EFFECTS OF WHITE-TAILED DEER DENSITY ON PHYSICAL CONDITION AND FOREST VEGETATION IN CUYAHOGA VALLEY NATIONAL PARK

by

Jacob J. Trowbridge

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A Thesis
Submitted in Partial Fulfillment of the Requirements for the
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THESIS APPROVAL

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Approved by:

Clayton K. Nielsen, Chair

Ryan J. Trimbath

Eric J. Holzmueller

Graduate School
Southern Illinois University Carbondale
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TITLE: EFFECTS OF WHITE-TAILED DEER DENSITY ON PHYSICAL CONDITION AND FOREST VEGETATION IN CUYAHOGA VALLEY NATIONAL PARK

MAJOR PROFESSOR: Dr. Clayton K. Nielsen

Given that overabundant white-tailed deer (*Odocoileus virginianus*) can exert lasting negative effects in forested ecosystems, management of deer has been a foremost conservation concern in eastern North America since the last century. Although knowledge of density impacts on body mass, pregnancy rates, and forest regeneration are vital for deer management, relatively few studies have assessed these relationships in the same study area for a >5-year period. I took advantage of a managed culling program to investigate the impacts of deer density on body mass, pregnancy rates, and native forest understory and trillium (*Trillium grandiflorium*) regeneration at Cuyahoga Valley National Park (CUVA), Ohio, during 2016–2022. Deer densities were estimated using distance sampling in November and deer were culled by sharpshooters the following January–March. Each deer culled was aged, sexed, weighed, and inspected for fetuses (recorded as present or absent). Deer densities ranged from 8.6–18.0 deer/km^2 and deer removed each study year varied between 205 and 450. Concurrently, the 1–6 tallest native seedlings per genera per subplot were measured in July–August in 25 fenced and unfenced paired plots and in long-term ecological monitoring (LTEM) plots. Browse was estimated in unfenced paired plots in alternating years. Trillium stem heights in both unfenced controls/fenced exclosures and browse in unfenced control plots were collected in April–June each year. Using a linear mixed model (LME), I analyzed change in body mass of culled deer and found a significant negative relationship with current deer density ($P < 0.001$), after controlling for age, sex, month, and zone

of removal. I used a generalized linear model to determine whether pregnancy rates of yearling and adult females were influenced by weight, age, and deer density with a ≤3-year time-lag. The top model for pregnancy rate incorporated a 3-year time-lag in parkwide density ($P < 0.001$) with a positive relationship; age and weight had a significant effect. I used a generalized linear mixed model (GLMM) to determine whether the mean seedling height per subplot of the 6 most common genera in CUVA were influenced by year and deer density with a ≤3-year time-lag. The top model found mean seedling heights increased with increased time since the initial measurement ($P = 0.006$) and incorporated an insignificant negative effect of deer density for the previous fall ($P = 0.091$). I used nonparametric statistical tests to analyze seedling heights, and taxonomic richness and diversity, respectively, in LTEM plots. Heights of all seedlings in LTEM plots ($P = 0.010$), taxonomic richness ($P = 0.029$), and diversity ($P = 0.036$) increased after 4 years of culling. Seedling browse decreased over time in 11/14 genera with ≥10 plots having browse for each genus. I analyzed trillium stem heights with LME and an ANOVA, and I analyzed trillium browse with a t-test, Wilcox test, and a GLMM. Plants were taller in fenced exclosures than unfenced controls ($P = 0.004$). Stem heights of trillium in unfenced plots were similar during low and high deer density years ($P = 0.123$). The top model for stem height incorporated a positive 2-year time-lag in spring deer density ($P < 0.001$) and negative effect of year ($P < 0.001$). Deer preferentially browsed taller plants ($P = 0.029$). Browse rates on all plants and large/reproductive plants were nearly greater during high density years ($P = 0.062$ and $P = 0.185$, respectively). Deer density as a numeric covariate did not affect browse rates ($P = 0.086$). Culling ≥30% of the deer population at CUVA improved deer body mass, pregnancy rates, and native forest understory regeneration. Pregnancy rates were driven by deer density 3 years prior, highlighting the importance of long-term monitoring. I suggest there may be a habitat feature

that has a long-lasting effect on pregnancy rates in this population, making it imperative to concurrently quantify potential habitat influences while managing deer numbers. Trillium stem height appeared to not have a useful relationship with deer density; however, this could be a result of legacy effects, thus continued monitoring of trillium is warranted.

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I would first like to thank Dr. Clay Nielsen who offered support, expertise, and a healthy stream of never ending edits. I would like to give Ryan Trimbath a thank you. He guided me on the complexity of deer management in Cuyahoga Valley National Park. He also gave me insight, support, and was willing to meet with me often, even during his busy schedule being a father, research scientist, and a Ph.D. candidate. It was a great pleasure to work with him and I would do so again during my career. Thank you, Dr. Eric Holzmueller, for serving on my committee. A big thank you to Adam Bump, for giving me the opportunity to see and experience wildlife management—if it was not for him, I may not have gotten to where I am at today.

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PREFACE

White-tailed deer (*Odocoileus virginianus*; hereafter, deer) are the most widespread ungulate species in North America (Rooney 2001, Côté et al. 2004), and are considered a keystone herbivore given their impacts on forest structure (Waller and Alverson 1997, Rooney 2001, Russell et al. 2017). Deer populations have become overabundant in many landscapes (Nielsen and Porter 2011, Urbanek et al. 2011), causing human-wildlife conflict such as deer-vehicle accidents (Nielsen et al. 2003), diseases (Côté et al. 2004, Wasserberg et al. 2009, Jennelle et al. 2014), human attacks (Hubbard and Nielsen 2009), and damage to native and ornamental vegetation (Bressette et al. 2012, Nuzzo et al. 2017, Schmit et al. 2020). Alverson et al. (1988) and McCabe (1997) estimated pre-European settlement deer densities to be 2–4 deer/km^2 and 3.1–4.2 deer/km^2, respectively. Deer densities today are 2–12 times higher, with some studies reporting densities >100 deer/km^2 (Peck and Stahl 1997, Royo et al. 2010, McShea et al. 2011, Urbanek et al. 2012c, Anderson et al. 2013). Numerous factors contribute to high deer densities including lack of predators, low to no hunting pressure, specific habitat components such as increased edges, and proliferation of non-natural food sources (Côté et al. 2004, McShea 2012). Population management of deer via controlled sharpshooting has now become commonplace to reduce deer population levels, and therefore alleviate deer-human conflict (Nielsen et al. 1997, DeNicola et al. 2000, DeNicola and Williams 2008, Mateus-Pinilla et al. 2013, Manjerovic et al. 2014).

Cuyahoga Valley National Park (hereafter, CUVA; Figure 1) provides a case study of deer population and habitat monitoring, followed by the implementation of a controlled sharpshooting program to manage overabundance. CUVA began monitoring their deer population in 1990 through spotlight surveys. Originally, an aggregate of deer observed

throughout the survey period served as an index for population trends (National Park Service 2014). Beginning in 1998, CUVA adopted distance sampling techniques (Buckland et al. 2001) to estimate the abundance of deer within the park through spotlight surveys (National Park Service 2014). Abundance estimates were used to determine a recruitment factor (i.e., a multiplier, accounting for births, deaths, immigration, and emigration), which estimates population growth between years and aids managers with decision making regarding deer management (National Park Service 2014).

CUVA also monitors specific vegetation metrics to determine deer impacts on woody vegetation (i.e., seedlings) and herbaceous plants (National Park Service 2014). CUVA implemented unfenced long-term ecological monitoring plots for vegetation in 1998, and in 2016, began periodically monitoring vegetation metrics using a paired plot-based (i.e., fenced exclosures and unfenced controls) design (National Park Service 2014; R. Trimbath, National Park Service, personal communication). These plot metrics were incorporated into CUVA's decision on whether deer management via sharpshooting was necessary on an annual basis.

CUVA is permitted by the National Park Service (hereafter, NPS), the Secretary of the Interior, and the NPS Organic Act (16 USC 1) to remove wildlife if that animal is causing detrimental damages to the park (National Park Service 2006). Moreover, the management of deer in CUVA is permitted because the deer population existed at an unnaturally high population which can prevent regeneration of vegetation (National Park Service 2006, 2014). In January 2016, CUVA began removing deer via controlled sharpshooting. Data are then collected to determine density-dependent effects on health using deer weights and pregnancy rates (National Park Service 2014).

I conducted an assessment of CUVA's deer management program using data collected by NPS staff and volunteers during 1998–2022. Such long-term case studies of deer management, involving a comprehensive set of data, are rare in the wildlife literature. I addressed the following 3 objectives: (1) analyze long-term spatial and temporal trends of deer population numbers, (2) evaluate the relationship between deer density and body condition and pregnancy rates, and (3) assess the relationship between deer density and vegetation trends. My goal was to provide natural resource managers with information useful for managing overabundant deer populations in park settings and yield further insight into the role of density-dependence in deer populations.

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CHAPTER 1

EFFECTS OF WHITE-TAILED DEER DENSITY ON PHYSICAL CONDITION AND FOREST VEGETATION IN CUYAHOGA VALLEY NATIONAL PARK

Introduction

Deer Density

Wildlife populations are limited by available habitat (Johnson and Arcata 2005, Morrison et al. 2006) and this limitation in population size is reflected in carrying capacity (Krebs 2002). Unrestricted populations are often subjected to boom-bust cycles (deCalesta and Eckley 2019). These cycles are evident in deer in many forest types, particularly oak (*Quercus* spp.) forest types (Ostfeld et al. 1996, deCalesta and Eckley 2019). Oak forests produce unusually large quantities of mast approximately 3–6 years depending on the forest (Sork et al. 1993, Dey 2002). These large increases in food availability can influence reproduction, survival, and thereby population size the following year of many species, such as deer, that occupy that forest (Ostfeld et al. 1996, McShea and Healy 2002, McShea et al. 2007). Deer populations that follow this pattern and exist near carrying capacity will overshoot the carrying capacity and food availability will not be sufficient the following year, potentially resulting in large die-offs (Price 1999). Deer populations typically have large impacts on forests, making it imperative to monitor the population and habitat. While population size alone is a not the most useful indicator of deer-forest impacts, it does serve as a metric that wildlife managers can use to monitor forest impacts (Putman et al. 2011). Thus, a sampling method for population density that is able to detect the nuances in deer population changes and produce robust estimates is necessary for management (Fryxell et al. 2014).

Distance sampling is a survey method that has produced reliable density estimates for a variety of species, including cervids, songbirds, whales, and plants (Ward et al. 2004, Heide-Jørgensen et al. 2010, Reidy et al. 2011, Schorr 2013, Beaver et al. 2014). Distance sampling involves (1) placing a transect, (2) measuring perpendicular distances to an object (i.e., an animal; a group of multiple animals is considered a cluster), and (3) fitting a monotonically decreasing detection function to these data (Buckland et al. 2001, Thomas et al. 2010, McShea et al. 2011). This detection function assumes decreased detection with increased distance and can incorporate environmental variables (e.g., topography, hydrology, land cover) that may influence detection (Buckland et al. 2001, Ruette et al. 2003, Marques et al. 2007, Zamboni et al. 2015, Montague et al. 2017). Many terrestrial wildlife studies employing distance sampling use spotlights or thermal imaging and utilize roads as transects, which may influence the detection function and produce unreliable estimates (Buckland et al. 2001, Marques et al. 2010, Beaver et al. 2014). However, the flexibility of analysis in distance sampling allows for the relaxation of the assumption that observations are independent of the transect, which accommodates the use of roads to be used as transects (Venturato et al. 2010, Erxleben et al. 2011, McShea et al. 2011).

Although differences arise in distance sampling protocols for deer, estimates appear robust. LaRue et al. (2007) found road-based distance sampling to yield more accurate density estimates of deer than traditional spotlight surveys due to the detection function modeling environmental variation. Montague et al. (2017) reported difficulty obtaining an adequate sample size with distance sampling but obtained consistent estimates when compared to harvest estimates. In variable landscapes, road-based and pellet-based distance sampling produced similar density estimates; however, deer may be attracted to roads in forested landscapes because of edge effects (Anderson et al. 2013). Conversely, deer may be repelled from roads, causing

positively biased detection and negatively biased density estimates (Stainbrook and Diefenbach 2012). Nevertheless, in forested landscapes, road-based distance sampling showed declining detection with distance while agricultural landscapes lacked declining detection (McShea et al. 2011).

The rigorous statistical basis of distance sampling gives it many advantages. Distance sampling allows for observations of animal clusters to be grouped, a posteriori, into bins making the analysis flexible (Ruette et al. 2003, McShea et al. 2011, Anderson et al. 2013, Montague et al. 2017). Moreover, distance sampling assumes imperfect detection except on the transect, and this is reflected in the detection function (Buckland et al. 2001, Thomas et al. 2010). The main logistical advantages of distance sampling are its relative ease of implementation and low cost (LaRue et al. 2007, Anderson et al. 2013), which is attractive to wildlife managers.

Weight as Indicator of Health and Pregnancy Rates

Numerous metrics have been used to indicate the health of deer including body mass, chest girth, hindfoot length, fat reserves, relative mass of specific organs, blood constituents, and levels of nitrogen in feces (Kie et al. 1983, Sams et al. 1998, Keyser et al. 2005, Kautz et al. 2020). Many agencies use antler characteristics such as the number of points, main beam length, and beam diameter to gauge health of deer populations (McCullough 1984, Keyser et al. 2005, Strickland and Demarais 2008). A simple and cost-effective measurement to monitor deer health is body mass. Across many deer species and age classes, the body mass of individuals in high density populations are significantly lower than different populations in similar habitats at low densities (Kie et al. 1983, Keyser et al. 2005, Richard et al. 2010). Although these populations demonstrated a density-dependent relationship for body mass (Sams et al. 1998, Hefley et al. 2013), the harvest regime typically mirrors selective harvest by hunters, which could lead to bias

in the data (Martınez et al. 2005, Leclerc et al. 2016, Allen et al. 2018). There are few studies that document the reversal of density-dependent effects in the same population (Putman et al. 2019). Nielsen et al. (1997) found following the removal of deer in a previously unregulated population through culling, the body mass of deer increased, albeit over a short time duration of ≤5 years.

It is advantageous for deer to have a healthy body mass. In high-density populations age at first reproduction is higher and fertility is lower, suggesting that a reduction in population size would improve fertility and animal body mass (Putman et al. 2019). Higher body mass in the pre-winter season was attributed to increased overwinter survival in both mule deer (*O. hemionus*) and white-tailed deer fawns, and northern ungulate populations, respectively (White and Bartmann 1998, Taillon et al. 2006, Kautz et al. 2020). In males, a higher body mass is heavily correlated with increased antler points, mass, and overall size (McCullough 1982, Newbolt et al. 2017). It is also well documented that increased antler or horn size in ungulates leads to higher reproductive success (Martin et al. 2016, Newbolt et al. 2017). Furthermore, body mass has been related to social structures where heavier fawns are more dominant (Taillon and Côté 2006). From a management perspective, in abundant deer populations, the simplest method to increase the mass of deer is to decrease is the density of deer through harvest or controlled removal methods.

However, there are instances where body mass has not been associated with deer density. Shea et al. (1992) did not report an increase in body mass when density was decreased by 75% and postulated this result was due to the study area having poor nutritional value, thus body mass was insensitive to density. It is hypothesized that density-dependent relationship between mass and density can only be observed when intraspecific competition for food resources exists (Eve

1981, Shea et al. 1992). Moreover, Warren et al. (1981) and Strickland et al. (2017) found deer mass can vary dramatically throughout the year, especially for males during the rut and females who had reared fawns. Therefore, it is imperative to use caution when using body mass as an index of deer population health, as habitat interactions and life history traits must also be considered.

Population wide pregnancy rates are occasionally responsive to white-tailed deer density (Swihart et al. 1998, Green et al. 2017, Ayotte et al. 2019). Typically, limitation of pregnancy rates is driven by resource availability, and in resource restricted populations, pregnancy rates tend to be lower across most age classes (Swihart et al. 1998). Pregnancy rates are also driven by age, with increased age resulting in increased pregnancy rates (Roseberry and Klimstra 1970). Additionally, weight of ungulates likely impacts pregnancy rates, including natality (i.e., number of offspring per individual), with heavier females more likely to go through gestation (Putman et al. 2019). Biologically, gestation is a nutritionally taxing event, and when compounded with winter, heavier massed females will likely go through gestation. Many of the factors that impact pregnancy, such as density and weight, are highly dependent on the availability of nutritional resources, which are a function of density. This circular relationship between density, body mass, pregnancy rates, and nutritional resources is an important positive feedback loop that highlights the importance of monitoring all 4 factors (Green et al. 2017).

Herbivory Impacts

Deer impacts on native vegetation have been extensively documented (Rooney and Waller 2003, Côté et al. 2004, Tanentzap et al. 2011, McShea 2012, Russell et al. 2017) and vary temporally, spatially, and across deer density gradients (Brown and Doucet 1991; Urbanek et al. 2011, 2012a; Royo et al. 2017). In the absence of predators and in unregulated populations, deer

can radically modify forest composition and structure, resulting in altered successional pathways, loss of habitat for wildlife, and homogenized forest types (Tanentzap et al. 2009, Roberson et al. 2016, Eichhorn et al. 2017, Parker et al. 2020). In severe cases of browse intensity, deer have arrested succession by causing recruitment failure, notably in eastern hemlock (*Tsuga canadensis*) and northern white cedar (*Thuja occidentalis*; Rooney 2001, Rooney and Waller 2003, Ramirez et al. 2019). Furthermore, deer can cause trophic cascades, influencing wildlife, plants, and insects (Nuttle et al. 2011, Bressette et al. 2012, Roberson et al. 2016). Consequently, increased deer densities have been linked to an increase in invasive species (Urbanek et al. 2012a), thereby decreasing native vegetation and habitat quality (Myers et al. 2004, Williams and Ward 2006, Knight et al. 2009b, Russell et al. 2017). Urbanek et al. (2012b) reported deer density to be (1) negatively correlated with species diversity and (2) positively related to species evenness. Rooney (2009), Royo et al. (2010), and Bloodworth et al. (2020) found no statistical changes in species richness, diversity, or evenness when deer populations were reduced. Nevertheless, Jenkins et al. (2014) observed species diversity, evenness, and richness significantly increased following deer reductions. Given these findings, inconsistencies in vegetative response to deer may be more reliant on site-specific qualities than deer density itself (Pendergast IV et al. 2016).

The ability to quantify the intensity of deer browse is central in wildlife management. Exclosures are regularly used to demonstrate the effects of deer on regeneration of forest understories (Horsley et al. 2003, Tanentzap et al. 2011, Urbanek et al. 2011, Royo et al. 2017, Parker et al. 2020). Exclosures and decreasing deer density gradients are typically indicative of increasing seedling heights (Trumbull et al. 1989, Horsley et al. 2003, Russell et al. 2017). However, Trumbull et al. (1989) found that the density of stems decreased as more stems

escaped the browse height of deer (i.e., 1.5 m) due to competition (Walters et al. 2016). Species that are able to escape browse when there is a lack of disturbances are often undesirable or browse tolerant (Horsley et al. 2003, Kelly 2019), and when coupled with excessive deer herbivory, the overstory will be dominated by browse insensitive and shade-tolerant species (Poznanovic et al. 2013, Walters et al. 2016). Ultimately, the intensity of deer browse on any given site is a function of deer density, quantity of vegetation, and vegetation species present (Royo et al. 2010, Urbanek et al. 2012a).

Deer browse on vegetative species disproportionately, thus impacting forest composition and regeneration. Vegetative species often experience interspecific competition, thereby exacerbating the effects of deer browse on regeneration. Given this, it is important to examine those effects concurrently with deer density and impacts. Decreased deer density led to fewer maples (*Acer* spp.), beeches (*Fagus grandifolia*), and cherries (*Prunus* spp.) showing signs of browse (Pierson and deCalesta 2015), contributing to the negative linear trends in height for maple and beech observed with deer density (Horsley et al. 2003, Walters et al. 2016). Relatively few relationships between deer density and severe browsing impacts have been established for cherry species (Horsley et al. 2003, Pierson and deCalesta 2015, Walters et al. 2016), indicating it is insensitive to browse or avoided by deer (Brown and Doucet 1991). Oak and hickory (*Carya* spp.) browse resilience has been documented, regardless of deer densities and accessibility, by height and abundance (Russell et al. 2017, Parker et al. 2020). However, oak survival increased within exclosures (Walters et al. 2016, Blossey et al. 2019). Dogwoods (*Cornus* spp.) and *Rubus* spp. were significantly taller and more abundant in exclosures than areas exposed to deer (Frerker et al. 2014, Roberts et al. 2014, Parker et al. 2020). In cafeteria and feeding studies, dogwoods were nearly always the most browsed twig (Brown and Doucet 1991) and *Rubus* spp.

were among the most preferred in summer (Dostaler et al. 2011). Black gum (*Nyssa sylvatica*) and sassafras (*Sassafras albidum*) interactions with deer browse is less studied. However, Forrester et al. (2006), Shelton et al. (2014), and Parker et al. (2020) found both species occurred more in exclosures compared to deer-accessed areas, and following 10 years of deer removals, sassafras stems increased significantly (Jenkins et al. 2015). Disproportionate browse, especially in areas with high deer density, can lead to decreased competition and increased introduced species (Russell et al. 2017). Introduced species, if invasive, can dominate the understory and midstory, shifting successional pathways and creating unsuitable habitat, thus contributing to biotic homogenization (Parker et al. 2020). This has become common in CUVA with multiflora rose (*Rosa multiflora*), privet (*Ligustrum* spp.), and Japanese barberry (*Berberis thunbergii*; R. Trimbath, National Park Service, personal communication). Therefore, it is essential to establish continual monitoring using multiple methods to determine the effects of high deer density and browsing (Pierson and deCalesta 2015).

Trophic cascades caused by large herbivores in the absence of population regulation, either by predators or human control, is well documented (Polis et al. 2000, Schmitz et al. 2000). Much of the current knowledge comes from utilizing deer exclosures or many sample plots across a large deer density gradient (Webster et al. 2005; Jenkins et al. 2007;Urbanek et al. 2012a, b). These studies demonstrate deer may impact seedling heights, regeneration, composition, and density (Csigi XIV and Holzmueller 2015, Flagel et al. 2016). Less understood are trophic cascades going in the opposite direction where regulation is implemented after a long absence of regulation within the same population (Ripple and Beschta 2007). Wolves (*Canis lupus*) cause trophic cascades in Yellowstone National Park by reducing elk (*Cervus canadensis*) densities thus reducing herbivory and allowing for the regeneration of aspen (*Populus* spp.;

(Ripple and Beschta 2007, 2012; Painter et al. 2015; Beschta and Ripple 2016; Beschta et al. 2018). Similar patterns in browse rates and seedling heights have occurred with willows (*Salix* spp.) in Yellowstone National Park (Beschta and Ripple 2007, Beyer et al. 2007, Painter and Tercek 2020). However, many of these studies utilize the sampling approach in Beschta and Ripple (2007) where they sampled the 5 tallest aspen seedlings per plot and called it the first recovering aspen (Beschta and Ripple 2013), or later the leading edge of recovery (Beschta et al. 2018). While there is debate if these trophic cascades are classified as behaviorally-mediated trophic cascades (Ripple and Beschta 2003, 2004, 2007; Kauffman et al. 2010; Beschta et al. 2018), or density-mediated trophic cascades (Flagel et al. 2016), it is known that a trophic cascade has occurred (Brice et al. 2022). Although the sampling scheme for a leading edge is a nonrandom design, Brice et al. (2022) found both leading edge and random designs showed a trophic cascade, but the leading edge design exaggerated the effects. Even fewer studies have shown the results of a human-mediated trophic cascade through culling (Tanentzap et al. 2012). Those studies have indicated variability in regeneration delays (Tanentzap et al. 2012); increased native vegetation richness, cover (Chollet et al. 2016), and herbaceous plant heights (Nuzzo et al. 2017); and decrease invasive plant cover (Schmit et al. 2020).

Temporal discrepancies exist regarding when forest regeneration will occur after deer density reduction; these delays in regeneration are called legacy effects (Royo et al. 2010, Tanentzap et al. 2011, Nuttle et al. 2014, Pendergast IV et al. 2016). Royo et al. (2010) attributed legacy effects to a lack of increase in species richness and diversity following 4 years of intensive deer reduction. Tanentzap et al. (2011) observed a decline in overstory trees while regeneration of the understory partially occurred during intensive deer reductions. Nuttle et al. (2014) documented seedlings and forbs in the understory influenced by deer 20 years after deer

were reduced from 15–30 deer/km^2 to 10–12 deer/km^2. It took 5 years to quantify a departure in species composition in exclosures compared to unfenced plots (Pendergast IV et al. 2016). Legacy effects can have long lasting influence on vegetation, making it imperative to select metrics for monitoring which detect forest regeneration.

Indicator species are commonly used to monitor the impact of wildlife on vegetation (Anderson 1994, Chevrier et al. 2012, Pierson and deCalesta 2015, Blossey et al. 2019). Indicator species should exist at moderately high abundances in the study site and have some characteristic impacted by deer (Kirschbaum and Anacker 2005). White-flowered trillium (*Trillium grandiflorum*; hereafter, trillium) height and density has served as a useful indicator of deer browse (Anderson 1994, Augustine and Frelich 1998, Royo et al. 2010), moreover, trillium is palatable and sensitive to deer browse (Augustine and Jordan 1998), making it a suitable indicator species. Trillium, however, has been an unreliable indicator in areas with high deer densities where significant decrease or extirpation of trillium have been documented (Royo et al. 2010). Trillium may also be locally rare naturally or extirpated due to heavy herbivory. Kirschbaum and Anacker (2005) determined trillium was an unreliable indicator of deer browse impacts while Koh et al. (2010) found trillium height decreased with increasing deer abundance.

Based on the aforementioned 3 objectives, I analyzed deer management at CUVA to provide the National Park Service with an evaluation of their management program and further expand upon the literature of overabundant deer management in protected settings. Most similar studies of deer populations are limited in duration (<5 yr; Nielsen et al. 1997, McShea et al. 2011, Urbanek et al. 2012c, Montague et al. 2017), thus unable to ascertain long-term impacts. The CUVA dataset consists of 6–25 years of data, depending on the specific dataset (R.

Trimbath, National Park Service, personal communication), allowing for a longer-term assessment of an overabundant deer management program.

Study Area

CUVA (Figure 1) is located in northeastern Ohio, south of Cleveland and north of Akron, within Cuyahoga and Summit counties. The 133 km^2 park contains ≥40 km of the Cuyahoga River and overlaps numerous political boundaries (National Park Service 2014, Jones et al. 2021, National Park Service 2021).The NPS protects 80 km^2, while Cleveland Metro Parks and Summit Metro Parks own approximately 33 km^2 (National Park Service 2014). Privately-owned recreational, residential, agricultural, and industrial land occupies the remaining 20 km^2 (National Park Service 2021). One hundred-sixty km of county roads with light to heavy traffic, 3 interstate highways, a historical railway, and remnants of the Ohio and Erie canals cross the park (National Park Service 2014). Human densities in Summit County and Cuyahoga County are 500 persons/km^2 and 1,080 persons/km^2, respectively (United States Census Bureau 2021). Due to proximity to large population centers, CUVA is one of the most visited National Parks in the National Park Service system, having >2 million visitors annually during the last 20 years (Jones et al. 2021).

CUVA is situated on the glaciated Allegheny Plateau (Hop et al. 2013), thus, the area is characterized by rolling hills, ridges, and valleys with elevation ranging from 305 m to 381m (National Park Service 2014). Annual rainfall varies from 5.1 cm to 10.4 cm per month (National Oceanic and Atmospheric Association 2021). Due to lake effect snow, the north side of the park receives ~173 cm of snow annually, while the south side receives ~118 cm (National Oceanic and Atmospheric Association 2021). Temperature also varies greatly annually, within a season, and with proximity to Lake Erie, making the northern portion of the park generally cooler. July is

the warmest, with a daily average of 23.4° C and January is the coldest, with a daily average of -2.2° C in the north and -2.9° C in the south (National Oceanic and Atmospheric Association 2021).

Although the glaciated Allegheny Plateau is characterized by poor soil drainage and unproductive cropland, agriculture is present (National Park Service 2014). Furthermore, the park features forest types of the Allegheny Plateau (Whitney 1990, Black et al. 2006). Mixed-mesophytic deciduous forests dominate at ~70% (National Park Service 2014). The species association in that forest type are oak/hickory, maple/oak, oak/beech/maple, maple/sycamore (*Platanus occidentalis*), and hemlock/beech (National Park Service 2014). Conifer forests exist in small patches (<1% of CUVA) with pine (*Pinus* spp.)/spruce (*Picea* spp.) associations (National Park Service 2014). Cropland and pastures, shrub/brush ranges, and wetlands represent 5.4%, 3.4%, and 2.7% of CUVA, respectively (National Park Service 2014). Other developed land, such as residential suburbs represent 13.3%, and 2.3% is water (National Park Service 2014). Much of CUVA's forests are heavily fragmented due to past land use practices, however, semi-contiguous tracts of forest do remain (National Park Service 2014). Much of the forests today are uneven-aged stands in numerous stages of succession and affected by disturbance regimes, primarily insect infestations and browse due to emerald ash borer (*Agrilus planipennis*) and deer, respectively (National Park Service 2014, Costilow et al. 2017, National Park Service 2020).

CUVA began the deer management process in 1993, when a deer management taskforce was created to identify problems and solutions to the issues caused by deer (National Park Service 2014). The taskforce recommended population control; ultimately however, the U.S. District Court prohibited the proposal based on a lack of environmental assessment (National

Park Service 2014). Neighboring parks began sharpshooting deer in 1998 and held controlled archery hunts in the early 2000s to reduce the population surrounding CUVA (National Park Service 2014). Additionally, private farmers within the park boundaries were issued deer damage permits by the State of Ohio (R. Trimbath, National Park Service, personal communication). In 2006 a science team was created to develop a plan of action to reduce the impacts caused by deer in CUVA (National Park Service 2014). A 5-year reduction plan was implemented and began winter 2016, with sharpshooting conducted by United States Department of Agriculture-Wildlife Services. Additional deer research and management activities conducted by CUVA include deer population surveys and vegetation monitoring.

Methods

Data Collection: Deer Density

Spotlight-based distance sampling, following Buckland et al. (2001), was used to gather observations of deer to estimate deer density in CUVA during 1998–2022. Approximately 51.5 km of roads and 12.9 km of railways (Figure 1) were sampled 30 min after sunset for 5 days during the last week of October and first week of November during 1998–2022 by National Park Service staff (National Park Service 2014). A spotlight was used to shine for deer and 2 crews each drove roughly half the transects per night (National Park Service 2014). Each crew consisted of a driver and 2 observers facing either roadside in a pick-up truck bed. Railroad transects were conducted using a hi-rail truck using the same methodology (National Park Service 2014). Transects were driven at approximately 16 km/h. Upon detecting deer, the observer directed the driver to position the truck perpendicular (i.e., 90º) to the deer. Deer were observed as individual animals or a cluster, defined as a group of ≥2 deer with a well-defined location for the group center (Buckland et al. 2001). When large groups of deer were seen in

open fields, cluster classification was attempted before obtaining perpendicular distance (m) to minimize flight response (National Park Service 2014). When deer exhibited a flight response, the observer noted their location and measured distance to that location (National Park Service 2014). During 1998–2004 observers ocularly binned sightings into the following 5 distance intervals: 0–≤30 m, 31–≤75 m, 76–≤150 m, 151–≤300 m, and >300 m (National Park Service 2014). During 2005–2022, exact distances were recorded using a laser rangefinder. Data collected during surveys were perpendicular distance, number of deer, and zone. A zone is an arbitrary delineation, using roads and rivers, CUVA staff used to stratify the park geographically (Figure 1). Observers also recorded whether deer were antlered, antlerless, or unknown.

Data Analysis: Deer Density

I analyzed distance sampling data collected during 1998–2022 using the Distance package (Miller et al. 2017) in R version 4.0.3 and 4.2.2 (R Core Team 2022). I pooled all observed distances on each transect across all sampling nights for each year (Buckland et al. 2001, Preston et al. 2021). I used the ds function (Miller et al. 2017) to fit a conventional distance sampling (CDS) model to my data (Buckland et al. 2001). A CDS model fits a selected detection function and series adjustment to the observed data to describe the decreased probability of detection of objects (i.e., deer) with increased distance from the observer (Buckland et al. 2001) and is used to estimate deer density. I used cluster size as a covariate that may affect density. I specified cut points (i.e., distance intervals) for all models using an automated script developed by Green et al. (2021) and Preston et al. (2021). Cut points group all distance observations within a specified interval (Buckland et al. 2001). This method used the recommendations by Buckland et al. (2001), such that: (1) each interval was ≥10 m, (2) no distance interval contained <4 observations, and (3) a histogram of the distance intervals

generally decreased as distance from the transect increased. Ideally, 4–6 intervals were created (Green et al. 2021, Preston et al. 2021). A new model was developed when a different key, series, covariate, or cut points were specified. Once a model was created, I plotted a histogram using the cut points, if specified, with the probability detection function to visually assess model fit (Buckland et al. 2001). Furthermore, I used the gof_ds function to conduct a Chi-squared goodness of fit test ($\alpha = 0.05$ throughout) if cut points are specified, to determine whether the model fitted the data based on P-values (Buckland et al. 2001, Miller et al. 2017). I evaluated the following 7 key and series adjustments recommended by Buckland et al. (2001): half-normal and hazard rate with no adjustment, cosine, Hermite polynomial, and uniform with a cosine adjustment, and I used size as a covariate for hazard-rate and half-normal key functions with no adjustment terms.

I analyzed data differently for 2 periods because of a change in how deer observations were recorded. Data collected during 1998–2004 were binned, therefore, the cut points were pre-specified and cannot be changed. Data collected during 2005–2022 were analyzed with various cut points since distances were exact using an automated cut-point generator (Green et al. 2021). I used the summarize_ds_model function to evaluate models within the same year that used identical cut points, using AIC (Burnham and Anderson 2004) for $P > 0.05$. I selected an overall top model for each year when it met the following criteria: (1) the coefficient of variation was minimized, (2) the P-value for the goodness of fit test was nonsignificant, and (3) detection probability was high (Miller et al. 2017). I estimated density from the top model using the dht2 function and stratified my data by region.label (i.e., zone). When stratifying using this methodology, I used the parkwide detection function to estimate density for each zone. I used a Mann-Kendall trend test to determine if the deer density in CUVA decreased during 1998–2022.

Data Collection: Weight as an Indicator of Health and Pregnancy Rates

Weight of deer at CUVA were collected from deer carcasses via sharpshooting, where USDA-WS used high powered, small-caliber rifles equipped with noise suppression and night vision devices used at close range (R. Trimbath, National Park Service, unpublished report). Sharpshooting generally occurred during January–March 2016–2022. Bait stations were placed throughout the park and at opportunistic locations where deer were known to congregate. Shooting took place on roads, parking lots, and open fields from elevated pickup trucks, including trucks equipped for railroads, as well as tree stands and existing structures. All activities followed federal firearm laws administered by the Department of Alcohol, Tobacco, and Firearms. All deer removed from CUVA were sexed, weighed to the nearest kg, and aged up to 4.5-yr using tooth replacement and wear (Severinghaus 1949). Also recorded were removal date, site, zone, and number of fetuses in females. All deer removed were processed and venison was donated to the local food banks (Greater Cleveland Foodbank and Akron-Canton Regional Foodbank).

Data Analysis: Weight as an Indicator of Health and Pregnancy Rates

For the body mass analysis, 2,270 deer were removed from CUVA from 2016–2022. I removed 2 individuals from analysis because the age, weight, or sex was unknown. I created a covariate, month, by assigning a calendar month to each deer based on the month that individual was culled. I assigned deer aged >4.5 years to 5.5 years. Deer aging based on tooth wear is unreliable beyond age classes of fawn, yearling, and adult (Gee et al. 2002). Therefore, I excluded 298 deer aged ≥4.5 years for my weight analysis. I modeled body mass of fawns (0.5 yr; n = 661) and adults (≥1.5 but ≤3.5 yr; n = 1309) separately using linear mixed effects models in the R package lme4 (Bates et al. 2014). I used park-wide or zone-based deer densities at 4

time-lags (i.e., D_{t-0}, D_{t-1}, D_{t-2}, D_{t-3}) using the densities estimated in objective 1, month of removal, sex, and age (for the adult model) as fixed effects. I treated the zone where deer were removed as a random effect since deer in the same area likely utilized the same resources and I expected their weights to be similar. I also treated month and sex as categorical variables to compare body mass and created 1 model for each time-lag, resulting in 16 models, 8 both for fawns and adults. No interactions were tested based on preliminary inspection of the data. There was no correlation among my predictor variables ($r > 0.7$). All models were visually inspected for normality and homogeneity of variances with Q-Q plots and a plot of residuals against the fitted values (Logan 2011). I selected the best fitted model using AICc (Burnham and Anderson 2004). All covariates with $P \leq 0.05$ were considered significant.

For the pregnancy rate analysis, I used 1,286 females removed from CUVA from 2016–2022, excluding deer removed in November and December due to difficulty in determining if a fetus was present that early in gestation. I removed 1 deer where age was unknown. I created a binomial response variable, 1 if a fetus was present or 0 if absent. I removed 233 deer aged ≥4.5 years because of the unreliability in tooth wear methods past 3.5 years (Gee et al. 2002). Although fawns (0.5 yr) in healthy populations can reproduce (Green et al. 2017), they typically reproduce at low levels. Sixteen fawns had 1 fetus and 5 fawns had 2 fetuses, but I removed all 306 fawns from my analysis to assess a change in pregnancy rates on strictly adults. I removed 9 outliers by weight using interquartile range. I used a generalized linear model with a logit link and a binomial response to determine whether pregnancy rates of females were influenced by weight, age, and deer density with a ≤3-year time-lag at the park-wide or zone-based deer densities. This resulted in 8 models. I used AIC to determine the best-fit model and all 2-way interactions were tested (Putman et al. 2019). Once a top model was selected, I used backward

elimination to find the most parsimonious model (Zuur et al. 2009). All covariates with $P \leq 0.05$ were considered significant.

Data Collection: Herbivory Impacts

Deer herbivory data were separated into 3 datasets (National Park Service 2014) for analysis: (1) Dataset 1 (i.e., seedling heights, change in seedling heights, and taxonomic richness and diversity), (2) Dataset 2 (i.e., seedling browse), and (3) Dataset 3 (i.e., trillium). Dataset 1 consisted of 2 data sources: paired plots (i.e., fenced exclosures and unfenced controls) and long-term unfenced ecological monitoring plots (hereafter, LTEMs). At 25 paired plots, 5 per zone, seedling height data were collected during July–August 2016–2021. Paired plots included a fenced 10 x 10 m plot where deer were excluded (i.e., fenced exclosure) and an adjacent 10 x 10 m plot accessible by deer (i.e., unfenced control). Forty-six LTEMs transects, with 3, 10 m radius plots were implemented in 1998 without fenced exclosure sites for comparison. For both paired plots and LTEMs, all woody vegetative plants >0.5 cm and <150 cm in height (i.e., seedlings) were counted and identified to the genus or species level. Seedling heights (cm) were recorded each sampling year for paired plots, and in 2017 and 2021 for LTEMs, by creating 3 seedling subplots 1 m in radius I each plot. The tallest species <150 cm in each subplot in both LTEM and paired plots were measured. For Dataset 2, from February–April during 2017, 2019, and 2021, the total number of buds and buds browsed were sampled on all seedlings using the 25 unfenced control plots and 46 LTEMs in 5 m radius plots to determine browse rates and selection. For Dataset 3, 22 paired plots (different from those mentioned above) and 29 additional unfenced control plots were monitored during April–July 2016–2022. Each paired plot was a 1 m^2 fenced exclosure and an adjacent 1 m^2 unfenced control, placed in areas where trillium was known to exist. Plants were tagged as they emerged to track individuals through the

season to document browse, and the height of each trillium stem (cm) from the ground to the leaf was measured. In 2019, additional metrics based on trillium leaf length and reproductive status (i.e., fruit development and pod size) began being collected and plants were classified as recommended by Knight et al. (2009a): (1) small 3-leaf, if leaves were <5 cm in length; (2) large 3-leaf, if leaves were >5 cm in length; and (3) reproductive, if leaves were >5 cm and the plant was reproductive. Additionally, browse on trillium was collected all identifiable plants.

Data Analysis: Herbivory Impacts

For Dataset 1, I used a nonparametric 2-sample Kolmogorov-Smirnov test to assess if seedlings grew taller in fenced exclosures than unfenced controls. I determined if deer density impacted seedling height using 2 datasets: (1) unfenced controls in the paired plots and (2) LTEM plot data. I used the 6 most common genera found in the study plots: *Acer*, *Carya*, *Fraxinus*, *Prunus*, *Quercus*, and *Ulmus*. I grouped by genus, site, year, and calculated the mean seedling height and the number of observations for each mean. I treated mean seedling height in each plot for each genus for each year as the unit of sample. Because I modeled mean seedling height, I used the number of observations for each mean as a weight in my models. I used glmmTMB (Magnusson et al. 2017) to create 4 candidate models, 1 for each time-lag in deer density ≤3 years and each model included year as a covariate. I scaled deer densities to help model convergence and calculate measurement errors. I included a random intercept for site to control for temporal correlation among measurements in the same site and unmeasured environmental factors (Brice et al. 2022). Since my model included multiple genera, I assumed each would be impacted by time and deer density differently; therefore, I included an additional random intercept for genus and a random slope for year for each genus. I used a gamma distribution with a log link, which uses non-negative right skewed data (Brice et al. 2022). I used

AIC to select the top model (Burnham and Anderson 2004). To assure my models conformed to assumptions, I used the simulateResiduals function in the DHARMa package (Hartig and Hartig 2017) and plotted the output. I checked for collinearity among fixed effects using the check_collinearity function in the performance R package (Lüdecke et al. 2021). All assumptions were met, and collinearity was absent. For the LTEM plot data, I used a nonparametric 2-sample Kolmogorov-Smirnov test to determine if there was a change in seedling heights from 2017 to 2021 in LTEM plots in 3 functional groups: community wide, shade tolerant, and genera (Comita and Hubbell 2009). Shade tolerance of a genera was determined using Hewitt (1998) and Niinemets and Valladares (2006). Only genera with ≥10 measured seedlings for each sampling year were analyzed.

Taxonomic richness and diversity in fenced and unfenced plots (n = 18) and LTEM subplots (n = 114) were calculated at the genus level. For paired plots, I used a mixed ANOVA with a pairwise t-test post hoc analysis using the "rstatix" package (Kassambara 2021). For LTEM plots, I used a Wilcoxon signed rank test with continuity correction to assess any differences between 2017 and 2021.

I calculated the mean change in seedling height by calculating the mean height of each genus per subplot and subtracted the difference of mean heights in both unfenced controls and fenced exclosures. This difference was only calculated if 2 consecutive years of measurements were obtained. To assess any difference in treatment type, I used a t-test with equal variances. This determined if height changes in fenced exclosures were greater than unfenced controls. I used mean differences in unfenced control plots in a linear regression with the upcoming fall deer density, $\hat{D}_{t-0}$, and the previous fall deer density, $\hat{D}_{t-1}$, to determine if the mean change was

predicted by deer density. I also scaled the covariates for model convergence and checked for collinearity.

I analyzed Dataset 2 using a chi-square goodness-of-fit test for each year (Brown and Doucet 1991, Kittredge and Ashton 1995) for native species with ≥30 available buds in a year. The observed values were the relative use of each species, calculated by taking the sum of the browsed buds for a species divided by the sum of all browsed buds (Neu et al. 1974). Expected values were the relative abundance of that individual species, expressed as a probability. The expected values were calculated by summing the number of available buds for a species and divided by the total available buds of all species (Neu et al. 1974). I determined which species were preferred versus avoided by comparing the availability of the species to the calculated simultaneous confidence intervals (Neu et al. 1974, Byers et al. 1984, White and Garrott 2012). Likewise, I conducted the same analysis for each year to determine if there were temporal differences in browsing selection. Additionally, I determined a temporal change in browse rates using a Kruskal-Wallis test for each genera and used a Wilcoxon multiple comparison test with a Bonferroni adjustment to compare any differences across years. Browse rates were calculated by summing the number of buds browsed divided by the total number of buds available for each genus in each plot. I only analyzed genera that had ≥10 sites for each year.

I analyzed Dataset 3 using linear mixed effects models to assess trillium stem heights in CUVA. I determined if trillium was indicative of deer browse and density by using a linear mixed effect model with time and treatment (i.e., fencing) and its interaction to determine what was affecting heights. I modeled 3639 observations after removing outliers and unmeasured plants. I considered all terms and interactions to be significant if $P \leq 0.05$. I used a t-test on plants in unfenced plots (n = 2262) to determine if deer preferentially browsed taller plants. To

further assess if ambient deer density impacted trillium stem heights, I used plants stem heights in unfenced plots as the response variable in a linear mixed effect model (Bates et al. 2014). I created 4 candidate models, 1 for each time-lag in deer density up to 3 years and each model included year as a covariate. I used the deer density estimate from the fall and assumed spring births equaled fall deaths. I included a random intercept for plot to capture temporal correlation in measurements and unmeasured environmental covariates. I used a deer density grouping, high (>10 deer/km^2) vs. low (≤10 deer/km^2) vs. fenced exclosures (0 deer/km^2) because impacts may not track linearly (Knight et al. 2009a). I used 10 deer/km^2 as the cutoff because it is cited as when regeneration in spring ephemerals and seedlings can happen (Royo et al. 2010). I used an ANOVA with stem height as the response and deer grouping as the independent variable and a pairwise t-test with a Bonferroni correction post-hoc test to determine any differences across the deer density grouping.

I assessed if browse rates on trillium in unfenced control plots could predict deer density by calculating the percentage browse per plot as the number of plants browse divided by the total number of plants present. I removed all measurements in the year 2020 because plants were only visited once due to COVID-19 restricting field work. Deer density groupings in the following analysis did not include fenced exclosures. I used a Wilcox test to determine if the deer density groupings impacted percentage of plants browsed. I further investigated deer density groupings on browse rates on only large 3-leaf and reproductive plants as defined by Knight et al. (2009a). I used a zero-inflated generalized linear mixed effect model with a beta family logit link in the "glmmTMB" R package (Magnusson et al. 2017) to determine if trillium browse rates could be predicted by deer density for the upcoming fall, $\hat{D}_{t-0}$. I used a zero-inflated model because many plots experienced no browse. I used a beta family logit link because it works for zero-inflated

proportional values, however, does not allow values of 1, so values of 1 were set equal to 0.999. I used the "DHARMa" R package (Hartig and Hartig 2017) to model the residuals to check assumptions.

Results

Deer Density

Twenty-five years of distance sampling surveys were conducted, and 936 models were developed. The hazard-rate key function performed best and was in 22 final models, followed by the half-normal key function in 2 models and uniform key function in 1 model. Cosine and Hermite polynomial adjustments were modeled 1 and 3 times, respectively. Group size was used 12 times as a covariate in a final model. A ≥10 m minimum bin size was selected 5 times, a ≥15 m minimum bin size was selected 7 times, and a ≥20 m minimum bin size was selected 6 times. The number of top performing models with 4, 5, or 6 cut points were 7, 6, and 5, respectively. I found no relationship between the minimum bin size, number of cut points, key function, or adjustment term and number of observations. The mean first bin size was 42.4 ± 3.2 m and mean bin size for all models was 46.8 ± 3.2 m.

Mean park-wide density during 1998–2022 was 15.9 deer/km^2 (range: 8.6–31.9 deer/km^2; Table 1, Figure 2). Mean zone-based density across all zones was 16.8 deer/km^2 (range: 2.7–44.4 deer/km^2; Table 1). Across all years, zone 4 had the lowest mean density ($\bar{x}$ = 11.7 deer/km^2), followed by zones 1, 2, 3, and 5 ($\bar{x}$ = 13.6, 18.0, 19.0, and 21.8, respectively) (Table 1). Deer density in CUVA decreased during 1998–2022 (τ = -0.593, $P < 0.001$, Figure 2). There was a decreasing trend in density estimates across both park-wide and zone-based spatial scales, however, temporal oscillations occurred (Table 1, Figure 2).

Weight as an Indicator of Health and Pregnancy Rates

Body mass (Appendix A) increased during 2016–2022 for all age classes in both sexes (Appendices B, C). The top model for body mass was the park-wide density at a time-lag of 0 for both adults and fawns (Tables 2 and 3). There was a negative effect of park-wide deer density on body mass of adults ($t_{1300.7} = -4.00$, $P < 0.001$) and fawns ($t_{651.3} = -3.85$, $P < 0.001$). Age was a strong predictor of body mass for adult deer ($t_{1298.6} = 23.04$, $P < 0.001$), as well as sex for both adults ($t_{1300.7} = 16.66$, $P < 0.001$) and fawns ($t_{650.8} = 9.33$, $P < 0.001$). Additionally, month of removal had a decreasing effect on body mass, however, this was only present in adults. Adult deer removed in November did not weigh significantly less than adult deer removed in December ($t_{1298.1} = -1.37$, $P = 0.172$), however, adult deer removed in January, February, and March weighed less than earlier removals (Table 2).

Among all females were 385 (29.9%), 226 (17.6%), 623 (48.4), and 52 (4.0%) that had 0, 1, 2, or 3 fetuses, respectively. Furthermore, among adult females (i.e., age ≥1.5 but ≤3.5 yr) 65 (8.8%), 168 (22.8%), 477 (64.6%), and 28 (3.8%) had 0, 1, 2, or 3 fetuses, respectively. Age specific pregnancy rates were variable, but highest in adults (Table 4). The top and most parsimonious model for pregnancy rate (Appendix D) incorporated a 3-year time-lag in park-wide density ($P < 0.002$) with a negative relationship (Table 5). Older females had higher pregnancy rates ($P = 0.007$) and increased weights resulted in lower in pregnancy rates ($P < 0.001$). An interaction with park-wide density at a time-lag of 3 years and weight (Figure 3) was also included in the model and significant ($P < 0.001$) with a positive effect.

Herbivory Impacts

Three-thousand twenty-five seedling measurement were taken during 2016–2021; 1,904, 1,329, and 602 seedlings were measured in fenced exclosures, unfenced controls, and unfenced

LTEM plots, respectively. Mean seedling heights in fenced exclosures were 27.0 ± 0.9 cm (median = 16.3), 20.6 ± 0.6 cm (median = 15.0) in unfenced controls, and 24.9 ± 0.9 cm (median = 17.0) in LTEM plots. Seedlings in fenced exclosures were taller than those in unfenced controls ($D = 0.11$, $P < 0.001$; Figure 4).

Mean seedling heights during 2016–2021 for all genera generally increased, although fluctuations occurred, notably in *Prunus* and *Quercus* (Table 6). I obtained 524 mean seedling heights from the 6 most common genera in unfenced control paired plots in CUVA. The top GLMM model incorporated a time-lag of 1 year for scaled deer density (Table 7), such that year had a significant positive effect on seedling height ($\beta = 0.05 \pm 0.02$, $P = 0.006$). Deer density had a nearly significant, and negative, effect on seedling height ($\beta = -0.02 \pm 0.1$, $P = 0.091$).

For LTEM plot data (Table 8), seedling heights increased during 2017–2021 at the community level ($D = 0.13$, $P = 0.010$). However, there were no changes in seedling heights in any of the shade tolerant functional groups: shade tolerant ($D = 0.09$, $P = 0.771$), shade intermediate ($D = 0.12$, $P = 0.298$), and shade intolerant ($D = 0.24$, $P = 0.059$). *Fraxinus* was the only genus to have taller seedlings in LTEM plots in 2021 than 2017 ($D = 0.23$, $P = 0.047$, Table 8).

Mean change in seedling height in fenced exclosures and unfenced controls were 2.4 ± 0.6 cm and 1.7 ± 0.4 cm, respectively (Figure 5). Seedling growth was similar in unfenced controls and fenced exclosure plots ($t_{207} = -0.96$, $P = 0.339$). Deer density and associated time lags did not affect mean change in seedling heights ($F_{3, 114} = 0.40$, $P = 0.756$, Adjusted $R^2 = -0.02$; Table 9).

A total of 36,906 buds were surveyed for browse impacts with 13,058, 11,027, and 10,741 buds used for analysis in 2017, 2019, and 2021, respectively. The number of buds

browsed decreased each year from 2,812 (21.5%) in 2017 to 991 (8.9%) in 2019 and 877 (8.2%) in 2021. Selective browse was observed for 2017 (χ^2_{18} =1058.1, P < 0.001), 2019 (χ^2_{19} = 629.9, P < 0.001) and 2021 (χ^2_{17} = 598.3, P < 0.001). Although deer utilized all genera, preferences across time were observed (Table 10).

Fourteen genera had ≥10 browse rates calculated for each year (Appendix E). Eleven of 14 genera had changes in browse rates (Table 11). Browse rates of *Carya* spp., *Crataegus* spp., *Fagus* spp., *Fraxinus* spp., *Lindera* spp., and *Prunus* spp. all decreased from 2017 to 2019 (Table 11, Appendix E). Browse rates of those same genera, excluding *Crataegus* spp., but including *Acer* spp., *Aesculus* spp., *Carpinus*/*Ostrya* spp., *Rubus* spp., and *Smilax* spp., all decreased at the plot level from 2017 to 2021 (Table 11, Appendix E). No significant changes in browse rates across any genera occurred from 2019 to 2021. Moreover, browse rates changed across all 14 genera from 2017 to 2019. Browse rates of only *Carpinus*/*Ostrya* spp. increased from 2017 to 2021, and browse rates of *Carpinus*/*Ostrya* spp., *Cornus* spp., and *Smilax* spp. increased from 2019 to 2021 (Appendix E). Browse rates did not statistically change during the study period for *Cornus* spp., *Ulmus* spp., and *Viburnum* spp. (Table 11).

Native shrub taxonomic richness in 114 unfenced LTEM subplots increased during 2017–2021 ($\bar{x}$ = 3.9 ± 0.3, median: 4.0, vs. $\bar{x}$ = 4.5 ± 0.3, median: 4.0, unique taxonomic groups per transect; V = 1264.5, P = 0.029). Similarly, Shannon's diversity index (*H'*) increased in the same unfenced LTEM transects from 2017–2021 ($\bar{x}$ = 0.8 ± 0.1, median: 0.8, vs. $\bar{x}$ = 0.9 ± 0.1, median: 0.9; V = 1792.5, P = 0.036).

Unfenced control and fenced exclosure paired plots showed similar results to the LTEM plots (Table 12). Native shrub taxonomic richness in 18 paired plots increased from 2017–2021. For native taxonomic richness, the interaction of year and treatment (i.e., fencing; $F_{1,31}$ = 1.89, P

= 0.179) and treatment ($F_{1,31}$ = 1.42, P = 0.242) alone were insignificant. Year, however, had a positive effect ($F_{1,31}$ = 14.42, P < 0.001). Similar patterns for *H′* from 2017 to 2021 occurred. The interaction ($F_{1,31}$ = 0.02, P = 0.879) and treatment ($F_{1,31}$ = 0.34, P = 0.567) were not significant, but year ($F_{1,31}$ = 12.15, P = 0.001) was significant.

Mean stem height of trillium during 2016–2022 in unfenced controls and fenced exclosures were 13.2 ± 0.1 cm and 14.9 ± 0.1 cm, respectively. Linear mixed effects models of trillium stem height with a year and treatment (i.e., fencing) and interaction as main effects with a random effect for site yielded highly significant results. The main effect of year ($t_{3253.9}$ = -11.58, β = -0.71, P < 0.001) and treatment ($t_{3602.0}$ = -2.91, β = -0.84, P = 0.004) both negatively affected trillium height. The treatment interaction was highly significant ($t_{3618.2}$ = -6.50, β = 0.56, P < 0.001) in the positive direction. Trillium mean stem height in control plots decreased, while trillium mean stem height in exclosures remained similar (Figure 6). Mean stem heights of unbrowsed plants ($\bar{x}$ = 13.1 ± 0.1 cm) were smaller (t_{2260} = 2.18, P = 0.029) than browsed plants ($\bar{x}$ = 14.0 ± 0.4 cm). The best performing model included a 2-year time-lag of spring deer density, such that increased spring deer density from 2 years prior had a positive effect on trillium stem heights (t = 3.62, β = 0.16, P < 0.001). Year had a strong negative effect (t = -5.62, β = -0.45, P < 0.001. The threshold of deer density (i.e., high deer density [>10 deer/km^2], low deer density [≤10 deer/km^2], exclosures [0 deer/km^2]) was highly significant ($F_{2, 3636}$ = 49.34, P < 0.001). High vs. low pairwise comparisons were the only nonsignificant comparison (P = 0.123; Figure 7). Stem heights were tallest in exclosures (14.9 ± 0.1 cm) followed by high spring density years (13.5 ± 0.2 cm) followed by low spring density years (13.0 ± 0.1 cm).

Browse rates of trillium plots were nearly greater (W = 7733, P = 0.062) in high deer density years than low deer density years. During high deer density years, mean browse rates

were 11.3 ± 2.0 % (median = 0.0, n = 109), while during low deer density years mean browse rates were 7.4 ± 1.6 % (median = 0.0, n = 104). Likewise, large 3-leaf and reproductive plants in high density years were browsed similarly (V = 2983, P = 0.185; $\bar{x}$ = 26.1 ± 4.0 %, median = 20.0, n = 51) to low density years ($\bar{x}$ = 20.8 ± 2.7 %, median = 6.2, n =104). Deer density as a numeric covariate was nearly significant and negative (β = -0.1, P = 0.086), indicating increased deer density led to decreased browse rates on all trillium plants; however, this model did not meet the heteroscedasticity assumption.

Discussion

Deer Density

Robust density estimates are needed for wildlife managers to effectively monitor populations and make management decisions (Fryxell et al. 2014). Numerous wildlife studies employ distance sampling because of its ease of implementation, easily met assumptions, thorough statistical support, and robust density estimates (Buckland et al. 2001). The density estimates I obtained occurred during 2 distinct timeframes annually: (1) pre-removal (9.7–31.9 deer/km^2; 1998–2015) and post-removal (8.6–18.0 deer/km^2; 2016–2022). Pre-removal estimates were similar to other suburban forests in Catoctin National Park (McShea et al. 2011), metropolitan Chicago (Witham and Jones 1990, Urbanek et al. 2012c), and Monocacy National Battlefield (Preston et al. 2021). I found higher density estimates at CUVA than in hunted populations in Minnesota (LaRue et al. 2007) and lower estimates than in hunted populations in New Jersey and Pennsylvania (Williams et al. 2013). Density comparisons among culled or hunted populations are difficult given different management goals among studies, but density estimates for CUVA were generally similar to other deer studies.

I was able to meet most of the key assumptions of distance sampling using roads as transects. Typically, road-based distance sampling violates 2 assumptions: (1) roads are not randomly placed on the landscape and, therefore, are not random transects; and (2) deer are not randomly distributed relative to roads. Ignoring such violations will lead to a positively biased detection estimate, thus an underestimated density (Stainbrook and Diefenbach 2012). However, I was able to overcome road bias by expanding the first cut point (Ward et al. 2004, McShea et al. 2011) and using a hazard-rate detection function during analysis. Additionally, the sampling scheme in CUVA has been consistent regarding timing, duration, and location of transects since 1998, making their continued use important for long-term assessments such as mine.

Increased accuracy of density estimates can be obtained by recording additional survey covariates while distance sampling. For example, I did not record whether the observations were taken in a field versus a forest. Undoubtedly, deer are more easily observed in fields than forests, thereby potentially violating the assumption of declining detection with increasing distance (Thomas et al. 2010, McShea et al. 2011). However, my study area was predominately forested, potentially making it difficult to obtain an adequate number of observations per habitat type to effectively model that variation. Detection of the object is paramount in distance sampling (Buckland et al. 2001) and landscape features can severely influence the ability of detection (Royle et al. 2004); particularly invasive plant species, such as autumn olive (*Elaeagnus umbellata*), amur honeysuckle (*Lonicera maackii*), and multiflora rose which grow along roadsides in dense clumps (Yates et al. 2004) and retained leaves when surveys at CUVA occurred. These roadside invasive plants can influence the detection probability by obstructing the view of the observer. In areas with these plants, I could not observe further than a few meters into the forest. Roadside invasives can also provide cover that deer can use to hide from the

observer. Thus, the presence of invasive plants at roadsides would violate the assumption of perfect detection of objects (i.e., deer) on the transect (Buckland et al. 2001).

Population dynamics of deer reflect complex and important interactions with their environment outside of population management (McShea and Schwede 1993, McShea et al. 2007). I noted 6 oscillations in density, roughly 2–5 yr apart. These oscillations were comprised of time at a low density, followed by an extreme high density, and are referred to as a "boom-bust" cycle. Nearly all density peaks were preceded by a relative minimum in density in the time series. These boom-bust cycles are typically caused by competition for nutritional resources (Doebeli et al. 2021). Oak mast (i.e., acorns) can result in large population increases in many wildlife species (Ostfeld et al. 1996). While I did not sample for oak mast directly, these timeframes for minimums/peaks coincide with when large crops of oak mast occur in eastern oak-hickory forests (Sork et al. 1993, Dey 2002). The low density estimates in the time series would be when the oak mast was a large crop, thus inflating doe reproduction and fawn survival during spring and summer. Increased reproduction and survival can cause high density estimates measured in the fall. However, in a resource restricted population, the density of deer would significantly decrease the following year because of resource limitation (Arnold 2021). The Ohio Department of Natural Resources monitors oak mast production at 38 wildlife areas; and in 2014 and 2019 the statewide mean mast production of red and/or white oaks were higher than the statewide long-term mean, but nearby sampled areas in those years were highly variable (Ohio Department of Natural Resources 2023). Another explanation for the peaks in density estimates may be density-dependence. At low densities, deer have higher reproduction rates and survival (McCullough 1979). Outside of removals, deer population dynamics in CUVA is likely strongly affected by a combination of density-dependence and nutritional resources.

I have confidence that density estimates are reflective of the long-term variability in deer density that has occurred at CUVA. The coefficient of variation was relatively low across all years, which indicated models had low variability. Thus, my estimates are most likely precise and track true density, even if inaccuracies may exist due to deer not being randomly distributed relative to road transects. Moreover, removals and population trends were reflected within the estimates, except when density was suppressed to around 10 deer/km^2. For example, deer density increased following the first year of removals (January 2016), which was likely caused by (1) deer previously existing near ecological carrying capacity and (2) removal levels were insufficient to reduce density below maximum sustained yield (McCullough 1984). The following year (January 2017) removal numbers were increased, and the population may have experienced increased natural mortality due to the higher density (Arnold 2021), which resulted in a dramatic decrease in density in November 2017. However, in there was an epizootic hemorrhagic disease outbreak in 2017 which likely contributed to a reduced density (R. Trimbath, National Park Service, personal communication). The following 2 years (January 2018 and 2019), ≥30 % of the population was removed which maintained a relatively low density of ≤10 deer/km^2. This 30% removal threshold is typically cited as being the minimum number required to appreciably decrease deer density (Xie et al. 1999, Ueno et al. 2010, Simard et al. 2013). Fewer deer removed in January 2020 resulted in an increased density estimate in November 2020. Nearly 30% of the population was removed in January 2021 and a negligible population increase occurred by 2022. Variation between years is inevitable, but a sustained cull of ≥30% of the population resulted in decreased population size which was reflected in the density estimates.

Weight as an Indicator of Health and Pregnancy Rates

Deer density at CUVA was inversely related to body mass where body mass was greatest at low deer densities and lowest at high densities, indicating a density-dependent relationship (Leberg and Smith 1993, Nielsen et al. 1997, Hefley et al. 2013, Putman et al. 2019). Fewer deer on the landscape likely resulted in more nutritional resources per capita (Skogland 1985, Ayotte et al. 2020). The density-dependent response was evident across all age- and sex-specific classes measured, implying all individuals benefitted from low densities, however, fawns and yearlings likely benefited the most (Strickland et al. 2008). Additionally, a density time-lag did not appear to influence body mass, which suggests the current year's deer density had the greatest impact on body mass. The absence of a deer density time-lag likely indicated an immediate release of nutritional stress occurred (Shea et al. 1992, Ashley et al. 1998), which differs from Keyser et al. (2005) who found a 2-year time-lag. Rather, my findings are similar to Hefley et al. (2013) who reported an inverse relationship between body mass and deer density. They, however, did not test for any density time-lags because the current year was correlated to body mass. Furthermore, Hefley et al. (2013) argued that testing for time-lags would make their results less meaningful to managers and reduce the quantity of data for analysis. While I agree with the latter half of their argument, I disagree with the former. Testing for density time-lags when using time series data should be forefront (Fryxell et al. 1991), because density-dependent relationships do not always occur immediately (Keyser et al. 2005, Putman et al. 2019). Shea et al. (1992) did not find a density-dependent body mass relationship in white-tailed deer and attributed it to a poor nutritional plane. Ayotte et al. (2020) documented deer density during the year of harvest did not impact body mass, but Pettorelli et al. (2002) observed the density during the year the individual was born was important. When density-dependent body mass relationships occur with the current year's deer density, it is most likely a result of a reduction in severe intraspecific competition for

nutritional resources (Ashley et al. 1998, Lesage et al. 2001). In deer populations where density was reduced but nutritional competition was limited or nonexistent, density-dependence may be more subtle; thus, the only way to observe those density-dependence is by testing for time-lags. Alternatively, in areas where habitat is depauperate from years of high populations and extensive browsing, vegetation may take years to regenerate and become present in the next trophic level (Royo et al. 2010, Pendergast IV et al. 2016). Moreover, not testing for time-lags could result in poor management decisions: not considering delays in density-dependent effects may result in misunderstanding deer-vegetation interactions and could impact forest regeneration (Russell et al. 2017).

Unsurprisingly, older deer had higher body mass than younger deer. Sexual dimorphism was present across all age classes with males weighing more than females (Leberg and Smith 1993, Hefley et al. 2013). Winter is a nutritionally taxing time for deer (Simard et al. 2014, Kautz et al. 2020) and as a result, adults lost body mass as winter progressed. Deer body mass in other temperate study areas yielded similar findings (DelGiudice et al. 1990, Taillon et al. 2006). Fawns reduce forage intake during winter (Taillon et al. 2006), which results in weight loss. I found fawns lost body mass during winter, however, mass loss occurred most rapidly just prior to vegetative green-up in March. This is similar to Taillon et al. (2006) who documented fawns lost mass during winter, but they found the loss in mass to be greater in magnitude than in my study, likely due to the northern climate. Additionally, fawns may not have significant loss in body mass because they do not go through the same physiological changes as adults and are still growing. Adults during winter reduce forage intake and females are beginning gestation, both of which are nutritionally demanding (Moen 1978, Beier and McCullough 1990, Pekins et al. 1998). Since most fawns were not reproductive in CUVA, they may not lose mass at the same

rate as adults. Additional environmental covariates that impact body condition could have been used in my analysis to model climate and landcover (Garroway and Broders 2005). While CUVA does experience strong seasonal climates, it is located in a mild winter area (Ford et al. 2022). McGraw et al. (2022) found the winter severity index in Wisconsin to not impact adult deer and minimally impact fawn body weight. On Anticosti Island, Ayotte et al. (2020) did not find their environmental winter metrics to influence body mass of white-tailed deer. These study areas experience much more severe winters than CUVA, therefore, I did not model any climatic variables. Additionally, many studies of deer are of rural populations which may have a dominant habitat type for an individual's home range. In suburban habitats such as CUVA, deer have access to forested, agricultural, and developed area for supplemental food in the form of plants, crops, bird seed, and ornamental plants (Kilpatrick and Spohr 2000).

In ungulates, increased body mass at low densities can influence reproduction rates and survival. Increased body mass heading into winter results in fewer deer dying from nutritional stress and less severe over winter weight loss, thus increasing survival (Kautz et al. 2020). Heavier doe body mass leads to increased fawn body mass in the spring (Hewison et al. 2005), which results in increased fawn survival (Carstensen et al. 2009, Michel et al. 2015, Michel et al. 2019). Heightened reproduction and survival ultimately inflate population productivity, resulting in increased abundance the following fall.

Density-dependent pregnancy rates in deer have been the subject of extensive research, as understanding the factors that influence reproductive success is essential for effective management. Pregnancy rates within CUVA increased with decreased deer density, indicating density-dependence (Albon et al. 1983, Swihart et al. 1998, Putman et al. 2019). I found a time-lag of 3-years in deer density to best influence pregnancy rates of white-tailed deer aged 1.5–3.5

years, differing from Putman et al. (2019) who found no time-lag for similar ages of red deer (*Cervus elaphus*) in Scotland. However, white-tailed deer would not be expected to follow the same pattern as red deer given differences in life history traits. My result was similar to Patterson and Power (2002) who found a 3-year time-lag of deer density affected yearling deer natality and no time-lag influenced fawn natality. Although I did not include fawns in the pregnancy analysis, fawns only produced twins when the density from 3-years prior was <10 deer/km^2, contributing correlative support for a 3-year time-lag. Additionally, in 2020, when the deer density 3-years prior was the highest during the study, 0/13 fawns were pregnant. I believe this 3-year time-lag to be potentially caused by 2 interacting factors: (1) maternal effects and (2) increased mast production. Maternal effects are environmental cues during gestation that can influence offspring phenotype independent of genotype (Bernardo 1996, Michel et al. 2016). For example, a first-time reproducers pregnancy rate in CUVA would be dependent on the deer density when their mother was a fetus. Maternal effects have increased body mass of roe deer fawns when they are a fetus during high mast years (Kjellander et al. 2006). Maternal effects have also increased antler characteristics (Michel et al. 2016) and body mass (Michel et al. 2019) of white-tailed deer. Although maternal effects have impacted pregnancy rates of root voles (*Microtus oeconomus*; Bian et al. 2015), maternal effects on pregnancy rates of wild deer remain unknown. Deer density in CUVA experienced a series of population oscillations every 2-5 years that may have been caused by increased oak mast availability (Ostfeld et al. 1996). Deer density is limited by resource availability, which also limits reproduction. Deer that were in utero during high mast years may have offspring more likely to have higher pregnancy rates than those offspring born in normal or low mast years. The stressors of not having high nutritional resources, or lack of stressors, can be passed on to offspring (Monteith et al. 2009, Michel et al. 2016). These findings

suggest increased food availability may have long lasting effects on this population through maternal effects.

Age and weight dictated pregnancy rates at CUVA such that older deer were more likely than younger deer to become pregnant and have increased twins and triplets (DelGiudice et al. 2007, Green et al. 2017). I found increased body mass decreased pregnancy rates, contradictory to many studies of ungulates (Albon et al. 1983, Putman et al. 2019). However, this is potentially an artifact of the data collection method; deer lost mass as winter progressed but were still pregnant. If all deer were removed at the same time during the removal period, I would likely have observed body mass to have a positive effect, however, the interactions of increased weight and increased deer density from 3-years prior resulted in increased pregnancy rates. Regardless of density in some ungulates, adults are somewhat insensitive to density-dependent effects on pregnancy rates (Bonenfant et al. 2002), but this insensitivity was not observed at CUVA. When deer densities were high at CUVA, heavier deer were more likely to go through gestation. At high deer densities, deer weigh less and gestation and winter further decrease weight, thereby requiring individuals to further minimize the risk of dying during pregnancy (Albon et al. 1983). At lower densities, however, more deer are more likely to be pregnant since food resources are not as restricted, making it appear as if lighter massed individuals are more likely to be pregnant.

I did not analyze density-dependence in litter size (as opposed to pregnancy rate, as in my analysis) because I was interested in investigating the pregnancy capabilities of the population during management. Green et al. (2017) noted that geographic location was important in determining the mean litter size of adult deer. My forested-suburban system yielded a similar adult litter size compared to many studies (Roseberry and Klimstra 1970, Nixon 1971, Green et al. 2017). However, I found a much lower fawn pregnancy rate than Green et al. (2017), while I

found a similar rate to Roseberry and Klimstra (1970) who used embryos. My study is unique because I had the ability to analyze a sharpshooting dataset which is typically unbiased in terms of age-classes of deer. Hunter harvest is a very popular data source, but it inherently contains bias because hunters selectively target large individuals (Martınez et al. 2005, Green et al. 2017, Allen et al. 2018). Fawns tend to have higher reproduction at low densities (Swihart et al. 1998), however, disparities in fawn pregnancy rates among studies are likely caused by both habitat quality and deer density (Green et al. 2017).

Herbivory Impacts

Heterogeneity in terms of vertical and horizontal diversity and species composition are important drivers of forest regeneration and are results of productive forests (LaRue et al. 2023), but given overabundant deer, these drivers may be suppressed or nonexistent (Côté et al. 2004, Royo and Carson 2022). Following deer culling in CUVA, I observed native seedling regeneration associated with increased seedling heights and increased species composition indices. Seedlings were taller in fenced exclosures than unfenced control plots, likely because the latter plots experienced deer herbivory (Walters et al. 2016). Seedlings in unfenced plots likely had their terminal bud browsed by deer which is required for vertical growth and seedling regeneration (Kupferschmid et al. 2019). However, this comparison is an environmental extreme because fenced exclosures represent a deer density of 0 deer/km^2, which likely exists nowhere on CUVA. Fenced exclosures can represent forest conditions entirely in the absence of deer herbivory and can be used for comparison to deer accessible areas. However, in the absence of deer herbivory, competition between seedlings will likely occur more intensely (Walters et al. 2020) potentially creating a new limiting factor for seedlings.

While it is certain deer impacted unfenced seedlings, I found marginal support that the tallest seedling heights increased linearly with the previous year's deer density during fall. For example, seedlings measured in July–August 2019 were most affected by the deer density from November 2018. It should be noted that this analysis used the tallest individuals per genera per subplot which may overestimate regeneration because it is not a random sample (Kauffman et al. 2013, Brice et al. 2022); however, I used the mean heights and weighted regression to offset any bias present. Additionally, I did not test if spring deer density impacted seedling heights because (1) browse occurred before, during, and after culling; (2) spring density is a function of fall density; and (3) the CUVA management plan related the seedling heights to fall densities. Testing for spring density effects may have been more biologically relevant, but the fall density is more important for management decisions in CUVA. While deer density was not a significant covariate, year was significant for increased seedling heights of 6 common genera. A likely explanation for increased seedling height is that deer density was suppressed below a unknown threshold to allow for positive regeneration to occur with time (Nagy et al. 2022). The upper limit of deer density to not be impacting forest regeneration is unique to each area and typically unknown, however, densities were kept below the suggested ≤12 deer/km^2 at CUVA, resulting in native seedling regeneration through time. Observing native seedling regeneration meant deer density was no longer a limiting factor for seedling heights, thus the native seedling population mean value could increase. Alternatively, I used the 6 most common tree genera in the unfenced control paired plots, not necessarily those most affected by deer, potentially causing deer density to be an insignificant effect. Furthermore, a comparison of LTEM plots from 2017 to 2021 yielded similar results. Mean deer density during 2017–2021 was 10.4 deer/km^2 after culling ≥30% of the population annually. Forest regeneration generally begins when deer densities are

≤12 deer/km^2 (Tanentzap et al. 2011, Urbanek et al. 2012a, Nagy et al. 2022). I observed measurable increases in regeneration of the community functional group and the *Fraxinus* spp. group, with the latter often regenerating quickly (Jenkins et al. 2015). Native seedling regeneration was less noticeable at finer taxonomic scales, although 9 functional groups either increased in mean height, median height, or the number of seedlings per subplot, thereby indicating that forest regeneration occurred. My results suggest the previous fall deer density was not linearly related to the tallest seedlings; however, maintained densities ≤12 deer/km^2 allowed for forest regeneration to occur.

I did not find support that mean change in seedling height per genera per plot is a useful metric for CUVA to determine if deer removal is needed. If mean change in seedling height was an indicative measure of deer impacts, I would have expected to detect a considerable difference in the mean change in seedling height between fenced exclosures and unfenced controls, but I did not. While seedlings may grow taller in fenced exclosures, they did not grow at an increased rate relative to seedlings in unfenced controls, although this conclusion may be confounded by competition (Walters et al. 2016, Walters et al. 2020). I also found no support that mean change in seedling height per plot in unfenced control plots increased with decreased deer density. Further investigation is necessary to determine the nature of this relationship.

Plant species richness and diversity increased in CUVA as a result of deer management, indicating deer browse may have decreased enough to allow for native seedling regeneration of additional species to begin (Horsley et al. 2003). Fenced exclosures had higher initial values than unfenced plots, but fencing overall did not contribute to increased richness and diversity. However, fencing was likely important, but richness and diversity metrics did not increase enough relative to the unfenced controls experiencing reduced deer densities to elucidate

differences. While fencing around plots did not yield changes in richness and diversity, those metrics might serve as an index of deer impacts if deer are appropriately managed.

It is well documented that deer selectively browse tree/shrub seedlings based on genera (Strole and Anderson 1992, Kittredge and Ashton 1995, Castleberry et al. 1999) and I found support for this hypothesis. I observed a decrease in browse rates for 10/14 genera from 2017 to 2021. I found many soft mast producing genera were selected for ≥2 of 3 years. This is potentially concerning because these genera often provide food for numerous wildlife species such as birds (Wood et al. 2012) and small mammals (McCracken et al. 1999). Additionally, strong selection by deer reduces the likelihood that these species will perpetuate into the future in the seed bank, mid-story, and overstory (Strole and Anderson 1992) and reduce overall forest complexity and heterogeneity (Kittredge and Ashton 1995). I also found *Aesculus* spp., *Fagus* spp., and *Fraxinus* spp. were heavily avoided; these species are also detrimental to forest complexity due to disease and pests. The ability for *Fraxinus* spp. to grow into the canopy layer is virtually nonexistent due to emerald ash borer (Burr and McCullough 2014). *Fagus* spp. are also at risk of a new pathogen infecting primarily seedling and saplings, beech leaf disease (*Litylenchus crenatae*), which defoliates the tree and eventually incurs mortality (Reed et al. 2022), in addition to beech bark disease. *Fraxinus* spp. and *Fagus* spp. are shade tolerant, dominate the understory, and can outcompete more sensitive species. Therefore, it is worrisome that these 2 species are avoided by deer and regenerating at CUVA, making it critically important to decrease deer browsing on preferred species, so they can compete with avoided species and produce heterogenous native canopies. However, it is promising that I documented significant reductions in seedling browse rates from 2017 to 2021. Immediate decrease in browse rates were documented on avoided genera and some neither avoided nor preferred genera,

however, *Prunus* spp. browse rates also decreased in 2 years, which was a preferred genus by deer. Four years elapsed to induce a noticeable decrease in browse rates among preferred species such as *Rubus* spp. and *Smilax* spp. and it may take even longer to observe a decrease in *Cornus* spp. Maintaining deer densities ≤10–12 deer/km^2 decreased browse rates in many genera, but not all. Due to years of extensive browse pressure, genera that are heavily preferred will likely need deer densities to be depressed for many years for regeneration to be observed. With widespread regeneration failure of forests in eastern North America (Trumbull et al. 1989, Miller et al. 2023), it is imperative to manage forests by maintaining deer densities below thresholds where native preferred species can regenerate and reproduce.

Trillium stem height has been considered to be an indicator of deer impacts, with lower deer herbivory resulting in taller stems (Anderson 1994, Koh et al. 2010). Trillium grew taller in fenced exclosure plots than unfenced control plots, likely because deer were unable to browse the flower in exclosures. When a trillium plant has been browsed, it will regenerate smaller in the following year from a loss in photosynthetic ability, potentially, flowering at a smaller stem height (Anderson 1994). My results marginally corroborate that finding. Trillium did flower at taller stem heights in fenced exclosures, but those exclosures are an environmental extreme of 0 deer/km^2 and are unrealistic at CUVA. Interestingly, I found mean stem height decreased in unfenced control plots while stem heights in fenced exclosures were relatively consistent. I explain these findings as such: (1) stem height was not indicative of deer impacts because deer density during the study was relatively low; or (2) the age of each plant was unknown, so regeneration in unfenced control plots occurred, but the regenerated plants were younger individuals and thus decreased the mean stem height. If the latter explanation was happening,

then this would be noticeable in control plots and not fenced exclosures because plants in fenced exclosures had replaced themselves allowing for young plants to grow while old plants senesced.

Among browsable plants, deer browsed taller stemmed trillium plants, ostensibly because taller trillium plants were more likely to be flowering and more nutritious than unflowered plants (Anderson 1994). Indicator species need to have a response to some quantifiable impact (Kirschbaum and Anacker 2005) and using tall, potentially flowering, individuals may work for deer impacts. If deer densities are not managed this can create a problematic situation because taller plants are likely reproductive and deer are browsing the flower before the plant can seed, thus not replacing itself and therefore not being a useful indicator species.

Decreased trillium stem height may not necessarily be indicative of increased deer density in CUVA because I found taller stems at high deer densities. Additionally, the top model included a 2-year time-lag in density meaning the mean trillium stem height for a given spring was dictated by deer density in the spring 2-years prior, although, the model that incorporated the current year's spring density did have a non-significant negative relationship with stem height. The threshold of high and low deer density did not correlate with trillium stem height. Understandably, fenced exclosures had the tallest plants, but grouping by spring deer density indicated plants were smaller when deer densities were lower (<10 deer/km^2), although the comparison was not significant. These analyses might be confounded by an increased number of young plants through regeneration which decreased stem heights, given plant age was not considered. However, I did find marginal support for having increased browse rates during high deer density years than low deer density years for all trillium plants. I found minimal support for increased browse on large 3-leaf and reproductive plants in high deer density years, albeit not significant. Browse rates on large 3-leaf plants can be used as an indicator of deer impacts

because browse is a direct effect on trillium, and when deer were culled, browse rates on trillium plots decreased. However, decreased browse rates could increase trillium abundance, leading to increased small plants, therefore decreased mean stem height. Therefore removing deer would initially decrease mean stem height, thus suggesting managers to remove more deer per the current CUVA deer management plan. Knight et al. (2009a) recommended ≤15% browse rates on large and reproductive plants was required to achieve a regenerating population of trillium. Neither density level yielded a mean of 15% browse rate at CUVA. In low density years 59% plots had <15% browse compared to 49% of plots having 15% browse in high density years. Many plants may have been experiencing heavy continuous browse and could demonstrate legacy effects (Royo et al. 2010) resulting in smaller stem height for a long period of time or indefinitely, thus, it may take many years of low deer density to have these effects vanish at CUVA.

Management Implications

CUVA currently utilizes a zone-based management approach for estimating deer density. While this is a practical approach, ideally each zone would have its own density estimate that was derived from its own detection function. It is recommended that ≥60 observations per stratification unit be observed (Buckland et al. 2001); therefore, I was unable to derive a detection function for individual zones during 2015–2022 due to insufficient sample sizes. Thus, I used the detection function for the entire park for each zone. This may potentially bias the estimates at the zone scale because the park is not uniform in its characteristics that would impact detection. Additionally, deer can move readily across all zones, given likely home ranges of 50–317 ha (Kilpatrick and Spohr 2000, Grund et al. 2002, Storm et al. 2007, Roden-Reynolds et al. 2022) making it an even less practical approach. However, deriving zone-based estimates

may be necessary to determine the magnitude of removals within an area. It is recommended that zone-based estimates be calculated and used to determine which zones may need more removals, but to base the whole management plan upon zones creates much statistical noise making interpretation difficult. Further ways to improve density estimates using the park-wide approach would be to measure additional covariates that may influence detection (e.g., environmental variables, habitat characteristics). If additional covariates are desired, I recommend that ≥30 observations per covariate be collected to obtain an accurate estimate (Anderson et al. 2013). It is also recommended that CUVA continues to use road-based distance sampling. The ability of the distance sampling protocol used in this study to track the nuances in deer population dynamics supports the use of the road-based distance sampling, given corrections are made to account for potential bias.

It is recommended that CUVA continue the use of sharpshooting. Sharpshooting directly resulted in a decreased deer abundance which increased physiological indicators of deer health. This supports strong intraspecific competition is occurring and alleviation of competition is necessary to improve deer condition. Culling enough deer to maintain density ≤10–12 deer/km^2 may be necessary for the physiological indicators measured in this study which are influenced by vegetation (Tanentzap et al. 2011, Urbanek et al. 2012a, Nagy et al. 2022).

The current vegetation monitoring framework in CUVA needs to be reevaluated in several ways. First, the tallest seedling heights are not a random sample of the understory. Measuring the tallest seedling violates randomization, a basic statistical assumption (Brice et al. 2022). I recommend that CUVA measure ≤3–5 random seedlings per genera per plot. This would remove any potential bias associated with measuring the tallest individuals and avoid exaggerating regeneration. Second, plots 4 m^2 in area were able to capture changes in seedling

stem counts more accurately than 12 m^2 plots, mostly due to observer error (Begley-Miller et al. 2018). CUVA currently has plots of 100 m^2 in area to count and measure seedlings. By using smaller plots, CUVA could implement more plots covering a broader range of environmental conditions (Urbanek et al. 2011). Third, microscale covariates (i.e., slope, aspect, canopy cover, basal area) should be recorded because those variables can influence regeneration (Robin-Abbott and Pardo 2017). I recommend that seedling abundances be recorded each year instead of every 4 years because competition affects seedling heights (Walters et al. 2016). The change in seedling height metric currently used showed no support for tracking deer density. Seedlings grew similarly across treatments and all deer densities. I recommend CUVA discontinue using this change in seedling height and focus on randomly sampling seedling heights and browse rates. Given the relationship with seedling heights I again recommend CUVA cull enough deer to maintain deer density no higher than ≤10–12 deer/km^2.

Trillium stem height should not be used as a phytoindicator of deer impacts at CUVA. It is worrisome that the current year's impact of trillium is what is determining deer management decisions when that may not be what is driving stem height based on the time-lag present in the analyses. Additionally, the disconnect between decreased browse but also decreased stem height indicates browse rates may be more useful than stem height. Based on Knight et al. (2009a), I recommend using browse rates on large 3-leaf and reproductive plants, aiming to have ≤15% of those plants browsed each year.

Future Research

I provide several directions for future research based on my observations at CUVA. Further research needs to be conducted to determine whether pregnant fawns are being reared by individuals that were born during high mast years to fully understand the 3-year time-lag

associated with pregnancy rates. Additionally, mast needs to be monitored (McShea et al. 2007) to see if that is the habitat characteristic that is involved in the aforementioned maternal effect. Long-term individual-based research should be conducted to fully understand maternal effects, habitat interactions, and how those influence population dynamics (Ostfeld et al. 1996, LaSharr et al. 2022). Obtaining genetic samples to construct maternity and GPS collaring females and inserting vaginal implant transmitters to study fawn maternity would help address these time-lags (LaSharr et al. 2022). Additionally, GPS collars would further address how deer move within CUVA, potentially answering the spatial scale at which management is necessary (Fattorini et al. 2020).

Further research is needed to separate the effects of competition, deer herbivory, and forest regeneration in CUVA. It is likely these and additional environmental variables are influencing regeneration at local and broad scales. Collecting additional site characteristic data (e.g., slope, aspect) would help understand these complex interactions. Utilizing smaller study plots for controls and exclosures to minimize data collection bias and increase precision of site-specific data would be needed (Begley-Miller et al. 2018). Additionally, knowledge of the abundances of each seedling genera, overstory canopy cover, soil type, browse on buds, seedling heights of random seedlings, and abiotic environmental variables would assist in teasing out regeneration due to competition versus deer herbivory or site characteristics (Walters et al. 2020). It is imperative that continued deer management to reduce deer density occurs. It is sure that the forest will only regenerate in some form when the deer impacts are reduced (Miller et al. 2023). Additionally, it becomes possible to observe the impacts of competition between genera when deer density is maintained at or below low levels (i.e., 10 deer/km^2; (Royo et al. 2010).

Table 1. Park-wide and zone-based deer density estimates (km^2) in Cuyahoga Valley National Park, Ohio, during 1998–2022.

	Park		Zone 1		Zone 2		Zone 3		Zone 4		Zone 5	
Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1998	21.8	1.5	18.0	2.3	27.9	3.3	27.0	2.6	13.6	1.4	32.5	5.9
1999	31.9	2.4	23.4	3.3	36.4	3.4	44.4	4.1	23.8	3.5	32.4	4.4
2000	22.6	1.8	16.4	2.5	30.3	3.9	24.7	3.3	18.1	2.7	30.3	5.7
2001	22.6	1.7	17.4	2.0	27.8	2.7	29.9	4.3	15.4	2.0	28.6	3.3
2002	23.4	1.8	20.7	2.0	37.5	5.3	24.6	3.0	14.3	2.6	37.6	4.7
2003	19.0	1.4	17.3	1.8	15.7	2.1	19.9	2.8	17.8	1.7	24.8	4.9
2004	26.1	2.5	15.9	1.9	36.0	5.8	32.0	4.9	20.6	4.1	30.6	3.0
2005	15.7	2.1	12.6	1.8	13.2	2.0	16.5	3.8	12.9	3.3	27.2	5.4
2006	13.0	1.2	8.5	1.8	16.3	2.4	15.2	1.9	9.2	1.7	20.6	3.5
2007	19.1	2.2	30.8	6.8	20.3	5.6	24.0	4.8	12.2	2.4	16.4	3.2
2008	13.4	1.3	13.8	2.3	19.2	2.9	13.1	2.9	9.1	1.7	21.5	2.5
2009	12.0	1.6	11.1	2.7	7.0	1.5	16.0	2.9	8.8	1.6	17.3	3.1
2010	11.9	1.2	9.4	2.1	10.1	2.8	14.4	2.1	7.3	1.8	23.3	4.0
2011	16.8	1.6	9.8	2.5	18.0	3.8	21.2	3.3	13.0	2.4	23.5	2.6
2012	11.5	1.1	6.3	1.0	2.7	0.8	12.2	1.8	14.4	2.0	13.6	2.9
2013	12.9	1.2	9.3	2.4	14.1	3.1	17.4	2.1	10.9	1.9	11.3	2.0
2014	9.7	1.3	7.3	1.0	10.2	2.7	10.2	2.7	7.8	1.6	16.2	3.8
2015	13.3	1.4	10.8	2.1	10.3	2.5	17.5	3.3	8.9	1.3	21.6	4.8
2016	18.0	1.6	18.0	2.6	24.5	4.1	24.4	3.4	8.9	1.6	24.8	6.3
2017	10.0	1.1	8.5	1.4	13.5	2.8	8.5	1.2	7.4	1.7	19.1	3.9
2018	8.6	1.1	8.4	1.9	14.3	2.2	9.8	2.5	4.6	0.9	13.3	2.9
2019	9.0	1.0	13.3	3.2	10.4	2.7	8.8	1.5	6.3	1.3	11.6	2.1
2020	12.8	1.6	9.1	1.9	10.7	2.0	14.8	3.2	11.9	3.0	15.7	3.6
2021	11.5	1.1	9.4	1.7	10.3	2.1	12.3	1.6	9.1	1.4	19.9	4.0
2022	11.9	1.2	14.8	2.3	14.1	2.3	14.3	2.9	7.3	1.3	12.5	2.0

Table 2. Best-fit model (deer density time-lag of 0 years) of the effect of park-wide deer density, sex, age, and month of removal on body weight (kg) on adult (i.e., ≥1.5 yr but ≤ 3.5 yr) white-tailed deer in Cuyahoga Valley National Park, Ohio, during 2016–2022. Bolded P-values indicate the variable was significant. Results of all models for adults are reported in Appendix B.

Variable	β	SE	t-value	P
(Intercept)	52.90	1.43	37.04	**<0.001**
Park Density$_{t-0}$	-0.25	0.06	-4.00	**<0.001**
Male	6.60	0.40	16.66	**<0.001**
Age	5.79	0.25	23.04	**<0.001**
December	-2.94	2.15	-1.37	0.172
January	-5.99	1.12	-5.36	**<0.001**
February	-7.19	1.11	-6.49	**<0.001**
March	-9.51	1.35	-7.02	**<0.001**

Table 3. Best-fit model (deer density time-lag of 0 years) of the effect of park-wide deer density, sex, and month of removal on body weight (kg) of fawn (i.e., ≤0.5 yr) white-tailed deer in Cuyahoga Valley National Park, Ohio, during 2016–2022. Bolded P-values indicate the variable was significant. Results of all models for adults are in Appendix C.

Variable	β	SE	t-value	P
(Intercept)	37.34	1.37	27.22	**<0.001**
Park Density$_{t-0}$	-0.21	0.06	-3.85	**<0.001**
Male	3.36	0.36	9.33	**<0.001**
December	3.58	2.00	1.79	0.075
January	-0.13	1.20	-0.11	0.915
February	-1.65	1.21	-1.37	0.172
March	-2.49	1.42	-1.76	0.078

Table 4. Pregnancy rates of females removed during January–March in Cuyahoga Valley National Park, Ohio, during 2016–2022.

Year	Age	N_0[a]	N_1	N_2	N_3	N_t[b]	Rate
2016	0.5	44	2	0	0	46	0.04
2016	1.5	6	12	7	0	25	0.76
2016	2.5	3	28	44	3	78	0.96
2016	3.5	2	8	39	0	49	0.96
2016	4.5	0	0	0	0	0	NA
2016	5.5	6	9	40	5	60	0.90
2017	0.5	76	2	0	0	78	0.03
2017	1.5	9	15	7	1	32	0.72
2017	2.5	3	17	51	3	74	0.96
2017	3.5	2	8	38	5	53	0.96
2017	4.5	7	14	27	9	57	0.88
2017	5.5	0	0	0	0	0	NA
2018	0.5	23	1	2	0	26	0.12
2018	1.5	2	5	9	0	16	0.88
2018	2.5	2	4	16	1	23	0.91
2018	3.5	1	3	15	2	21	0.95
2018	4.5	2	2	7	0	11	0.82
2018	5.5	0	0	0	0	0	NA
2019	0.5	37	5	0	0	42	0.12
2019	1.5	1	23	23	1	48	0.98
2019	2.5	0	7	35	1	43	1.00
2019	3.5	1	3	26	3	33	0.97
2019	4.5	5	7	31	6	49	0.90
2019	5.5	0	0	0	0	0	NA
2020	0.5	13	0	0	0	13	0.00
2020	1.5	0	3	8	1	12	1.00
2020	2.5	0	1	12	1	14	1.00
2020	3.5	0	3	14	0	17	1.00
2020	4.5	3	1	7	1	12	0.75
2020	5.5	0	0	0	0	0	NA
2021	0.5	45	2	2	0	49	0.08
2021	1.5	3	6	9	0	18	0.83
2021	2.5	3	2	27	1	33	0.91
2021	3.5	2	6	24	3	35	0.94
2021	4.5	1	2	10	0	13	0.92
2021	5.5	1	2	2	2	7	0.86

2022	0.5	47	4	1	0	52	0.10
2022	1.5	3	7	16	1	27	0.89
2022	2.5	18	3	34	0	55	0.67
2022	3.5	7	6	26	2	41	0.83
2022	4.5	3	1	9	0	13	0.77
2022	5.5	3	2	5	0	10	0.70

[a]$N_{\#}$: Number of females with that number of fetuses.

[b]N_t: Number of females total with and without a fetus present.

Table 5. Most parsimonious model (deer density time-lag of 3 years) of the effect of park-wide deer density, age, body weight (kg), and density-weight interaction on pregnancy rates of adult (i.e., ≥1.5 yr) females white-tailed deer in Cuyahoga Valley National Park, Ohio, during 2015–2022. Bolded P-values indicate the variable is significant. Results of all models are in Appendix D.

Variable	β	SE	z-value	P
(Intercept)	25.76	8.1	3.18	**0.001**
Park Density$_{t-3}$	-2.28	0.7	-3.07	**0.002**
Age	0.58	0.2	2.71	**0.007**
Weight	-0.51	0.1	-3.59	**<0.001**
Park Density$_{t-3}$*Weight	0.05	0.0	3.58	**<0.001**

Table 6. Mean, standard error, and sample size of 12 common genera seedling heights (cm) in Cuyahoga Valley National Park, Ohio, during 2016–2021.

	2016			2017			2018			2019			2020			2021		
Genus	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n
Acer	8.7	0.4	49	9.1	0.7	29	9.7	0.5	40	10.2	0.7	39	10.6	1.0	41	11.0	0.8	36
Carpinus/Ostrya	14.1	2.8	11	29.3	7.4	10	NA	NA	NA	32.6	7.6	12	31.1	8.6	16	30.8	5.2	23
Carya	11.8	0.9	20	12.7	1.0	20	12.7	1.0	21	14.0	1.2	25	15.1	1.1	15	15.7	1.7	17
Cornus	20.0	3.0	5	27.0	0.0	2	NA	NA	NA	15.5	7.8	3	NA	NA	NA	24.0	7.5	3
Craetagus	13.9	1.8	9	15.6	2.4	7	NA	NA	NA	16.6	3.7	9	16.0	2.2	6	15.3	3.0	7
Fagus	47.2	13.7	7	45.0	16.8	6	54.0	16.1	7	70.8	23.0	5	52.1	16.4	8	63.6	21.4	7
Fraxinus	22.2	2.1	60	23.1	2.3	55	28.6	2.8	54	32.5	3.0	52	35.3	3.5	53	40.2	4.2	52
Liriodendron	10.9	*2.1*	7	11.2	1.7	5	12.0	3.3	5	16.3	5.2	3	10.4	2.8	5	10.0	2.9	5
Prunus	16.5	1.9	36	14.3	1.8	37	17.7	2.1	39	16.8	2.2	33	18.1	1.7	31	15.3	1.4	32
Quercus	11.9	0.8	22	12.1	0.9	17	12.1	0.9	13	11.6	1.4	17	12.8	1.2	12	12.9	1.0	20
Sassafras	18.0	2.7	5	13.0	3.0	2	17.5	1.3	3	23.7	5.9	3	25.0	11.5	3	61.0	NA	1
Ulmus	12.6	1.0	23	15.7	1.6	19	20.9	2.8	16	22.6	3.7	18	22.3	3.3	18	26.2	3.6	19

Table 7. Top generalized linear mixed model results for seedling heights in Cuyahoga Valley National Park, Ohio, during 2016–2021. Top model is year since study began (e.g., 0, 1, 2, etc.) and scaled deer density with a time-lag of 1 year. Bolded P-values indicate the variable is significant.

Variable	β	SE	z-value	P
(Intercept)	2.57	0.1	19.61	**<0.001**
Year	0.05	0.0	2.77	**0.006**
Deer Density$_{t-1}$	-0.02	0.0	-1.69	0.091

Table 8. Summary statistics for unfenced LTEM plot seedling heights (cm) in Cuyahoga Valley National Park, Ohio in 2017 and 2021. Three functional groups were used: community (i.e., all species combined), shade tolerance, and 9 common genera. Bolded P-values indicate the variable is significant.

	2017				2021					
Functional Group	n	$\bar{X}$	SE	median	n	$\bar{X}$	SE	median	Statistic	P
Community	282	22.9	1.3	15.5	320	26.7	1.4	18.0	0.13	**0.010**
Shade Tolerant	100	25.1	2.7	15.5	102	25.1	2.6	16.5	0.09	0.771
Shade Intermediate	126	22.5	1.7	15.0	151	27.7	2.0	17.0	0.12	0.298
Shade Intolerant	56	20.0	2.2	17.0	67	26.9	2.3	21.0	0.24	0.060
Acer	31	10.5	1.1	8.0	35	10.2	0.6	9.0	0.27	0.182
Carpinus/Ostrya	26	32.8	5.9	26.0	19	31.8	5.7	26.0	0.15	0.974
Carya	29	16.2	1.8	16.0	32	24.0	2.5	21.5	0.26	0.261
Creatagus	11	33.1	7.8	58.0	19	29.2	5.4	45.0	0.18	0.975
Fagus	11	66.1	12.0	22.0	11	63.5	15.0	32.5	0.27	0.808
Fraxinus	71	26.8	2.4	12.0	68	39.0	3.4	13.5	0.23	**0.047**
Prunus	39	19.0	2.9	17.0	42	22.4	3.6	22.0	0.16	0.670
Quercus	15	11.8	1.2	15.5	40	14.0	0.9	18.0	0.18	0.892
Ulmus	20	21.1	2.7	15.0	25	26.8	3.1	17.0	0.27	0.393

Table 9. Results from the linear model for change in mean seedling heights in unfenced control plots in Cuyahoga Valley National Park, Ohio during 2016–2021. Deer density variables were scaled. Year is time since study began (e.g., 0, 1, 2, etc.). Bolded P-values indicate the variable is significant.

Variable	β	SE	t-value	P
(Intercept)	3.35	1.6	2.10	**0.038**
Park Deer Density$_{t-0}$	0.43	0.6	0.68	0.500
Park Deer Density$_{t-1}$	-0.48	0.6	-0.85	0.396
Year	-0.54	0.5	-1.05	0.295

Table 10. Browse preference of seedlings in Cuyahoga Valley National Park, Ohio in 2017, 2019, and 2021.

Year	Genus	Sampled Browsed	Sampled Un-browsed	Sampled Total	Prop. of Total	Expected Browse Rate	Observed Browse Rate	χ^2	Cum. Sum χ^2	Lower CI	Upper CI	Pref.[a]
2017	Acer	80	349	429	0.03	92.37	0.03	1.66	1.66	0.02	0.04	o
2017	Aesculus	30	230	260	0.02	55.99	0.01	12.06	13.72	0.00	0.02	-
2017	Carp/Ostrya[b]	135	820	955	0.07	205.67	0.05	24.28	38.00	0.04	0.06	-
2017	Carya	28	88	116	0.01	24.97	0.01	0.37	38.37	0.00	0.02	o
2017	Cornus	62	97	159	0.01	34.25	0.02	22.48	60.85	0.01	0.03	+
2017	Craetagus	61	139	200	0.02	43.08	0.02	7.45	68.31	0.01	0.03	o
2017	Fagus	575	3363	3938	0.30	848.04	0.20	87.91	156.22	0.18	0.23	-
2017	Fraxinus	191	1591	1782	0.14	383.75	0.07	96.82	253.04	0.05	0.08	-
2017	Hamemelis	18	28	46	0.00	9.90	0.01	6.63	259.67	0.00	0.01	o
2017	Lindera	620	2152	2772	0.21	596.93	0.22	0.89	260.56	0.20	0.24	o
2017	Nyssa	37	9	46	0.00	9.90	0.01	74.21	334.76	0.01	0.02	+
2017	Prunus	281	575	856	0.07	184.33	0.10	50.70	385.47	0.08	0.12	+
2017	Ribies	47	19	66	0.01	14.20	0.02	75.76	461.22	0.01	0.02	+
2017	Rubus	40	24	64	0.00	13.78	0.01	49.90	511.12	0.01	0.02	+
2017	Smilax	299	129	428	0.03	92.18	0.11	464.06	975.18	0.09	0.12	+
2017	Toxico.[c]	6	47	53	0.00	11.42	0.00	2.57	977.75	0.00	0.00	o
2017	Ulmus	76	163	239	0.02	51.46	0.03	11.70	989.45	0.02	0.04	o
2017	Vaccinium	122	162	284	0.02	61.16	0.04	60.52	1049.97	0.03	0.05	+
2017	Viburnum	104	261	365	0.03	78.60	0.04	8.21	1058.18	0.03	0.05	o
2019	Acer	19	242	261	0.02	23.46	0.02	0.85	0.85	0.01	0.03	o
2019	Aesculus	7	166	173	0.02	15.55	0.01	4.70	5.55	0.00	0.02	-

2019	Amelanchier	2	39	41	0.00	3.69	0.00	0.77	6.32	0.00	0.01	o
2019	Carp/Ostrya[a]	120	1062	1182	0.11	106.23	0.12	1.79	8.10	0.09	0.15	o
2019	Carya	2	54	56	0.01	5.03	0.00	1.83	9.93	0.00	0.01	o
2019	Cornus	18	76	94	0.01	8.44	0.02	10.82	20.75	0.01	0.03	o
2019	Craetagus	25	91	116	0.01	10.43	0.03	20.38	41.13	0.01	0.04	o
2019	Fagus	167	2599	2766	0.25	248.58	0.17	26.77	67.90	0.13	0.20	-
2019	Fraxinus	24	1657	1681	0.15	151.07	0.02	106.88	174.78	0.01	0.04	-
2019	Hamemelis	9	79	88	0.01	7.91	0.01	0.15	174.93	0.00	0.02	o
2019	Lindera	180	2280	2460	0.22	221.08	0.18	7.63	182.57	0.14	0.22	-
2019	Prunus	84	496	580	0.05	52.13	0.08	19.49	202.06	0.06	0.11	+
2019	Quercus	3	42	45	0.00	4.04	0.00	0.27	202.32	0.00	0.01	o
2019	Ribies	3	85	88	0.01	7.91	0.00	3.05	205.37	0.00	0.01	o
2019	Rubus	35	56	91	0.01	8.18	0.04	88.01	293.38	0.02	0.05	+
2019	Sassafras	17	32	49	0.00	4.40	0.02	36.08	329.46	0.00	0.03	+
2019	Smilax	66	136	202	0.02	18.16	0.07	126.09	455.55	0.04	0.09	+
2019	Ulmus	44	144	188	0.02	16.90	0.04	43.48	499.02	0.02	0.06	+
2019	Vaccinium	68	172	240	0.02	21.56	0.07	99.99	599.02	0.04	0.09	+
2019	Viburnum	98	528	626	0.06	56.26	0.10	30.97	629.99	0.07	0.13	+
2021	Acer	14	227	241	0.02	19.68	0.02	1.64	1.64	0.00	0.03	o
2021	Aesculus	1	158	159	0.01	12.98	0.00	11.06	12.70	0.00	0.00	-
2021	Amelanchier	4	70	74	0.01	6.04	0.00	0.69	13.39	0.00	0.01	o
2021	Carya	3	122	125	0.01	10.21	0.00	5.09	18.48	0.00	0.01	+
2021	Craetagus	46	202	248	0.02	20.25	0.05	32.74	51.22	0.03	0.07	+
2021	Fagus	137	2312	2449	0.23	199.96	0.16	19.82	71.04	0.12	0.19	-
2021	Fraxinus	16	1786	1802	0.17	147.13	0.02	116.87	187.92	0.00	0.03	-
2021	Hamemelis	1	37	38	0.00	3.10	0.00	1.43	189.34	0.00	0.00	o

2021	Lindera	188	2486	2674	0.25	218.33	0.21	4.21	193.56	0.17	0.26	o
2021	Liriodendron	1	53	54	0.01	4.41	0.00	2.64	196.19	0.00	0.00	-
2021	Prunus	65	640	705	0.07	57.57	0.07	0.96	197.15	0.05	0.10	o
2021	Quercus	10	108	118	0.01	9.64	0.01	0.01	197.17	0.00	0.02	o
2021	Ribies	14	108	122	0.01	9.96	0.02	1.64	198.80	0.00	0.03	o
2021	Rubus	27	111	138	0.01	11.27	0.03	21.96	220.76	0.01	0.05	+
2021	Smilax	88	177	265	0.02	21.64	0.10	203.56	424.33	0.07	0.13	+
2021	Ulmus	85	312	397	0.04	32.41	0.10	85.31	509.64	0.07	0.13	+
2021	Vaccinium	56	214	270	0.03	22.05	0.06	52.28	561.92	0.04	0.09	+
2021	Viburnum	121	741	862	0.08	70.38	0.14	36.41	598.33	0.10	0.17	+

[a]Preference, o: neither aoivded/preferred, –: avoided, +: preferred
[b]Carpinus/Ostrya
[c]Toxicodendron

Table 11. Change in browse rates for genera with ≥10 sites measured during each sampling year in Cuyahoga Valley National Park, Ohio, during 2017, 2019, and 2021. Bolded P-values indicate the variable is significant.

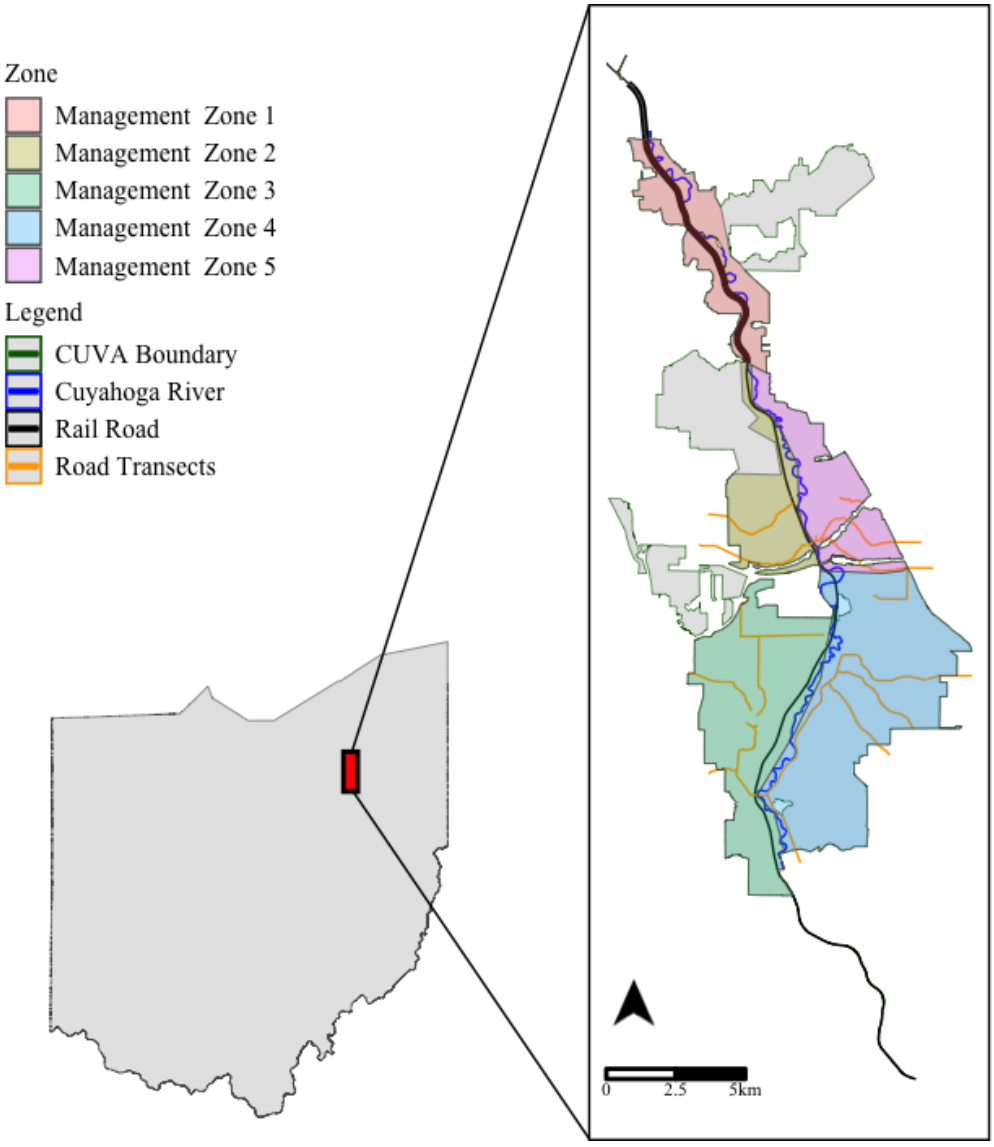
	Kruskal-Wallis test	Wilcox Multiple Comparison Tests[a]		
Genus	P	2017:2019	2017:2021	2019:2021
Acer	**0.029**	ns	*	ns
Aesculus	**0.031**	ns	*	ns
Carpinus/Ostrya	**0.022**	ns	*	ns
Carya	**0.004**	*	*	ns
Cornus	0.171	ns	ns	ns
Craetagus	**0.019**	*	ns	ns
Fagus	**<0.001**	***	****	ns
Fraxinus	**<0.001**	****	****	ns
Lindera	**<0.001**	***	***	ns
Prunus	**0.004**	*	*	ns
Rubus	**<0.001**	ns	***	ns
Smilax	**0.007**	ns	*	ns
Ulmus	0.465	ns	ns	ns
Viburnum	0.774	ns	ns	ns

[a]ns: P > 0.5, *: P < 0.5, **: P < 0.01, ***: P < 0.001, ****: P < 0.0001

Table 12. Summary statistics for species richness and Shannon's Diversity Index (*H'*) for each year and treatment group in Cuyahoga Valley National Park, Ohio, during 2017–2021.

Variable	Treatment	Year	n	Min	Max	Median	$\bar{X}$	SD	SE	CI
Diversity	Control	2017	17	0.0	2.1	0.3	0.5	0.7	0.2	0.3
Diversity	Control	2021	17	0.0	2.1	0.7	0.7	0.7	0.2	0.3
Diversity	Exclosure	2017	18	0.0	1.8	0.4	0.7	0.7	0.2	0.4
Diversity	Exclosure	2021	17	0.0	2.4	1.0	0.9	0.7	0.2	0.4
Richness	Control	2017	17	0.0	11.0	2.0	2.4	3.0	0.7	1.6
Richness	Control	2021	17	0.0	10.0	2.0	3.2	3.0	0.7	1.5
Richness	Exclosure	2017	18	0.0	11.0	2.5	3.4	3.5	0.8	1.7
Richness	Exclosure	2021	17	0.0	17.0	4.0	5.4	5.0	1.2	2.6

Figure 1. Cuyahoga Valley National Park, Ohio. White-tailed deer management zones are the highlighted areas with 1 at the north end and 2–5 below going counter-clockwise beginning in the northwest corner during 1998–2022. The green outline is the park boundary, the blue line is the Cuyahoga River, the black line is a railroad, while the thicker black line is the railroad transect, and yellow lines are road transects. Areas shaded in grey, but within the green outline are other parks that operate within the National Park.



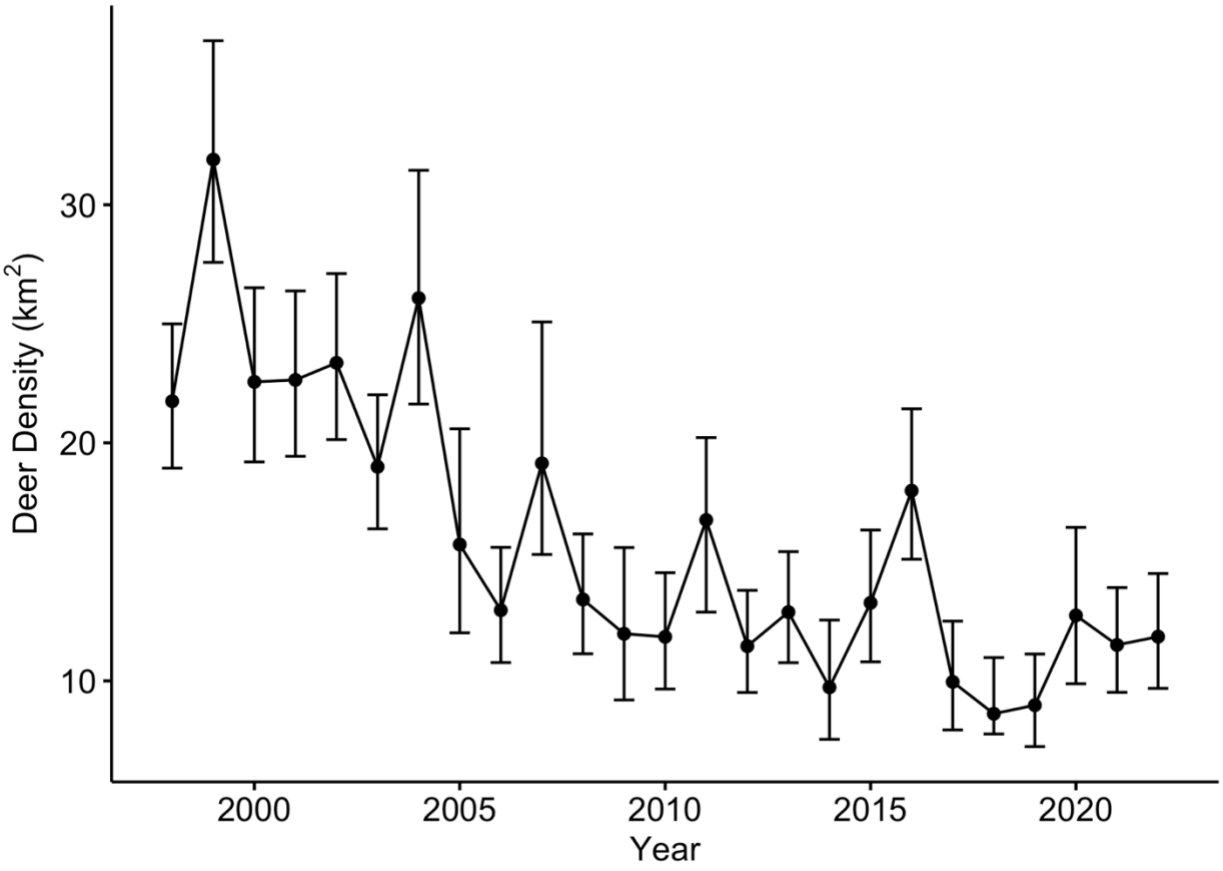


Figure 2. Park-wide deer density estimates (km^2) in Cuyahoga Valley National Park, Ohio, during 1998–2022. Error bars represent a 95% confidence interval.

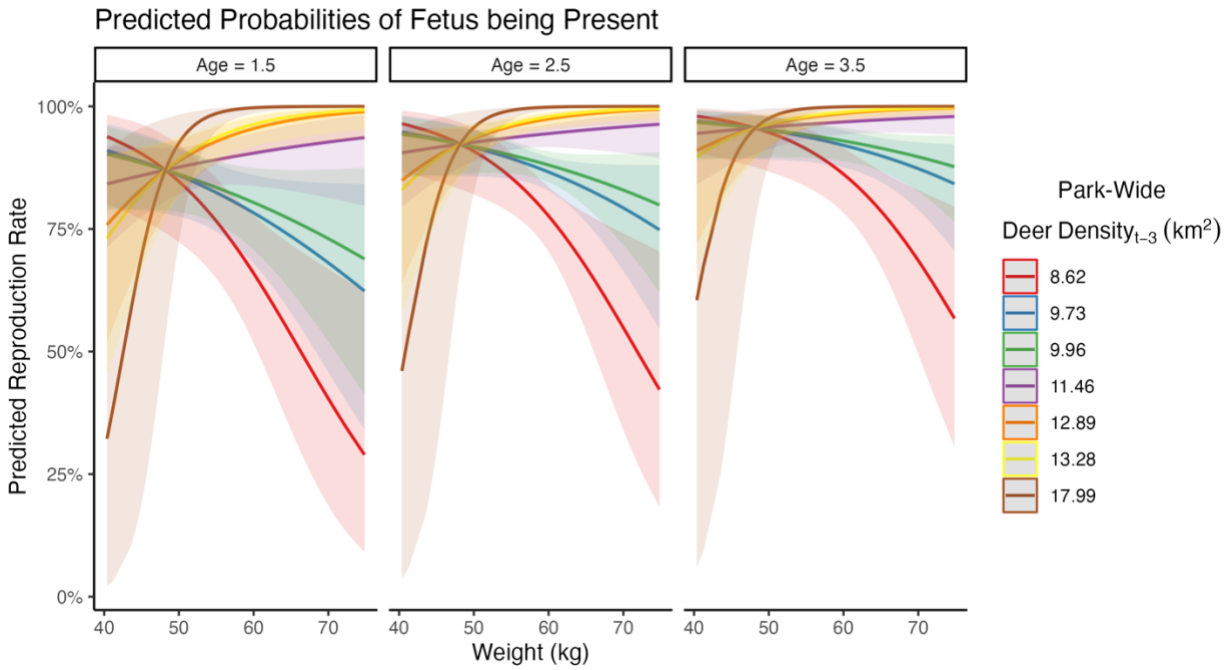


Figure 3. Predicted interaction term between 3-year parkwide deer density and body mass of female white-tailed deer in Cuyahoga Valley National Park, Ohio during 2016–2022.

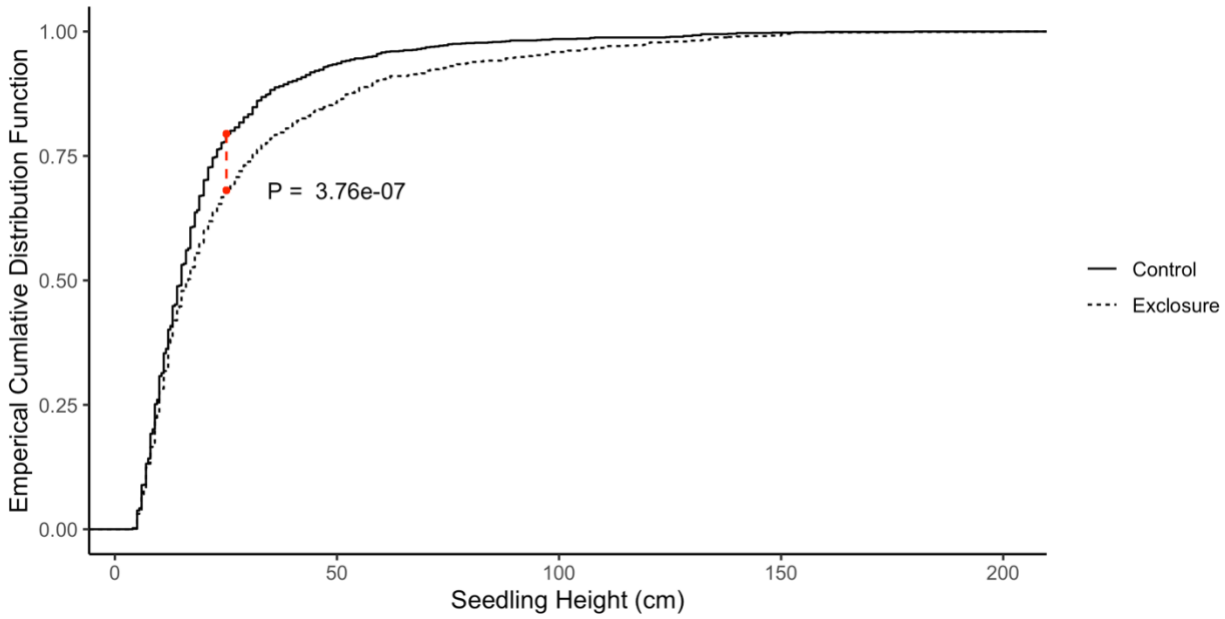


Figure 4. Empirical cumulative distributions of seedling heights (cm) in unfenced control plots and fenced exclosures in Cuyahoga Valley National Park, Ohio, during 2016–2022.

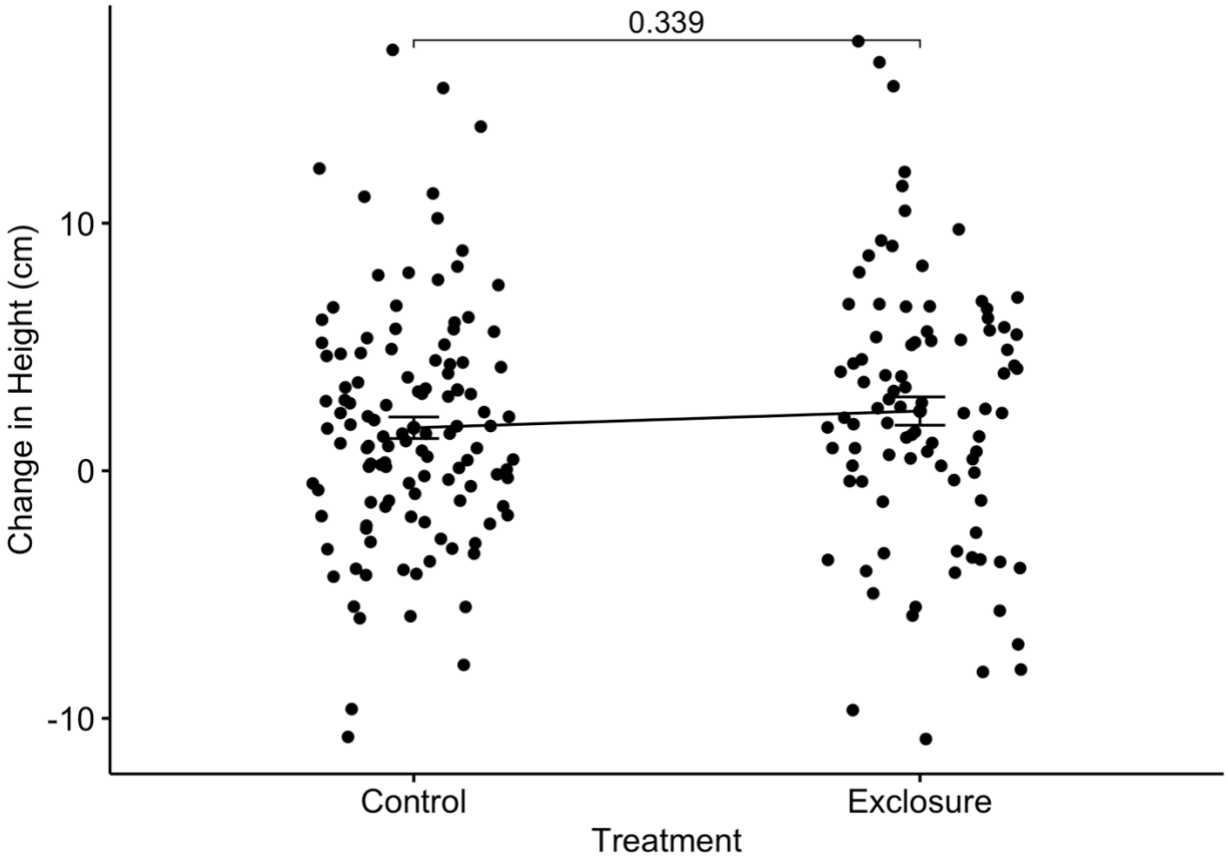


Figure 5. Change in mean seedling heights (cm) of seedlings in paired plots (i.e., unfenced controls and fenced exclosures) in Cuyahoga Valley National Park, Ohio during 2016–2021. Center dots connected by line is the mean of each treatment and the error bars are standard error.

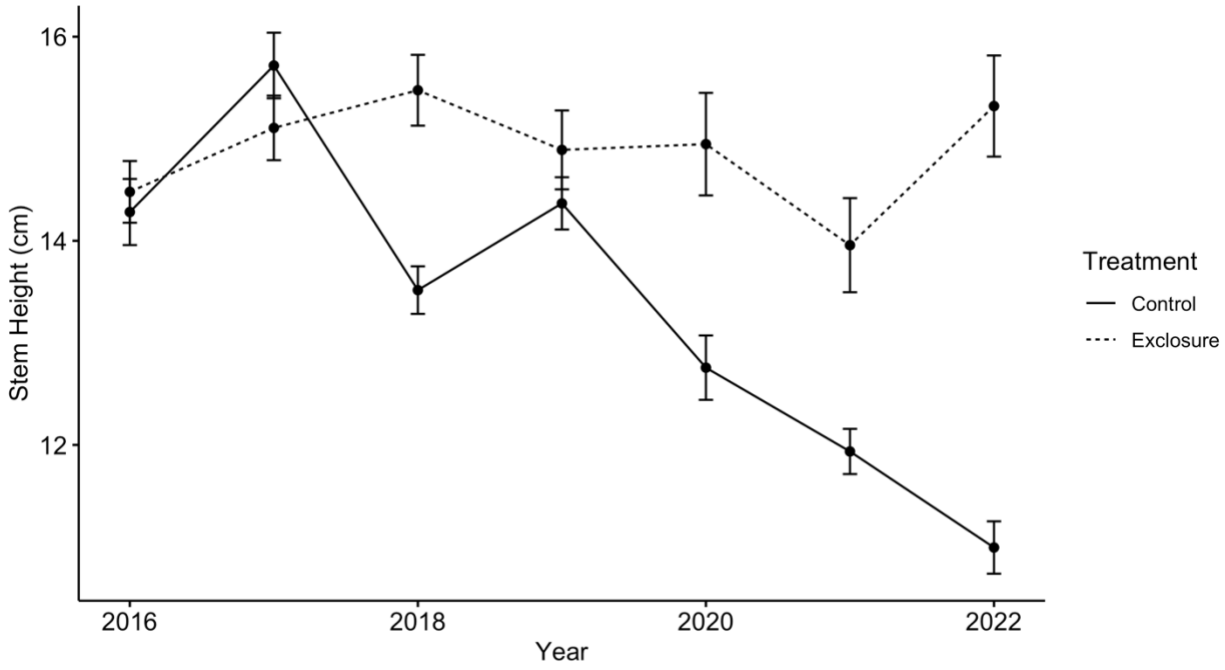


Figure 6. Trillium mean stem heights (cm) in fenced exclosures and unfenced control paired plots in Cuyahoga Valley National Park, Ohio during 2016–2022. Error bars represent standard error.

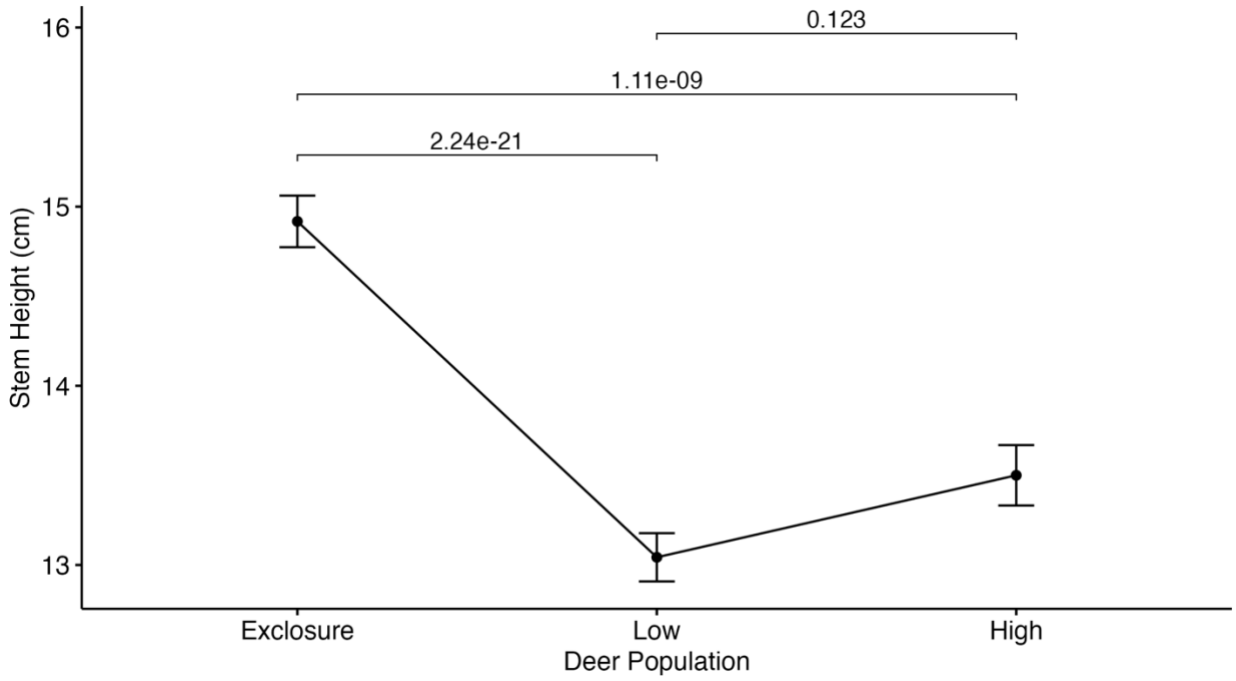


Figure 7. Pairwise comparison of mean trillium stem heights (cm) in Cuyahoga Valley National Park, Ohio during 2016–2022. The above brackets compare the treatments, and the associated number is the P-value. The error bars represent standard error.

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APPENDIX A

Age- and sex-specific summary statistics of body weight (kg) for white-tailed deer removed in Cuyahoga Valley National Park, Ohio, during 2016–2022.

Year	Age	Sex	n	$\bar{X}$	SE	Min	Median	Max	IQR[a]
2016	0.5	F	46	32.7	0.8	21.8	33.1	49.4	6.6
2017	0.5	F	78	33.0	0.4	24.9	33.8	42.6	5.8
2018	0.5	F	44	33.7	0.8	25.9	33.3	48.1	7.0
2019	0.5	F	42	35.0	0.7	27.2	34.0	45.4	5.8
2020	0.5	F	25	36.2	1.2	24.9	35.4	49.7	7.7
2021	0.5	F	49	34.6	0.7	23.1	35.4	45.4	6.4
2022	0.5	F	52	33.9	0.8	20.9	34.2	49.4	6.5
2016	1.5	F	25	49.3	1.6	27.7	49.4	65.8	10.0
2017	1.5	F	32	51.4	1.1	39.0	51.3	68.0	9.0
2018	1.5	F	36	52.3	1.1	43.5	51.7	74.4	7.9
2019	1.5	F	48	52.0	0.8	36.3	52.2	59.9	5.2
2020	1.5	F	23	57.4	0.9	49.9	57.6	66.7	5.1
2021	1.5	F	18	53.9	1.2	46.3	53.5	63.0	6.2
2022	1.5	F	27	55.0	0.7	49.9	54.4	64.4	5.0
2016	2.5	F	78	57.0	0.8	37.6	56.7	70.3	10.3
2017	2.5	F	74	57.3	0.6	46.3	56.7	71.2	7.7
2018	2.5	F	59	60.2	0.8	49.9	59.9	77.6	7.0
2019	2.5	F	43	58.8	0.7	48.5	58.1	68.0	3.6
2020	2.5	F	29	60.7	0.9	52.6	60.3	71.9	5.9
2021	2.5	F	33	59.0	0.8	51.7	58.1	68.9	8.2
2022	2.5	F	55	58.7	0.5	49.9	58.5	68.5	5.2
2016	3.5	F	49	59.3	1.0	45.4	57.2	82.1	8.2
2017	3.5	F	53	60.8	0.8	49.4	60.3	74.8	8.2
2018	3.5	F	35	61.4	1.1	49.9	61.2	82.6	7.7
2019	3.5	F	33	62.1	0.9	51.3	62.1	79.4	5.0
2020	3.5	F	23	64.3	1.1	56.7	63.5	75.3	9.3
2021	3.5	F	35	63.5	0.9	50.3	63.5	71.7	8.2
2022	3.5	F	41	63.4	0.8	53.5	64.0	78.0	5.0
2016	4.5	F	8	56.3	2.7	47.6	52.8	68.0	9.0
2017	4.5	F	57	60.3	0.8	45.8	59.0	75.3	7.7

2018	4.5	F	24	62.5	1.4	46.7	62.6	79.4	10.7
2019	4.5	F	49	63.7	1.1	49.0	63.0	79.4	10.0
2020	4.5	F	18	64.1	1.3	56.2	64.2	77.1	8.2
2021	4.5	F	13	63.9	1.6	57.2	62.1	75.8	9.5
2022	4.5	F	13	69.8	1.5	58.5	68.9	79.8	5.9
2016	5.5	F	53	60.4	0.8	44.5	59.4	78.0	8.6
2020	5.5	F	3	66.7	2.8	61.7	67.1	71.2	4.8
2021	5.5	F	7	61.2	4.5	50.8	56.2	83.9	9.5
2022	5.5	F	10	62.5	1.9	54.9	60.3	71.2	9.3
2016	0.5	M	45	35.5	0.7	24.5	36.3	44.5	7.7
2017	0.5	M	76	35.8	0.4	24.0	35.8	45.4	2.7
2018	0.5	M	44	36.9	0.7	27.2	36.3	45.4	6.6
2019	0.5	M	38	37.9	0.7	29.5	36.7	49.9	6.6
2020	0.5	M	37	38.7	0.8	29.9	39.0	49.9	8.2
2021	0.5	M	33	39.1	0.7	28.6	40.8	45.8	5.4
2022	0.5	M	52	38.3	0.7	28.6	37.6	53.1	6.6
2016	1.5	M	12	54.1	2.5	38.1	54.7	65.8	9.1
2017	1.5	M	23	57.0	1.6	40.8	56.7	77.1	1.8
2018	1.5	M	24	55.8	1.4	43.5	55.8	73.0	7.8
2019	1.5	M	19	58.4	2.0	46.3	56.7	72.6	13.8
2020	1.5	M	25	59.6	1.1	51.7	59.4	73.7	6.8
2021	1.5	M	24	57.2	1.1	48.5	57.6	68.9	7.8
2022	1.5	M	28	55.2	0.9	48.1	54.0	71.2	3.7
2016	2.5	M	22	62.1	1.5	51.7	59.4	73.0	10.7
2017	2.5	M	31	61.5	1.6	31.8	63.5	74.8	9.1
2018	2.5	M	53	64.1	1.2	49.0	62.1	87.1	9.1
2019	2.5	M	30	68.4	1.5	56.7	67.4	86.2	16.3
2020	2.5	M	13	72.3	2.1	60.3	71.7	88.5	6.4
2021	2.5	M	20	66.6	1.9	48.5	65.3	80.7	9.6
2022	2.5	M	26	63.2	0.9	54.4	62.8	78.5	4.4
2016	3.5	M	7	64.2	1.9	58.5	65.8	69.4	9.8
2017	3.5	M	20	71.2	2.5	56.7	68.9	97.1	9.5
2018	3.5	M	19	70.0	2.9	45.8	72.6	88.5	20.4
2019	3.5	M	10	75.2	3.1	60.3	74.6	90.7	11.1
2020	3.5	M	5	88.1	4.7	74.4	89.8	102.5	8.6
2021	3.5	M	14	71.5	3.5	54.9	69.9	95.3	16.3

2022	3.5	M	35	74.8	1.2	57.2	75.8	87.5	6.1
2016	4.5	M	1	90.7	NA	90.7	90.7	90.7	0.0
2017	4.5	M	5	72.3	2.9	64.9	70.3	79.4	10.9
2018	4.5	M	11	71.3	5.5	44.9	77.1	93.0	31.3
2019	4.5	M	2	68.0	1.4	66.7	68.0	69.4	1.4
2020	4.5	M	3	83.9	11.0	65.8	82.1	103.9	19.1
2021	4.5	M	2	72.6	8.2	64.4	72.6	80.7	8.2
2022	4.5	M	7	90.7	2.7	85.3	88.5	106.1	4.5
2016	5.5	M	4	88.5	7.4	69.4	89.4	105.7	11.1
2020	5.5	M	1	87.1	NA	87.1	87.1	87.1	0.0
2021	5.5	M	2	73.7	17.0	56.7	73.7	90.7	17.0
2022	5.5	M	5	86.5	2.3	78.5	88.9	91.2	4.5

[a]Interquartile Range

APPENDIX B

Summary of the models of the effects of white-tailed deer densities at 4 time-lags and 2 spatial scales, sex, age, and month of removal on body weight (kg) for adult white-tailed deer (age ≥ 1.5 yr but ≤ 3.5 yr) in Cuyahoga Valley National Park, Ohio during 2016–2022. P-values in bold are significant at the 0.05 level.

Time lag (years)	Scale	Variable	β	SE	t-value	P	Delta AIC
0	Park	(Intercept)	52.90	1.43	37.04	**<0.001**	0.00
		Park Density$_{t-0}$	-0.25	0.06	-4.00	**<0.001**	
		Male	6.60	0.40	16.66	**<0.001**	
		Age	5.79	0.25	23.04	**<0.001**	
		December	-2.94	2.15	-1.37	0.172	
		January	-5.99	1.12	-5.36	**<0.001**	
		February	-7.19	1.11	-6.49	**<0.001**	
		March	-9.51	1.35	-7.02	**<0.001**	
1	Park	(Intercept)	51.18	1.45	35.39	**<0.001**	15.33
		Park Density$_{t-1}$	-0.05	0.06	-0.74	0.461	
		Male	6.68	0.40	16.68	**<0.001**	
		Age	5.72	0.25	22.70	**<0.001**	
		December	-2.95	2.16	-1.36	0.173	
		January	-6.78	1.12	-6.03	**<0.001**	
		February	-7.68	1.13	-6.82	**<0.001**	
		March	-10.37	1.35	-7.71	**<0.001**	
2	Park	(Intercept)	49.13	1.55	31.76	**<0.001**	10.62
		Park Density$_{t-2}$	0.16	0.07	2.24	**0.025**	
		Male	6.70	0.40	16.81	**<0.001**	
		Age	5.75	0.25	22.83	**<0.001**	
		December	-2.95	2.16	-1.37	0.171	
		January	-7.04	1.09	-6.43	**<0.001**	
		February	-8.40	1.13	-7.46	**<0.001**	
		March	-11.00	1.36	-8.07	**<0.001**	
3	Park	(Intercept)	50.01	2.08	24.00	**<0.001**	15.01
		Park Density$_{t-3}$	0.04	0.09	0.50	0.617	
		Male	6.66	0.40	16.66	**<0.001**	
		Age	5.73	0.25	22.68	**<0.001**	

		December	-2.95	2.16	-1.37	0.172	
		January	-6.68	1.24	-5.40	**<0.001**	
		February	-7.58	1.23	-6.14	**<0.001**	
		March	-10.18	1.44	-7.08	**<0.001**	
0	Zone	(Intercept)	52.01	1.41	36.87	**<0.001**	9.22
		Zone Density$_{t-0}$	-0.12	0.04	-2.73	**0.007**	
		Male	6.67	0.40	16.78	**<0.001**	
		Age	5.72	0.25	22.73	**<0.001**	
		December	-2.90	2.16	-1.34	0.180	
		January	-6.53	1.10	-5.91	**<0.001**	
		February	-7.55	1.10	-6.84	**<0.001**	
		March	-10.16	1.34	-7.57	**<0.001**	
1	Zone	(Intercept)	50.61	1.42	35.53	**<0.001**	16.39
		Zone Density$_{t-1}$	0.02	0.04	0.44	0.660	
		Male	6.64	0.40	16.62	**<0.001**	
		Age	5.72	0.25	22.67	**<0.001**	
		December	-2.93	2.16	-1.36	0.175	
		January	-7.02	1.10	-6.36	**<0.001**	
		February	-7.91	1.11	-7.14	**<0.001**	
		March	-10.44	1.34	-7.78	**<0.001**	
2	Zone	(Intercept)	49.31	1.48	33.27	**<0.001**	9.43
		Zone Density$_{t-2}$	0.12	0.05	2.68	**0.008**	
		Male	6.68	0.40	16.80	**<0.001**	
		Age	5.74	0.25	22.82	**<0.001**	
		December	-2.93	2.16	-1.36	0.174	
		January	-6.83	1.09	-6.24	**<0.001**	
		February	-8.12	1.10	-7.37	**<0.001**	
		March	-10.66	1.34	-7.95	**<0.001**	
3	Zone	(Intercept)	48.29	1.64	29.43	**<0.001**	9.17
		Zone Density$_{t-3}$	0.12	0.05	2.71	**0.007**	
		Male	6.63	0.40	16.67	**<0.001**	
		Age	5.75	0.25	22.85	**<0.001**	
		December	-2.65	2.16	-1.23	0.220	
		January	-6.00	1.15	-5.23	**<0.001**	
		February	-6.84	1.16	-5.89	**<0.001**	
		March	-9.17	1.42	-6.47	**<0.001**	

APPENDIX C

Summary of the models of the effects of white-tailed deer densities at 4 time-lags and 2 spatial scales, sex, and month of removal on body weight (kg) for fawn white-tailed deer (age = 0.5 yr) in Cuyahoga Valley National Park, Ohio during 2016–2022. P-values in bold are significant at the 0.05 level.

Time lag (years)	Scale	Variable	B	se	t value	P	Delta AIC
0	Park	(Intercept)	37.34	1.37	27.22	**<0.001**	0.00
		Park Density$_{t-0}$	-0.21	0.06	-3.85	**<0.001**	
		Male	3.36	0.36	9.33	**<0.001**	
		December	3.58	2.00	1.79	0.075	
		January	-0.13	1.20	-0.11	0.915	
		February	-1.65	1.21	-1.37	0.172	
		March	-2.49	1.42	-1.76	0.078	
1	Park	(Intercept)	36.35	1.40	25.89	**<0.001**	11.50
		Park Density$_{t-1}$	-0.11	0.06	-1.69	0.092	
		Male	3.39	0.36	9.32	**<0.001**	
		December	3.57	2.02	1.76	0.078	
		January	-0.60	1.22	-0.49	0.624	
		February	-2.03	1.22	-1.66	0.098	
		March	-3.01	1.42	-2.12	**0.034**	
2	Park	(Intercept)	33.53	1.47	22.74	**<0.001**	6.34
		Park Density$_{t-2}$	0.19	0.07	2.82	**0.005**	
		Male	3.41	0.36	9.40	**<0.001**	
		December	3.51	2.01	1.74	0.082	
		January	-1.12	1.19	-0.94	0.346	
		February	-2.98	1.21	-2.45	**0.014**	
		March	-4.01	1.44	-2.78	**0.006**	
3	Park	(Intercept)	35.13	1.93	18.18	**<0.001**	13.88
		Park Density$_{t-3}$	0.02	0.08	0.21	0.830	
		Male	3.38	0.37	9.26	**<0.001**	
		December	3.52	2.03	1.74	0.083	
		January	-0.92	1.30	-0.70	0.482	
		February	-2.30	1.31	-1.75	0.080	
		March	-3.08	1.49	-2.07	**0.039**	

0	Zone	(Intercept)	35.95	1.36	26.42	**<0.001**	13.60
		Zone Density$_{t-0}$	-0.05	0.04	-1.32	0.187	
		Male	3.38	0.36	9.27	**<0.001**	
		December	3.56	2.02	1.76	0.079	
		January	-0.81	1.20	-0.67	0.504	
		February	-2.20	1.21	-1.81	0.071	
		March	-3.08	1.42	-2.17	**0.030**	
1	Zone	(Intercept)	35.29	1.39	25.35	**<0.001**	14.99
		Zone Density$_{t-1}$	0.01	0.04	0.29	0.770	
		Male	3.39	0.36	9.29	**<0.001**	
		December	3.54	2.03	1.75	0.081	
		January	-1.06	1.20	-0.89	0.376	
		February	-2.44	1.21	-2.02	**0.044**	
		March	-3.17	1.42	-2.24	**0.026**	
2	Zone	(Intercept)	34.45	1.43	24.01	**<0.001**	12.17
		Zone Density$_{t-2}$	0.08	0.05	1.69	0.091	
		Male	3.39	0.36	9.33	**<0.001**	
		December	3.57	2.02	1.77	0.078	
		January	-0.89	1.19	-0.74	0.458	
		February	-2.47	1.20	-2.06	**0.040**	
		March	-3.36	1.42	-2.36	**0.018**	
3	Zone	(Intercept)	33.45	1.55	21.56	**<0.001**	10.01
		Zone Density$_{t-3}$	0.10	0.04	2.28	**0.023**	
		Male	3.35	0.36	9.20	**<0.001**	
		December	4.08	2.03	2.01	**0.045**	
		January	-0.19	1.24	-0.15	0.880	
		February	-1.54	1.26	-1.22	0.223	
		March	-2.16	1.48	-1.45	0.147	

APPENDIX D

Model comparison for 4 time-lags and 2 spatial scales of pregnancy rate in Cuyahoga Valley National Park, Ohio during 2016–2022.The top model underwent backward elimination.

Model	K[a]	AICc[b]	Delta AICc[c]	AICcWt[d]	Cum.Wt[e]	LL[f]
Park Model T-3	7	400.72	0.00	1	1	-193.28
Park Model T-2	7	424.00	23.29	0	1	-204.92
Zone Model T-2	7	428.02	27.31	0	1	-206.93
Zone Model T-3	7	432.69	31.97	0	1	-209.27
Zone Model T-0	7	432.83	32.11	0	1	-209.34
Park Model T-0	7	435.29	34.58	0	1	-210.57
Park Model T-1	7	440.73	40.01	0	1	-213.29
Zone Model T-1	7	443.42	42.71	0	1	-214.64

[a]Number of parameters
[b]Corrected Akaike Information Criterion
[c]Change in Akaike Information Criterion from top model
[d]Corrected Akaike Information Criterion model weight
[e]Cumulative model weight
[f]Log-likelihood

APPENDIX E

Genera browse percentage across all plots in Cuyahoga Valley National Park, Ohio, during 2017, 2019, and 2021.

Genus	2017	2019	2021
Acer	0.19	0.07	0.06
Aesculus	0.12	0.04	0.01
Amelanchier	0.05	0.05	0.05
Asimina	0.00	0.00	NA
Betula	NA	NA	0.05
Carpinus/Ostrya	0.14	0.10	0.14
Carya	0.24	0.04	0.02
Cornus	0.39	0.19	0.30
Craetagus	0.31	0.22	0.19
Fagus	0.15	0.06	0.06
Fraxinus	0.11	0.01	0.01
Hamemelis	0.39	0.10	0.03
Juglans	NA	NA	0.00
Juniperus	0.22	NA	NA
Lindera	0.22	0.07	0.07
Liriodendron	0.04	0.05	0.02
Lonicera	NA	NA	0.06
Magnolia	0.00	0.00	0.17
Nyssa	0.80	1.00	0.14
Pinus	0.55	0.14	0.17
Platanus	0.50	NA	0.16
Populus	NA	NA	0.20
Prunus	0.33	0.15	0.09
Quercus	0.17	0.07	0.09
Ribies	0.71	0.03	0.12
Rosa	0.00	NA	NA
Rubus	0.63	0.39	0.20
Salix	NA	NA	0.00
Sassafras	0.62	0.35	0.14
Smilax	0.70	0.33	0.33

Tilia	0.00	0.00	NA
Toxicodendron	0.11	NA	NA
Ulmus	0.32	0.23	0.21
Vaccinium	0.43	0.28	0.21
Viburnum	0.29	0.16	0.14

VITA

Graduate School
Southern Illinois University Carbondale

Jacob J. Trowbridge

Jacobtrowbridge18@gmail.com

Michigan State University
Bachelor of Science, Fisheries and Wildlife – Wildlife Biology and Management, May 2020

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Major Professor: Clayton K. Nielsen