and the location error is sufficiently small to inform the speed parameter estimates (Noonan et al., 2019).

This study introduces continuous-time estimated *diffusion rate* as a robust and versatile metric for quantifying animal movement and proposes it as an alternative to discrete and continuous time estimates of mean speed, especially for coarse telemetry data. We define diffusion rate as the expected square displacement over a finite period of time, which can be interpreted as the variance in locations per unit of time (see S2: Supplement A). Unlike speed, diffusion rates offer insights into how extensively an animal explores space over time (Moorcroft & Lewis, 2013, allowing researchers to investigate cumulative displacement patterns less sensitive to sampling bias.

This paper had two main aims: (1) to demonstrate and describe the relationship between mean speed and diffusion in animal trajectories and (2) to demonstrate why and when diffusion rate is a better metric of animal movement. Our analysis draws on empirical tracking data from a large dataset of 108 white-tailed deer (117 seasonal trajectories; *Odocoileus virginianus* Zimmermann) from New York, USA. We applied CTSD models to generate estimates of mean speed and diffusion rate and demonstrate the relationship between the two as well as how sampling frequency affects their estimates and effective sample size. Finally, to show how speed estimation performs under increasingly coarse conditions, we used simulations from a known movement model to assess the accuracy and robustness of both mean speed and diffusion rate as a function of sampling interval. This study demonstrates the broader applicability of diffusion rate in ecological research and provides a foundation for more reliable movement modeling.

Methods

Diffusion rates measure how broadly an animal's location spreads over time by quantifying the rate of increase in spatial variance with respect to time, providing insight into how quickly an animal expands its range (Okubo & Levin, 2001). The diffusion rate D can be defined as the variance in displacements per unit time-lag or

$$D(\tau) = d/d\tau \ \mathrm{VAR}[x(t+\tau)-x(t)] \qquad (1)$$

where $x(t)$ is the location process at some initial time t, and τ is the time lag under consideration (Okubo & Levin, 2001). Unlike mean speed, which captures the average rate of movement per unit time, the diffusion rate considers both speed and directional changes. Mean speed or daily distance traveled can provide an important indicator of an animal's energetic expenditure (Carbone et al., 2005), whereas diffusion rate can inform on space use and movement efficiency (Okubo & Levin, 2001).

2.1 Relationship between mean speed and diffusion rate in white-tailed deer telemetries

To quantify the relationship between speed and diffusion, we used the mgcv package (Wood, 2017) for R (R Core Team, 2024) to fit a Hierarchical Generalized Additive Model (HGAM; Pedersen et al., 2019) to the moving-window estimates of mean speed and diffusion produced in DeNicola et al. (2024). To remove potential confounds due to differences in sampling intervals (discussed below), we constrained the analyses to windows with a median sampling interval of 1 hour (95.13% of the estimates with finite speed and diffusion). The HGAM had a population-level linear term of log-transformed diffusion and a factor smooth term of log-transformed diffusion for each animal to account for individual-level deviations from the population average (see model GS in Pedersen et al., 2019). The model had a Gamma family of distributions with a log link function, so the population-level model (i.e., ignoring individual animal-level trends) can be written as

$$log\ (\mu_S)\ =\ \beta_0 + \beta_1 log(\mu_D), \qquad (2)$$

where μ_S is mean speed and μ_D is mean diffusion. We discretized the covariates (discrete = TRUE) and the smoothness parameter was estimated via fast REML (method = “fREML”) to reduce fitting time with no substantial loss to accuracy.

2.2 Effects of sampling interval on robustness of estimates in white-tailed deer telemetries

To estimate the effects of sampling interval on the relationship between mean speed and diffusion as well as one’s ability to obtain estimates of speed and diffusion rate, we thinned all trajectories with progressively coarser sampling intervals. Starting from the estimates that had a median sampling interval of 1 hour (117 seasonal trajectories from 108 distinct deer, with 9 tracked in two separate seasons), we thinned the data at intervals of 2, 3, 4, …, 46, 47, and 48 hours and fit movement models to each trajectory using the ctmm.select() function for a total of 5,616 movement models. We then modeled the effects of diffusion and sampling interval on mean speed using a second HGAM. In addition to the terms from model (2), this second HGAM included a population-level smooth term of sampling interval. As with the first HGAM, this model used a Gamma family of distributions and a log link function, and the smoothing parameter was estimated via fast REML with discretization of the covariates. We can thus write the population-level model as

$$log\ (\mu_S)\ =\ \beta_0 + \beta_1 log(\mu_D) + f(\Delta t), \quad (3)$$

where $f(\Delta t)$ is a (smooth) function of the sampling interval.

2.3 Relationship between speed and diffusion rate in simulated trajectories

To demonstrate the consequences of forcing speed estimation when data are too coarse, we simulated 1,000 trajectories from a known movement model. The model had a directional persistence of 1 hour, a range crossing time of 24 hours, and a spatial variance of 1 km^2, which resulted in a mean speed of 6.14 km/h and a mean diffusion of 1.74 km^2/h. We thinned each of the 1,000 trajectories as above using sampling intervals of 1, 2, 3, …, 46, 47, and 48 hours. We then fit Ornstein-Uhlenbeck-Foraging (OUF) movement models via the ctmm.fit() function to obtain estimates of both speed and diffusion rate for all sampling intervals, forcing estimates for coarse data.

Results

The deer had a mean estimated directional persistence of 10.2 minutes (median 9.7 minutes; range: 2.5-26.9 minutes, all below the sampling interval of 1 hour) and a mean estimated range crossing time of 27.8 hours (median 9.1 hours; range: 3.7 hours to 33 days).

3.1 Relationship between mean speed and diffusion rate in white-tailed deer telemetries

The model for the 1-hour moving window data demonstrated a good fit, explained 80.9% of the deviance, and did not show evidence of heteroskedasticity in the residuals (Fig. 2). It produced the estimated relationship in SI units

$$log\ (\mu_S) = 3.09 + 0.40\ log\ (\mu_D), \quad (4)$$

where μ_S and μ_D are the estimated mean speed and diffusion in SI units, respectively. The equation can be rewritten as the estimated power relationship

$$\mu_S = 21.99\ {\mu_D}^{0.40}, \quad (5)$$

from which we can derive that speed increases with diffusion sublinearly (because the 0.40 < 1), and a 1% increase in diffusion results in an approximate 0.40% increase in mean speed (99% CI: (0.38, 0.42); see S2: Supplement B).

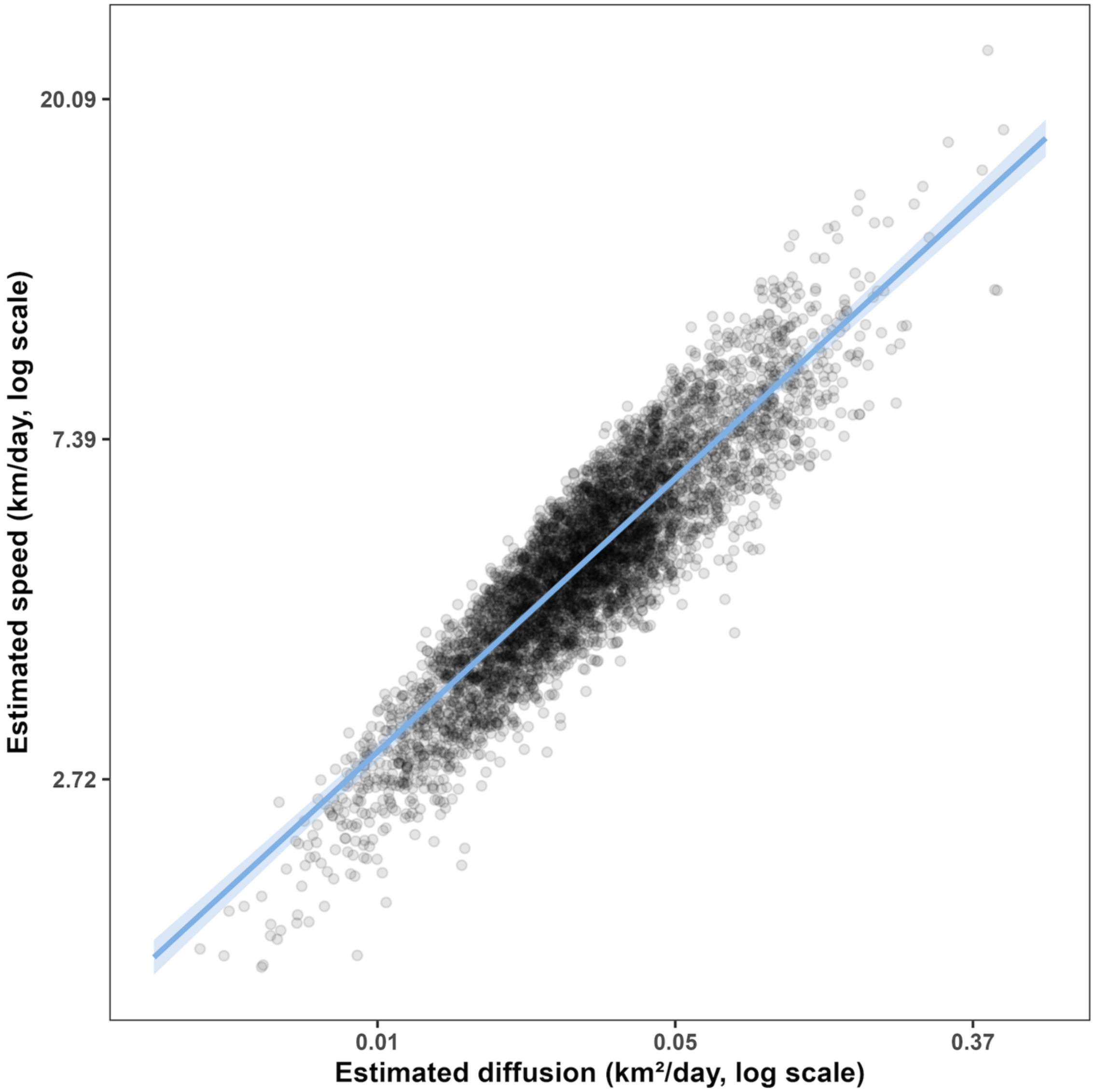

Figure 2 — Estimated speed and diffusion have a linear relationship on a log-log scale for deer telemetries. Movement rates were estimated using continuous-time movement models using the ctmm.select() function from the ctmm package for R. The line indicates the estimated relationship, while the shaded ribbon indicates the 99% credible interval of the posterior. The points are 5,180 7-day mean speed and diffusion estimates from 108 deer estimated in DeNicola et al., 2024 (Chapter 3 in this thesis).

3.2 Effects of sampling interval on robustness of estimates in white-tailed deer telemetries

Of the 5,616 movement models fit to the thinned white-tailed deer telemetries, only 984 (17.5%) had finite estimates of speed, but 4219 (75.1%) had finite estimates of diffusion. All models with finite speed also had finite diffusion. The HGAM fit to these data revealed a similar relationship to the one described in Eq. (5) after accounting for the effect of sampling interval (Fig. 3). However, the relationship between mean speed, μ_S, and sampling interval, Δt, was nonlinear, so we included its effect as the nonlinear (smooth) function $f(\Delta t)$, which can be treated as a constant for a given Δt. The model produced the power relationship

$$\mu_S = (3.20\, f(\Delta t))\, \mu_D{}^{0.50} \qquad (6)$$

and had a very good fit, as it explained 97.7% of the deviance. The estimated exponent was 0.504 (99% credible interval: (0.463, 0.545)).

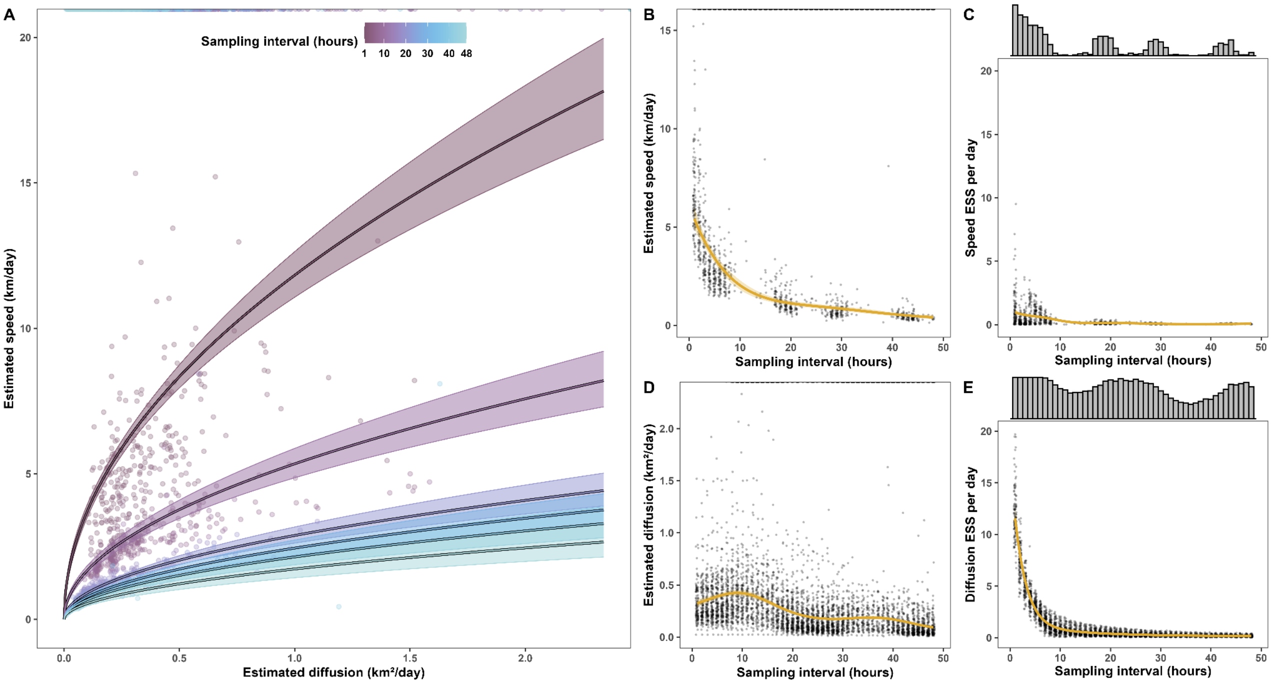

Figure 3 — Estimated speed and diffusion estimated from deer telemetries have a nonlinear power relationship (A). The line indicates the estimated relationship, while the shaded ribbon indicates the

99% credible interval. The points at the top of the figure show the distribution of non-finite estimates of speed (top) and diffusion (top right corner). Speed estimates (B) and effective sample size (C) decrease rapidly with sampling interval and show substantial gaps where speed estimation was inappropriate (see marginal histograms in C). Diffusion estimates (D) and effective sample size (E) also decrease with sampling interval. Still, diffusion estimates do not change substantially for sampling intervals $\lesssim$ 15 hours, effective sample sizes are much higher than those for speed, and the estimate gaps are less pronounced. Orange lines and ribbons indicate the relationships estimated by Gamma GAMs fit via ggplot2's geom_smooth() function, while points at the top of panels B and D indicate non-finite speed and diffusion estimates, respectively. Marginal histograms in C and E indicate the number of finite speed and diffusion estimates, respectively.

Diffusion estimates and effective sample size were substantially more robust to sampling interval than speed estimates. Mean-speed estimates decreased with sampling interval, and mean-speed effective sample size was > 5 in only 0.08% of the estimates. In contrast, diffusion rate estimates did not change substantially across sampling intervals $\lesssim$ 15 hours. Approximately 5.48% of all thinned telemetries had a diffusion effective sample size > 5, including all those with a 1-hour sampling interval. Both parameters showed oscillations in the number of models with finite estimates, but the oscillations were much more accentuated for mean speed. All sampling intervals had more than 40 diffusion estimates (out of 117 movement models), but 41 of 48 sampling intervals had only 40 speed estimates or less.

3.3 Relationship between speed and diffusion rate in simulated trajectories

The results from the simulated trajectories mirror those from the previous two subsections: Speed estimates were reasonably accurate and precise for sampling intervals $\lesssim$ 4 hours (Fig. 4A;

also see Noonan et al., 2019), while diffusion estimates were reasonably accurate and precise for sampling intervals ≲ 23 hours (Fig. 4B). Sampling intervals as low as 6 hours resulted in infinite speed point estimates, while 99.82% of all diffusion-rate point estimates were finite, albeit often excessively large for sampling intervals ≳ 35 hours. As in the previous section, effective sample size for speed decreased faster over the sampling interval than for diffusion but note that it was substantially larger when the sampling interval was near the true directional persistence timescale of 1 hour (Fig. 4C-D).

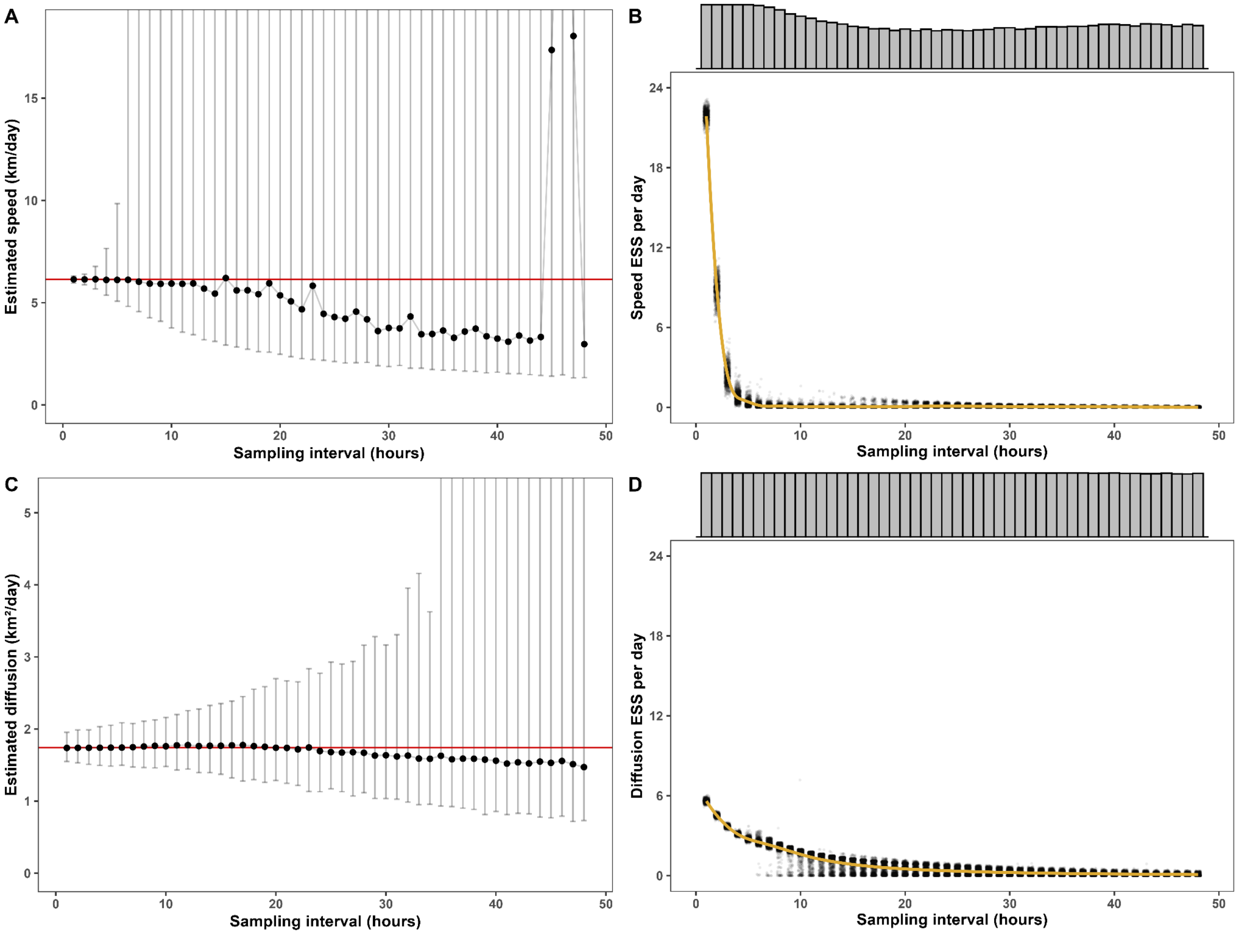

Figure 4 — Estimated speed (A) and diffusion (C) and corresponding estimated effective sample sizes (ESS) for speed (B) and diffusion (D) from 1,000 Ornstein-Uhlenbeck-Foraging (OUF) movement models fit via the ctmm.fit() function from the ctmm package to simulated trajectories.

The points and error bars in panels A and C indicate the median estimate and the 99% quantile interval, respectively, while the red line indicates the true speed and diffusion parameters. In panels B and D, the points indicate the data, jittered horizontally by no more than ±0.25, while the orange line indicates the estimated trends fit via ggplot2's geom_smooth() function. The marginal histograms indicate the proportion of finite estimates at each sampling interval.

Discussion

Fine-scale animal movement is often characterized using speed and distance traveled to answer questions about foraging patterns, resting habits, and travel routes while linking movement intensity to an animal's responses to environmental stimuli (Fryxell et al., 2008; Turchin, 1998; Wilson et al., 2015). An animal's diffusion rate reflects the individual's short-term space use by integrating movement speed and tortuosity to reveal larger-scale processes such as site fidelity or exploration (Codling et al., 2008; Smouse et al., 2010). Higher diffusion rates suggest exploratory behavior or dispersal, whereas lower rates indicate either inactivity or more localized activities, such as the use of den sites, foraging patches, or breeding behavior (Codling et al., 2008; Giuggioli & Kenkre, 2014). Taken together, speed and diffusion rate provide complementary insights into an individual's movement behavior. Speed captures the rate and intensity of movement, while diffusion links movement to broader spatial and ecological processes (Börger et al., 2008). Using both metrics together, researchers can effectively characterize the proximate behaviors driving movement and the ultimate ecological consequences of space use. Additionally, when accurate speed estimation is not possible due to limitations such as coarse sampling intervals, measurement errors, or low effective sample sizes, diffusion rate can be used as a robust proxy for mean speed. While diffusion rate does not directly measure speed, it incorporates information on movement rate and directional persistence, offering insights into overall movement activity. Our findings highlight that, at coarse sampling intervals, diffusion rate is a more accurate, robust, and consistent measure of an animal's movement behavior that can be used in place of mean speed.

4.1 Relationship between mean speed and diffusion rate in white-tailed deer telemetries

Our results showed that mean speed and diffusion rate scale with a sublinear power relationship, suggesting that diffusion can be used to make population-level inferences about speed. However, this relationship does depend on movement behavior at the individual level. Because diffusion reflects the combined effects of speed and tortuosity, it can provide a better proxy for mean speed when tortuosity is less variable in the population, whether that be an ecological population or a statistical population of different behaviors. Tortuosity can vary from predominantly ballistic movement (e.g., moving between patches without exploring much) with low tortuosity and high directional persistence to predominantly exploratory movement (e.g., moving within patches) with high tortuosity and low directional persistence. Animals exhibiting highly directed ballistic movement (Visser & Kiørboe, 2006) will generate both large diffusion rates and mean speeds. In contrast, animals with highly tortuous movement that explore a large area will have high mean speeds but comparatively lower diffusion rates, as the space they fill does not scale linearly with speed. Therefore, all else being equal, increasing tortuosity will increase mean speed without substantially impacting the diffusion rate. This relationship highlights how movement characteristics—such as directional persistence and tortuosity—shape the scaling of speed and diffusion rates.

We expected a positive association between mean speed and diffusion rate within populations, and our results suggest this association is approximately linear on a log-log scale (i.e., sublinear on natural scales). However, this relationship may vary depending on the extent to which mean speed and tortuosity differ across individuals within the population, given differences in movement behavior and physiology. Further research on a broader range of species is needed to determine whether diffusion rate remains a simple proxy for mean speed and distance traveled at the population level. While diffusion rate is a measure of large-scale movement patterns and a useful alternative when speed estimates are unavailable or unreliable, it cannot be assumed to be proportional to speed or used as a direct proxy without consideration of the nonlinear scaling between the two variables and species- or individual-specific movement characteristics.

4.2 Effects of sampling interval on robustness of estimates in white-tailed deer telemetries

Our results demonstrated that diffusion rate is substantially more robust to coarse sampling intervals than speed and that it is easier to obtain realistic and accurate diffusion estimates under marginal data conditions. However, the oscillations in the mean and number of estimates over the sampling interval suggest that the ability to produce accurate estimates of diffusion (or any estimates at all) depends in part on the animals' heterogeneity in movement behavior. Unlike the simulations we present in section 3.3 and discuss below, animals do not have stochastic movement behaviors with a single mean. Instead, they often switch between behaviors (i.e., many different means, e.g., foraging, exploration, sleeping), so estimates of any movement behavior parameters will depend strongly on whether the sampling interval is a (sub)multiple of the animal's activity cycles: locations taken every 6 hours may provide highly biased estimates of home range size, speed, and diffusion if the animal of interest returns to its den every 6 hours to rest. This would be particularly visible in the unlucky case that all locations are taken when the animal is resting at its den and ignore the movement between each rest. For white-tailed deer, the oscillations in speed and diffusion estimates seem to occur on a 12-hour cycle with peak mean diffusion at 12-hour and 36-hour sampling intervals and lower mean diffusion at sampling intervals of 24 and 48 hours. These findings may correlate with white-tailed deer's tendency to be less active during certain periods of the day (Roden-Reynolds et al., 2022). Still, these results further demonstrate the robustness of diffusion rate over speed in terms of both effective sample size and estimate stability, supporting the use of diffusion rate as a reliable metric for analyzing movement in coarse or irregular telemetry datasets. An interesting perspective would be to combine location data with activity data and read variations of mean speed and diffusion rates against diel activity cycles (Hertel et al., 2017).

4.3 Relationship between speed and diffusion rate in simulated trajectories

The results from the simulated telemetries supported the empirical findings while also demonstrating why estimating speed is not always appropriate. Forcing a model to estimate speed when telemetry data do not contain (sufficient) information on an animal's speed and movement trajectory results in estimates that are most often biasedly low. This occurs because thinning telemetry data removes crucial fine-scale resolution on the tortuosity of the movement. While this is also true for diffusion, diffusion estimates are more reliant on the spatial variance of the locations (i.e., the area they cover) than the movement path.

While the results from the simulations strongly agree with the empirical results, they also demonstrate an important difference between the timescales of speed and diffusion. Because animals will change direction more often than they change their diffusion rate, speed changes at a faster rate than diffusion rate. Consequently, very fine sampling intervals will produce a large effective sample size for speed, but they will have a lesser impact on effective sample size for diffusion. This is because fine-scale sampling allows continuous-time models such as those fit by ctmm to obtain many independent estimates of speed (Noonan et al., 2019), but the number of independent diffusion values will be lower and often unaffected by sampling interval because it changes over longer timescales. Thus, if one is interested in estimating fine-scale, instantaneous estimates of speed (rather than simply mean speed), we echo the suggestion of Noonan et al. (2019) of choosing a sampling interval that is substantially ($\gtrsim$ 3 times) smaller than the directional persistence of the species of interest.

4.4 Implications and future research

Our results emphasize the complementary role of speed and diffusion rate in understanding animal movement and highlight the robustness and stability of diffusion rate when data quality is compromised due to coarse sampling or large measurement errors. In the absence of reasonable speed estimates, diffusion rate can serve as an effective alternative that allows inferences about movement patterns, space use, and energetics. By integrating both metrics, researchers can gain a more comprehensive understanding of movement behavior by using speed to assess fine-scale activity and energetics and diffusion to explore large-scale spatial patterns and ecological processes. This complementary approach allows researchers to infer behavioral and ecological dynamics even in challenging datasets and proposes diffusion rate as an essential tool for movement ecology alongside traditional metrics like mean speed and distance traveled. However, the nuances in the relationship between diffusion and speed highlight the need for continued research into how diffusion relates to movement energetics and activity budgets. Understanding these dynamics could enhance the ecological insights derived from metrics of diffusion, especially across species and movement contexts, for example, complementing location and accelerometry data (see also dead-reckoning approaches, e.g., Magowan et al., 2022). By leveraging both metrics in future studies, researchers can bridge the gap between fine-scale behaviors and larger-scale ecological processes while achieving a more holistic view of animal movement and its implications for individuals, the surrounding community, and the landscape.

Data Availability Statement

The data and code used in this study are publicly available on the Open Science Framework (OSF) repository at the following link: https://osf.io/4hgev?view_only=c6ac7024b1454cffb662db8c5d79c3aa. This includes all datasets and analytical scripts necessary to reproduce the results presented in this manuscript.

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CHAPTER 3. EFFECTS OF VASECTOMY ON BREEDING-RELATED MOVEMENT AND ACTIVITY IN FREE-RANGING WHITE-TAILED DEER

Movement Ecology
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Abstract

Background: An abundance of white-tailed deer (*Odocoileus virginianus*) in suburban communities can lead to problems such as increased deer-vehicle collisions (DVCs), tick-borne illnesses, and forest degradation. Deer populations can be managed using traditional lethal methods; however, these methods are often impractical, ineffective, or socially unacceptable, prompting interest in management alternatives, including fertility control. Some fertility control methods (such as vasectomy, tubal ligation, and porcine zona pellucida-based vaccines) cause unsuccessfully bred females to experience multiple estrous cycles, potentially altering their movement behavior and fine-scale activity. Such changes could increase the risk of DVCs and negatively affect the physical condition of the animals. However, the effects of such treatments on animal behavior remain poorly understood, specifically in terms of breeding-related movements and energetics. This study aimed to evaluate the behavioral impacts of a large-scale vasectomy program on white-tailed deer.

Methods: We conducted a 2-year study using a treatment/control design and analyzed biologging data of white-tailed deer at two sites near New York City, USA. We used a moving-window approach to assess the effects of a large-scale vasectomy program on the seasonal changes in movement behavior (home-range size, distance traveled, diffusion, and excursivity) and fine-scale activity (time spent in low-activity states and the daily number of state transitions).

Results: There were no biologically significant differences in movement behavior or activity trends in either sex between the treatment and control groups. Females in both groups exhibited similar trends in all movement metrics, but females at the treatment site tended to switch between activity states more often in winter. Males at the treatment site expanded their space use less than control males during peak breeding season but otherwise exhibited similar movement behavior trends. Mortality rates and causes were similar at both sites.

Conclusions: The vasectomy program, despite causing extra estrus periods in unsuccessfully bred females, is unlikely to cause appreciable behavioral changes that could exacerbate management-related issues at the time scales investigated. Fertility control methods inducing extra estrus periods could be implemented alone or alongside other strategies to reduce abundant deer populations with minimal impact on behavior.

Keywords: accelerometer, contraception, ctmm, fertility control, GPS, *Odocoileus* sp., population management, suburban wildlife

Introduction

Over the last century, deer populations have expanded in suburban and urban areas across North America, Europe, and Asia, leading to a range of human-deer conflicts and ecosystem impacts [1]. Among the most pressing concerns are deer-vehicle collisions (DVCs) [2], damage to agricultural and residential landscapes [3], overbrowsing of native vegetation [4, 5], and the spread of tick-borne diseases [6]. Local reductions in deer densities, achieved through lethal methods (e.g., controlled hunting and culling), translocation, and fertility control, have been shown to reduce these conflicts [5, 7, 8]. While lethal methods remain the most common approach, they are often impractical, ineffective, or socially unacceptable in densely populated suburban and urban environments, leading to increased interest in non-lethal alternatives like fertility control [9].

Fertility control methods include surgical (e.g., vasectomy, ovariectomy, and tubal ligation) and non-surgical (e.g., immunocontraceptive vaccines and hormonal methods) options [10]. These approaches aim to reduce or eliminate reproductive output and, over time, lower population densities. These techniques have shown success in cases where reproduction is reduced to near zero, and immigration is minimal [11, 12]. However, some fertility control techniques prevent conception without halting estrous cycles in unbred females, leading to concerns that this behavioral change could alter movement patterns and increase human-wildlife conflicts. In particular, treatments such as vasectomy, tubal ligation, and porcine zona pellucida (PZP) immunocontraceptive vaccines result in repeated estrous cycling in unsuccessfully bred females, which may prolong movement-intensive breeding behaviors and elevate the risk of DVCs [13-15]. Several studies suggest that DVC rates increase during the breeding season due to increased movement and activity [16, 17]. Concerns about movement change due to repeated estrous cycling are frequently cited in debates over the suitability of fertility control as a management tool but have rarely been tested in free-ranging populations [10, 13-15].

Breeding-related movement behavior in male and female white-tailed deer (*Odocoileus virginianus* Zimmerman; hereafter, deer) has been studied extensively [18–22]. The breeding season results in the first annual estrous period in females and peak testosterone levels in males [23, 24]. Female deer generally show increased movement and activity during the breeding season, with peak activity occurring around conception [22]. Excursive behavior may increase a female's chances of encountering a male during receptivity, especially in populations with low densities or female-biased sex ratios [18, 22]. Male deer exhibit distinct movement patterns during the breeding season, characterized by increased activity and larger home ranges [20, 21]. Females who fail to conceive due to fertility control measures may have repeated estrous cycles (~1–2 days every ~25 days), potentially into late winter [13, 14, 15]. These additional cycles may lead to extended breeding activity and movement [14, 15], which, in turn, may increase the animals’ energetic expenditures and the risk of DVCs [16, 17, 25]. Evaluating the overall effectiveness and applicability of fertility control treatments thus requires understanding the treatment's side effects on animal behavior [10]. This research aimed to address these concerns by quantitatively assessing the implications of a large-scale vasectomy program that induces multi-estrous cycling in female deer through a semi-experimental, multi-scale, treatment-control study.

Between 2016 and 2024, New York City Parks and Recreation conducted an in-situ research program at Staten Island, New York, USA, to assess the potential effectiveness of a large-scale male vasectomy program in reducing the local deer population [26]. This study aimed to assess the behavioral impacts of this fertility control initiative, providing critical insights into its effects on movement behavior and activity in an urban/suburban deer population. Between 2021 and 2023, we collected Global Positioning System (GPS) and accelerometry data from biologging devices on male and female deer at the treatment site and compared them with the data of untreated males and females at a nearby control site. We examined the movement and activity patterns over time, focusing on trends during the expected period of additional estrous cycles (January–April; see S3: Table 4). We hypothesized that females at both sites would exhibit increased movement and activity during estrus periods, but that male movement and activity would peak only during the November-December breeding season, regardless of treatment status due to naturally declining testosterone levels [23]. By quantifying these patterns, this study provides much-needed empirical evidence on the behavioral impacts of fertility control, informing future management decisions in suburban deer populations.

Materials and methods

Study areas

Treatment site – Staten Island, New York, USA

Staten Island (SI) is a borough of New York City (NYC), New York, USA (40.598237, −74.144319; Fig. 5A) that covers an area of ~155 km^2, ~35% of which is considered deer habitat (e.g., grassland, deciduous hardwood forest, and marsh areas greater than ~2 ha) [26]. It is the least populated of the five boroughs of NYC (2022 human population: 495,925) and contains nearly 5,000 ha of protected parkland. The remaining area is a mix of single- and multi-family housing development, commercial development, other open spaces (e.g., golf courses and cemeteries), and roads. Over 97% of antlered SI males have been vasectomized, and hunting is prohibited within NYC limits [26]. We focused our capture efforts on The Greenbelt and Freshkills areas of SI (bounded area in Fig. 5A), specifically targeting these areas to closely resemble the contiguous open space at the control site. The area used by the individuals in this study encompassed 45.7 km^2 of open spaces and developed areas.

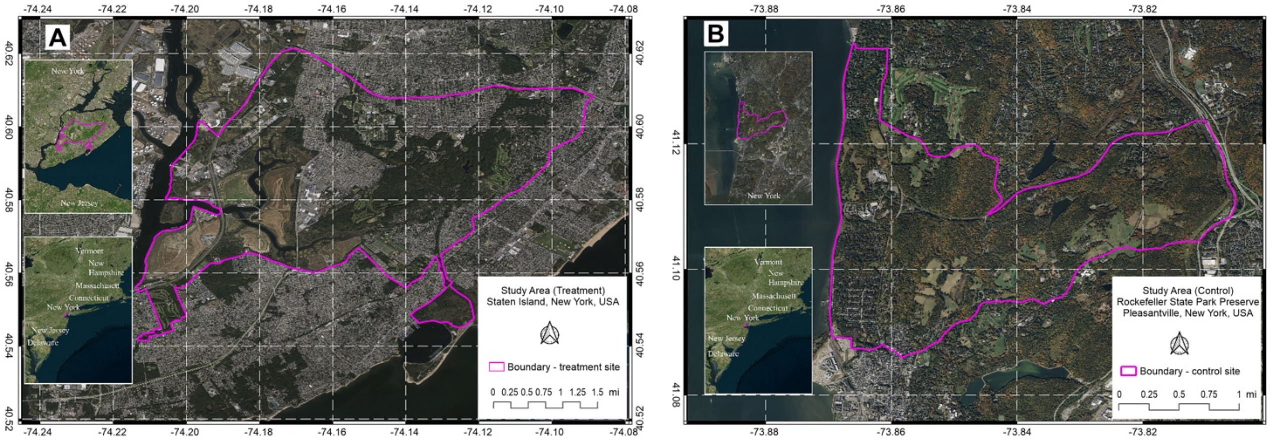

Figure 5 — A. Map of the treatment study area in Staten Island and its location in New York State and the northeastern United States. B. Map of the control study area in Rockefeller State Park Preserve in the context of New York State and the northeastern United States. The control site is located ~50 km north of the treatment site.

Control site – Rockefeller State Park Preserve, Pleasantville, New York, USA

The Rockefeller State Park Preserve (RSPP; 41.107083, −73.839131; Fig. 5B) is located in Pleasantville, New York, USA, in Westchester County. This site is ~50 km north of the treatment site. The preserve encompasses 7.2 km^2 of deciduous hardwood forests, agricultural pastures, grasslands, and aquatic habitats (J. DiPaola; personal communication; 13 February 2023). The forested area is dominated by several species of oak (*Quercus* spp.), tulip poplar (*Liriodendron tulipifera*), maple (*Acer* spp.), and American beech (*Fagus grandifolia*). Several water bodies are in the preserve, including the centrally located 7.7 ha Swan Lake and numerous interconnected streams. An ~88.5 km network of carriage roads serves as trails for both pedestrian and equestrian traffic. Several roadways run adjacent to and intersect portions of the preserve, with certain boundaries of the park demarked by fences 2.5 m or higher. Many of these fences lack consistent maintenance and feature breaches that facilitate wildlife passage. The preserve is surrounded by ~8.1 km^2 of residential property with lot sizes varying from 0.4 to 5 ha. During the first year (2021–2022), deer hunting was allowed in the eastern section of the preserve (east of Route 448). Between September and December 2022, several hunters were also active in small areas on the northwestern side of the park. None of the study deer and only two non-study animals were harvested during the study period. We focused our capture efforts in areas where hunting was restricted. The area used by the individual deer in this study comprised 14.1 km^2 of open spaces and developed areas.

At both study sites, peak breeding normally occurred in mid-November, with the breeding season starting in late October and ending in late December [23].

Capture and data collection

We aimed to collect the data comprising a minimum of 10 adult males and 20 adult females at each study site during each of the two study years, and we captured additional individuals when mortalities occurred. We immobilized adult deer using dart projectors [27] and the capture protocol outlined in DeNicola & DeNicola [12]. All captured deer were fitted with biologging devices (Vertex Plus with a 32 Hz Advanced 3-axis acceleration sensor; Vectronic Aerospace GmbH, Berlin, Germany) that contained GPS loggers, triaxial accelerometers, and an automatic drop-off mechanism. We estimated the weight based on chest girth measurements and age based on tooth wear [28]. No fawns or yearlings (deer younger than two years old) were handled to better reflect the expected age structure in a high-treatment vasectomy program, where the population would primarily consist of adult individuals if reproduction were reduced or eliminated. While approximate ages were estimated, all individuals were classified as adults due to the inherent imprecision of live aging in deer. All capture and handling procedures were conducted in accordance with the New York Department of Environmental Conservation Scientific Collection Permit (LCP #2100). All male deer included in the study at the treatment site underwent vasectomies during the previous field seasons, and ~97% of antlered male deer at the treatment site were vasectomized [26]. Population dynamics are beyond the scope of this study.

We scheduled the GPS devices to obtain 1-h fixes. To extend the battery life, only six daily GPS fixes (one every 4-h) were transmitted via satellites. The remaining 18 daily fixes were stored in the collar until retrieval. Triaxial accelerometers were used to record data at 32 Hz with a sensitivity of ±4 g (surge (X-axis), sway (Y-axis), and heave (Z-axis)). We defined the behavioral periods as pre-breeding (22 September–18 October), breeding (20 October–4 January), peak breeding (10 November–30 November), and post-breeding/extra estrus periods (5 January–1 April) [23]. During Year 1 (August–May 2022), collars were removed on 30 May 2022 to ensure device refurbishment for Year 2 deployment. In Year 2 (August 2022 to June 2023), the collars were removed on 20 June 2023. Data were collected between the device deployment and remote drop-off or animal death.

GPS data analyses

We preprocessed the raw GPS data after downloading from MoveBank (MoveBank Study ID: 1879977576; S3: Table 5) and then estimated the changes in movement over time for each animal using the continuous-time speed and distance (CTSD) method [29]. This method is based on the continuous-time movement modeling workflow via the ctmm package (1.2.0) [30] in R (4.4.0) [31]. To quantify the changes in movement behavior, we modeled each animal's telemetry data using a moving-window approach [32] (also see the empirical example by [33], in which each window had a size and slide of seven and three days, respectively, resulting in overlapping 7-day estimates. We selected a 7-day window to identify fine-scale temporal variations in movement behavior (e.g., peak breeding season, proestrus/estrus) [14, 23] while maintaining sufficiently abundant range crossings (e.g., frequent movements across the boundaries of the estimated home range to provide enough data points to define home range reliably) to produce reasonable estimates of home-range (HR) size [34]. Because deer collared after late August were not tracked during summer (S3: Fig. 11B), the dates for each window were converted to the number of days after 1 August to ensure continuity between December and January of the following year (S3: Fig. 11C).

We fit a movement model to each 7-day subset of telemetry data using the ctmm.select() function to determine the best-fitting model as a function of sampling frequency and the degree of autocorrelation in the tracking data [30]. From each model, we extracted the animal's 7-day HR size and, when possible, the average daily anomalous diffusion, average daily distance traveled (i.e., average speed), and excursivity. Diffusion was calculated as the asymptote of the time-dependent expected square displacement over a finite period of time, which results in superdiffusion for time lags below an animal's foraging timescale, linear diffusion for time lags greater than the foraging timescale but smaller than the range-crossing timescale, and asymptotic diffusion for time periods longer than the range-crossing timescale [35]. Excursivity was determined by calculating the daily mean quantile of each animal's utilization distribution [36], which we estimated using Autocorrelated Kernel Density Estimation [37] on the full telemetry dataset of each individual (keeping the two years separate; see S3: Fig. 12).

Modeling movement behavior

We estimated the differences in movement behavior over time between sexes at each site using the mgcv package [38] in R software to fit four hierarchical generalized additive models for location and scale (HGAMLS) [38–41]. Specifically, we fit HGAMLSs with gamma location-scale families of distributions to 7-day HR size, average daily distance traveled, and average daily diffusion (because all three were strictly positive; see S3: Table 6), whereas we modeled excursivity using an HGAMLS with a beta location-scale family of distributions. The code for the family was provided to us by Dr. Simon Wood, the developer and maintainer of the mgcv package, and is available in our GitHub repository.

All four models had the same set of three terms for both the mean and scale linear predictors: (1) A group-level fixed-effect intercept and smooth term of time (days since 1 August) accounted for differences across each combination of sex and treatment level. (2) A "sum-to-zero" smooth term of time between the two study years (for each combination of sex and treatment level) accounted for the differences between study years while weighing each year equally. (3) A factor-smooth interaction term for each animal in each study year accounted for individual-level deviations from the group-level mean. See S3: Table 13 for additional model details.

Accelerometer data analyses

To quantify fine-scale movement behavior, we defined accelerometer-based activity states for each animal that we derived using vectorial dynamic body acceleration (VeDBA) [41], a rotationally invariant metric proportional to body movement that is strongly and positively associated with energy expenditure [42]. We estimated the static acceleration using the three mean acceleration axes (X, Y, and Z) in non-overlapping 2-s intervals, and we calculated the log mean VeDBA for each interval to quantify the intensity of activity [43]. To account for differences among devices, animals, and the positioning of the devices on animals' necks, we defined behavioral states for each individual based on each collar's local minima in the distributions of log mean VeDBA, with VeDBA = 0 (log mean VeDBA = − Inf) as a no-activity state. We thus had four states, namely no, low, medium, and high activity. We visually inspected the log mean VeDBA histograms for each month for 10 individuals to ensure consistent minima values over time. To quantify changes in daily behavior, we computed the daily proportion of time spent in each activity state and the daily number of transitions between different states. Additional details can be found in Additional file 7.

Modeling time in activity states and transitions

To estimate the effects of the treatment on fine-scale movement behavior, we used the mgcv R package [38] to fit hierarchical generalized additive models (HGAMs) to the proportion of time spent in the no- or low-activity states and the daily number of transitions between states (S3: Table 7). The first HGAM used a beta distribution and logit link function, whereas the second HGAM used a negative binomial family of distributions and a log link function. The HGAMs had the same terms as the HGAMLSs described in the previous section (S3: Table 6) but assumed a common and constant mean-variance relationship (i.e., a common and constant scale parameter).

Results

Capture and collaring

Between 23 August and 13 December 2021 (Year 1) and 14 August 2022 and 8 January 2023 (Year 2), 158 adult deer (a total of 52 males and 106 females in SI and RSPP; S3: Table 8) were captured and fitted with biologging devices. Seven devices failed to transmit GPS fixes (S3: Fig. 11A); therefore, we included only collar-stored GPS fixes (e.g., one fix/4-h) and accelerometry data for these animals in the analyses. In Year 1, we excluded 10 individuals from the study who died before the first frost due to unknown causes during a known epizootic hemorrhagic disease outbreak (the tracking duration was typically less than 45 days and not during the periods of interest). Similarly, we excluded 23 individuals from the study with tracking periods of <28 days and one owing to collar failure. At both sites, eight females and two males were tracked in both years. Our final sample, therefore, included data from 21 males and 42 females in Year 1 and 19 males and 42 females in Year 2 (Table 3).

Table 3 — Number of individuals captured and the number of individuals included in the study (# individuals captured; # individuals included in the study) at the treatment site in Staten Island, NY, USA and at the control site in Rockefeller State Park Preserve, Pleasantville, NY, USA in both study years (2021–2022; 2022–2023).

	Year 1		Year 2	
	SI	RSPP	SI	RSPP
Females	34; 21	27; 21	24; 22	21; 20
Males	17; 11	13; 10	12; 10	10; 9

Among the animals in the study from Year 1, we recorded nine mortalities (collars collected on 30 May 2022), whereas in Year 2, we recorded five (collars collected on 20 June 2023; S3: Table 9 and Table 10). None of the animals in the study were harvested through hunting at the control site; however, poachers killed two study individuals at the control site. In the final set of monitored deer, we recorded seven DVC-related mortalities (4 in SI and 3 in RSPP) and four owing to unknown causes (1 in SI and 3 in RSPP). The mortality rate of individuals in the study was overall lower at the treatment site, but there were no significant differences at the $\alpha = 0.10$ level, even within sexes. Fisher's exact test produced the following estimated odds ratios (treatment relative to control): 0.55 overall ($P = 0.3861$), 1.4 ($P = 1.0$) for males, 0.29 for females ($P = 0.1511$).

Movement behavior

We produced HR size estimates for all 7-day windows for all individuals and removed 99 estimates (1.05% of the total; S3: Table 11) because of a lack of range residency that resulted in excessively large estimates (>10 km^2; range: 10–179 km^2). Only 60.3% of the ctmm movement models had sufficiently fine telemetry data to estimate the daily distance traveled, but almost all movement models (98.9%; S3: Table 11) could produce daily diffusion estimates.

Females in both groups exhibited similar sizes and trends over time in all four movement metrics (Fig. 6; S3: Table 12 and Table 13). Males in the control site increased their 7-day HR size, daily distance traveled, daily diffusion, and daily excursivity around the peak of the November breeding season (all four approximate p-values < 2.7e-06; see Fig. 6, S3: Table 12 and Table 13). After early December, the daily distance traveled, daily diffusion, and excursivity measures declined to previous values and remained approximately constant, whereas the 7-day HR size exhibited a less noticeable increase and decrease. Males in the treatment site did not change their HR size significantly over time (approximate p-value = 0.60) and had less pronounced peaks in diffusion (approximate p-value: < 2e-16) and excursivity (approximate p-value: 7.87e-05), but we found no appreciable differences between the temporal trends in the mean daily distances traveled by the treated and control males. All four models explained ≥80% of the deviance.

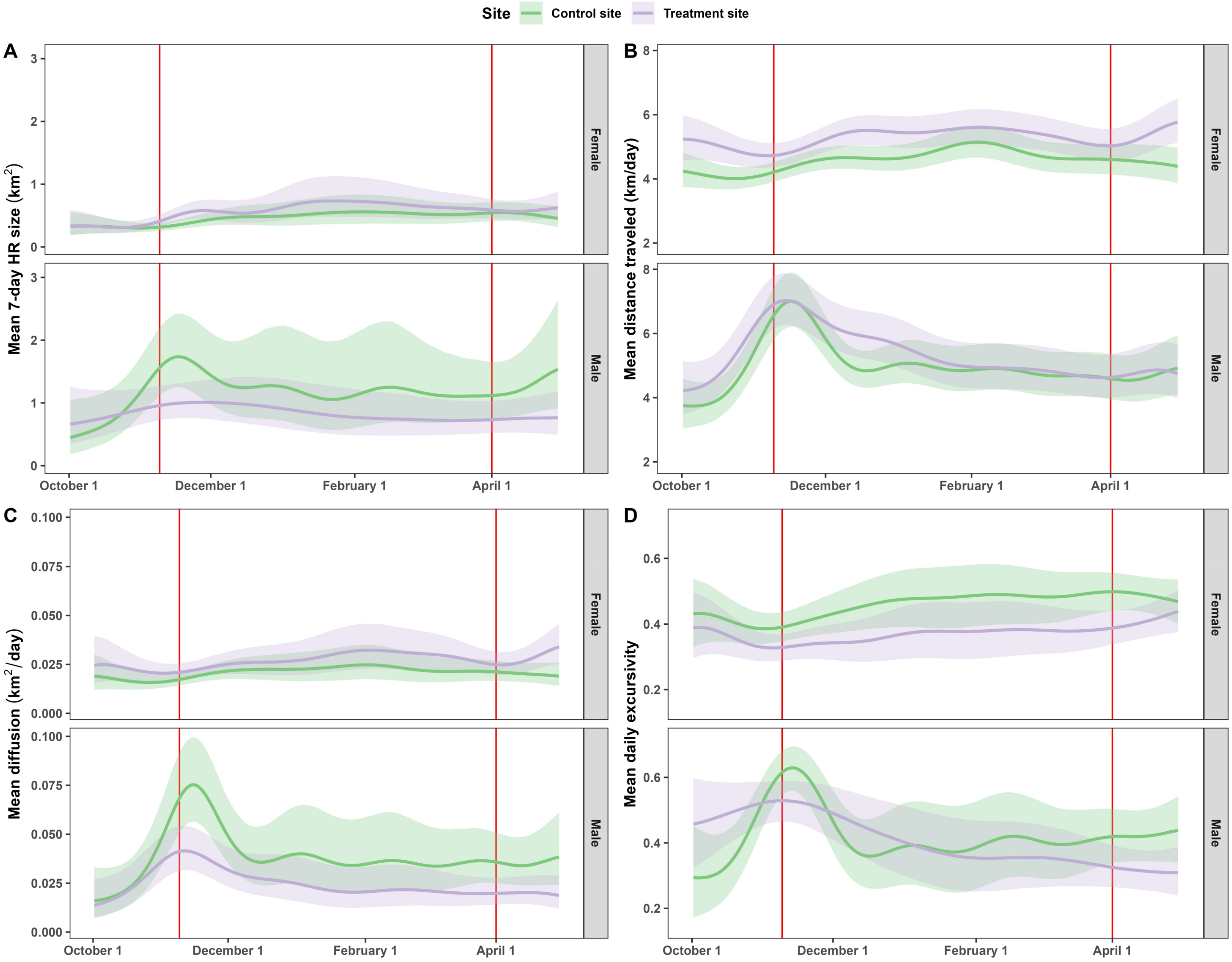

Figure 6 — Trends in the mean 7-day home range (A), daily distance traveled (B), daily diffusion (C), and daily excursivity (D) over the day of the year by sex and treatment status. The 95% Bayesian credible intervals were estimated using a Gaussian assumption of the residuals and account for uncertainty in the scale parameter. The first red line indicates the beginning of peak breeding season (10 November), and the second indicates the end of the potential extra estrus periods (1 April).

Activity

The log mean VeDBA distribution included three distinct peaks across all individuals in our study (S3: Fig. 13). Upon inspecting the subset of 10 individuals, we found no differences in the histogram's monthly local minima values compared with that of the full year (S3: Fig. 14), indicating that these peaks could be used as activity levels to consistently characterize behavior across individuals.

Vasectomized males tended to spend a greater proportion of time in the no- or low-activity states, but we found no appreciable difference between females at the two sites (Fig. 7A; S3: Table 12 and Table 13). At both sites, males showed comparable increases in daily state transitions in fall and similar values throughout the year (Fig. 7B). Treatment-site females exhibited more daily behavioral transitions in winter, but there were no appreciable differences between fall, late winter, and spring (Fig. 7B). Both models explained most of the deviance (state: 64.4%, daily transitions: 70.7%).

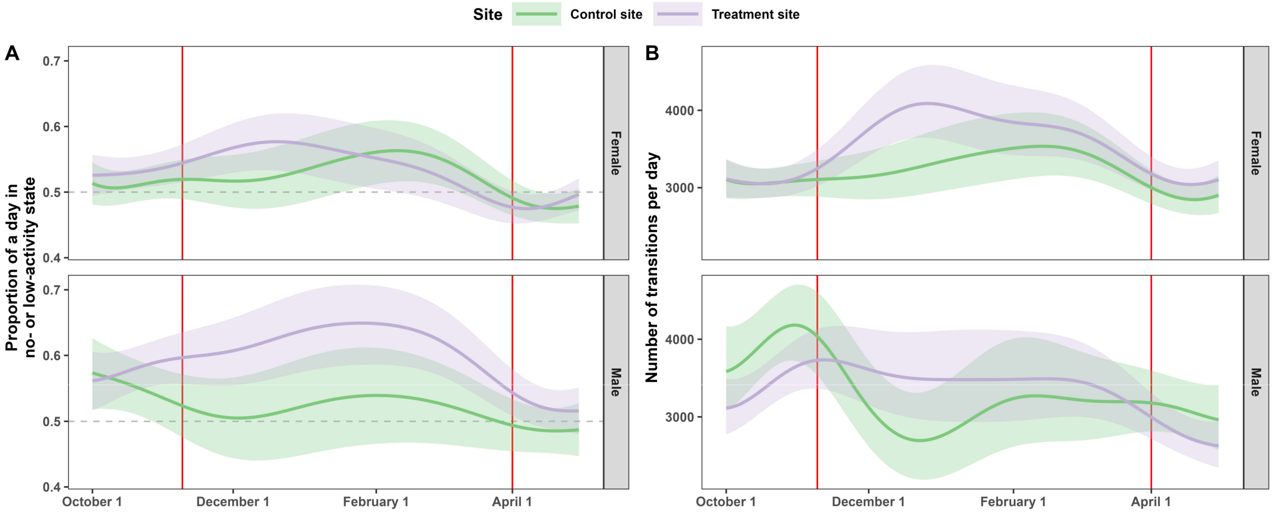

Figure 7 — Mean trends over the day of the year in the proportion of time spent in the no- or low-activity state (A) and the daily number of transitions between states (B) by sex and treatment status. The colored line shows the model-predicted mean, whereas the shaded ribbons indicate the

associated 95% Bayesian credible intervals (under the assumption of Gaussian residuals). The first red line indicates the beginning of peak breeding season (10 November), and the second indicates the end of the potential extra estrus periods (1 April).

Discussion

This study examined the effects of a high-percentage vasectomy program (>97%) on breeding-related movement and activity behaviors of free-ranging deer [26]. We focused on whether males and females in the treatment area exhibited prolonged breeding-related movements and increased activity beyond the peak breeding season due to repeated estrus periods in unsuccessfully bred females. We hypothesized that males would not exhibit any biologically significant differences in movement behavior or activity between sites, whereas females would show differences in fine-scale activity but not movement behavior during extra estrus periods (S3: Table 4). Overall, our findings revealed minimal differences in movement behavior and activity between the treatment and control sites, with no appreciable variations attributable to extra estrous cycling at the treatment site. Treatment site movement behavior and activity were consistent with the hormonally-driven patterns exhibited at the control site. At both sites, female patterns were relatively stable throughout the study period, and male movement behavior peaked in November and declined throughout winter. This consistency in pattern between sites supports the conclusion that fertility control methods leading to extra estrus periods can be implemented with minimal population-level behavioral alterations at the time scale studied.

Female deer movement behavior and activity

As hypothesized, we did not find appreciable differences between the groups' large-scale movement behaviors during the extra estrus periods. While this may be due to the brief duration of estrus bouts and pre/post conception activity (48-96 hours) [14, 22] relative to the window size (7 days), narrower windows would have likely produced less accurate movement metrics (particularly HR size) owing to insufficient effective sample sizes [34]. A lack of synchronization across estrus periods could also cause the HGAMLS to fail to detect common oscillations, but sensitivity analyses showed little to no change in both the group-level and individual-level smooth terms, even for very large basis sizes (k = 30; not shown).

The slight tendency of treated females to spend more time in lower activity states while exhibiting more state transitions per day suggests that they may be less active overall but more responsive to nearby males during additional estrus periods. However, this difference does not appear substantial enough to negatively impact body condition, especially because females at the treatment site are unlikely to be gravid [26]. Existing studies comparing PZP-treated and untreated females indicate that non-gravid, non-lactating treated females tend to maintain or even improve body condition relative to gravid or lactating females [15]. This suggests that females at the treatment site may similarly maintain or improve body condition, as they are not subjected to the high metabolic demands of gestation, parturition, and lactation. Finally, mortality rates were lower at the treatment site, further suggesting that the program had minimal adverse effects and reinforcing the program's safety.

Male deer movement behavior and activity

Our analysis found no substantial differences in the movement behavior of male deer between treatment and control groups. While treated males had lower measures and smoother curves for HR size, diffusion, and excursivity during the breeding season, there were minimal variations thereafter, suggesting that both groups behaved similarly (e.g. males increase movement during peak breeding and decrease it in subsequent months). These patterns align with the findings of previous studies on breeding-related behavior [19–21] in which expanded breeding-related movement in male deer is linked to day length and peak testosterone levels [24]. As we expected, males at the treatment site did not maintain the larger breeding-related movement levels in January–March, despite female's extra estrus periods. The flatter trends at the treatment site suggest a less pronounced peak breeding season. This could indicate that unsuccessfully bred females can enter estrus earlier in the year because they do not expend energy in gestation and lactation [45] and that males may remain active as unsuccessfully bred females return to estrus in mid-to-late December; however, their overall patterns remained similar to males at the control site. An alternative explanation for the less pronounced peak could be related to differences in habitat between the two sites. Suburban environments provide high-quality edge habitat, offering reliable anthropogenic food sources, such as ornamental plantings, bird feeders, and landscaped green spaces [46, 47]. These anthropogenic resources can reduce the need for long-distance foraging movements, potentially leading to more localized activity patterns compared to deer in more rural or agricultural settings [48–50]. Although the two sites had comparable habitat in areas where we captured deer, individuals on Staten Island ultimately occupied more habitat that included impervious surfaces (e.g., dwellings, office parks), which may have increased their access to anthropogenic resources and contributed to reduced overall space use (S3: Table 14) [49].

Contrary to previous observations on breeding behavior [20, 21], the 7-day HR size did not decrease to early-fall levels after December at either site. Testosterone-linked movements associated with breeding typically diminish in late December, leading to more localized, sedentary feeding behavior [24]. Nevertheless, there were clear differences in how males moved within their HR post-peak breeding (daily distance traveled, daily diffusion, and excursivity all declined), which suggests behavioral shifts following the breeding season.

Treatment-site males showed a marginally higher tendency to spend more time in the no- and low-activity states than control-site males, but the higher number of transitions between activity states, especially in December and January, may suggest extended responsiveness to females in estrus. However, this did not correlate with any variation in activity levels that could be associated with illness or compromised health [51, 52], such as an increased proportion of time in low-activity states indicating illness. This conclusion is also supported by the lack of unexplained male mortalities (see Methods) and a consistent long-term pattern in carcass pickups (no increase during or after extra estrus periods; S3: Table 10).

Implications and future research

This study provides a comprehensive analysis of the breeding-related movement and activity patterns of free-ranging deer using precise, high-resolution data that surpasses the limitations of coarse datasets and captive animal studies that have influenced the existing literature. Our findings challenge the primary management concerns related to fertility control programs, specifically the potential for increased DVCs and reduced body condition due to prolonged breeding-related movements. We observed no evidence of negative outcomes during the study period, suggesting that vasectomy programs may induce negligible behavioral and social changes without significant impacts on population health or public safety. To further bolster our conclusions, closely monitored DVCs have declined by 75%, and the overall population has declined by 45% since the inception of the vasectomy program in 2016 [26]. However, the results of this study should not be assumed to be universally applicable to other ungulate populations. Nevertheless, the absence of appreciable negative outcomes in this context supports the continuous use of this program as a safe and humane management tool.

However, several limitations must be considered. Movement patterns may have been influenced by the fragmented suburban habitat at the treatment site and the agriculturally productive habitat at the control site [46, 47]. However, we were able to observe movement changes in males during the peak breeding season and subsequent declines post-breeding regardless of treatment status–we would expect to see this behavioral change in any habitat at any density. Additionally, we could not determine the reproductive status of all females, though we assumed most treatment-site females were non-reproductive based on population estimates and a ~95% reduction in fawning at the treatment site [26]. Investigating the effects of late gestation and parturition on female movement could provide additional insights. Future research on the effects of age-class distribution and density on breeding-related movements would facilitate the evaluation of the broader implications of this program.

Conclusions

We presented the first fine-scale study of the effects of a high-percentage vasectomy program on a population of deer. While fertility control methods are often disregarded owing to concerns about behavioral changes, we used a multi-scale, treatment-control, semi-experimental design with robust quantitative analysis to demonstrate that using high-percentage vasectomies as a means of population control had no biologically significant adverse effects on deer's movement behavior or activity. The approach used in this study can inform broader management practices, and this framework may be adapted to evaluate other wildlife management interventions, offering valuable insights into their long-term ecological impacts.

Availability of data and materials

Data and code are available on GitHub at https://github.com/StefanoMezzini/ny-deer-vasectomy, where we provide all derived data required to run our analysis (e.g., R code and data). Raw GPS data supporting this research are sensitive and not available publicly but are available to qualified researchers; use of these data will be restricted to research, and users will not be allowed to distribute the data. Raw GPS data for white-tailed deer are owned by Field Engine Wildlife Research and Management and are available by contacting the organization (vickie.denicola@fieldengine.com) and requesting the GPS data from New York City white-tailed deer vasectomy program between 2021 and 2023.

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CHAPTER 4. MONITORING THE EFFECTS OF OVARIECTOMY ON SEASONAL MOVEMENT BEHAVIOR IN SUBURBAN FEMALE WHITE-TAILED DEER USING IOT-ENABLED DEVICES

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Abstract

Conflicts caused by abundant deer populations in suburban communities are common, but traditional population reduction methods, such as controlled hunting, can be challenging to implement in these contexts. Fertility control, specifically through ovariectomy, can limit reproduction and reduce populations in certain settings, yet its effects on movement behavior remain poorly understood. Concerns persist that hormonal changes affecting movement could lead to increased energetic costs and influence deer-vehicle collision (DVC) risks.

We evaluated the effects of ovariectomy-induced anestrus on the seasonal movement behavior in female white-tailed deer (*Odocoileus virginianus* Zimmermann) using Internet of Things (IoT) biologging devices connected via a low-power wide-area network (LPWAN). From 17 January 2023 to 1 June 2024, we collected telemetry data from ovariectomized (treated) and untreated (control) female deer in South Euclid, Ohio, USA, and quantified seasonal movement patterns using continuous-time movement models with a moving-window approach to estimate 7-day home-range (HR) size, daily diffusion, and daily excursivity.

Treated females maintained stable movement patterns year-round, whereas untreated females exhibited seasonal increases in HR size, diffusion, and excursivity leading up to and during the breeding season (late July–November). During and after parturition (late May), untreated females reduced HR size and overall mobility. These findings suggest that ovariectomy removes the hormonal triggers that typically drive seasonal movement changes. We found no clear evidence that ovariectomy increased energetic costs or excursive behavior, nor that it led to higher DVC risk, although our sample size was limited.

Additionally, LPWAN-enabled IoT tracking proved to be a viable, low-cost, low-power, lightweight method for wildlife monitoring, as compared to traditional GPS biologgers, but base-station-dependent data download was irregular, at times. We recommend further research to build on our findings, which provide insights into the viability of ovariectomy to manage deer populations and highlight the potential and limitations of IoT-based biologging for wildlife research.

Keywords: deer management, fertility control, GPS, IoT devices, Odocoileus spp., population management

Introduction

Managing abundant deer populations is a significant concern in suburban and urban areas globally (Nugent et al., 2011; Krausman et al, 2014; Curtis, 2020). Expanding deer populations contribute to increased deer-vehicle collisions (DVCs; Bissonette et al., 2008; DeNicola and Williams, 2008), landscape damage (Waller and Alverson, 1997), and the spread of tick-borne diseases (Kuehn, 2013; Telford, 2017). Traditional deer management strategies rely on controlled and recreational hunting (Boulanger et al., 2014; Curtis, 2020), but fertility control has gained interest as a potential management alternative in suburban settings where hunting is often restricted or impractical (Fagerstone et al., 2006).

Fertility control methods, including surgical sterilization and immunocontraceptive vaccines, have been studied for their ability to limit reproduction (Matschke, 1977; Warren and Warnell, 2000; Boulanger et al., 2012; Massei and Cowan, 2014; DeNicola and DeNicola, 2021). However, little is known about how these interventions influence movement behavior, which is critical in assessing their management implications (Gray and Cameron, 2010). Hormonally driven changes in space use can influence energy expenditure, social behavior, and human-wildlife interactions such as DVCs (Bertrand et al., 1996; Beier and McCullough, 1990; Hothorn et al., 2015; Stickles et al., 2015). Female white-tailed deer (*Odocoileus virginianus* Zimmermann; hereafter, deer) often exhibit distinct movement shifts associated with reproduction, including increased mobility before breeding and parturition, followed by reduced movement post-parturition (Bertrand et al., 1996; D'Angelo et al., 2005; Kolodzinski et al., 2010; Debeffe et al., 2014; Sullivan et al., 2017; Wright et al., 2021). Methods that eliminate estrous cycling and, subsequently, parturition—such as ovariectomy and GnRH immunocontraceptive vaccines—may disrupt these movement cycles, potentially leading to more stable, year-round movement patterns.

Recent advances in wildlife tracking now enable low-cost, lightweight, low-power, long-term movement data collection through Internet of Things (IoT) biologging devices. While traditional GPS collars are widely used in wildlife research, the devices are costly, require large battery units, and have relatively expensive data transmission costs, making deployment challenging, particularly for studies with budget constraints. In contrast, IoT biologging devices, such as those used in this study, leverage existing low-power wide-area networks (LPWANs) to provide an alternative tracking method (Wild et al., 2023). This technology can use existing LPWANs where coverage exists, or the user can set up commercially available cellular-connected base stations to provide data transmission capabilities. These systems enable continuous, high-frequency data collection at a fraction of the cost of traditional GPS systems.

Beginning in January 2022, the city of South Euclid, Ohio, USA adopted an integrated deer management strategy, combining professional sharpshooting with surgical sterilization via ovariectomy to manage an abundant deer population in a densely developed suburban environment (Boulanger and Ellingwood, 2024). In this free-range treatment-control study, we used IoT biologging devices connected via a LPWAN to evaluate seasonal movement patterns in ovariectomized and untreated female deer in South Euclid. To understand the effects of ovariectomy-induced anestrus, we tracked individuals from January 2023 to June 2024 and quantified movement behavior across reproductive seasons.

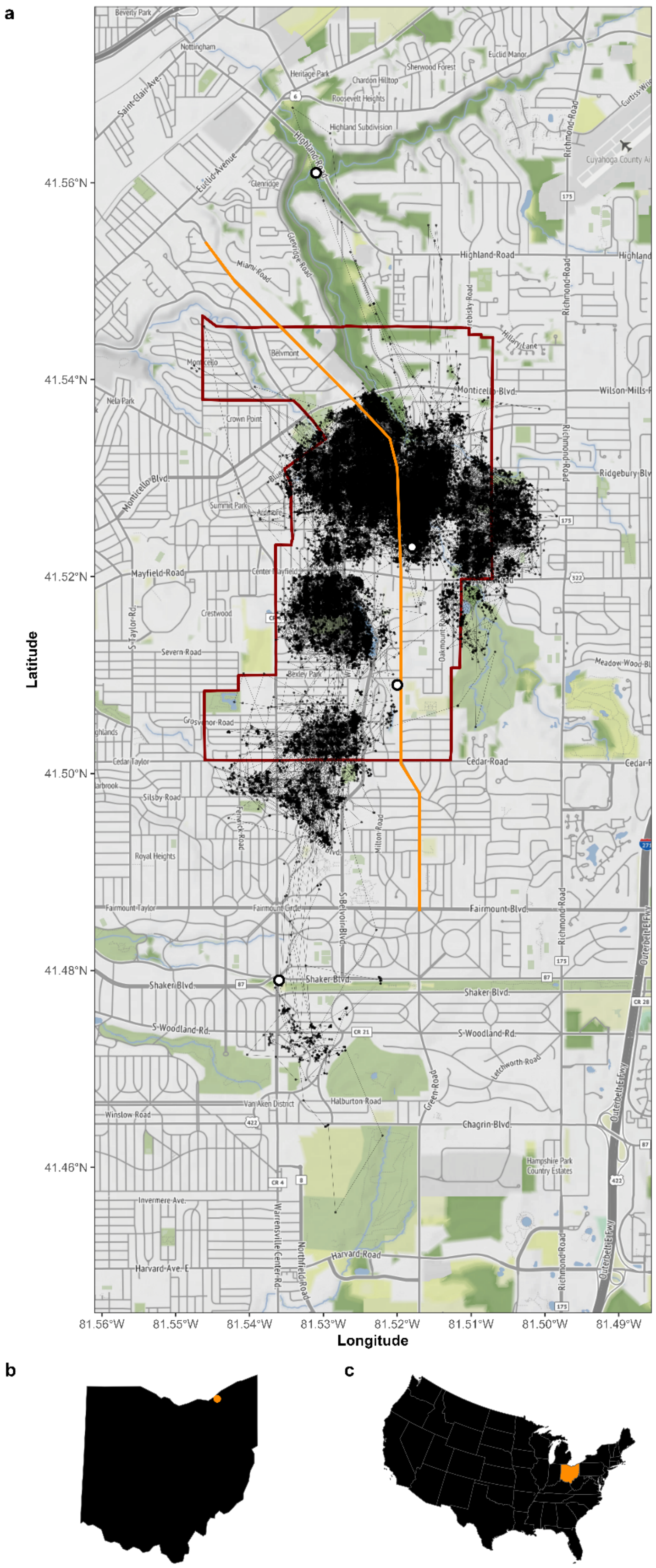
We assessed three key movement metrics: (1) home-range size, which quantifies the spatial extent of an animal’s local movements; (2) diffusion rate, which reflects movement variability and range exploration; and (3) daily excursivity, the tendency for an individual to move outside core-use areas.

We hypothesized that ovariectomized females, lacking hormonal cues from estrus and parturition, would exhibit stable movement patterns throughout the year. In contrast, untreated females would expand their movement leading up to the breeding season and reduce movement following parturition. We expected peak breeding season to occur annually between 3 and 16 November and peak parturition between 18 May and 7 June (Nixon, 1971). Our study provides new insights into how ovariectomy-induced anestrus influences seasonal movement patterns in female deer and demonstrates the application and limitations of IoT-based biologging as a scalable, low-cost tool for wildlife monitoring.

Methods

Study site

The city of South Euclid (41.52311, −81.51846; SE; Fig. 8) is a suburban community in Cuyahoga County, Ohio, USA, located in the northeastern part of the state (Boulanger and Ellingwood, 2024). The topography is relatively flat, with a shallow forested ravine at the northern end of the city. At the time of the study, the community covered approximately 12.2 km^2 and consisted of residential neighborhoods, small commercial areas, and interspersed green spaces, including parks, riparian corridors, and privately owned wooded properties. Despite being heavily developed (2019 census: 1,768 people/km^2 in 9,071 households), the distribution of green spaces provides a suitable habitat for deer. Similarly developed communities with green spaces and connectivity via riparian and green space corridors border South Euclid.


a
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81.50°W
81.49°W
Highland Road
Monticello Blvd.
Mayfield Road
Cedar Road
Fairmount Blvd.
Shaker Blvd.
S Woodland Rd.
Chagrin Blvd.
Richmond Road
Euclid Avenue
Cuyahoga County Airport

Figure 8 – Study site, deer movement data, and base station locations in South Euclid, Ohio, USA. (a) Map of the study area showing the geographic boundaries of the deer movement study. White points indicate the locations of the four micro base stations, while the orange line represents South Green Road. Treatment deer were captured west of South Green Road and control deer were captured in the east. (b) The location of South Euclid within Ohio. (c) The position of Ohio within the USA. Maps are presented using the Universal Transverse Mercator (UTM) projection (zone 17N). The basemap was provided by Stadia Maps, Stamen Design, OpenMapTiles, and OpenStreetMap contributors.

The region has a humid continental climate with four distinct seasons, including cold, snowy winters and warm, humid summers (99 cm average annual precipitation, including, 173 cm average annual snowfall). The forested areas are characteristic of the eastern deciduous forest biome, dominated by oak (*Quercus spp.*), maple (*Acer spp.*), American beech (*Fagus grandifolia*), and hickory (*Carya spp.*).

Recreational hunting is not permitted within the community. During the study, no non-human predators were present that could appreciably limit deer populations. The city has experienced increasing deer-related conflicts, including rising DVC rates, landscape damage, and concerns regarding tick-borne disease transmission (Boulanger and Ellingwood, 2024). In January 2022, the local deer population was estimated at 36 deer/km², highlighting the need for alternative management strategies (Boulanger and Ellingwood, 2024).

Animal capture and handling

Between January 2023 and January 2024, we immobilized adult female deer using projectors with 2 mL transmitter darts (Pneu-Dart Inc., Williamsport, PA, USA; Kilpatrick et al., 1997). Each dart administered 1.5 mL BAM (butorphanol 0.65 mg/kg, azaperone 0.22 mg/kg, medetomidine 0.26 mg/kg; Wildlife Pharmaceuticals, Inc., Fort Collins, CO, USA) combined with 0.5 mL of 200 mg/mL ketamine. We approached deer by vehicle on public and private roadways and properties where permission had been granted. Working in coordination with local law enforcement, we used radio telemetry to locate each immobilized deer 15 minutes post-dart deployment.

We captured and fitted 20 adult female deer with IoT biologging devices (Sensolus Tracker – SNT3 Compact track 1010, Ghent, Belgium; Wild et al., 2023) affixed to nylon collars. These lightweight (95 g) devices were selected for their low power consumption, extended battery life (~18-24 months), and cost-effectiveness (USD 95 per unit, plus USD 20 for the collar). The devices recorded a location every 60 minutes when moving and every 6 hours regardless of movement status. The devices also logged stop events when an individual remained stationary for more than 5 minutes and start events after 1 minute of continuous movement. Telemetry data were transmitted via four internet-connected (via cellular data) micro base stations (SMBS T4 Micro Base Station, Sigfox, Labège, France; 110v powered; USD 539/unit; data cost USD 20/month; Fig. 8a), which were strategically deployed in collaboration with the manufacturer to ensure the best possible coverage, given the sites made available by the community. Each individual was also fitted with numbered ear tags for individual identification.

Deer captured east of South Green Road were assigned to the control group *(n* = 10), while those captured west of the road were assigned to the treatment group (*n* = 10). This boundary was selected due to permit restrictions governing the larger management study, but both groups could move freely across this road. No fawns or yearlings (individuals younger than two years old) were handled to better mimic the expected age class in a high-treatment ovariectomy program, where adult females would dominate if reproduction ceased. While approximate ages were recorded using methods described in Severinghaus (1949), all individuals were classified as adult females because the live aging of deer is inherently imprecise.

Control females were released after collaring, whereas treatment females were transported to a public property where surgical ovariectomy was performed following the protocol described by DeNicola and DeNicola (2021). Following the procedure, all animals were returned to their original capture location, selecting release sites with minimal human disturbance to facilitate post-handling recovery. We administered atipamezole (50 mg IM) and naltrexone (25 mg IM) as reversal agents and monitored each deer during recovery.

Data collection continued until battery depletion, mortality, or the individual left the base station coverage area. All procedures were conducted under the Ohio Department of Natural Resources Scientific Collection Permit (#SC210047).

Data processing and analysis

We downloaded telemetry data from the manufacturer's website (Sensolus.com) and transferred it to MoveBank (Study ID: 2689852069; 100,374 locations). After downloading the data, we identified and removed outlier fixes using visual inspection of telemetry data and diagnostic plots of minimum speed (straight-line displacement), deviation from the median location, turning angle, and time intervals between locations (procedure available on GitHub; see the code availability statement).

Our primary objective was to compare seasonal trends in movement behavior between treatment and control females over time. We estimated changes in movement parameters using continuous-time stochastic movement models, following the workflow outlined by Calabrese et al. (2016) for *ctmm* (version 1.2.0) in R (4.4.0, R Core Team, 2024), to account for data gaps in movement data and irregular telemetry intervals while addressing inherent autocorrelation. We analyzed three key movement metrics:

1. 7-day home-range (HR) size – the estimated area needed by an individual within a 7-day period, which we estimated using the 95th percentile of the Autocorrelated Kernel Density Estimate AKDE (Silva et al., 2022);
2. Daily diffusion rate – a measure of mean squared displacement per unit time, reflecting the rate at which an individual explores space over time; and
3. Daily excursivity – a metric based on AKDE quantiles, that indicates whether an individual is remaining in core-use areas (low excursivity) or venturing into peripheral areas (high excursivity) and provides insight into exploratory behavior.

We modeled the telemetry data for each animal (S4: Fig. 15) using a moving-window approach with 7-day windows and 3 days between windows that resulted in a 4-day overlap between adjacent windows. The window's short duration provided insights into behavioral changes that occurred over biologically relevant time scales (e.g. proestrus/estrus, breeding, pre-parturition, post-parturition; Nixon, 1971; Ozoga and Verme, 1975) while ensuring that each window's effective sample size was sufficiently high for robust estimates of HR size and diffusion rates (Fleming and Calabrese, 2017; Fleming et al., 2018; Fleming et al., 2019). We were unable to assess the effects of the treatment on the animals' speed (i.e., daily distance traveled) because the data were too coarse to estimate speed accurately (Noonan et al., 2019).

After removing all 7-day subsets of telemetry data with 5 or fewer locations, we fit movement models to each subset using the `ctmm::ctmm.select()` function, which considers the data's sampling frequency and degree of temporal autocorrelation when selecting among models (Calabrese et al., 2016). From each model, we extracted the animal's 7-day HR size and, when possible, daily diffusion. To estimate the degree of excursive behavior, we first used each animal's full telemetry dataset to estimate its Autocorrelated Kernel Density Estimate (AKDE; Fleming and Calabrese, 2017; Alston et al., 2022; Silva et al., 2022). We then extracted the quantile for each telemetry location and calculated each animal's daily mean AKDE quantile. A value near 0 indicated that the individual remained in high-use areas, whereas a value near 1 indicated that the individual spent more time in "peripheral" areas and engaged in more excursive behavior (Fig. 9).

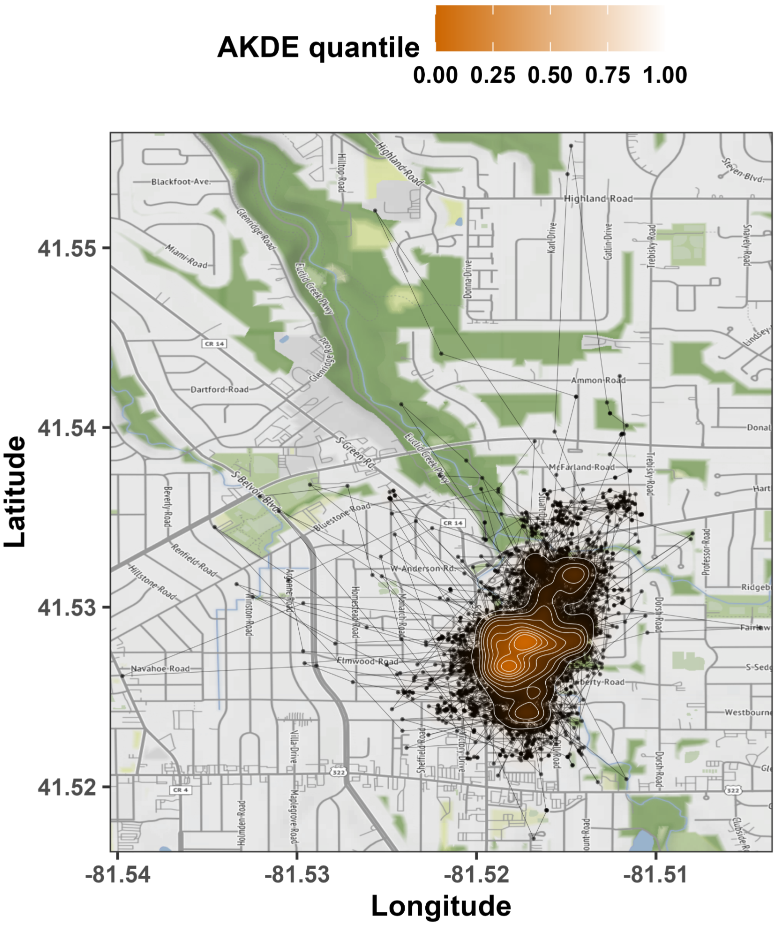

Figure 9 – Telemetry data (dots) and Autocorrelated Kernel Density Estimate (AKDE; shading) for deer C_100. The contours indicate quantiles at intervals of 0.1 from 0.1 to 0.9. Excursivity was measured as the mean daily AKDE quantile for each telemetry fix. The basemap was provided by Stadia Maps, Stamen Design, OpenMapTiles, and OpenStreetMap contributors.

To quantify the seasonal changes in movement behavior, we fitted three Hierarchical Generalized Additive Models (HGAMs; Pedersen et al., 2019) using the mgcv package (1.9-1, Wood, 2017) for R. HGAMs allow one to model complex nonlinear relationships using flexible, nonlinear, and smooth relationships that are informed by the data rather than by relationships determined a priori by the analyst. The HGAMs for the 7-day HR size and daily diffusion used a gamma family of distributions with a log link function, whereas the HGAM for daily excursivity used a beta distribution with a logit link function. Each model included three terms (see the code below): (1) a fixed intercept of group (control or treatment) to account for the group-level mean, (2) a cyclic smooth term (‘bs = “cc”’) of day of year for each group, with group-level smoothness selection (by = group) to account for group-level seasonal trends, and (3) a cubic-regression factor smooth interaction term of day of year for each animal in each year (‘doy_cr’, ‘animal_year’) by group, which accounted for animal-level variation in seasonal trends while keeping each group separate. We did not force the latter factor smooth term to be cyclical because environmental conditions and data availability differed between the start and end of the year. We optimized smoothness selection using fast REML. To test whether sampling intensity differed between the groups, we fitted a fourth HGAM with the same terms to model the number of daily telemetry fixes each animal had from the deployment of the collar until the day of the last fix (including days with no fixes).

```
Y ~
 group +
 s(doy, by = group, k = 10, bs = “cc”) +
 s(doy_cr, by = group, animal_year, k = 10, bs = ”fs”, xt = list(bs = “cr”))
```

Results

Between 17 January 2023 and 18 January 2024, we handled 20 adult female deer (10 treatment; 10 control; S4: Table 15). Two telemetry devices failed to transmit data when the individuals left the area (C_101, C_103) and were excluded from the analysis. One control individual was omitted due to having only 16 recorded locations and was observed in the area (C_201; S4: Fig. 16). Data collection concluded on 1 June 2024, with the final dataset comprising seven control and ten treated females. One base station was offline due to technical difficulties between 15 March and 1 July 2023, which reduced data coverage for some individuals but did not prevent data collection (S4: Fig. 16). We recorded a DVC and a cull in each group, for a total of four mortalities during the study period (S4: Table 15).

Data quality and movement behavior estimates

After data cleaning, the final dataset included 100,358 telemetry fixes, with 162 outliers removed (0.16%). The median sampling interval was 47 min (S4: Fig. 17). Across individuals, the median fix intervals ranged from 33 min to 64.5 min. Four individuals had devices that transmitted data for a limited duration (S4: Table 15; S4: Fig. 16). Three of these individuals (C_106, C_107, T_159) were subsequently observed outside of the study area in neighboring communities, while one was observed in the study area (T_160). On average, treated females had ~38% fewer daily GPS fixes than controls, but the posterior distribution indicated substantial uncertainty in this difference (P = 0.671, 95% credible interval: (-93%, 467%); S4: Fig. 18). Daily fixes declined from 25 February to 1 July 2023, likely due to the base station outage. Additionally, variability in data collection may be influenced by increased sedentary behavior (no fix collection while sedentary) or individuals moving beyond the base station coverage area. Notably, this decline was more pronounced in the control group.

The effective sample size was above 3 for the great majority of windows for both HR size (1288 out of 1342; 96.0%) and diffusion (1310 out of 1342; 97.6%), which indicated that the 7-day moving window was sufficiently large to obtain robust estimates of both HR size and diffusion (Calabrese et al., 2016; Fleming and Calabrese, 2017).

One treated deer (T_169) exhibited movement patterns associated with short-term commuting behavior that resulted in lack of range residency within approximately 16 windows, relative to the 7-day window size. This resulted in 15 unreliable HR estimates that were 10 times larger than the group mean, and a single outlier diffusion estimate 6 times greater than the group mean (S4: Fig. 19). Upon visual inspection, this individual repeatedly moved between two distinct areas of the study site, making eight such transitions during monitoring (S4: Fig. 19), showing commuting behavior between two non-contiguous areas (Cagnacci et al. 2016, Gurarie et al. 2017). We had another single 7-day window in individual T_158 where commuting behavior was observed. We excluded these windows from further analysis, as they spuriously included the areas traversed, but not used within HRs. Further, we obviously excluded windows where locations were missing or sparse (n < 5 locations). Out of 692 7-day windows of 7 control animals, we could analyze: 90.8% windows for HR size, 88.7% for diffusion, and 92.1% for excursivity. Out of 1082 7-day windows of 10 treatment animals, we could analyze: 64.5 windows for HR size, 64.3% for diffusion, and 67.9% for excursivity (S4: Fig. 20; S4: Table S16).

Seasonal movement trends

All HGAMs exhibited reasonably good fits, though residual histograms showed slightly heavy tails (S4: Fig. 21). The models explained 74.0% of the deviance in 7-day HR size, 56.8% of the deviance in daily diffusion, and 31.1% of the deviance in daily excursivity.

As expected, control deer followed seasonal physiological cycles, increasing movement leading into the breeding season (late July–November) and reducing movement during and after parturition (April–June; Fig. 10). In contrast, treated deer maintained approximately stable movement patterns year-round for all metrics, except for a slight increase in June and July, when control deer had the lowest HR size, diffusion, and excursivity.

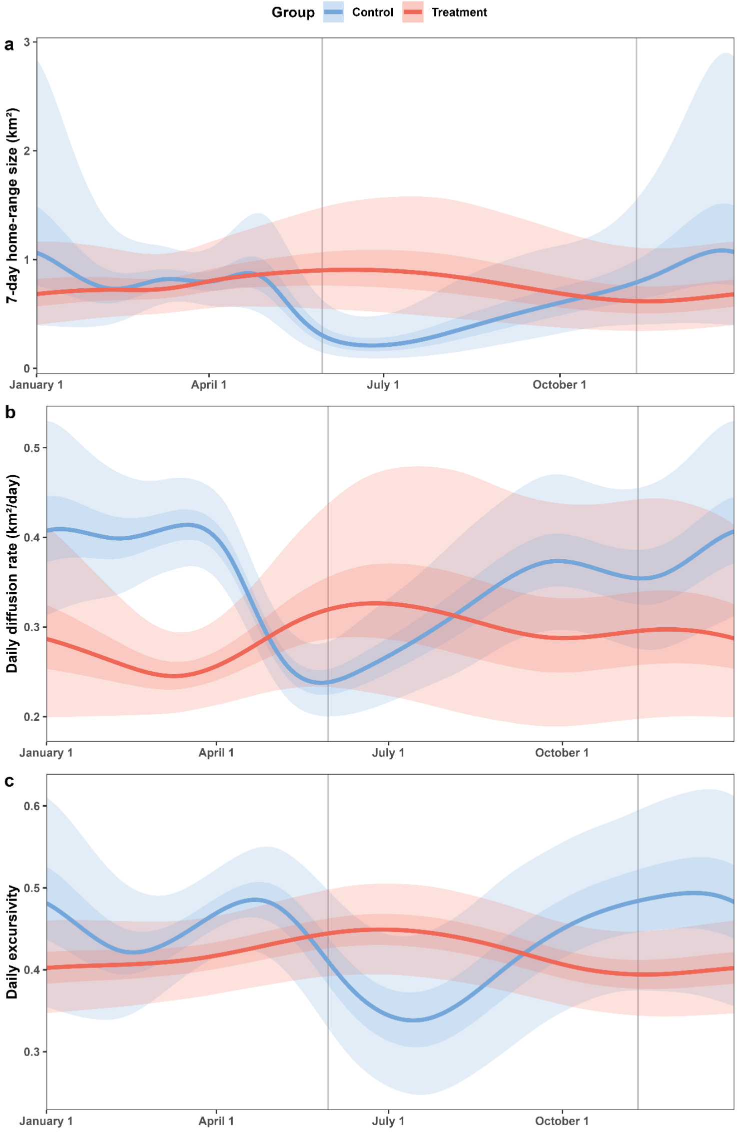

Figure 10 – Mean trends in 7-day home-range size (a), daily diffusion rate (b), and daily excursivity (c) for the control and treated deer populations. Shaded ribbons indicate the 95% and

50% Bayesian credible intervals (under the assumption of Gaussian coefficient estimates). The gray lines indicate the peak of parturition (30 May) and the peak of the breeding season (10 November) in Ohio (Nixon, 1971).

Differences between the groups' overall means (i.e., averaged across day of year; the model intercepts) were relatively small, highly uncertain, and not credible at the 95% level (HR: +18%, 95% CI: (-20%, +73%), P = 0.408; diffusion: -16%, 95% CI: (-33%, +5%), P = 0.121; excursivity: -1%, 95% CI: (-7%, +5%), P = 0.691; see S4: Fig. 22a). Control deer exhibited a clear seasonal contraction in HR size in late April, whereas treated deer showed little to no seasonal change (Fig. 10A). Although control deer moved less between 1 April and 31 May, their diffusion values remained comparable to those of treated females (~0.3 km^2/day). Control deer also exhibited increased excursivity prior to breeding and reduced movement post-parturition. All control individuals changed their HR size concomitantly prior to April 1, while trends among treated deer were highly variable (see the individual-level deviations in S4: Fig. 22). Seasonal trends in HR size and diffusion were more variable among treated individuals than among control individuals (S4: Fig. 22 but notice that the y-axes differ among groups).

Discussion

Our findings indicate that deer in both groups had similar home-range sizes, diffusion, and excursive behavior, as indicated by strong similarity and lack of significant difference between the model intercepts (S4: Fig. 22). However, while ovariectomized deer maintained relatively stable movement patterns year-round, untreated control females exhibited expected seasonal shifts associated with reproductive cycles. The increase in control females' HR size, diffusion, and excursivity during the pre-breeding and breeding seasons is consistent with an increase in fawn mobility that occurs in summer (Webb et al., 2010; Holland et al., 2024) as well as the decreases in resource availability (Mezzini et al., 2024) and mate-searching behavior that are typical of late fall and winter (D'Angelo et al., 2005; Kolodzinski et al., 2010; Sullivan et al., 2017). During parturition (May–June), untreated females exhibited an expected contraction in movement as they selected fawning sites and engaged in maternal care (D'Angelo et al., 2005; Webb et al., 2010; Wright et al., 2021), while treated females increased their HR size, diffusion, and excursivity slightly, possibly due to reduced competitive pressure from other deer. Thus, our results support our hypothesis that eliminating estrous cycling removes the hormonal cues that drive reproductive-linked shifts in movement behavior, and they also suggest that ovariectomy mitigates hormonal influences on movement without introducing concerning differences in space use (e.g., increases in HR size, exploratory behavior). While treated deer had, on average, greater HR size, diffusion, and excursivity than control deer post-parturition, this difference is unlikely to result in increased energetic costs for treated deer, because ovariectomized deer do not undergo gestation, parturition, or lactation, all of which would have higher metabolic demands than the routine movement seen during this period (Hewitt, 2011). Furthermore, if fawning is reduced in treated deer, both spring and fall DVCs would likely decline, as spring collisions often coincide with behavioral displacement during parturition, while fall collisions are driven by yearling male dispersal (Ramakrishnan et al., 2005, Marcoux et al., 2005). Still, this difference warrants consideration in management applications, as treated deer's relatively higher movement rates during summer could influence space use, social interactions, or potential exposure to anthropogenic risks. While we found no evidence of differences in DVC related mortality among treated females, we recognize that our sample size was limited, and future studies should investigate movement during this period in greater detail and over a longer period of time.

The lack of concurrent changes in the movement of ovariectomized deer prior to parturition suggests that, unlike control deer, treated females did not exhibit group-level changes in movement behavior. Thus, the movement behavior of treated females appears to depend more on external factors (e.g., habitat selection, food availability, and social interactions; see Nathan et al., 2008) rather than reproductive status and hormonal changes. Future studies should explore whether this variability has implications for space use and resource competition in treated populations.

We observed instances of commuting behavior and range shifts among a subset of individuals, which are well-documented movement behaviors in ungulates (Cagnacci et al., 2016). One individual (T_169) exhibited a distinct commuting pattern, moving between two areas for a period of time. Additionally, three individuals emigrated from the study area and were subsequently reported by residents in neighboring communities (one treatment and two control). These behaviors were equally common in both groups, suggesting that they represent natural variation rather than an effect of ovariectomy. Despite these individual deviations, the majority of animals exhibited resident movement patterns. While we cannot entirely rule out the possibility that commuting and range-shifting behavior represent an altered response to ovariectomy, it is more likely that these movements reflect normal responses to resource distribution.

Device performance and data limitations

A key limitation of our study was the reliance on biologging devices that required base station coverage for data transmission. While the Sigfox IoT network has coverage in 70+ countries, there was no coverage in the USA at the time of this study (https://sigfox.com/coverage/). To collect data, we needed to deploy and maintain commercially available limited-range micro base stations that required power and cellular-based connectivity. While this system provided a cost-effective alternative to traditional GPS collars, it introduced challenges related to data completeness, as gaps between fixes could occur as a consequence of failed transmission. Our use of continuous-time movement models was particularly valuable given the irregular sampling and variable data quality, allowing us to appropriately model movement despite these challenges (Calabrese et al., 2016). Although treated females averaged fewer GPS fixes per day than controls, the wide credible interval indicates substantial uncertainty, making it unclear whether a meaningful difference exists. This variability could be influenced by factors such as base station outages, increased sedentary behavior lowering fix rate, or individuals moving beyond the coverage area. When an individual left the coverage area, its movement could not be tracked, and without VHF capabilities, fate determination was not possible. Two individuals, C_101 and C_103 left the study area, reported no data, and were seen repeatedly in a nearby community. Four other individuals reported data for a portion of the study period. Three of these individuals (C_106, C_107, T_159) were subsequently seen in neighboring communities, while two (T_160, C_201) were seen in the study area with failed devices. Additionally, a base station outage between ~15 March and July 2023 contributed to further data irregularities.

Despite these challenges, the system provided valuable insights into seasonal movement trends. The affordability, lightweight design, and extended battery life make it a viable option for wildlife monitoring, particularly in settings where cost, collar weight, or long-term deployment are constraints. However, as the base stations and devices were not explicitly designed for wildlife tracking, they posed logistical challenges. To improve the reliability of IoT biologging for wildlife studies, future deployments could integrate additional base stations, employ manual data retrieval efforts (e.g., drone or vehicle data collection), or incorporate hybrid tracking technologies such as VHF for real-time detection. While the system proved effective for monitoring fine-scale movement in this suburban setting, researchers should consider the limitations when applying similar methods in broader landscapes with more extensive animal movements, such as migrations or lack of range residency.

Sample size and data collection considerations

While the small sample size and irregular data collection impacted the uncertainty of estimates, our findings appear to be informative and representative of the potential effects of ovariectomy on deer. The similarity in seasonal trends among control individuals suggests that the telemetry data are representative of the movement of the individuals in the sample. Additionally, the continuous-time movement models fit by the ctmm package are well-suited for complex telemetry data, including data that are not missing at random and uneven sampling over space and time (Calabrese et al., 2016; Noonan et al., 2019; Silva et al., 2022). Furthermore, HGAMs leverage the information across individuals' time series to produce statistically sound estimates of population-level trends along with appropriate across-the-function measures of uncertainty (Wood, 2017; Simpson, 2018; Pedersen et al., 2019; Marra and Wood, 2012). Still, we suggest that future studies aim for larger sample sizes and improved device reliability.

Management implications and future research directions

The efficacy of fertility control in limiting deer population growth over time has been well studied (Gray and Cameron, 2010; Boulanger et al., 2012; DeNicola and DeNicola, 2021), but potential behavioral side effects have received less attention. Our findings suggest that ovariectomy does not induce changes in movement behavior that compromise the health of treated individuals. However, given our small sample size and the treated deer's relatively higher movement rates in summer, it is not possible to credibly conclude whether the treatment affects the incidence of DVCs. Future research should evaluate the interaction between fertility control and movement behavior with larger samples and across different environmental contexts while also assessing the treatment's long-term impacts. Particular attention should be given to how landscape features, health status, and social interactions shape movement behavior, as these factors likely become central drivers of movement in the absence of hormonal and reproductive cues (Nathan et al., 2008). As conflicts with abundant deer populations continue to increase in suburban landscapes worldwide, alternative management strategies must remain a priority.

Data archiving statement

All the data, R scripts, supporting figures, and supplementary materials are available at https://osf.io/qwf9t/?view_only=ed0e3d8960294dfa99222e7831a7d63d.

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CHAPTER 5. GENERAL CONCLUSIONS

This thesis examined the effects of two common fertility control methods on the movement behavior of white-tailed deer, addressing concerns about their potential viability as management strategies due to impacts on movement behavior. Fertility control is increasingly relevant as wildlife populations expand in human-dominated landscapes, where traditional lethal management strategies often face social, legal, and logistical barriers (DeNicola et al., 2000; Barfield et al., 2005; McShea et al., 2012; Boulanger et al., 2014; Stinchcomb et al., 2023). Our findings reinforce the viability of vasectomy and ovariectomy as tools to manage abundant deer populations while minimizing unintended behavioral consequences. We found that vasectomy, despite inducing additional estrous cycles in unbred females, did not significantly alter movement patterns or activity levels. Similarly, ovariectomy, which induces anestrus in treated females, did not result in abnormal roaming behavior or increased activity that might suggest elevated energetic needs or stress. These results should alleviate concerns that these methods cause behavioral change (USNPS, 2014) or increase the risk of DVCs. The consistency of movement behavior and limited effect following these interventions in this thesis provide strong evidence supporting these fertility control techniques in urban and suburban deer management. In fact, by reducing deer numbers over time, fertility control will contribute to fewer collisions in the long run, as smaller or more behaviorally predictable herds may interact less often with vehicles (though immediate effects on DVC rates would be minimal until population size declines). Just as importantly, the lack of aberrant movement or extensive wandering in treated deer is an encouraging sign for deer health and welfare. We observed no evidence that either sterilization treatment caused undue energetic costs or trauma that would manifest in altered movement. In past fertility control research, a key worry was that altered reproductive cycles might lead to prolonged breeding behaviors or other physiological side effects (e.g., prolonged breeding activity could increase injury rates, or repeated cycling could affect body condition). Our findings help allay these fears: the treatment groups maintained biologically normal behaviors and did not suffer higher mortality or morbidity rates relative to untreated groups during the study. In sum, linking movement ecology to safety and wellness outcomes, we conclude that fertility control via vasectomy or ovariectomy did not aggravate risks of DVCs or compromise well-being, reinforcing the notion that these non-lethal interventions are behaviorally benign management tools. This is a critical insight for stakeholders concerned that fertility control might “do more harm than good” – on the contrary, our data suggest it can reduce deer population growth without creating new public safety hazards or welfare issues.

Comparative Context: Urban Deer and Other Human–Wildlife Conflicts

The challenges of balancing wildlife management with public safety and property protection are not unique to suburban white-tailed deer; they echo across many species and landscapes worldwide. If our findings are placed in a broader context, we can better understand the applicability and limits of fertility control as a management strategy. A pertinent parallel is the case of wild boar (*Sus scrofa*) encroaching into suburban and peri-urban areas in Europe and elsewhere (Massei, 2015). Much like abundant deer, wild boar frequently come into conflict with humans: they cause significant crop and yard damage, raid garbage, and are involved in a large share of wildlife-vehicle collisions in regions where they thrive near cities (Massei, 2023). In some European countries, boar and roe deer together account for nearly 80% of reported wildlife-vehicle collisions, with wild boar alone inflicting millions of euros in damage to agriculture and infrastructure annually (Massei, 2023). Traditionally, intensive culling or hunting has been used to control boar populations, but in suburban settings, these lethal methods face many of the same obstacles encountered with urban deer management – legal restrictions on the discharge of firearms, public opposition to killing animals, and the practical difficulty of safely removing animals in densely populated areas. As a result, managers have started exploring fertility control for boar, aiming to mitigate their population growth humanely. Notably, trials with immunocontraceptive vaccines (such as GnRH agonists like GonaCon) in wild boar have shown promising results: treated females can remain infertile for 4–6 years after a single dose, with no adverse effects on their physiology or behavior observed in controlled studies (Massei, 2023). Treated sows did not display abnormal aggression or expanded ranging; because GnRH-based vaccines suppress gonadal hormones, treated boar largely ceased reproductive behaviors and did not experience the repeated drives to mate that intact boar do (Massei, 2008). This is a contrast to immunocontraception in deer using PZP (porcine zona pellucida vaccines), where treated females continue to have repeated estrous cycles but fail to conceive, leading to concerns about an extended mating seasons (Miller, 2001). The boar example underscores that the specific method of fertility control (hormonal vaccine vs. surgical sterilization vs. PZP, etc.) can determine whether animals continue reproductive activities or not, which in turn influences individual movement and conflict potential. More broadly, the boar case confirms that human–wildlife conflicts in suburban landscapes often share common threads: high densities of adaptable mammals, limitations on lethal control, and public demand for humane solutions. Other instances include suburban black bear populations that raid bird feeders and garbage, urban coyote encounters with pets, or overpopulations of feral horses and monkeys in certain reserves and cities – all situations where authorities have considered fertility control as part of the management toolkit (often in tandem with other measures) when culling is untenable or undesirable (Gray & Cameron, 2010; Massei, 2023). By comparing deer with these examples, we highlight that the success of any wildlife fertility control program hinges on both the biological response of the animal and the anthropogenic context. Our studies contribute valuable evidence that sterilization does not cause the sort of movement or activity that could worsen human-wildlife interactions or contribute to the physical deterioration of the animal. For wildlife agencies, such findings build confidence that fertility control can reduce wildlife conflicts (by gradually lowering population density) while keeping animal behaviors within normal bounds, an outcome desirable for coexistence. Cross-species parallels also remind us that wildlife management must be adaptive: strategies that work for suburban deer – a relatively sedentary, philopatric species – might need adjustment for species like boar that are highly mobile and capable of rapid range expansion. Nevertheless, the overarching lesson is that non-lethal management, supported by scientific monitoring of animal behavior, holds promise for a variety of human–wildlife conflict scenarios.

Long-Term Ecological and Evolutionary Consequences of Fertility Control

While our research confirms the short-term consequences of deer fertility control from a behavioral standpoint, it also prompts forward-looking questions about the long-term ecological, behavioral, and evolutionary impacts of the use of such interventions. Wildlife populations are dynamic systems; altering the fundamental demographic process of reproduction may have gradual, cascading effects that only become apparent over years or decades. One foreseeable outcome of sustained fertility control is a shift in population age structure. By curtailing annual fawn recruitment, fertility control will, over time, skew a population towards older age classes. In a treated deer herd, the average age of individuals would increase as fewer young are added each year and existing adults continue to survive. This demographic aging can have several consequences. Ecologically, older deer may have different impacts on vegetation and different space use patterns than a more juvenile-heavy population. For instance, mature females without fawns (a likely scenario if most breeding is prevented) might range more widely during summer because they are not restricted by the need to hide and nurse fawns – although our findings did not show a significant increase in movement, one might expect subtle shifts in habitat use when maternal behaviors are largely absent. Additionally, an older population might experience density declines more slowly (because adult survival still drives numbers) and could potentially stabilize at a lower growth rate. From a social behavior perspective, widespread infertility could disrupt typical behavioral rhythms and social structures. In normal deer populations, reproductive events (breeding, gestation, fawning) strongly influence behavior and group dynamics: the fall breeding season triggers increased movement and competition, and spring brings dispersed, secretive behavior as females give birth. If fertility control is universal, these seasonal pulses would diminish. Under an ovariectomy or GnRH-vaccine regime where females do not enter estrus at all, one would effectively remove the breeding-related behaviors from the system – males would find no estrus females but would have high testosterone levels, potentially changing the dynamics of typical breeding behavior. This might alter herd social structure (for example, males could remain in bachelor groups longer, and females might not separate for fawning because fawning does not occur). Conversely, under a vasectomy or PZP immunocontraception strategy where females do cycle and exhibit estrus but fail to conceive, the breeding season could be prolonged. Females may be healthier and enter estrus earlier in the fall, and the breeding season may extend into December because testosterone levels remain high and females enter the second estrus period. In a long-term, population-wide application of such a treatment, we might expect an earlier, slightly longer breeding season each year. A longer breeding season could slightly elevate the window of risk for breeding-related deer–vehicle collisions or intraspecific injuries, as sexually active deer roam and chase for an atypically extended time. However, it is important to note that in our vasectomy-treated cohort, despite the potential for multiple estrus periods, we did not observe a marked increase in movement or range size during the breeding season, but did see a flattening of some male measures, including diffusion, excursivity and mean 7-day HR, suggesting the potential for a longer, less intense breeding season. Wildlife managers should remain vigilant for behavioral shifts (e.g., breeding season lengthening, changes in grouping) as a fertility-controlled population evolves over multiple years. Another critical consideration is the genetic and evolutionary impact of long-term fertility control. By preventing a large fraction of individuals from reproducing, we are effectively reducing the number of breeders and the gene pool in each generation. Over many generations, this could subtly reduce genetic diversity in the population. If, for example, only 10–20% of females in a town are left fertile (due to incomplete treatment coverage or deliberate strategy), those females (and the males that breed with them) will contribute all the offspring, concentrating the gene flow through a much smaller set of parents than in an unmanaged population. In small or isolated populations, this could increase the risk of inbreeding and reduce adaptive potential. Even in larger, open populations, there might be evolutionary selection pressures at play. Animals that are not treated (either because they evade capture or because they are biologically less susceptible to the contraceptive method) will have higher fitness by default (producing more offspring). Over time, one might expect more “trap-shy” **or** contraception-resistant individuals to form a greater share of the breeding pool. For instance, in a dart-delivery immunocontraception program, the most elusive deer (those that avoid coming within darting range or do not visit bait stations) could disproportionately escape treatment and thus reproduce, potentially selecting for wariness or altered behavior in the population. Likewise, if there were any genetic basis for responding to a contraceptive (e.g., some females might not mount a strong immune response to a vaccine and thus remain fertile), those individuals would contribute more offspring, possibly passing on whatever trait allowed them to bypass infertility. These evolutionary scenarios remain largely speculative, as fertility control programs in wildlife are relatively recent and typically too short-lived to have measured such effects. It will be important for future research to monitor treated populations not just for immediate behavioral responses, but also for any signs of longer-term demographic or genetic shifts. Age structure changes, altered social dynamics, and reduced genetic variability could all influence the resilience of a population. For example, an older-skewing herd might be more prone to die-offs during harsh winters (if few prime-aged adults or fawns are present), or it might interact differently with predators (e.g., predators might have fewer fawns to prey on and could turn to other prey or leave the area). Managers might need to adapt by periodically allowing some reproduction (as has been done in certain wild horse herds managed with contraception) to refresh age structure and gene flow, especially if the goal is to maintain a population at some lower level rather than eliminate it. Overall, while our study did not observe negative long-term effects in its timeframe, it lays the groundwork for considering these broader ecological questions. Fertility control appears to steer deer populations toward a lower growth trajectory without behavioral upheaval, but continuous monitoring is advisable to ensure that unforeseen consequences (like altered age distributions or loss of genetic diversity) do not undermine the conservation objectives. In summary, the long-term use of fertility control in wildlife must strike a balance between achieving the desired reduction in population and preserving the natural characteristics and adaptability of that population. We advocate for an adaptive management approach: implement fertility control, study its impacts on behavior, demography, and genetics over multiple years, and adjust management actions as needed to safeguard both the population's health and the ecosystem's integrity.

Implications for Suburban Wildlife Management and Conservation Strategies

Taken together, these findings and the related discussions point to several important implications for wildlife management in suburban environments. First and foremost, this research bolsters the case that fertility control can be a viable and effective tool for managing abundant deer in areas where traditional culling is impractical or publicly opposed. The success of both ovariectomy and vasectomy in limiting deer population growth without inducing significant behavioral side effects addresses a major concern that has historically made managers hesitant to adopt fertility control. Fears that sterilized deer would range widely into roads or neighborhoods or suffer health declines are not supported by our data. Instead, treated deer continued to behave much like their fertile counterparts, meaning that communities can reap the benefits of population stabilization (and eventual reduction) without incurring new problems in the interim. This evidence-based reassurance is crucial for gaining public support and regulatory approval for fertility control programs, which often face scrutiny regarding human safety and animal welfare. Our study also exemplifies how modern technology and analytical methods (like IoT-enabled tracking and continuous-time movement modeling) can be leveraged to inform management decisions. By rigorously monitoring how wildlife respond to interventions, managers can proceed with confidence or detect early warning signs of issues. In the case of South Euclid, tracking deer allowed us to confirm that sterilization did not inadvertently increase deer–human conflicts; such data-driven validation can similarly guide programs for other species (e.g., verifying that an urban boar contraception program does not cause boar to forage more aggressively or expand into new areas). The broader conservation strategy emerging from this work is one of proactive, humane management that seeks to balance human interests with ecological stewardship. Suburban ecosystems are inherently human dominated, yet they still harbor wildlife that may perform important ecological roles (for instance, deer as herbivores shaping plant communities). Completely removing or eradicating these animals is often neither feasible nor desirable. Fertility control offers a compromise solution: it reduces population pressure to a level that the landscape and community can tolerate (often defined by a “social carrying capacity”; Massei, 2023), but it does so in a way that maintains the animals on the landscape, allowing natural behaviors and interactions to continue, just at lower intensity. In other words, it aims for coexistence through population moderation rather than elimination. There are, of course, limitations and context dependencies. Fertility control is not a one-size-fits-all remedy; it requires substantial upfront investment, repeated effort in some cases, and works more slowly than lethal removal in reducing numbers. In scenarios where an immediate reduction in wildlife is needed (e.g., a disease outbreak or a population truly at crisis levels), fertility control alone may be insufficient. However, as our work underlines, in settings where the situation allows for a longer-term solution and where community values favor humane treatment, fertility control can play a pivotal role. It may be best employed as part of an integrated wildlife management strategy that includes an initial cull to reduce a deer or boar population to a manageable size, and then fertility control keeps it low over subsequent years. This way, the immediate impact is achieved, and the long-term maintenance is humane and socially acceptable. Finally, considering evolutionary and behavioral feedback loops (as discussed above) is essential for truly sustainable management. Managers implementing fertility control should also implement monitoring programs for demographics and genetics, ensuring that the managed population retains healthy age distribution and diversity. If signs of unintended consequences appear, strategies can be adjusted—such as treating a smaller fraction of animals, switching contraceptive methods, or temporarily halting treatments to allow some rebound. The key is adaptability and informed decision-making, principles that are at the heart of modern conservation management. In conclusion, this dissertation’s findings reinforce that non-lethal fertility control can mitigate human-wildlife conflicts in suburban deer without provoking new problems, all while upholding animal welfare standards. When compared with similar challenges in species like wild boar, our results contribute to a growing body of evidence that thoughtful application of fertility control can aid in the coexistence of humans and wildlife in shared landscapes. As suburban communities continue to expand and wildlife adapts to these environments, developing and refining tools like fertility control will be increasingly important. A long-term vision would include a suite of management strategies that are effective, ethical, and ecologically sound – strategies that reduce conflicts, preserve biodiversity, and foster a more peaceful human-wildlife relationship in our ever-more crowded world.

APPENDIX

Supplementary material to Chapter 2 (S2)

Supplement A — Derivations

To compare the diffusion rates of different, selected stochastic process models, we first consider time-lag dependence of diffusion via the semi-variance function (SVF):

$$\gamma(\tau) = \frac{1}{4}\mathrm{E}\big[(x(t+\tau)-x(t))^2 + (y(t+\tau)-y(t))^2\big] \,, \tag{1.1}$$

which is a quarter of the time-averaged mean square displacement (ISD), defined so that $\gamma(\tau)$ limits to the average variance:

$$\lim_{\tau\to\infty} \gamma(\tau) = \sigma_0 = \frac{1}{2}\left(\mathrm{VAR}[x(t)] + \mathrm{VAR}[y(t)]\right) , \tag{1.2}$$

for a stationary movement process, so that

$$\gamma(\tau) = \sigma(0) - \sigma(\tau) \,, \tag{1.3}$$

in terms of the autocorrelation function (ACF), $\sigma(\tau)$.

The autocorrelation and semi-variance functions for our continuous-time stochastic process models are given in Fleming et al. (2015, 2017). From this perspective, the diffusion rate can be defined in two different ways:

$$D(\tau) \equiv \frac{d\gamma}{d\tau}(\tau) = -\frac{d\sigma}{d\tau}(\tau) \,, \qquad \text{or} \qquad D(\tau) \equiv \frac{\gamma(\tau)}{\tau} \,, \tag{1.4}$$

which both measure how the MSD increases with increasing time lag. To compare diffusion rates across different stochastic process models, we will compare the maximum diffusion rates:

$$D_{\max} = D(\tau_{\max}) \qquad \text{where} \qquad \tau_{\max} = \arg\max_{\tau} D(\tau)\,. \tag{1.5}$$

As we will show, this definition of the maximum diffusion rate produces the commonly accepted parameters of comparison between Brownian motion (BI), Ornstein-Uhlenbeck (OU), and integrated Ornstein-Uhlenbeck (IOU) processes. Furthermore, we will use the first definition, which relies on differentiation, because our parameters of interest can then be solved in closed form, from either $\gamma''(\tau) = 0$ or $\sigma''(\tau) = 0$. However, while all of the SVFs we consider are monotonically increasing functions, the second diffusion-rate definition would be advantageous if that were not the case, as the maximum slope might not be particularly meaningful then.

1.1 Brownian motion

The Brownian motion SVF is simply linear

$$\gamma(\tau) = D\,\tau \tag{1.6}$$

with the maximum diffusion rate given by the slope, *D*, which is the only diffusion rate for this process.

1.2 Ornstein-Uhlenbeck motion

The Ornstein-Uhlenbeck ACF is given by:

$$\sigma(\tau) = \sigma_0\, e^{-\frac{\tau}{\tau_p}} \tag{1.7}$$

in terms of the position autocorrelation timescale, τ_p. The maximum diffusion rate is then given by the instantaneous diffusion rate:

$$D_0 = \frac{\sigma_0}{\tau_p} \,. \tag{1.8}$$

1.3 Integrated Ornstein-Uhlenbeck motion

The integrated Ornstein-Uhlenbeck SVF is given by:

$$\gamma(\tau) = D_\infty \left(\tau - \tau_v \left(1 - e^{-\frac{\tau}{\tau_v}} \right) \right) , \tag{1.9}$$

in terms of the velocity autocorrelation timescale, τ_v. The maximum diffusion rate given by the asymptotic diffusion rate, D_∞.

1.4 OUF motion

The OUF ACF is given by (Fleming et al., 2014):

$$\gamma(\tau) = \sigma_0 \frac{\tau_p \, e^{-\frac{\tau}{\tau_p}} - \tau_v \, e^{-\frac{\tau}{\tau_v}}}{\tau_p - \tau_v} . \tag{1.10}$$

By differentiating the ACF twice, we find the maximum diffusion rate to occur at time lag

$$\tau_{\mathrm{max}} = \frac{\log \theta}{\theta - 1} \tau_p \,, \qquad \text{where} \qquad \theta \equiv \frac{\tau_p}{\tau_v} \,, \tag{1.11}$$

and by plugging this back into the derivative of the SVF, we find the maximum diffusion rate to be:

$$D_{\mathrm{max}} = \frac{1}{\sqrt[\theta-1]{\theta}} \frac{\sigma_0}{\tau_p} \,. \tag{1.12}$$

1.5 OUO motion

The oscillatory OUF ACF—termed OUO in `ctmm`—is given by (Fleming et al., 2017):

$$\gamma(\tau) = \sigma_0 \left(\cos(\omega\tau) + \frac{\sin(\omega\tau)}{\omega\tau_p} \right) e^{-\frac{\tau}{\tau_p}} \, , \tag{1.13}$$

in terms of the oscillation frequency, ω. Again, by differentiating the ACF twice, we find the maximum diffusion rate to occur at time lag

$$\tau_{\max} = \frac{\tan^{-1}\epsilon}{\epsilon}\,\tau_p \, , \qquad \text{where} \qquad \epsilon \equiv \omega\tau_p \, , \tag{1.14}$$

and by plugging this back into the derivative of the SVF, we find the maximum diffusion rate to be:

$$D_{\max} = \sqrt{1+\epsilon^2}\, e^{-\frac{\tan^{-1}\epsilon}{\epsilon}}\, \frac{\sigma_0}{\tau_p} \, . \tag{1.15}$$

1.6 OUf motion

The Ouf ACF, which is OUF where $\tau_p = \tau_v$ or OUO where $\omega = 0$, is given by:

$$\gamma(\tau) = \sigma_0 \left(1 + \frac{\tau}{\tau_p} \right) e^{-\frac{\tau}{\tau_p}} \, . \tag{1.16}$$

The maximum diffusion rate is easily obtained from the $\omega \to 0$ limit of the OUO result:

$$D_{\max} = \frac{1}{e}\,\frac{\sigma_0}{\tau_p} \, . \tag{1.17}$$

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Supplement B — Interpreting the relationship between speed and diffusion

The model we are using estimates log mean speed as a function of log diffusion:

$$\log(\mu) = \beta_0 + \beta_1 \log(d) \Rightarrow \mu = \exp\big(\beta_0 + \beta_1 \log(d)\big) \qquad (1)$$

If we used a linear model of the form $\mu = \beta_0 + \beta_1 d$, the additive change in speed, $\Delta\mu$, for a change in diffusion, Δd, would be $\Delta\mu = \mu_1 - \mu_0 = (\beta_0 + (d + \Delta d)\beta_1) - (\beta_0 - d\beta_1) = (d + \Delta d - d)\beta_1 = \Delta d\beta_1$. In this case, β_1 indicates the additive change in μ for an additive change in diffusion, Δd.

If we used a GLM with a log link function, the model would be $\log(\mu) = \beta_0 + \beta_1 d \Rightarrow \mu = \exp(\beta_0 + \beta_1 d)$, and the relative change in speed, R_s, for an additive change in diffusion, Δd becomes

$$R_s = \mu_1/\mu_0 = \frac{\exp(\beta_0 + (d + \Delta d)d\beta_1)}{\exp(\beta_0 + d\beta_1)} = \frac{e^{\beta_0} e^{d\beta_1} e^{\Delta d\beta_1}}{e^{\beta_0} e^{d\beta_1}} = e^{\Delta d\beta_1}.$$

Now a Δd additive change in diffusion would result in a relative change of $R_s = e^{\Delta d\beta_1}$. But because we log both speed and diffusion in our model, the relative change in speed is

$$R_s = \mu_1/\mu_0 = \frac{\exp\big(\beta_0 + \beta_1 \log(d + \Delta d)\big)}{\exp\big(\beta_0 + \beta_1 \log(d)\big)} = \exp\big(\beta_0 + \beta_1 \log(d + \Delta d) - \beta_0 - \beta_1 \log(d)\big) =$$

$$= \exp\left(\beta_1 \log\left(\frac{d + \Delta d}{d}\right)\right) = \exp\big(\beta_1 \log(R_d)\big) = \exp\left(\log\left(R_d^{\beta_1}\right)\right) = R_d^{\beta_1},$$

where R_d is the relative change in diffusion and β_1 is the slope of the log-log model shown in Equation (1). Given the estimate from Fig. 2 of the manuscript $\hat{\beta}_1 = 0.40$, a 1% increase in diffusion corresponds to an approximate 1.004-fold increase (a 0.4% additive increase) in speed:

$$R_s = (101\%)^{0.40}/(100\%)^{0.40} = 1.01^{0.40}/1 \approx 1.003988 = 100.3988\% \approx 100.40\%.$$

This corresponds to an additive change in mean speed of $\Delta\mu \approx 100.40\% - 100\% = 0.40\%$, which is approximately β_1, but note the relationship between μ and d is nonlinear, so a doubling (a 100% increase) in diffusion does not correspond to a doubling in speed but rather an approximately 1.32-fold change (a 32% additive increase) in speed:

$$R_s = (200\%)^{0.40} = (2)^{0.40} = 1.319508 = 131.9508\% \Rightarrow \Delta\mu = 31.9508\%.$$

Supplementary material to Chapter 3 (S3)

S3: Table 4 — Summary of the study design and related hypotheses, predictions, data, consequences, and methods used in assessing the impact of vasectomy on breeding-related movement behavior and activity in free-ranging white-tailed deer. This study was conducted at a treatment site in Staten Island, NY, USA (SI) and at a control site in Rockefeller State Park Preserve, Pleasantville, NY, USA (RSPP) between 2021 and 2023.

Hypothesis	Prediction (Control- RSPP)	Prediction (Treatment- SI)	Data Source and Measure	Consequence	Method
Male white-tailed deer increase exploratory behavior in response to elevated testosterone levels.	Male white-tailed deer at the control site will show peak home range, distance traveled, diffusion, and excursivity during late October - December. These measures will decrease as testosterone levels drop in early January.	No expected differences with respect to Control	1 GPS fix/hour; 7-day home range, daily distance traveled, daily diffusion, daily excursivity	Increased deer-vehicle collisions, decreased body condition	Measures derived via ctmm in R with 7-day moving window/3-day slide; Modeled with HGAMLS
Female white-tailed deer show increases in exploratory behavior in response to estrus periods.	Female white-tailed deer at the control site will show increases in home range, distance traveled, diffusion, and excursivity in November - December during a window around their estrus period. Owing to the short duration of estrus, these changes may not be noticeable in the modeled data.	No expected differences with respect to Control, despite extra-estrus, as these changes might not be noticeable in the modeled data.	1 GPS fix/hour; 7-day home range, daily distance traveled, daily diffusion, daily excursivity	Increased deer-vehicle collisions, decreased body condition	Measures derived via ctmm in R with 7-day moving window/3-day slide; Modeled with HGAMLS
Male white-tailed deer become more active with elevated testosterone levels.	Male white-tailed deer at the control site will show peak activity during late October - December. These measures will decrease as testosterone levels drop in early January.	No expected differences with respect to Control	32 Hz tri-axial accelerometry; # of activity state transitions/day; proportion of time/day spent in no/low activity state	Increased deer-vehicle collisions, decreased body condition	Derived measures using 2-s window log (VeDBA); states identified via clustering with GMM; modeled with HGAM

Female white-tailed deer show increases in activity in response to estrus periods.	Female white-tailed deer at the control site will increase activity in November - December during a window around their estrus period. Owing to the short duration of estrus, these changes may not be noticeable in the modeled data.	Female white-tailed deer at the treatment site will increase in activity from November - March during a window around their estrus periods (extra-estrus).	32 Hz tri-axial accelerometry; # of activity state transitions/day; proportion of time/day spent in no/low activity state	Increased deer-vehicle collisions, decreased body condition	Derived measures using 2-s window of log (VeDBA); states identified via clustering with GMM; modeled with HGAM

S3: Table 5 — Detailed description of data cleaning and processing for telemetry data from both study sites.

After downloading raw GPS data (n = 735,270) from MoveBank we removed events without coordinates (n = 15,854), those from individuals tracked for < 28 days, and those from individuals in Year 1 who died of unknown causes before the first frost (known Epizootic Hemorrhagic Disease outbreak; n = 20,566). We removed outlier locations (n = 37) based on the visual inspection of telemetry data and the relationships between the minimum speed (assuming straight-line displacement) and deviation from the median location, turning angle, and time between locations. For each individual, we removed the first 10 and last 2 days of data from the analysis to reduce disturbance from the capture event and to limit the potential for inclusion of data after the collar had dropped off [1]. The median sampling interval for each individual included in the final sample is shown in S3: Fig. 11A.

S3: Table 6 — Hierarchical generalized additive models for location and scale (HGAMLSs) used to estimate the effect of the vasectomy treatment on movement behavior. The response variables are 7-day 95% home range size (km^2; `hr_est_95`), daily distance traveled (km/day; `speed_est`), daily diffusion (km^2/day; `diffusion_est`), and daily excursivity (unitless; `excursivity`). The predictor variables are the four combinations of sex and treatment status (`sex_treatment`), day of year (`days_since_aug_1`), study year (`study_year`), and animal ID for each study year (i.e., each collaring event; `animal_year`).

Response	HGAMLS Model

7-day home range size (km^2)

```
gam(formula = list(
  # linear predictor for the mean
  hr_est_95 ~
        sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
        s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
          xt = list(bs = 'cr')),
  # linear predictor for the scale (sigma2 = mu^2 * scale)
  ~ sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
        s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
        xt = list(bs = 'cr'))),
  family = gammals(),
  data = d,
  method = 'REML')
```

Distance traveled (km/day)

```
gam(formula = list(
  # linear predictor for the mean
  speed_est ~
        sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
```

```
        s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
          xt = list(bs = 'cr')),
  # linear predictor for the scale (sigma2 = mu^2 * scale)
  ~ sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
        s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
          xt = list(bs = 'cr'))),
  family = gammals(),
  data = d,
  method = 'REML')
```

Diffusion (km^2/day)

```
gam(list(
  # linear predictor for the mean
  diffusion_est ~
        sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
        s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
          xt = list(bs = 'cr')),
  # linear predictor for the scale (sigma2 = mu^2 * scale)
  ~ sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
        s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
          xt = list(bs = 'cr'))),
  family = gammals(),
  data = d,
  method = 'REML')
```

Daily excursivity

```
gam(formula = list(
  # linear predictor for the mean
  excursivity ~
        sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
        s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
```

```
        xt = list(bs = 'cr')),
# linear predictor for the scale (sigma2 = mu * (1-mu) * scale)
~ sex_treatment +
      s(days_since_aug_1, by = sex_treatment, k = 15, bs = 'tp') +
      s(days_since_aug_1, study_year, by = sex_treatment, k=15, bs='sz')+
      s(days_since_aug_1, animal_year, k = 15, bs = 'fs',
        xt = list(bs = 'cr'))),
family = betals(),
data = d,
method = 'REML')
```

S3: Table 7 — Hierarchical Generalized Additive Models (HGAMs) used to estimate the effect of the vasectomy treatment on activity states. The response variables are the daily proportion of time spent in a no- or low-activity state (vs a medium- or high-activity state; `p_low`), and the daily number of transitions between activity states (no, low, medium, high; `n_transitions`). The predictor variables are sex and treatment status of individuals (`sex_treatment`), day of year (`days_since_aug_1`), study year (`study_year`), and animal ID in each study year (`animal_year`).

Response	HGAM Model

Daily proportion of time spent in no- low-activity state

```
bam(
  p_low ~
        sex_treatment +
        s(days_since_aug_1, by = sex_treatment, k = 10, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=10,
bs='sz')+
        s(days_since_aug_1, animal_year, k = 10, bs = 'fs',
          xt = list(bs = 'cr')),
  family = betar(link = 'logit'),
  data = d,
  method = 'fREML',
  discrete = TRUE)
```

Daily number of transitions between activity states

```
bam(
  n_transitions ~
        sex_treatment +
    s(days_since_aug_1, by = sex_treatment, k = 10, bs = 'tp') +
        s(days_since_aug_1, study_year, by = sex_treatment, k=10,
bs='sz')+
        s(days_since_aug_1, animal_year, k = 10, bs = 'fs',
          xt = list(bs = 'cr')),
  family = nb(link = 'log'), # data is clearly over-dispersed
  data = d,
  method = 'fREML',
  discrete = TRUE)
```

S3: Table 8 — The data for the animals captured and fitted with biologging devices in the vasectomy study at Rockefeller State Park Preserve, Pleasantville, NY, USA (control) and Staten Island, NY, USA (treatment). The details include Animal ID, collar deployment start and end dates, number of days the collar was deployed, study status of individuals (e.g., why removed, 4 hr data noted, individuals in both years noted), estimated birth year, sex, site, and study year of individuals in the movement behavior study in New York, USA. White-tailed deer were treated with vasectomy starting in 2016, and during the time of the study, 97% of the antlered male deer were vasectomized on Staten Island.

Animal ID	Collar deployment start	Collar deployment end	Number of days deployed	Included in both years (y) or 4 hr data (4)	Estimated birth year	Sex	Site	Study year
2	2021-08-24	2022-05-30	279		2019	F	Treatment	1
3	2021-08-24	2022-05-30	279		2018	F	Treatment	1
148	2021-08-24	2022-05-30	279		2015	M	Treatment	1
1074	2021-08-24	2022-05-30	279		2013	M	Treatment	1
4a	2021-08-24	2021-08-30	6		2017	F	Treatment	<28 days
7	2021-08-25	2021-10-17	53		2016	F	Treatment	Potential EHD
629	2021-08-25	2022-05-11	259		2013	M	Treatment	1
1	2021-08-27	2022-05-30	276	y	2017	F	Treatment	1
8	2021-08-27	2021-09-23	27		2018	F	Treatment	<28 days
9	2021-08-27	2021-10-10	44		2016	F	Treatment	Potential EHD
11	2021-08-27	2022-05-30	276		2015	F	Treatment	1
12	2021-08-27	2022-05-30	276		2015	F	Treatment	1
13	2021-08-27	2021-10-18	52		2013	F	Treatment	Potential EHD
20a	2021-08-27	2022-05-30	276		2018	F	Treatment	1
5a	2021-08-27	2021-09-21	25		2017	F	Treatment	<28 days
16	2021-08-28	2022-05-30	275	y	2018	F	Treatment	1
18	2021-08-28	2022-05-30	275		2019	F	Treatment	1
403	2021-08-28	2021-10-10	43		2013	M	Treatment	Potential EHD
14a	2021-08-28	2021-09-15	18		2016	F	Treatment	<28 days
15a	2021-08-28	2021-09-08	11		2015	F	Treatment	<28 days
17a	2021-08-28	2021-08-29	1		2017	F	Treatment	<28 days
19a	2021-08-28	2021-10-09	42		2018	F	Treatment	Potential EHD
6a	2021-08-28	2022-05-30	275		2019	F	Treatment	1
219	2021-08-29	2022-05-30	274		2013	M	Treatment	1
674	2021-08-29	2021-09-25	27		2013	M	Treatment	<28 days
825	2021-08-29	2021-09-24	26		2016	M	Treatment	<28 days
1573	2021-08-29	2021-11-23	86		2019	M	Treatment	1
1891	2021-08-29	2021-10-08	40		2018	M	Treatment	Potential EHD
21a	2021-08-29	2022-05-30	274		2019	F	Treatment	1
23a	2021-08-29	2021-08-30	1		2018	F	Treatment	<28 days
28	2021-08-30	2022-01-30	153		2013	F	Control	1
264	2021-08-30	2021-09-22	23		2013	M	Treatment	<28 days
26	2021-08-31	2021-09-30	30		2013	F	Control	Potential EHD
30	2021-08-31	2022-05-30	272	y	2017	F	Control	1
31	2021-08-31	2022-05-30	272		2019	F	Control	1
33	2021-08-31	2022-03-06	187	4	2016	F	Control	1

34	2021-08-31	2021-09-01	1		2013	M	Control	<28 days
35	2021-08-31	2022-05-30	272		2019	M	Control	1
22	2021-09-01	2022-05-29	270	4	2018	F	Control	1
27	2021-09-01	2022-05-30	271	y	2016	F	Control	1
29	2021-09-01	2022-05-30	271	y	2013	F	Control	1
36	2021-09-01	2021-09-08	7		2013	F	Control	<28 days
37	2021-09-01	2021-09-09	8		2016	F	Control	<28 days
38	2021-09-01	2022-05-12	253	4	2013	M	Control	1
39	2021-09-01	2022-05-30	271		2017	M	Control	1
40	2021-09-01	2022-05-30	271		2018	F	Control	1
41	2021-09-01	2022-03-31	211	4	2018	M	Control	1
42	2021-09-02	2022-05-30	270		2016	F	Control	1
43	2021-09-02	2022-05-30	270	y	2018	M	Control	1
46	2021-09-02	2022-05-30	270		2013	F	Control	1
32a	2021-09-02	2021-11-14	73		2018	F	Control	1
44	2021-09-03	2022-02-28	178		2013	F	Control	1
45	2021-09-03	2022-05-30	269		2018	F	Control	1
47	2021-09-03	2022-05-30	269		2017	F	Control	1
23b	2021-09-03	2022-05-30	269		2013	F	Treatment	1
4b	2021-09-03	2022-05-30	269	y	2017	F	Treatment	1
48	2021-09-04	2021-10-12	38		2019	F	Control	Potential EHD
49	2021-09-04	2022-01-08	126		2013	F	Control	1
50	2021-09-04	2022-05-30	268		2018	M	Control	1
51	2021-09-04	2022-05-30	268	y	2018	F	Control	1
53	2021-09-04	2021-11-09	66		2017	M	Control	1
54	2021-09-22	2022-05-03	223		2016	F	Control	1
52	2021-09-23	2022-05-30	249		2018	F	Control	1
59	2021-09-28	2021-09-29	1		2019	M	Control	<28 days
561	2021-09-28	2022-05-30	244		2016	M	Treatment	1
1429	2021-09-28	2021-10-10	12		2017	M	Treatment	<28 days
14b	2021-09-28	2022-05-30	244		2015	F	Treatment	1
15b	2021-09-28	2022-05-30	244		2017	F	Treatment	1
5b	2021-09-28	2021-11-18	51		2018	F	Treatment	1
57	2021-09-29	2022-04-12	195	4	2018	M	Control	1
58	2021-09-29	2021-10-24	25		2018	M	Control	<28 days
24	2021-10-28	2021-11-01	4		2017	F	Treatment	<28 days
56	2021-10-28	2022-05-30	214		2015	F	Control	1
61	2021-10-28	2022-05-30	214		2017	M	Control	1
1319	2021-10-28	2022-05-30	214		2016	M	Treatment	1
17b	2021-10-28	2022-05-30	214		2018	F	Treatment	1
19b	2021-10-28	2021-11-04	7		2018	F	Treatment	<28 days
21b	2021-10-28	2022-05-30	214		2016	F	Treatment	1
25	2021-10-29	2022-05-30	213	y	2017	F	Treatment	1
62	2021-10-29	2022-05-30	213		2016	F	Control	1
133	2021-10-29	2022-05-30	213		2013	M	Treatment	1
170	2021-10-29	2022-04-22	175		2013	M	Treatment	1
1123	2021-10-29	2022-05-30	213	y	2018	M	Treatment	1
66	2021-11-05	2022-05-30	206		2017	F	Treatment	1
20b	2021-11-05	2022-05-30	206		2017	F	Treatment	1
63	2021-11-11	2022-04-29	169		2018	M	Control	1
32b	2021-11-27	2021-11-27	0		2020	F	Control	<28 days
32c	2021-11-30	2021-11-30	0		2018	F	Control	<28 days
6b	2021-12-01	2022-05-30	180		2018	F	Control	1
80	2021-12-13	2022-05-30	168		2018	F	Treatment	1
1584	2021-12-13	2022-05-30	168		2018	M	Treatment	1
51	2022-08-14	2023-06-21	311	y	2018	F	Control	2
82	2022-08-14	2023-06-21	311		2019	M	Control	2
83	2022-08-15	2023-06-21	310		2020	F	Control	2
84	2022-08-15	2023-06-21	310		2018	F	Control	2
85	2022-08-15	2022-12-30	137		2020	F	Control	2
102	2022-08-16	2023-06-21	309		2019	F	Treatment	2
1123	2022-08-17	2023-02-07	174	y	2018	M	Treatment	2

116	2022-08-18	2023-06-21	307		2017	F	Treatment	2
113	2022-08-20	2023-06-21	305		2018	F	Treatment	2
115	2022-08-20	2022-09-08	19		2015	F	Treatment	<28 days
117	2022-08-20	2023-06-21	305		2016	F	Treatment	2
123	2022-08-21	2023-06-21	304		2019	F	Treatment	2
1979	2022-08-21	2023-06-21	304		2018	M	Treatment	2
25	2022-08-22	2022-11-14	84	y	2017	F	Treatment	2
118	2022-08-22	2023-06-21	303		2015	F	Treatment	2
119	2022-08-22	2023-06-21	303		2018	F	Treatment	2
120	2022-08-22	2023-06-21	303		2016	F	Treatment	2
122	2022-08-22	2023-06-21	303		2017	F	Treatment	2
481	2022-08-22	2022-08-23	1		2015	M	Treatment	<28 days
1286	2022-08-22	2023-06-21	303		2017	M	Treatment	2
4b	2022-08-22	2023-06-21	303	y	2017	F	Treatment	2
351	2022-08-23	2023-03-16	205		2016	M	Treatment	2
1143	2022-08-23	2023-06-21	302		2018	M	Treatment	2
1580	2022-08-24	2022-10-05	42		2018	M	Treatment	Potential EHD
1713	2022-08-24	2023-06-21	301		2020	M	Treatment	2
1716	2022-08-24	2023-06-21	301		2020	M	Treatment	2
41y	2022-08-24	2023-06-21	301		2017	F	Treatment	2
121	2022-08-28	2022-10-05	38		2015	F	Treatment	Potential EHD
124	2022-08-28	2023-06-21	297		2019	F	Treatment	2
125	2022-08-28	2023-06-21	297		2018	F	Treatment	2
127	2022-08-28	2023-06-21	297		2015	F	Treatment	2
126	2022-08-29	2023-06-21	296		2019	F	Treatment	2
1782	2022-08-30	2023-06-21	295		2019	M	Treatment	2
128	2022-08-31	2023-06-21	294		2019	F	Treatment	2
16	2022-09-02	2023-06-21	292	y	2018	F	Treatment	2
1159	2022-09-04	2023-06-21	290		2017	M	Treatment	2
63	2022-09-08	2022-10-29	51		2018	M	Control	Failure
88	2022-09-08	2023-06-21	286		2017	F	Control	2
92	2022-09-08	2023-06-21	286		2018	F	Control	2
99	2022-09-08	2023-06-21	286		2018	F	Control	2
100	2022-09-08	2023-06-21	286		2016	F	Control	2
27	2022-09-09	2023-06-21	285	y	2016	F	Control	2
29	2022-09-09	2023-06-21	285	y	2013	F	Control	2
87	2022-09-09	2023-06-21	285		2017	F	Control	2
89	2022-09-09	2023-06-21	285		2018	F	Control	2
90	2022-09-09	2023-06-21	285		2020	M	Control	2
98	2022-09-09	2023-06-21	285		2015	F	Control	2
182	2022-09-09	2023-06-21	285		2020	F	Control	2
183	2022-09-09	2022-09-19	10		2017	F	Control	<28 days
192	2022-09-09	2023-06-21	285		2020	F	Control	2
30	2022-09-10	2023-06-21	284	y	2017	F	Control	2
91	2022-09-10	2023-06-21	284	4	2019	M	Control	2
97	2022-09-10	2023-06-21	284		2019	F	Control	2
184	2022-09-10	2023-06-21	284		2020	F	Control	2
185	2022-09-10	2023-06-21	284		2016	F	Control	2
43	2022-09-11	2023-06-21	283	y	2018	M	Control	2
187	2022-09-11	2023-06-21	283		2019	M	Control	2
1	2022-10-22	2023-06-21	242	y	2017	F	Treatment	2
93	2022-10-22	2023-06-21	242		2019	M	Control	2
94	2022-10-22	2023-06-21	242		2020	F	Control	2
107	2022-10-22	2023-06-21	242		2020	F	Treatment	2
2009	2022-10-22	2023-06-21	242		2019	M	Treatment	2
95	2022-11-08	2023-06-21	225		2020	M	Control	2
96	2022-11-08	2023-06-21	225		2017	M	Control	2
188	2022-11-08	2023-06-21	225		2016	M	Control	2
132	2022-12-11	2023-06-21	192		2017	F	Treatment	2
139	2023-01-08	2023-06-21	164		2020	F	Treatment	2

S3: Table 9 — Mortality data and cause for individuals included in the movement study at the treatment site in Staten Island and at the control site at Rockefeller State Park Preserve in both study years (2021–2022; 2022–2023).

	Year 1		Year 2	
	SI	RSPP	SI	RSPP
Females	1 DVC (11/20/2021)	3 Unknown (1/8/2022, 1/30/2022, 3/1/2022) 2 DVC (11/14/2021, 5/29/2021)	1 Unknown (11/14/2022)	1 Poaching (12/30/2022)
Males	1 DVC (4/22/2022)	1 DVC (11/9/2021)	2 DVC (2/7/23, 3/16/2023)	1 Poaching (10/29/2022)

S3: Table 10 — Individual deer carcasses (monthly percentage of total) reported to the New York Department of Sanitation for pick-up on both public and private lands in Staten Island, NY, USA, between July 2016 and June 2024 [1].

	2016–17	2017–18	2018–19	2019–20	2020–21	2021–22*	2022–23**	2023–24
July	8 (5%)	7 (3%)	4 (1%)	8 (6%)	3 (2%)	2 (2%)	3 (5%)	1 (2%)
August	10 (6%)	9 (3%)	8 (3%)	5 (4%)	4 (3%)	8 (9%)	2 (3%)	0 (0%)
September	10 (6%)	14 (5%)	11 (4%)	10 (7%)	7 (5%)	15 (16%)	4 (6%)	2 (4%)
October	22 (13%)	36 (13%)	37 (14%)	19 (13%)	12 (8%)	8 (9%)	13 (20%)	6 (12%)
November	41 (24%)	44 (16%)	52 (19%)	31 (22%)	23 (15%)	6 (7%)	9 (14%)	17 (34%)
December	9 (5%)	21 (8%)	38 (14%)	10 (7%)	30 (20%)	8 (9%)	9 (14%)	5 (10%)
January	13 (8%)	38 (14%)	27 (10%)	17 (12%)	20 (13%)	6 (7%)	5 (8%)	3 6%)
February	15 (9%)	30 (11%)	23 (9%)	9 (6%)	12 (8%)	10 (11%)	4 (6%)	4 (8%)
March	10 (6%)	23 (8%)	34 (13%)	6 (4%)	23 (15%)	11 (12%)	3 (5%)	4 (8%)
April	8 (5%)	23 (8%)	13 (5%)	5 (4%)	7 (5%)	5 (5%)	5 (8%)	3 (6%)
May	12 (7%)	24 (9%)	14 (5%)	13 (9%)	4 (3%)	8 (9%)	5 (8%)	3 (6%)
June	11 (7%)	11 (4%)	7 (3%)	9 (6%)	7 (5%)	5 (5%)	3 (5%)	2 (4%)
Total	169	280	268	142	152	92	65	50

* Data represents Year 1 of the research program and was the year an Epizootic Hemorrhagic Disease outbreak occurred.

**Data represents Year 2 of the research program.

References

1. New York City Department of Parks and Recreation (NYCDPR). Managing deer impacts on Staten Island; 2024. https://storymaps.arcgis.com/stories/e3a5f6d544594690a313693d1e88d9ef Accessed 12 Sep 2024

S3: Table 11 — Percentage of movement parameter estimates used in the analysis after excluding NA, non-finite, and excessively large values, as described in the text.

Sex (Site)	7-day home range size (%)	Daily distance traveled (%)	Daily diffusion (%)	Daily excursivity (%)
Female (RSPP)	100	54.4	99.7	100
Female (SI)	97.7	55.4	99.7	100
Male (RSPP)	99.9	75.2	96.6	100
Male (SI)	98.7	56.2	99.7	100
Total	98.9	60.3	98.9	100

S3: Table 12 — Families of distributions, percentages of deviance explained, and scale estimates ($\hat{\theta}$) for HGAMs presented, listed by response variable: home range size, daily distance traveled, daily diffusion, daily excursivity, proportion of time spent in no- or low-activity state by day, and number of transitions between states by day. The deviance explained (%) is a measure of goodness of fit that shows the proportion of the total deviance that the model accounts for. Deviance explained is not currently available for the `betals` family, as it is currently not included in the `mgcv` package. The scale estimate measures the dispersion of the response variable. Scale estimates are not included for location-scale models because they depend on the covariates. The estimated variance for the Beta and Negative Binomial families, respectively, are $\widehat{Var(Y)} = \hat{\mu}(1-\hat{\mu})/(1+\hat{\theta})$ and $\widehat{Var(Y)} = \hat{\mu} + \hat{\mu}^2/\hat{\theta}$, where $\hat{\mu}$ is the estimated mean.

Response variable	Family of distributions	Deviance explained (%)	Scale estimate ($\hat{\theta}$)
7-day home range size (km^2)	Gamma location-scale	94.5	Not a constant
Daily distance traveled (km/day)	Gamma location-scale	79.5	Not a constant
Daily diffusion (km^2/day)	Gamma location-scale	89.1	Not a constant
Daily excursivity	Beta location-scale	NA	Not a constant
Daily proportion of time in no- or low-activity state	Beta	64.5	102.019
Daily number of transitions between states	Negative binomial	70.7	63.215

S3: Table 13 — Model summaries for hierarchical generalized additive models for location and scale (HGAMLSs) and hierarchical generalized additive models (HGAMs) used to estimate the effect of the vasectomy treatment on movement behavior. The response variables are 7-day 95% home range size (km^2; `hr_est_95`), daily distance traveled (km/day; `speed_est`), daily diffusion (km^2/day; `diffusion_est`), daily excursivity (unitless; `excursivity`), the daily proportion of time spent in a no- or low-activity state (vs a medium- or high-activity state; `p_low`), and the daily number of transitions between activity states (no, low, medium, high; `n_transitions`). The predictor variables are the four combinations of sex and treatment status (`sex_treatment`), day of year (`days_since_aug_1`), study year (`study_year`), and animal ID for each study year (i.e., each collaring event; `animal_year`).

Response variable	Model summary
7-day 95% home range size (km^2; `hr_est_95`)	

```
Family: gammals
Link function: identity log

Formula:
hr_est_95 ~ sex_treatment + s(days_since_aug_1, by = sex_treatment,
    k = 15, bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))
~sex_treatment + s(days_since_aug_1, by = sex_treatment, k = 15,
    bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))

Parametric coefficients:
                              Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -0.83072    0.07205 -11.529  < 2e-16 ***
sex_treatmentf staten_island   0.20332    0.10129   2.007   0.0447 *
sex_treatmentm rockefeller     0.91205    0.13196   6.911 4.80e-12 ***
sex_treatmentm staten_island   0.61185    0.12702   4.817 1.46e-06 ***
(Intercept).1                  3.46953    0.09291  37.341  < 2e-16 ***
sex_treatmentf staten_island.1  1.40047    0.13128  10.668  < 2e-16 ***
sex_treatmentm rockefeller.1    1.08324    0.17177   6.306 2.86e-10 ***
sex_treatmentm staten_island.1  1.67883    0.16271  10.318  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                            edf   Ref.df
Chi.sq  p-value
s(days_since_aug_1):sex_treatmentf rockefeller           11.463   12.027
56.477  < 2e-16 ***
s(days_since_aug_1):sex_treatmentf staten_island         12.652   13.187
102.613  < 2e-16 ***
s(days_since_aug_1):sex_treatmentm rockefeller           11.841   12.487
56.323 2.66e-06 ***
s(days_since_aug_1):sex_treatmentm staten_island          4.759    5.455
3.971  0.60464
s(days_since_aug_1,study_year):sex_treatmentf rockefeller     2.000    2.000
0.757  0.68501
```

```
s(days_since_aug_1,study_year):sex_treatmentf staten_island      2.001    2.001
12.864  0.00161 **
s(days_since_aug_1,study_year):sex_treatmentm rockefeller        9.105    9.979
10.837  0.35272
s(days_since_aug_1,study_year):sex_treatmentm staten_island     11.444   12.437
21.654  0.03148 *
s(days_since_aug_1,animal_year)                               1000.112 1687.000
72037.164  < 2e-16 ***
s.1(days_since_aug_1):sex_treatmentf rockefeller                11.871   12.908
91.294  < 2e-16 ***
s.1(days_since_aug_1):sex_treatmentf staten_island              11.425   12.485
121.693  < 2e-16 ***
s.1(days_since_aug_1):sex_treatmentm rockefeller                 3.996    4.660
4.602  0.40296
s.1(days_since_aug_1):sex_treatmentm staten_island               1.000    1.000
8.409  0.00373 **
s.1(days_since_aug_1,study_year):sex_treatmentf rockefeller      2.000    2.000
5.035  0.08068 .
s.1(days_since_aug_1,study_year):sex_treatmentf staten_island   11.873   13.030
59.071  < 2e-16 ***
s.1(days_since_aug_1,study_year):sex_treatmentm rockefeller      8.831   10.054
17.181  0.07154 .
s.1(days_since_aug_1,study_year):sex_treatmentm staten_island    7.451    8.607
19.899  0.04369 *
s.1(days_since_aug_1,animal_year)                              596.901 1670.000
4657.330  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Deviance explained = 94.5%
-REML = -66.723  Scale est. = 1         n = 9288
```

Daily distance traveled (km/day; `speed_est`)

```
Family: gammals
Link function: identity log

Formula:
speed_est ~ sex_treatment + s(days_since_aug_1, by = sex_treatment,
    k = 15, bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))
~sex_treatment + s(days_since_aug_1, by = sex_treatment, k = 15,
    bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))

Parametric coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                     1.50542    0.03605  41.755  < 2e-16 ***
sex_treatmentf staten_island    0.16129    0.05058   3.189  0.00143 **
sex_treatmentm rockefeller      0.05578    0.06442   0.866  0.38656
sex_treatmentm staten_island    0.10141    0.06345   1.598  0.10998
(Intercept).1                   2.78682    0.07110  39.194  < 2e-16 ***
sex_treatmentf staten_island.1  0.60058    0.09920   6.054 1.41e-09 ***
sex_treatmentm rockefeller.1    0.34508    0.12422   2.778  0.00547 **
sex_treatmentm staten_island.1  0.68142    0.12306   5.537 3.07e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                                   edf   Ref.df
Chi.sq  p-value
s(days_since_aug_1):sex_treatmentf rockefeller                  10.705   12.014
58.004  < 2e-16 ***
s(days_since_aug_1):sex_treatmentf staten_island                11.012   12.260
76.175  < 2e-16 ***
s(days_since_aug_1):sex_treatmentm rockefeller                  13.056   13.665
141.405  < 2e-16 ***
s(days_since_aug_1):sex_treatmentm staten_island                12.140   13.189
100.907  < 2e-16 ***
s(days_since_aug_1,study_year):sex_treatmentf rockefeller        6.418    7.442
10.509  0.15144
```

```
s(days_since_aug_1,study_year):sex_treatmentf staten_island    11.704   13.011
55.410 2.32e-06 ***
s(days_since_aug_1,study_year):sex_treatmentm rockefeller       2.015    2.019
3.054  0.21978
s(days_since_aug_1,study_year):sex_treatmentm staten_island     2.013    2.016
6.946  0.03111 *
s(days_since_aug_1,animal_year)                               538.894 1607.000
15610.431  < 2e-16 ***
s.1(days_since_aug_1):sex_treatmentf rockefeller                1.003    1.004
0.483  0.48469
s.1(days_since_aug_1):sex_treatmentf staten_island              3.242    3.899
14.126  0.00759 **
s.1(days_since_aug_1):sex_treatmentm rockefeller                9.039   10.546
52.670 2.33e-06 ***
s.1(days_since_aug_1):sex_treatmentm staten_island              4.831    5.803
51.349  < 2e-16 ***
s.1(days_since_aug_1,study_year):sex_treatmentf rockefeller     2.670    2.934
1.590  0.57919
s.1(days_since_aug_1,study_year):sex_treatmentf staten_island   2.002    2.002
1.878  0.39124
s.1(days_since_aug_1,study_year):sex_treatmentm rockefeller     2.004    2.006
3.733  0.15448
s.1(days_since_aug_1,study_year):sex_treatmentm staten_island   2.002    2.004
2.869  0.23849
s.1(days_since_aug_1,animal_year)                             208.192 1601.000
725.253  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Deviance explained = 79.6%
-REML = 7886.7  Scale est. = 1         n = 5445
```

Daily diffusion (km^2/day; `diffusion_est`)

```
Family: gammals
Link function: identity log

Formula:
diffusion_est ~ sex_treatment + s(days_since_aug_1, by = sex_treatment,
    k = 15, bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))
~sex_treatment + s(days_since_aug_1, by = sex_treatment, k = 15,
    bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))

Parametric coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                    -3.91469    0.06725 -58.207  < 2e-16 ***
sex_treatmentf staten_island    0.28460    0.09438   3.015  0.00257 **
sex_treatmentm rockefeller      0.53841    0.12211   4.409 1.04e-05 ***
sex_treatmentm staten_island    0.06146    0.11768   0.522  0.60147
(Intercept).1                   3.72217    0.06787  54.844  < 2e-16 ***
sex_treatmentf staten_island.1  0.94987    0.09616   9.878  < 2e-16 ***
sex_treatmentm rockefeller.1    0.30712    0.12857   2.389  0.01690 *
sex_treatmentm staten_island.1  0.98776    0.11949   8.267  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                                  edf   Ref.df
Chi.sq  p-value
s(days_since_aug_1):sex_treatmentf rockefeller                 11.935   12.545
59.229 2.34e-06 ***
s(days_since_aug_1):sex_treatmentf staten_island               12.794   13.307
171.159  < 2e-16 ***
s(days_since_aug_1):sex_treatmentm rockefeller                 13.073   13.453
143.199  < 2e-16 ***
s(days_since_aug_1):sex_treatmentm staten_island               11.843   12.661
64.331  < 2e-16 ***
s(days_since_aug_1,study_year):sex_treatmentf rockefeller       2.014    2.017
1.375 0.505948
```

```
s(days_since_aug_1,study_year):sex_treatmentf staten_island    10.467   11.540
14.520 0.263509
s(days_since_aug_1,study_year):sex_treatmentm rockefeller       8.586    9.507
14.627 0.105467
s(days_since_aug_1,study_year):sex_treatmentm staten_island     2.046    2.056
7.894 0.017046 *
s(days_since_aug_1,animal_year)                               957.768 1679.000
53860.569  < 2e-16 ***
s.1(days_since_aug_1):sex_treatmentf rockefeller                9.313   10.713
37.534 9.01e-05 ***
s.1(days_since_aug_1):sex_treatmentf staten_island             10.372   11.638
110.147  < 2e-16 ***
s.1(days_since_aug_1):sex_treatmentm rockefeller                7.576    8.862
32.581 0.000227 ***
s.1(days_since_aug_1):sex_treatmentm staten_island              5.272    6.264
25.602 0.000359 ***
s.1(days_since_aug_1,study_year):sex_treatmentf rockefeller     2.013    2.017
2.402 0.302130
s.1(days_since_aug_1,study_year):sex_treatmentf staten_island  11.696   12.944
70.499  < 2e-16 ***
s.1(days_since_aug_1,study_year):sex_treatmentm rockefeller    10.025   11.417
45.790 1.43e-05 ***
s.1(days_since_aug_1,study_year):sex_treatmentm staten_island   2.011    2.014
2.461 0.294433
s.1(days_since_aug_1,animal_year)                             469.380 1667.000
2699.844  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Deviance explained = 89.1%
-REML = -30616  Scale est. = 1         n = 9320
```

Daily excursivity (unitless; `excursivity`)

```
Family: betals
Link function: identity identity

Formula:
density ~ sex_treatment + s(days_since_aug_1, by = sex_treatment,
    k = 15, bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))
~sex_treatment + s(days_since_aug_1, by = sex_treatment, k = 15,
    bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 15, bs = "sz") + s(days_since_aug_1, animal_year, k = 15,
    bs = "fs", xt = list(bs = "cr"))

Parametric coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                    -0.19699    0.05235  -3.763 0.000168 ***
sex_treatmentf staten_island   -0.29277    0.07335  -3.992 6.56e-05 ***
sex_treatmentm rockefeller     -0.15977    0.09633  -1.658 0.097217 .
sex_treatmentm staten_island   -0.23254    0.09171  -2.536 0.011227 *
(Intercept).1                  -2.69152    0.05645 -47.680  < 2e-16 ***
sex_treatmentf staten_island.1  0.06305    0.07914   0.797 0.425664
sex_treatmentm rockefeller.1    0.37802    0.10364   3.647 0.000265 ***
sex_treatmentm staten_island.1  0.33703    0.09939   3.391 0.000697 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                                  edf   Ref.df
Chi.sq  p-value
s(days_since_aug_1):sex_treatmentf rockefeller                 11.786   12.562
61.758  < 2e-16 ***
s(days_since_aug_1):sex_treatmentf staten_island               11.898   12.699
51.020 5.09e-06 ***
s(days_since_aug_1):sex_treatmentm rockefeller                 13.142   13.579
195.427  < 2e-16 ***
s(days_since_aug_1):sex_treatmentm staten_island                7.681    8.807
34.464 7.87e-05 ***
s(days_since_aug_1,study_year):sex_treatmentf rockefeller       2.003    2.004
0.937 0.626764
```

```
s(days_since_aug_1,study_year):sex_treatmentf staten_island     2.041    2.050
4.853 0.082115 .
s(days_since_aug_1,study_year):sex_treatmentm rockefeller      11.374   12.460
24.608 0.013818 *
s(days_since_aug_1,study_year):sex_treatmentm staten_island     7.049    8.001
3.853 0.869719
s(days_since_aug_1,animal_year)                               969.229 1696.000
55845.107  < 2e-16 ***
s.1(days_since_aug_1):sex_treatmentf rockefeller                9.982   11.333
19.673 0.055103 .
s.1(days_since_aug_1):sex_treatmentf staten_island             10.884   12.123
50.849 6.03e-06 ***
s.1(days_since_aug_1):sex_treatmentm rockefeller                1.014    1.018
0.042 0.856879
s.1(days_since_aug_1):sex_treatmentm staten_island              1.005    1.006
0.131 0.720167
s.1(days_since_aug_1,study_year):sex_treatmentf rockefeller     2.005    2.006
1.028 0.599549
s.1(days_since_aug_1,study_year):sex_treatmentf staten_island   8.070    9.271
7.745 0.481704
s.1(days_since_aug_1,study_year):sex_treatmentm rockefeller     2.014    2.017
1.513 0.473243
s.1(days_since_aug_1,study_year):sex_treatmentm staten_island  11.262   12.593
35.179 0.000566 ***
s.1(days_since_aug_1,animal_year)                             790.163 1681.000
6465.661  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Deviance explained =   NA%
-REML = -16743  Scale est. = 1         n = 29856
```

Daily proportion of time spent in a no- or low-activity state (vs a medium- or high-activity state; `p_low`)

```
Family: Beta regression(102.019)
Link function: logit

Formula:
p_low ~ sex_treatment + s(days_since_aug_1, by = sex_treatment,
    k = 10, bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 10, bs = "sz") + s(days_since_aug_1, animal_year, k = 10,
    bs = "fs", xt = list(bs = "cr"))

Parametric coefficients:
                             Estimate Std. Error t value Pr(>|t|)
(Intercept)                   0.13369    0.02281   5.860 4.68e-09 ***
sex_treatmentf staten_island -0.03043    0.03204  -0.950    0.342
sex_treatmentm rockefeller   -0.01673    0.04714  -0.355    0.723
sex_treatmentm staten_island  0.19752    0.03987   4.954 7.30e-07 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                                  edf   Ref.df
F p-value
s(days_since_aug_1):sex_treatmentf rockefeller                  8.781    8.843
21.299 < 2e-16 ***
s(days_since_aug_1):sex_treatmentf staten_island                8.338    8.531
12.249 < 2e-16 ***
s(days_since_aug_1):sex_treatmentm rockefeller                  6.286    6.670
2.873 0.00436 **
s(days_since_aug_1):sex_treatmentm staten_island                8.371    8.517
7.497 < 2e-16 ***
s(days_since_aug_1,study_year):sex_treatmentf rockefeller     2.013    2.016
0.137 0.87511
s(days_since_aug_1,study_year):sex_treatmentf staten_island   9.269    9.479
5.687 < 2e-16 ***
s(days_since_aug_1,study_year):sex_treatmentm rockefeller     2.048    2.056
0.128 0.88945
s(days_since_aug_1,study_year):sex_treatmentm staten_island   6.133    6.570
1.196 0.30591
s(days_since_aug_1,animal_year)                             820.849 1069.000
25.378 < 2e-16 ***
---
```

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.621   Deviance explained = 64.4%
fREML = -17043  Scale est. = 1         n = 28168
```

Daily number of transitions between activity states (no, low, medium, high; `n_transitions`)

```
Family: Negative Binomial(63.215)
Link function: log

Formula:
n_transitions ~ sex_treatment + s(days_since_aug_1, by = sex_treatment,
    k = 10, bs = "tp") + s(days_since_aug_1, study_year, by = sex_treatment,
    k = 10, bs = "sz") + s(days_since_aug_1, animal_year, k = 10,
    bs = "fs", xt = list(bs = "cr"))

Parametric coefficients:
                             Estimate Std. Error t value Pr(>|t|)
(Intercept)                  8.123078   0.017926 453.134   <2e-16 ***
sex_treatmentf staten_island 0.022158   0.024967   0.887    0.375
sex_treatmentm rockefeller   0.043288   0.036710   1.179    0.238
sex_treatmentm staten_island 0.005262   0.030953   0.170    0.865
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                                edf   Ref.df
F p-value
s(days_since_aug_1):sex_treatmentf rockefeller                 8.681    8.784
18.200 < 2e-16 ***
s(days_since_aug_1):sex_treatmentf staten_island               8.528    8.675
18.164 < 2e-16 ***
s(days_since_aug_1):sex_treatmentm rockefeller                 8.816    8.876
29.269 < 2e-16 ***
s(days_since_aug_1):sex_treatmentm staten_island               8.769    8.833
18.137 < 2e-16 ***
s(days_since_aug_1,study_year):sex_treatmentf rockefeller     8.488    8.858
2.895 0.00316 **
s(days_since_aug_1,study_year):sex_treatmentf staten_island   9.243    9.467
6.391 < 2e-16 ***
s(days_since_aug_1,study_year):sex_treatmentm rockefeller     6.641    7.098
1.008 0.54605
s(days_since_aug_1,study_year):sex_treatmentm staten_island   7.574    8.018
3.076 0.00180 **
s(days_since_aug_1,animal_year)                             808.212 1071.000
41.796 < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.694   Deviance explained = 70.7%
fREML =  42373  Scale est. = 1         n = 28220
```

S3: Table 14 — Percentage habitat composition for female and male deer at treatment and control sites in Year 1. Habitat composition was determined using GLC_FCS30D land cover data [1] overlaid with the 50% home range estimated via Autocorrelated Kernel Density Estimation (AKDE) in ctmm [2]. The area of each habitat type within the 50% AKDE was calculated for each individual, and group-level percentages represent the habitat composition across all individuals in that category.

Control site females	
Habitat class	**%**
Closed deciduous broadleaved forest	77.18
Herbaceous cover cropland	14.28
Impervious surfaces	3.07
Shrubland	1.34
Closed evergreen needle-leaved forest	1.17
Open evergreen broadleaved forest	0.96
Open mixed leaf forest (broadleaved and needle-leaved)	0.57
Grassland	0.54
Rainfed cropland	0.43
Open evergreen needle-leaved forest	0.28
Open deciduous broadleaved forest	0.12
Irrigated cropland	0.05

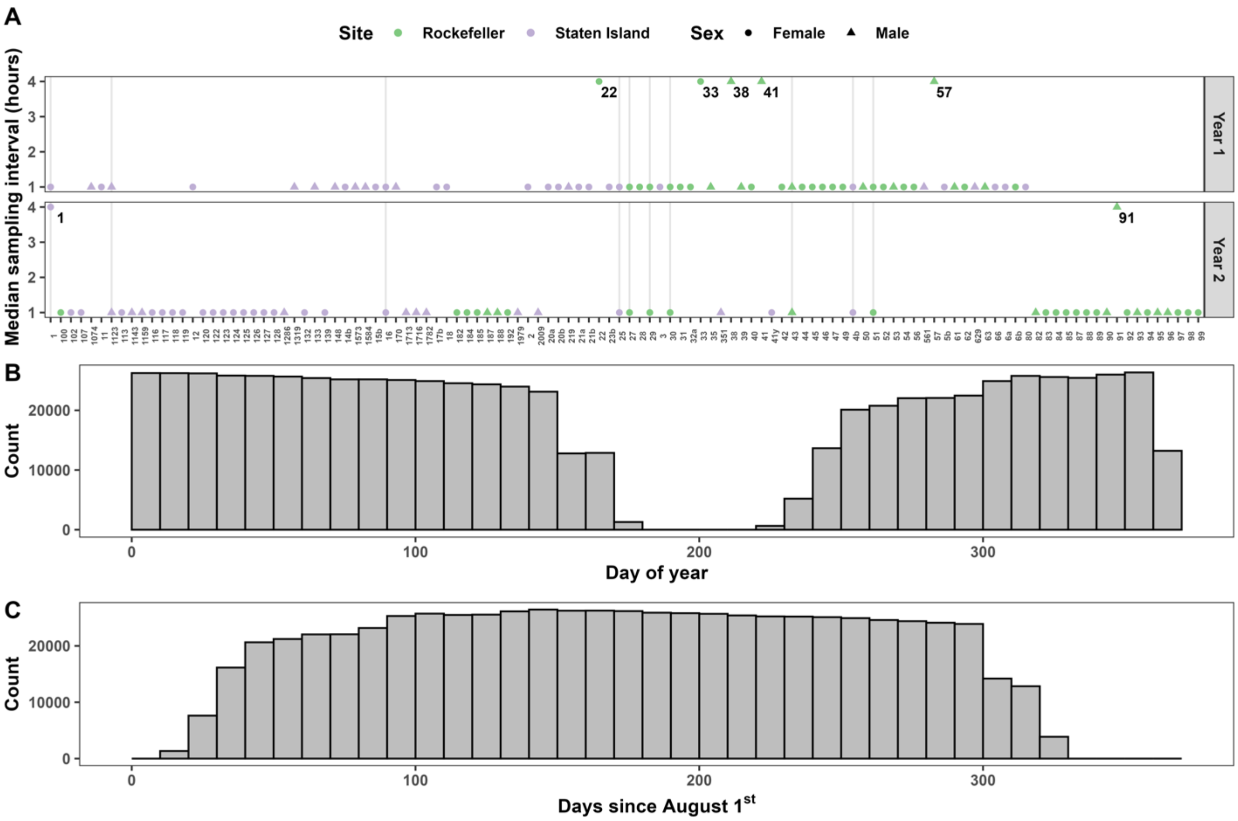
Control site males	
Habitat class	**%**
Closed deciduous broadleaved forest	70.17
Impervious surfaces	12.71
Herbaceous cover cropland	8.39
Closed evergreen needle-leaved forest	3.58
Rainfed cropland	1.04
Shrubland	0.99
Open evergreen needle-leaved forest	0.7
Open mixed leaf forest (broadleaved and needle-leaved)	0.53
Water body	0.5
Open evergreen broadleaved forest	0.34
Salt marsh	0.24

Grassland	0.2
Swamp	0.2
Open deciduous needle-leaved forest	0.09
Open deciduous broadleaved forest	0.07
Closed deciduous needle-leaved forest (fc >0.4)	0.06
Irrigated cropland	0.04
Marsh	0.04
Closed evergreen broadleaved forest	0.03
Sparse vegetation	0.03
Bare areas	0.01
Evergreen shrubland	0.01

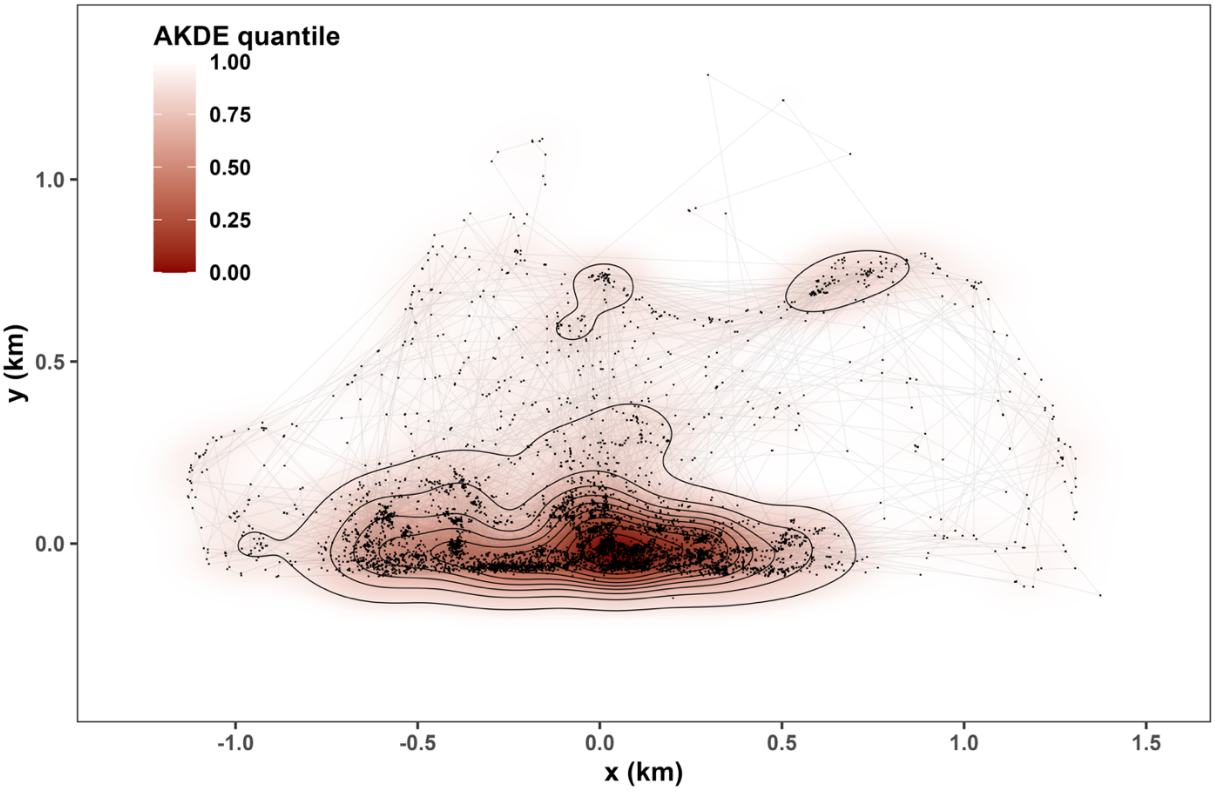
Treatment site females	
Habitat class	**%**
Closed deciduous broadleaved forest	46.61
Impervious surfaces	24.18
Herbaceous cover cropland	12.82
Closed evergreen needle-leaved forest	4.89
Salt marsh	4.76
Shrubland	1.88
Open evergreen broadleaved forest	1.15
Open evergreen needle-leaved forest	0.85
Rainfed cropland	0.53
Water body	0.53
Tidal flat	0.37
Lichens and mosses	0.32
Swamp	0.3
Closed deciduous needle-leaved forest (fc >0.4)	0.27
Open mixed leaf forest (broadleaved and needle-leaved)	0.19
Grassland	0.16
Open deciduous broadleaved forest	0.09
Sparse vegetation	0.09

Treatment site males	
Habitat class	**%**
Impervious surfaces	37.71
Closed deciduous broadleaved forest	24
Herbaceous cover cropland	21.29
Water body	4.01
Salt marsh	3.93

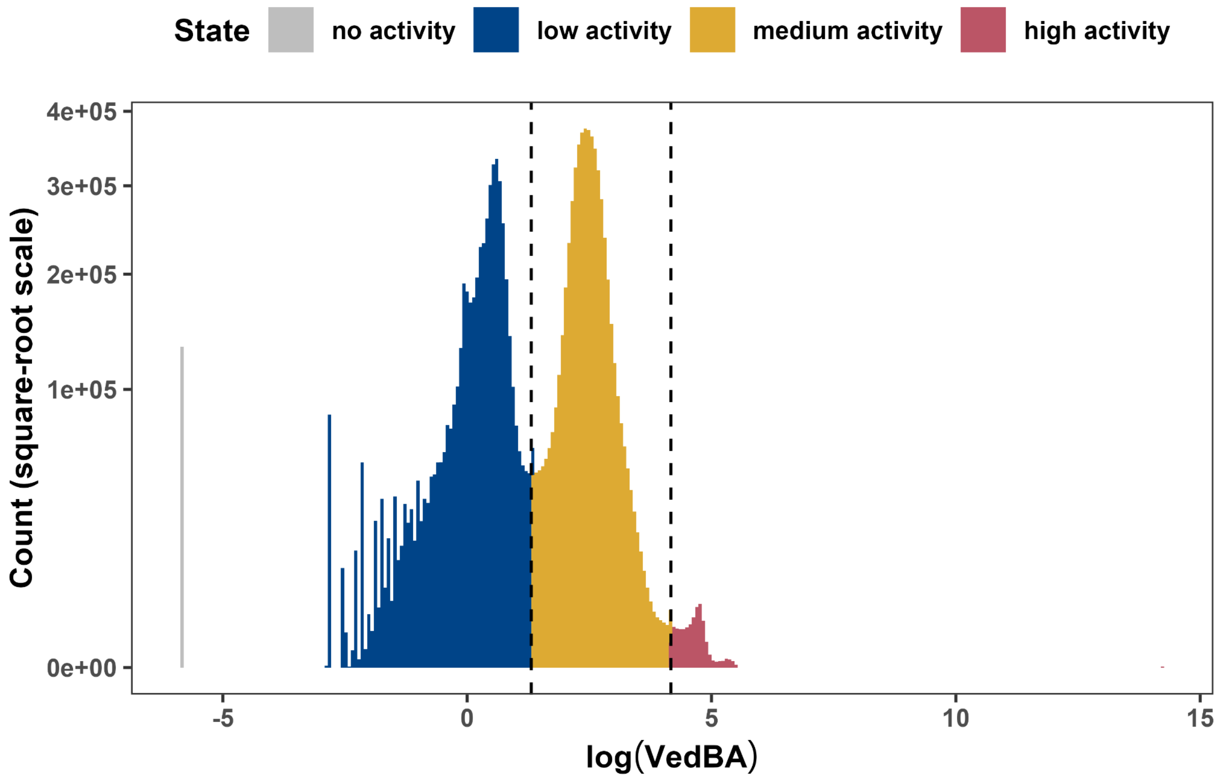
Closed evergreen needle-leaved forest	3.2
Open evergreen broadleaved forest	1.29
Rainfed cropland	1
Swamp	0.92
Open evergreen needle-leaved forest	0.81
Shrubland	0.65
Open deciduous broadleaved forest	0.34
Marsh	0.26
Grassland	0.14
Sparse vegetation	0.14
Tidal flat	0.14
Open mixed leaf forest (broadleaved and needle-leaved)	0.06
Bare areas	0.03
Closed deciduous needle-leaved forest (fc >0.4)	0.03
Irrigated cropland	0.03
Closed evergreen broadleaved forest	0.01



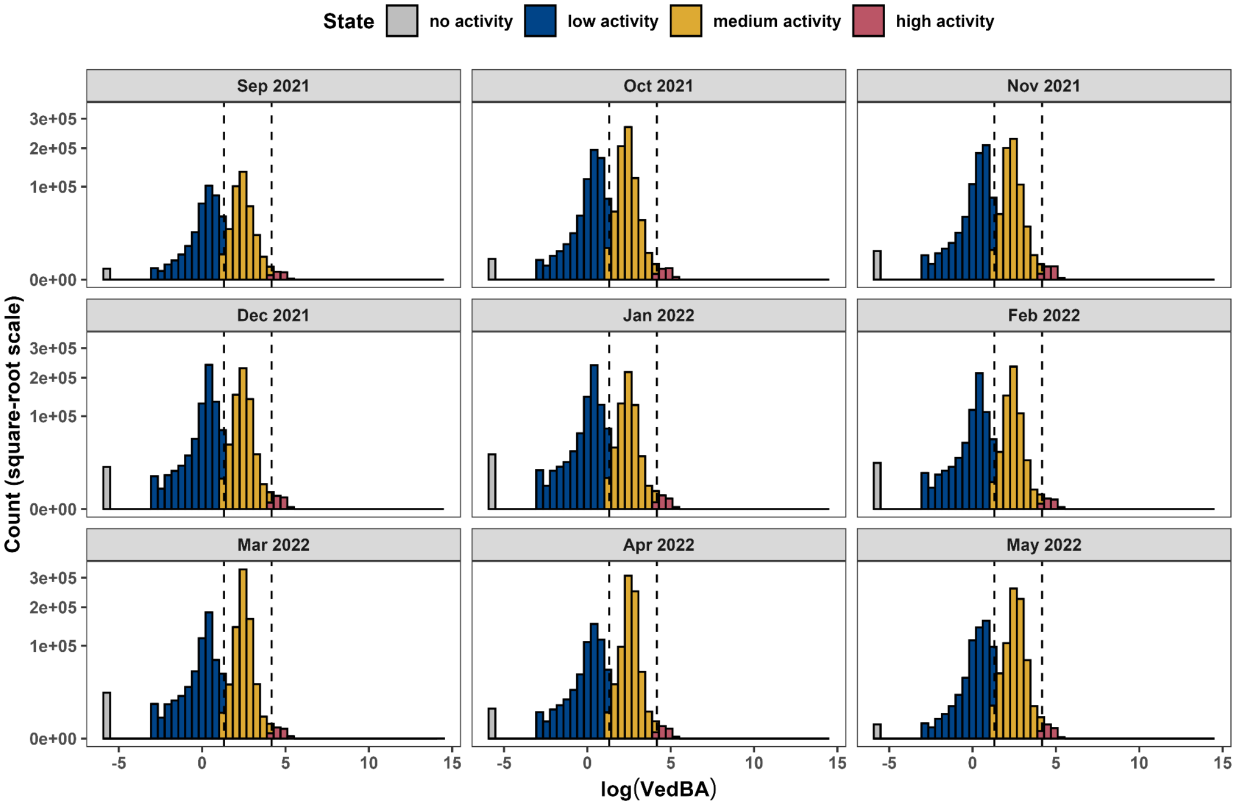
S3: Figure 11 — Median GPS fix rate for individuals in the final sample. Text labels indicate which deer had a 4-h sampling interval, whereas gray vertical lines indicate which deer were tracked in both years (A). Total number of GPS fixes over day of year (i.e., days since December 31st of the previous year; (B) and days since 1 August (C). In panel B, note the lack of continuity between December and January as well as the gap between the end of data collection in May/June and the deployment of collars and contrast this with panel B, where dates are shown as the number of days since 1 August.



S3: Figure 12 — Telemetry data (dots) and Autocorrelated Kernel Density Estimate (shading) for deer 148 in Year 1 (2021–22) with a two-point equidistant projection. The contours indicate quantiles at intervals of 0.1. Excursivity was measured by taking the average quantile of the locations for each day. A value close to 0 indicated the deer used high-use areas, whereas a value of 1 indicated that the deer used more "peripheral" areas that were generally only used during excursions.



S3: Figure 13 — Trimodal distribution of log mean VeDBA values for 2-s intervals for one individual. Low (log(VeDBA) < 1.12), medium (1.12 < log(VeDBA) < 4.2), and high (log(VeDBA) > 4.2) activity states are represented by the three distribution peaks. The small peak represents the high activity state at ~4.5. The same 3-peak pattern was observed in all individuals. VeDBA values of 0 (log(VeDBA) = -∞) are shown at the minimum finite log(VeDBA) - 3 for ease of readability.



S3: Figure 14 — Monthly trimodal distribution of log mean VeDBA values for 2-s intervals for one individual. The boundaries of low, medium, and high states did not change by month when 10 individuals were examined.

Reference

1. Liangyun Liu, Xiao Zhang, & Tingting Zhao. (2023). GLC_FCS30D: the first global 30-m land-cover dynamic monitoring product with fine classification system from 1985 to 2022 [Data set]. Zenodo. https://doi.org/10.5281/zenodo.8239305
2. Calabrese JM, Fleming CH, Gurarie E. ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol Evol. 2016;7:1124–32. https://doi.org/10.1111/2041-210X.12559

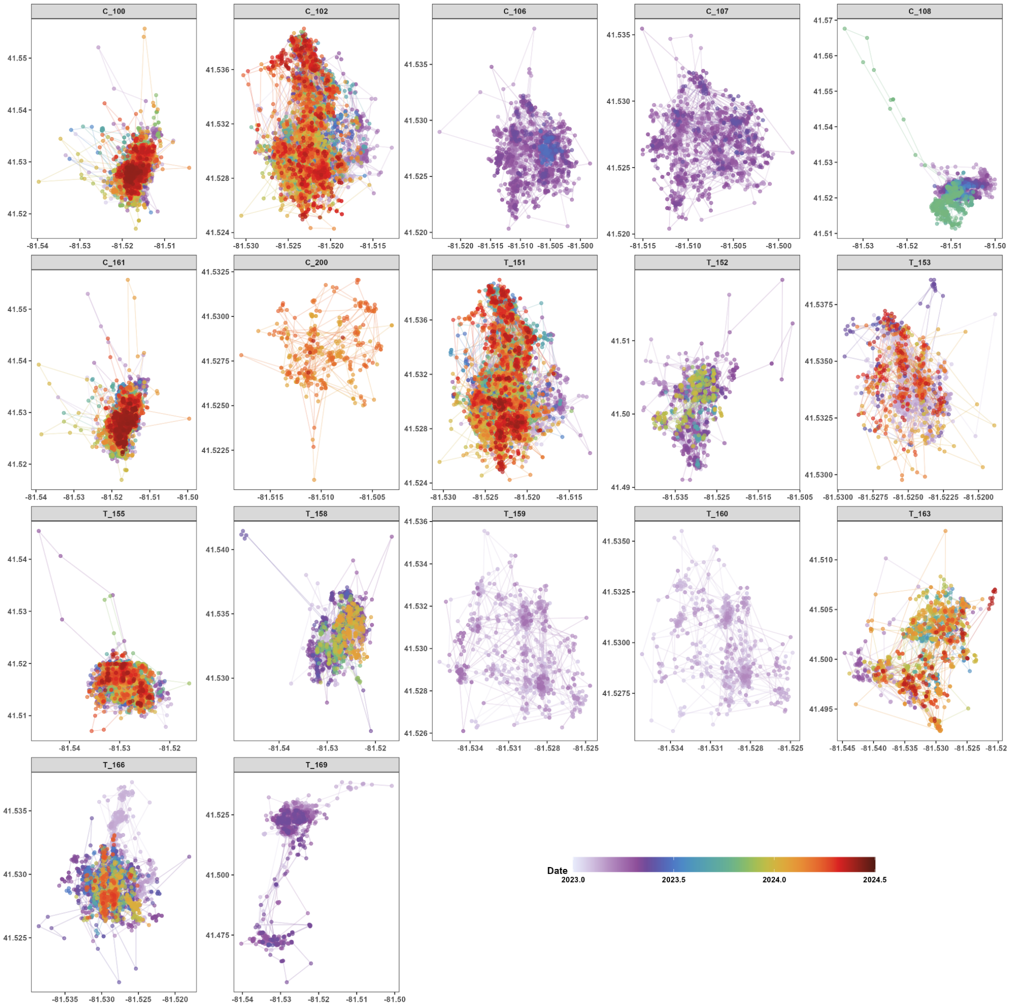
Supplementary material to Chapter 4 (S4)

Individual ID	Capture date	Number of fixes	Mortality date (cause)
C_100	18 Jan 2023	18,799	
C_101	19 Jan 2023	0	
C_102	19 Jan 2023	12,887	
C_103	20 Jan 2023	0	17 May 2023 (DVC)
C_106	20 Jan 2023	2,418	
C_107	20 Jan 2023	2,032	
C_108	21 Jan 2023	3,316	26 Oct 2023 (cull)
C_161	18 Jan 2023	15,560	
C_200	18 Jan 2024	395	
C_201	18 Jan 2024	0	
T_151	17 Jan 2023	13,989	
T_152	18 Jan 2023	2,096	
T_153	17 Jan 2023	1,389	
T_155	18 Jan 2023	10,992	
T_158	17 Jan 2023	2,473	29 Feb 2024 (cull)
T_159	18 Jan 2023	1,127	
T_160	18 Jan 2023	812	
T_163	18 Jan 2023	1,698	
T_166	18 Jan 2023	5,419	
T_169	18 Jan 2023	3,480	30 May 2023 (DVC)

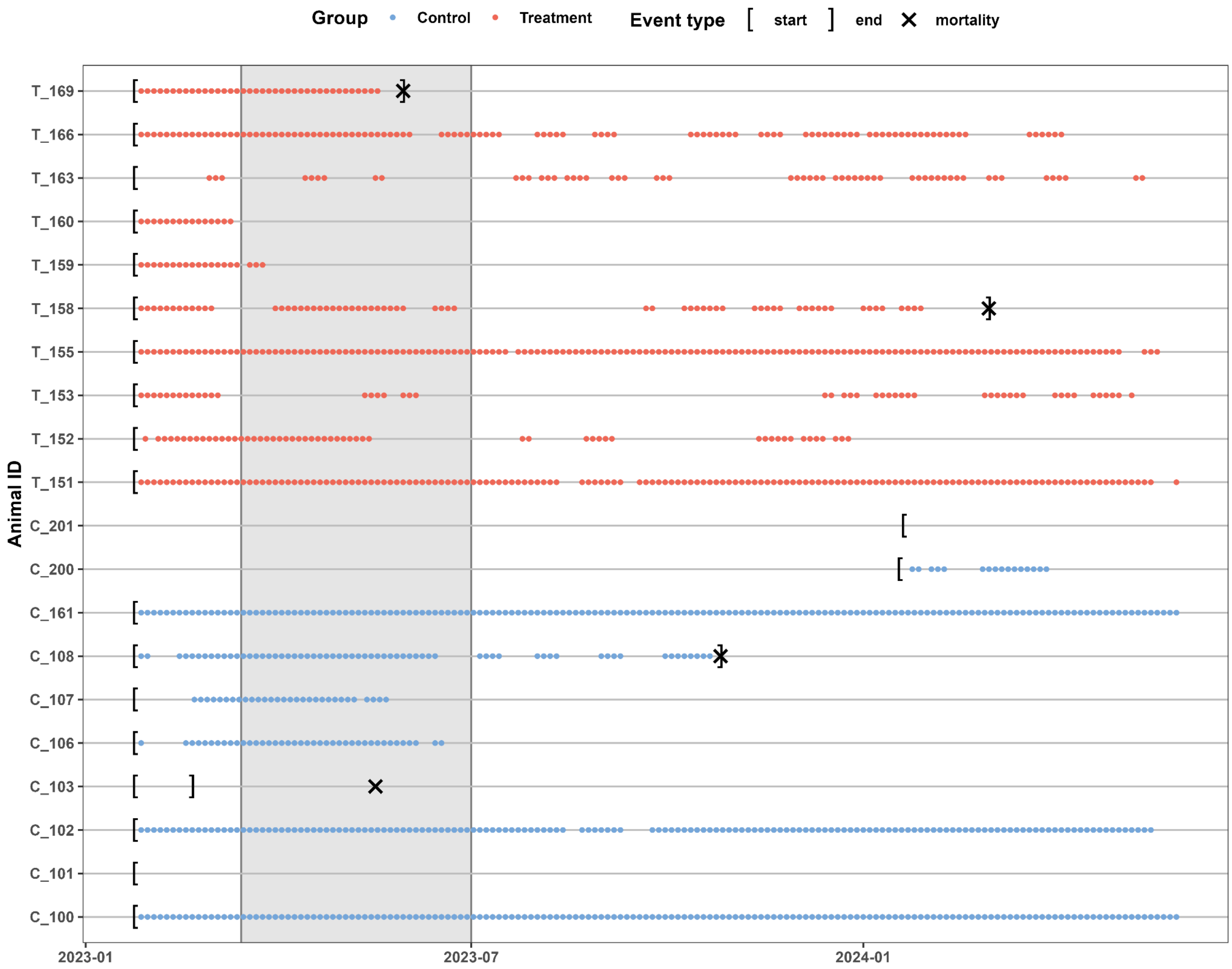
S4: Table 15 — Individual deer ID, capture date, number of fixes, mortality date (cause), and data status for individuals in the movement behavior study in South Euclid, Ohio, USA. All individuals were adult females. The first character of the individual ID indicates whether the animal was part of the treatment (T) or control (C) groups.

S4: Table 16 — Number (and percentage) of windows with parameter estimates used in the HGAM analysis after excluding NA, and excessively large values, as described in the text, along with the total number of windows (including those with NA and excessively large values).

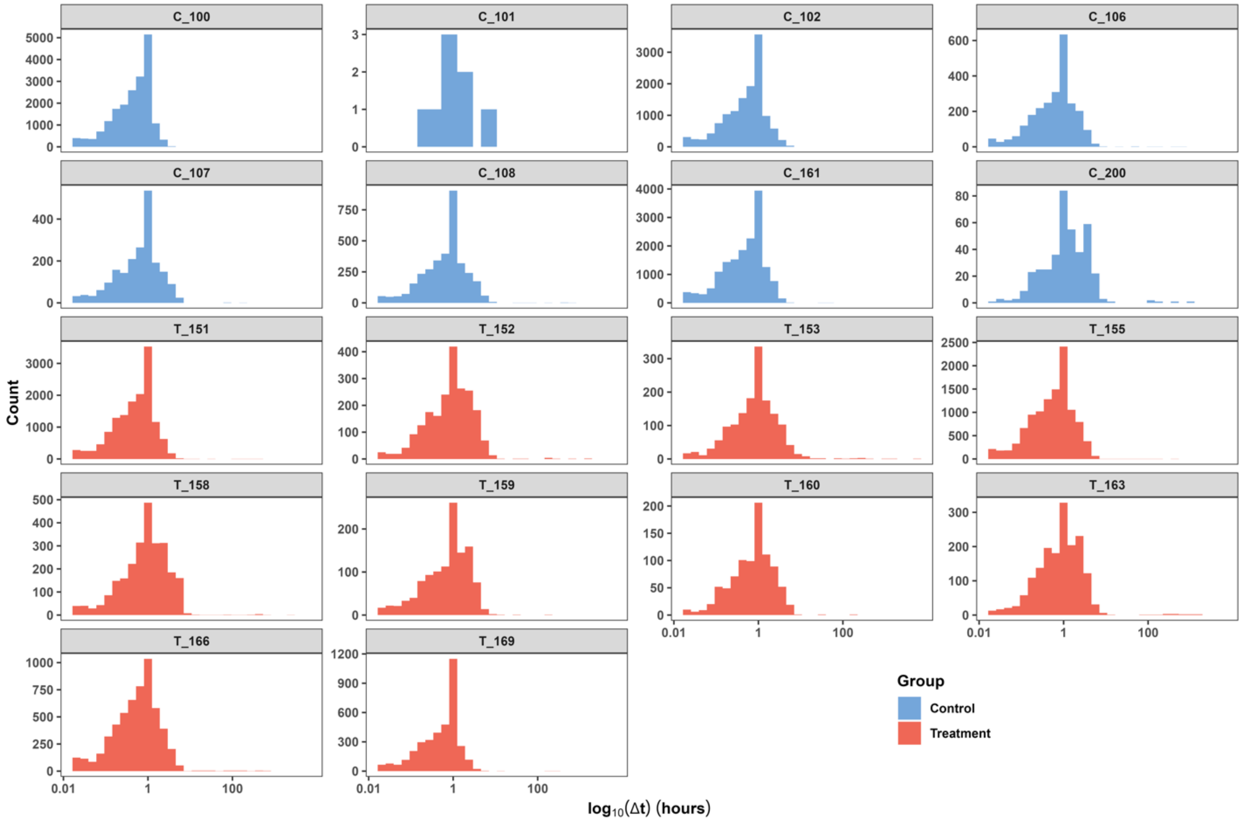
Group	7-day HR size	Diffusion	Excursivity	Total windows
Control	628 (90.8%)	614 (88.7%)	637 (92.1%)	692 (100%)
Treatment	698 (64.5%)	696 (64.3%)	735 (67.9%)	1082 (100%)
Total	1326 (74.7%)	1310 (73.8%)	1372 (77.3%)	1774 (100%)



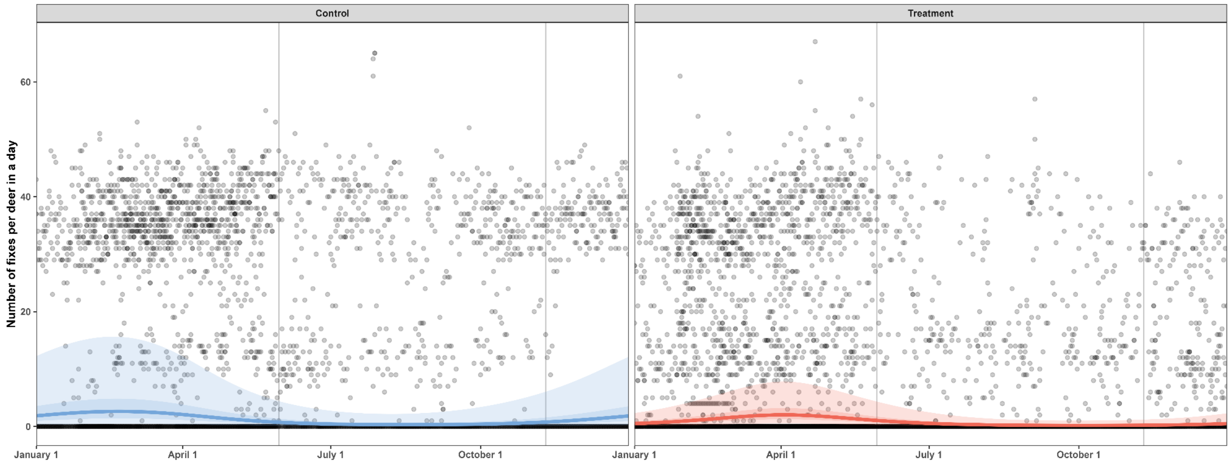
S4: Figure 15 — Telemetry data of the deer in South Euclid, Ohio, USA included in this study. Facet labels with “C” indicate control deer, whereas facet labels with “T” indicate deer treated with ovariectomy. The color of the points indicates the date the location was taken. The lines indicate the sequence of locations but are not appropriate reconstructions of the paths taken by the animals.



S4: Figure 16 — Sampling events from biologging devices for the treatment (T) and control (C) individuals in South Euclid, Ohio, USA deer movement study. Each dot represents the center of a 7-day window with at least 5 fixes. The gray band reflects the period when the base station was offline between 15 March and 1 July 2023.



S4: Figure 17 — Sampling intervals from biologging devices for the treatment (T) and control (C) individuals in the deer movement behavior study in South Euclid, Ohio, USA.



S4: Figure 18 — The number of daily fixes in a day from 1 January until 31 December for the treatment and control individuals in the South Euclid, Ohio, USA deer movement study. The lines indicate the estimated mean daily number of fixes for a deer in each group, whereas the shaded areas indicate the corresponding 50% and 95% Bayesian credible intervals under the assumption of Gaussian coefficients on the link scale. Note that daily fixes decrease from 25 February until 1 July. This decline may be attributed to a base station outage from 15 March to 1 July 2023. Variability in data collection could also result from increased sedentary behavior, or individuals moving beyond the coverage area. Notably, the decline is more pronounced in the control group. Gray lines mark the peak of parturition and the breeding season in Ohio [1].

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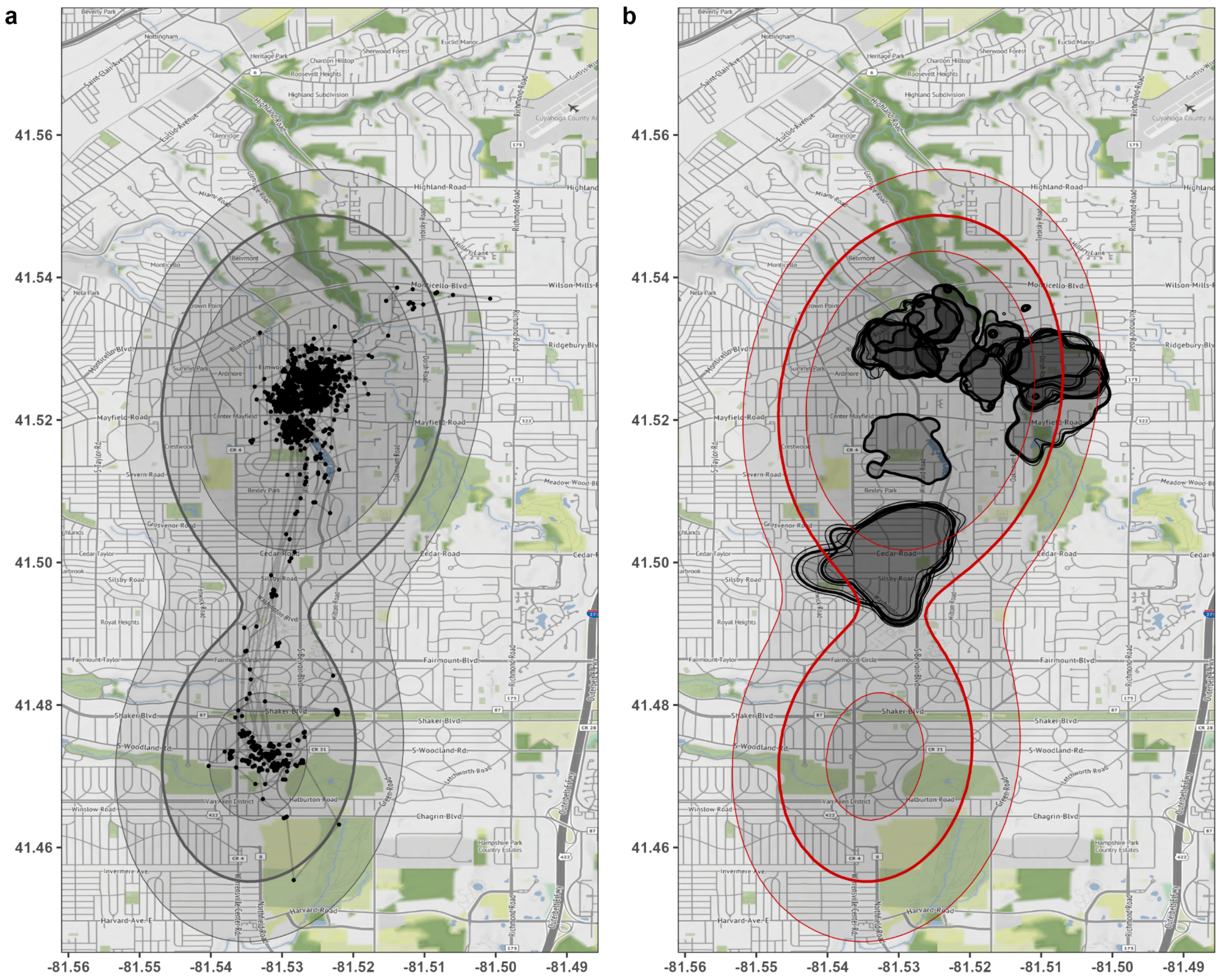
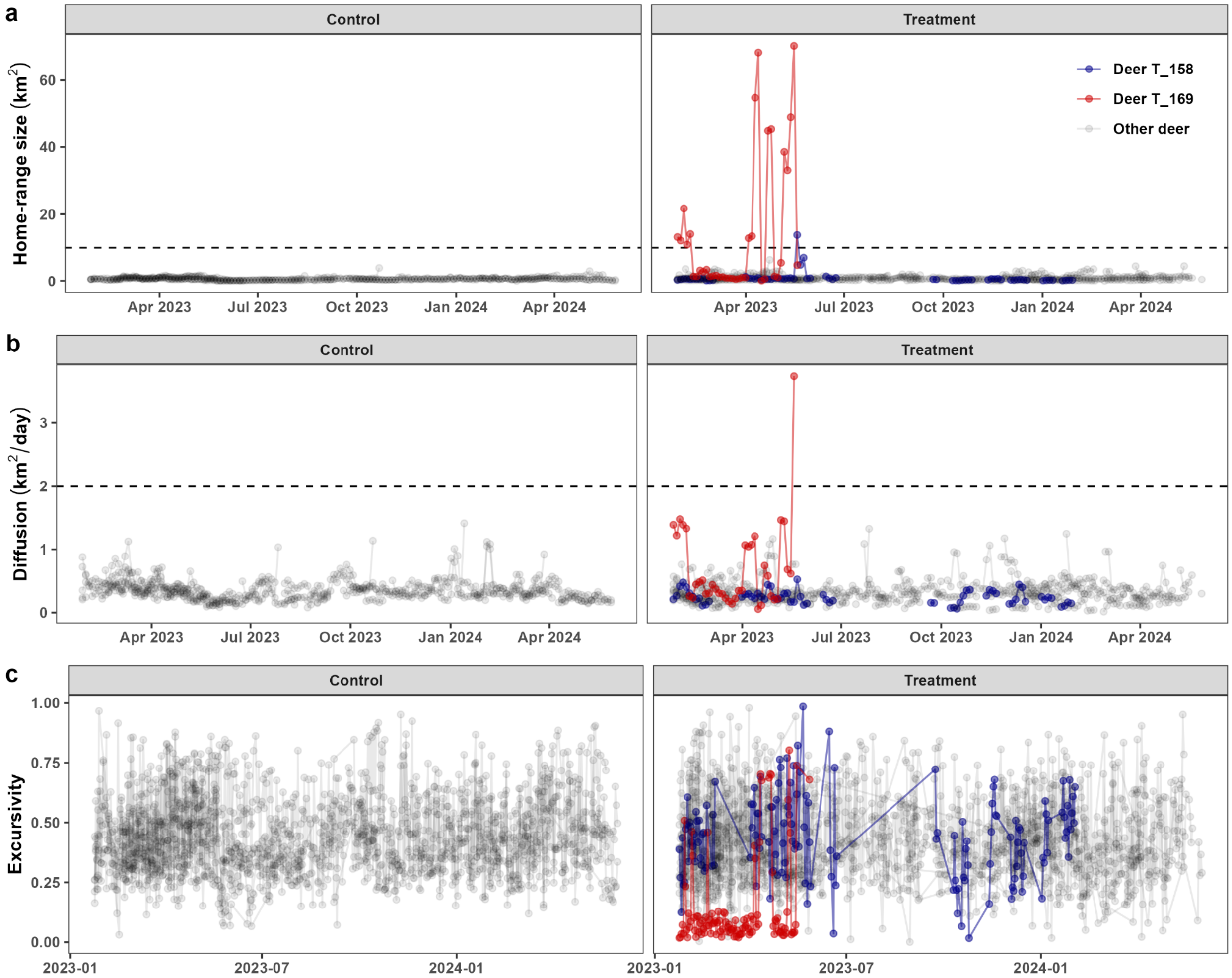
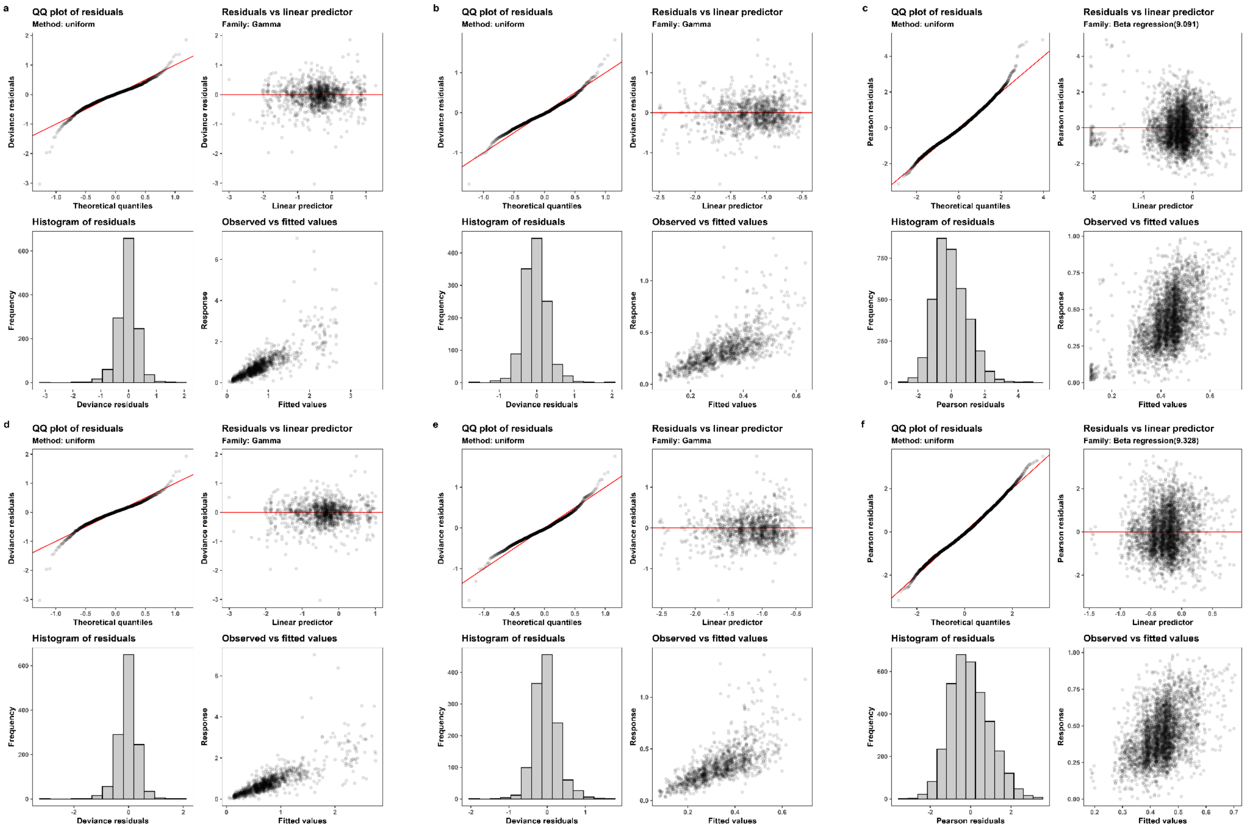
1. Nixon, C.M. 1971. Productivity of white-tailed deer in Ohio. The Ohio Journal of Science, 71(4):217–225.



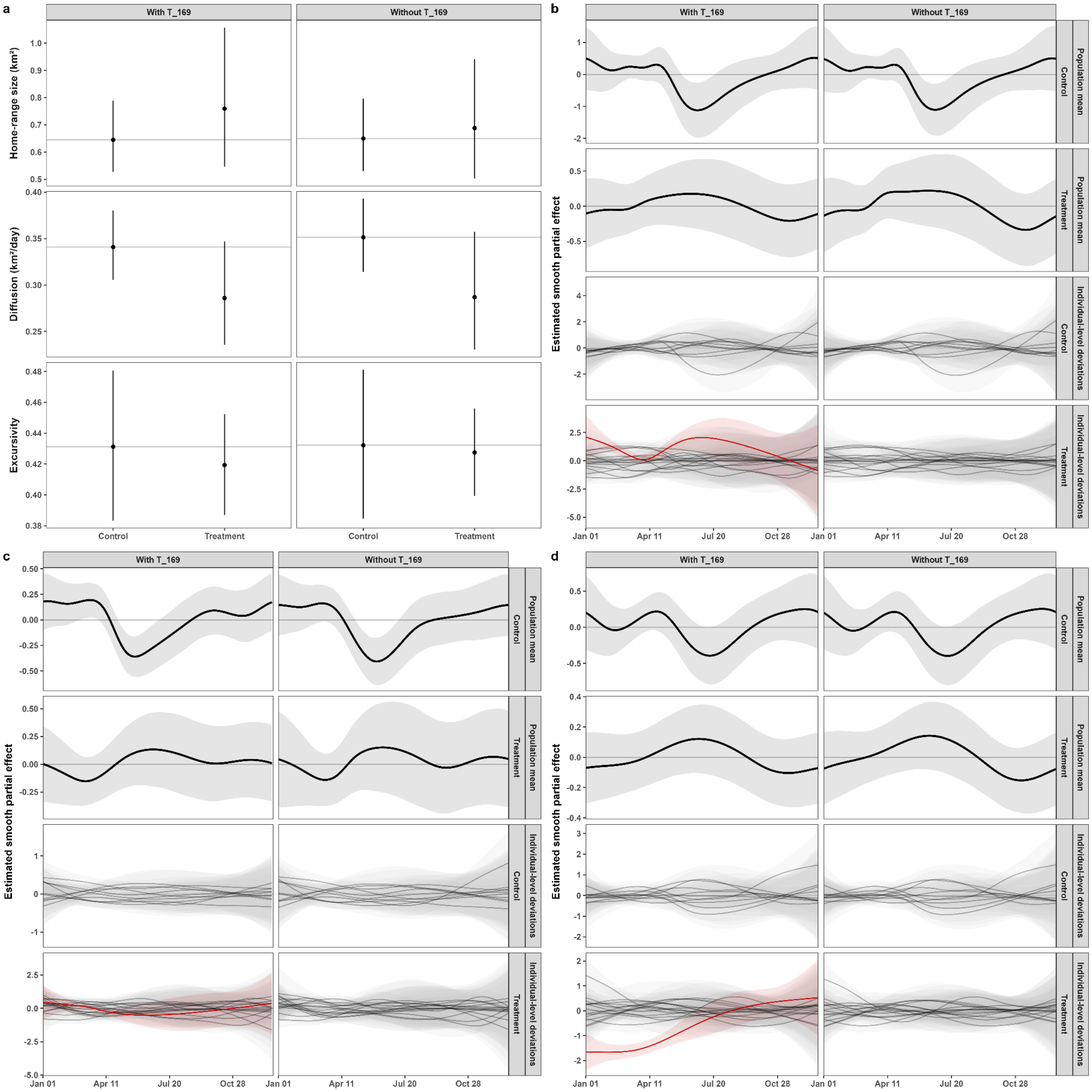
S4: Figure 19 — Telemetry and Autocorrelated Kernel Density Estimate for individual T_169 before excluding the 7-day windows of transition between the two commuting sites (a) and the Autocorrelated Kernel Density Estimates for all individuals in the South Euclid, Ohio, USA deer movement study are shown in black, with T_169 shown in red (b). The basemap was provided by Stadia Maps, Stamen Design, OpenMapTiles, and OpenStreetMap contributors.



S4: Figure 20 — Estimated 7-day home-range (a), daily diffusion (b), and daily excursivity (c) for all the treated and control individuals in the South Euclid, Ohio, USA deer movement study, with deer T_169 indicated in red and deer T_158 in blue. Note the substantially different estimates relative to all other deer.



S4: Figure 21 — Diagnostic plots used to examine the fit of the three HGAMs used in the South Euclid, Ohio, USA deer movement study with T_169 (a-c) and without T_169 (d-f) of home-range size (a, d), diffusion (b, e), and excursivity (c, f). Deer T_169 moved between two areas of the study site eight times during monitoring. The lack of stationary behavior led to a total of 15 biasedly large home-range estimates and overall biasedly small excursivity, but such differences were accounted for using deer-level random effects within each group. After the removal of unreliable estimates (i.e., home-range and diffusion estimates > 10 times the group mean, the addition or removal of T_169 did not impact the HGAMs substantially (also see Fig. S9).



S4: Figure 22 — Link-scale partial effects and corresponding 95% Bayesian credible intervals (under the assumption of Gaussian coefficients on the link scale) of the intercept terms (a) and smooth effects (b-d) of the HGAMs with and without deer T_169, which is shown in red. Removal of T_169 did not change the model fits to an appreciable degree. Panels B-C show the partial effects of day of year for 7-day home-range size (b), daily diffusion (c), and excursivity (d).

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CHAPTER 6. ADDITIONAL PAPERS PUBLISHED DURING THE PHD COURSE

DeNicola A., **DeNicola V.** (2021) Ovariectomy as a Management Technique for Suburban Deer Populations. Wildlife Society Bulletin, https://doi.org/10.1002/wsb.1218

Fleming CH, Drescher-Lehman J, Noonan MJ, Akre TSB, Brown DJ, Cochrane MM, Dejid N, **DeNicola V**, et al. (2020) A comprehensive framework for handling location error in animal tracking data. bioRxiv 2020.06.12.130195; doi: https://doi.org/10.1101/2020.06.12.130195

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VanAcker M.C., **DeNicola V.L.**, DeNicola A.J., Aucoin S.G., Simon R., Toal K.L., et al. (2023) Resource selection by New York City deer reveals the effective interface between wildlife, zoonotic hazards and humans. Ecology Letters, 26, 2029–2042. Available from: https://doi.org/10.1111/ele.14326

Williams S.C., Linske M.A., DeNicola A.J., **DeNicola V.L.**, Boulanger J.R. (2023) Experimental oral delivery of the systemic acaricide moxidectin to free-ranging white-tailed deer (Artiodactyla: Cervidae) parasitized by *Amblyomma americanum* (*Ixodida: Ixodidae*), Journal of Medical Entomology, Volume 60, Issue 4, July 2023, Pages 733–741, https://doi.org/10.1093/jme/tjad056

CHAPTER 7. ETHICAL STATEMENTS AND CODE AVAILABILITY

Ethical statements and code availability references are included separately in the appropriate chapters.