# Unveiling drivers of fecundity in an urban white-tailed deer population over 20 years of active management

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## Abstract (250 words max)

White-tailed deer (*Odocoileus virginianus*; hereafter "deer") are keystone herbivores that exert considerable ecosystem impacts. Quantifying drivers of urban deer demography, including fecundity (number of fetuses/doe), is paramount for understanding deer ecology and making management decisions, but this information is lacking for urban deer populations. In non-urban areas, doe age, population density, winter severity, and plant primary productivity influence fecundity. Increased forage availability in urban areas may dampen climatic effects on deer reproduction, but other threats and stressors might mitigate the positive effects of anthropogenic resources. We investigated how management, habitat, winter severity, and forage availability influenced deer pregnancy and fecundity using structural equation models using 20 years of data from a deer management program in a large urban park system. The proportion of pregnant fawns, yearlings, and adults were 0.16, 0.95, and 0.97, respectively, while fecundity (fetuses/doe) was 0.17, 1.59, and 1.88. Low fawn pregnancy rates and stable adult fecundity rates indicated a robust deer population. Age and body condition were the strongest predictors of fecundity. Unexpectedly, management, habitat (including urbanization), winter severity, and forage availability did not directly affect fecundity. Winter severity had a counterintuitive positive effect on adult deer body mass. Management affected yearling body masses: higher deer removal in the previous year was associated with increased current year removal and lower yearling body masses. Together, these results indicate that the environmental factors that commonly affect rural populations do not drive fecundity in this system, potentially reflecting unique characteristics of managed urban deer populations. .

## Acknowledgements

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## Introduction

Urbanization is globally expanding and impacting wildlife populations in numerous ways, both positively and negatively. For example, urbanization can provide novel habitats, alter wildlife activity patterns, and increase pathogen loads (Baker et al. 2003; Gallo et al. 2022; Albery et al. 2022). Recent work highlights how urbanization can also affect key demographic parameters such as reproductive success and fecundity, which has important implications for urban wildlife population dynamics (Shochat et al. 2006; Grimm et al. 2008). For instance, urbanization can increase survival and lead to higher annual recruitment and site fidelity for urban-adapted mammals such as raccoons (*Procyon lotor*; Prange et al. 2003). In contrast, densities of some species increase in urban areas without direct shifts in demographic or population parameters like reproductive rates or body condition, potentially due to behavioral changes or reduced competition leading to larger aggregations in urban areas (e.g., as in little brown bats, *Myotis lucifugus;* Coleman and Barclay 2011). Such examples notwithstanding, substantial knowledge gaps regarding the effects of urbanization on demographic parameters remain for many species, particularly wide-ranging mammals whose demographics can be challenging to study over long timescales (e.g., decades). Quantifying connections of this type would help clarify how such mammals adapt to urban environments and could inform management and conservation strategies (Adams and Lindsey 2010; Gehrt et al. 2010).

Assessing the factors driving patterns in ungulate demography is critical for successful population and ecosystem management. Ungulates are frequent research subjects because of their important role as game species and their substantial effects on vegetation communities and agricultural crops (Leopold et al. 1947; Waller and Alverson 1997; Côté et al. 2004; Seager et al. 2013; Readyhough et al. 2024). Much recent work on ungulates has also focused on their disease ecology (e.g., chronic wasting disease and COVID-19; Grear et al. 2006; Hale et al. 2022). One such species is white-tailed deer (*Odocoileus virginianus,* hereafter "deer"), which is a keystone herbivore due to the cascading ecosystem effects it triggers via vegetation browsing (Waller and Alverson 1997). Deer are now the most abundant ungulate in North America after populations increased prodigiously in the last half-century, with current continental population estimates of over 30 million (Murphy 2011). Several factors contributed to this population increase, including reforestation, changes in harvest regulations, and local extirpations of natural predators (Leopold et al. 1947; Waller and Alverson 1997; Hewitt 2011). Deer populations have also increased in urban areas over the last several decades (McAninch et al. 1993). Virtually absent in many urban areas of the Midwestern USA in the 1970s, deer now commonly reach problematically high densities in cities throughout the region (Conover et al. 1995; Bowman 2011). A combination of productive habitats, alternative forage in the form of landscape plantings, bird feeders, and direct feeding by the public, and restrictions on hunting within city limits contribute to these high densities (McAninch et al. 1993; Conover et al. 1995; Kilpatrick and Spohr 2000). Therefore, deer are not only an important urban-dwelling species ecologically, but also a key species in human-wildlife interactions and conflict (Bowman 2011). In urban habitats, deer can come into conflict by eating garden vegetation, being involved in vehicle collisions, and degrading natural landscape fragments through over-browsing (Conover et al. 1995; Côté et al. 2004; Bowman 2011). Accordingly, deer are often intensively managed in urbanized landscapes using various means, including managed and public hunts, targeted sharpshooting, and contraceptives (Hansen and Beringer 1997; Rudolph 1999; Kilpatrick et al. 2007; Howard et al. 2020).

Despite the widespread recognition that urban deer populations require targeted management and the common practice of intensively managing such populations (Roseberry and Woolf 1991), the factors influencing fecundity in urban herds are poorly understood. For example, we initiated this analysis by conducting a literature review in November 2023 using the Web of Science (WoS). Searching across all WoS databases with the search terms "Odocoileus virginianus" and "fecundity OR reproductive success" and "urban OR urbanization" yielded zero relevant studies. Filling this knowledge gap would aid in management decisions while revealing the degree to which urban deer ecology differs from that of their non-urban counterparts (Honda et al. 2018). A deeper understanding of such ecological differences would, in turn, support critical evaluations of the relevancy of traditional (i.e., non-urban) management strategies for urban herds. More broadly, despite an emerging body of literature situated in urban environments (Ebersole 2006; Denicola et al. 2008; Honda et al. 2018), research on urban deer demography is still in its infancy (cf. Etter et al. 2002; Bowman 2011).

Here, we investigated drivers of two important demographic parameters, pregnancy and fecundity (number of fetuses *in utero*; DelGiudice et al. 2007), among an actively managed, urban deer population inhabiting a large park system in a major metropolis in the midwestern USA. Overall, we expected that fecundity would be strongly affected by individual stage (fawn, yearling, adult) and body condition (represented by whole body mass). We hypothesized that higher deer body mass and older age would increase the probability of pregnancy and individual fecundity. We further hypothesized that these two driving factors in turn would be influenced by several covariates related to management, habitat, winter severity, and forage and that urbanization would act as a mediating factor for several of these relationships. Specifically, we used structural equation models to evaluate causal hypotheses related to deer pregnancy and fecundity using data collected from 3,986 female deer that were lethally removed during management activities over a 20-year period from 2000-2021 in Cleveland, Ohio, USA. We discuss the implications of our results for urban white-tailed deer ecology and the management of urban deer populations.

## Methods

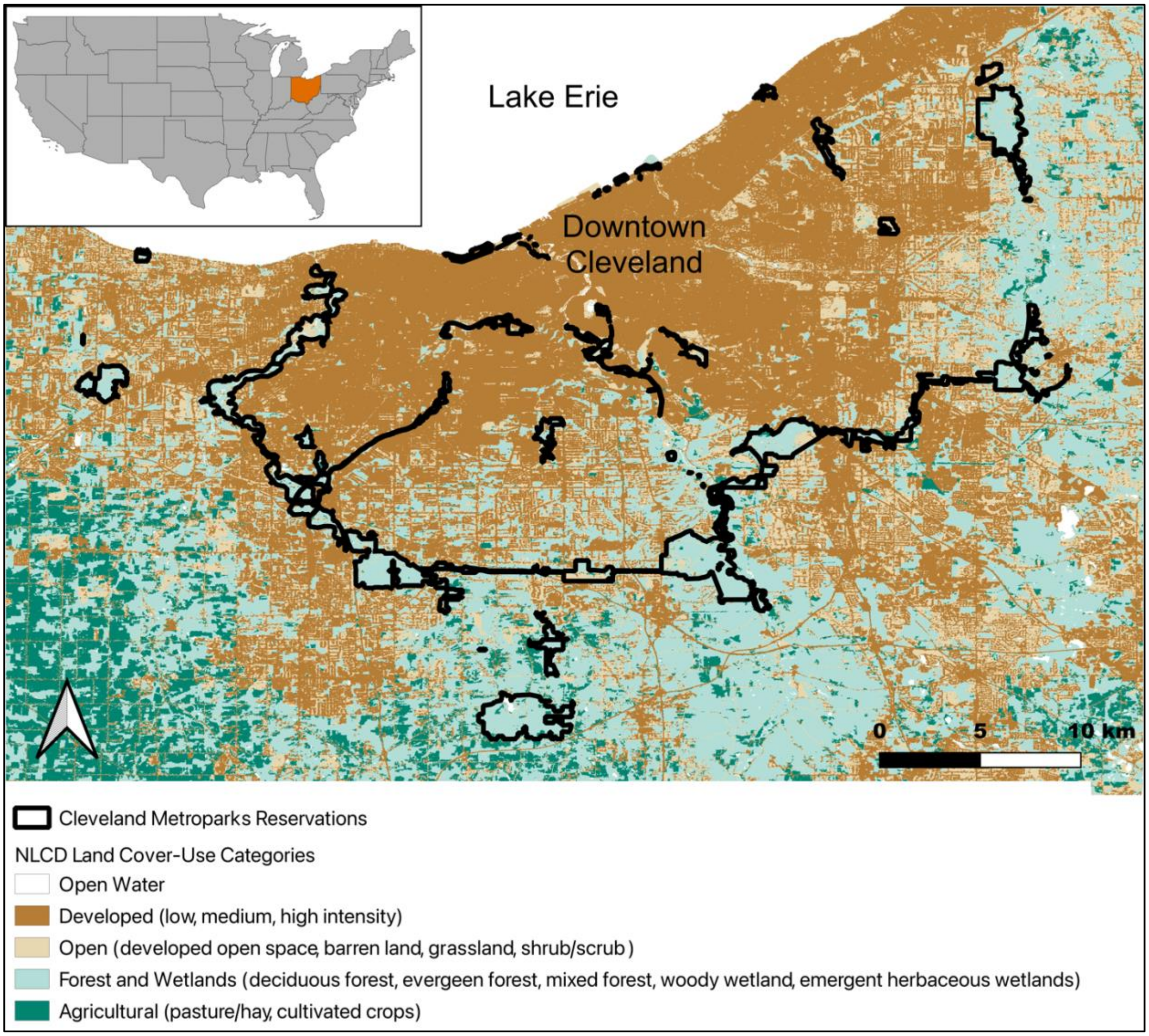

Figure 1. Cleveland Metroparks Reservations (black outlines) are a series of forested fragments surrounded by a gradient of urbanization and land covers in the Cleveland, OH, USA area. Inset: Ohio (orange) within the contiguous USA (grey).

*Study Area*

The Cleveland Metroparks system consists of more than 25,000 acres (10,117 ha) of green space throughout northeast Ohio, USA (Figure 1). This ecosystem includes 18 reservations within the greater Cleveland metropolitan area (population: c. 2 million; Cleveland Metroparks 2021). The reservations vary in size by nearly two orders of magnitude, ranging from 59 to 4,210 acres (23.9 - 1,703.7 ha). Levels of urbanization also vary strongly between reservations. For example, impervious surface ranges from 5.2% - 60.3% in reservations, with the most urban reservations near downtown Cleveland containing higher impervious surface area and lower urban tree canopy area (Hanou 2011). Urban tree canopy averages 71-77% across the reservations, but like impervious surface, tree canopy varies strongly across the reservations, ranging from 12.1% to 75% (Hanou 2011). The dominant forests of the region are beech/maple mixed hardwood and wet-mesic red maple forest (Hausman and Volk 2023). The most common tree species are sugar maple (*Acer saccharinum*) and red maple (*Acer rubrum*) with other common species including American beech (*Fagus grandifolia*), wild black cherry (*Prunus serotina*), green ash (*Fraxinus pennsylvanic*a) and Northern red oak (*Quercus rubra*; Hausman and Volk 2023). Reservations also include an interconnected series of streams, wetlands, meadows, golf courses, picnic areas, mixed-use trails, and waterfront recreational areas (Cleveland Metroparks 2021). Average winter (December-February) temperature is 35.0°F (standard deviation (sd) = 3.4°F; approximately 1.7°C; sd = 6°C) with an average of 54.0 inches (sd = 20.5in; approximately 137cm; sd = 52cm) of total snowfall for this three-month period (Cleveland Hopkins International Airport Weather Station 2023). Average summer (June-August) rainfall is 16.6 inches (sd = 4.0in; approximately 42cm; sd = 10cm; Cleveland Hopkins International Airport Weather Station 2023). In 2021, the Cleveland Metroparks recorded annual park use of 19,714,148 visits (Cleveland Metroparks 2021). Recreational hunting is not permitted in the Cleveland Metroparks and management activities vary among 49 neighboring municipalities from no deer management to various levels of hunting and/or sharpshooting efforts (J. Cepek pers. comm.).

### *Deer Management*

In 1998, Cleveland Metroparks began a deer management program in response to severe habitat degradation attributed to deer over-browsing in multiple reservations. Pilot management actions included the lethal removal of deer in 1998 and 1999, and an expanded deer management program began in 2000. Since that time, a team of trained sharpshooters have annually removed deer during winter (January-March) across reservations with an average take of 300 deer/year. Cleveland Metroparks has conducted deer management in 11 out of the 18 reservations due to staff access, observed impacts on understory vegetation, and the logistics of removing deer in an urban park system. Cleveland Metroparks submits a permit annually to the Ohio Division of Natural Resources Department of Wildlife for management activities in a subset of the reservations. Since 2000, Cleveland Metroparks has removed 9,249 deer. Park staff recorded the location, time, and date of all removed deer, and transferred deer to a Cleveland Metroparks processing facility. There, staff recorded the whole body mass, estimated age based on tooth development and wear (Severinghaus, 1949), sex, and fecundity (number of fetuses *in utero*) of each deer. To test our hypotheses, we used data on removal location, age, body mass, and pregnancy status of 3,986 individual female deer collected between 2000 and 2021 for which we had complete data (Table S1).

### *Modeling Framework and Hypotheses*

A conceptual diagram of the causal modeling framework is depicted in Figure 2. As noted above, we evaluated hypotheses regarding the effects of management, habitat, winter severity, and forage on deer pregnancy and fecundity as mediated through deer age, body mass, and urbanization (Figure 2). We hereafter use the general term fecundity to refer to both pregnancy rate (for fawns) and number of fetuses per doe (for yearlings and adults). We used deer life history stages (fawn, yearling, adult) rather than age as preliminary analyses suggested there were negligible differences between adult age classes with respect to body condition and fecundity, as has been detected in other populations (e.g., DelGiudice et al. 2007). For management effects, we hypothesized that as more deer were removed from a reservation, deer density would decrease, and the remaining deer would have higher nutritional condition (using body mass as an indicator of nutritional condition) and higher fecundity (Feldhamer et al. 1989; Keyser et al. 2005; Ebersole 2006). We therefore predicted that the previous year's deer removal would have a positive effect on deer body mass and fecundity during the current year and that the current year's deer removal would decrease when the previous year's deer removal was high in a reservation due to lower deer densities. The effort-controlled number of deer removed during the current season could vary due to a myriad of factors, including deer densities, deer attraction to bait sites, sharpshooter skill, and daily weather. Therefore, we expect that the factors captured by current removal may affect deer fecundity and body mass, but we could not predict the direction of these impacts. We operationalized the deer removal covariate as the average number of deer removed per hour of effort in each reservation (catch per unit effort). For habitat effects, we hypothesized that sites with more edge habitat or open vegetation would sustain higher densities of deer than sites with less edge or more forest cover (Stoll and Parker 1986; Beier and McCullough 1990; Ford et al. 1997). We also hypothesized that more urban sites would include anthropogenic resources (e.g., lawns, gardens, bird feeders) that would support higher deer densities compared to less urban sites (Swihart and DeNicola 1993; Grund et al. 2002). We used the National Land Cover Database (NLCD; temporal range 2001-2021), to develop covariates representing the proportion of a 1000 m buffer around each location that fell in an urban development category (categories 22- developed, low intensity, 23- developed, medium intensity, 24- developed, high intensity) and the proportion of the buffer area that was categorized as deciduous, mixed, or evergreen forest (categories 41- deciduous forest, 42- evergreen forest, 43- mixed forest; Dewitz 2021). NLCD uses a modified Anderson Land Cover Classification to assign 30m$^2$ pixels to 20 unique land cover classes (see Dewitz 2021 for detailed descriptions of each class). We chose the 1000 m buffer as the spatial scale for these covariates based on previous work in this system that indicated that deer responses to landscape covariates were strongest at the 1000m scale (Moll et al. 2020). Additionally, we used the *landscapemetrics* package (Hesselbarth et al. 2019) in R to calculate the edge density between land cover types within that 1000m buffer around each location (Table S3). For all land cover covariates, we used the NLCD dataset from time periods that aligned with the year of deer removal (see Table S4).

We hypothesized that more severe winters (i.e., colder temperatures, more days with snow on the ground, and larger snowstorms) would decrease food availability and increase stress on deer resulting in lower body masses and decreased fecundity (Morton and Cheatum 1946; Mech et al. 1987). We tested for lag effects, where previous severe winters ranging from 1 to 3 years prior would decrease deer fitness and fecundity in the current year, as lag effects have been significant in other studies (e.g., Mech et al. 1987; Feldhamer et al. 1989). We modeled winter severity using monthly weather data from the Cleveland Hopkins International Airport weather station due to its central location within the Cleveland metropolitan area (National Centers for Environmental Information 2023). We averaged data on winter temperature, snow accumulation, and days with >1 inch (2.54 cm) of snow on the ground from the preceding November-March period of each management season.

Finally, we hypothesized that forage availability would impact deer health, and therefore, fecundity (Morton and Cheatum 1946; Stoll and Parker 1986; Feldhamer et al. 1989; Wentworth et al. 1992; Ford et al. 1997). Specifically, we hypothesized that high acorn mast years would positively impact deer body mass and by extension, fecundity (Feldhamer et al. 1989; Wentworth et al. 1992; Ford et al. 1997). We also hypothesized that years with high growing season precipitation would increase forage availability, leading to increased body mass and fecundity (Morton and Cheatum 1946; Stoll and Parker 1986; Ford et al. 1997). We modeled acorn mast by compiling the state-wide proportion of oak (*Quercus* spp.) masting for each year preceding deer removal using data from the Ohio Department of Natural Resources Division of Wildlife (B. Plasters pers. comm.). We quantified growing season precipitation again using weather data from Cleveland Hopkins International Airport by averaging monthly precipitation from June-September of the year preceding the deer removal date (National Centers for Environmental Information 2023). We also considered 1- to 3-year lagged effects for these covariates. We only included data on deer removed after January 1st of each management season in our models to increase our confidence in accurately detecting fetuses as pregnancy can be difficult to detect early on. Since deer body condition declines throughout the winter (Mautz 1978; Nicholson et al. 2008; Parker et al. 2009), we included Julian date of deer collection as a covariate in our body mass models. Finally, we included time (year) and reservation as random effects in our models to control for spatial and temporal variation not captured by our other covariates.

### *Model implementation*

We used R and RStudio for all data analyses (R version 4.2.3, R Core Team 2023, RStudio version 2023.03.0+386, RStudio Team 2023). To understand relationships between management, habitat, winter severity, and forage covariates and female deer fecundity, we fit piecewise structural equation models (SEM) using the *piecewiseSEM* package (Lefcheck 2016).

SEMs are designed specifically to facilitate casual inference between covariates due to their explicit modeling framework that quantifies both direct and indirect effects, which correspond to the hypotheses described above (Grace et al. 2010; Lefcheck 2016). Preliminary analyses indicated that fawns had low pregnancy rates and rarely carried more than one fetus, so we used a binary variable (1 = pregnant, 0 = not pregnant) as our response variable in the fawn SEM and modeled relationships assuming a Bernoulli distribution. Since yearlings and adults were almost always pregnant, we used fetuses/doe as the response variable in the yearling and adult SEMs and modeled relationships assuming a Poisson distribution. As noted above, we refer to both demographic parameters as fecundity but make distinctions in interpreting our results as necessary to relate our findings to other work.

Prior to modeling we tested for collinearity using the *cor.test* function in base R to calculate Pearson's product moment correlation between covariates. Forest cover and urbanization were highly correlated with each other (Pearson's r = -0.9; highly correlated per Dormann et al. 2013). Thus, we excluded forest from our models under the assumption that as urbanization increased, forest cover decreased. Additionally, the winter covariates (winter temperature, snow accumulation, days with snow depth >1 inch) were highly correlated with each other (all r > 0.7; Dormann et al. 2013). As we were interested in testing specific causal relationships, we used the strongest of these predictors based on effect size and explanatory power ($R^2$), winter temperature, in all subsequent models. No other pairs of covariates were significantly correlated (all r < 0.5; Dormann et al. 2013). We compared competing SEMs that included lag effects (1-, 2-, or 3-years preceding deer removal) for winter temperature, acorn masting, growing season precipitation, and deer removal using Fisher's C, Chi-square goodness-of-fit tests, $R^2$ values, and $\Delta$AIC, as recommended for piecewise SEMs that include generalized linear models (Lefcheck 2021). We selected a final model that had the best fit and highest explanatory power based on these metrics (Lefcheck 2021). Our final models included a 1-year lag effect for winter temperature, growing season precipitation, and deer removal, but 2- or 3-year lag effects were not significant and did not improve model fit, and thus were not included in our final models (Tables S5-7). Covariates included in our final models incorporated the results of tests of directed separation (dSep tests) which indicated additional significant pathways between environmental covariates (current and previous year: winter temperature, growing season precipitation, and acorn mast) and the Deer Removal response variable (Tables S5-S7). We also included Julian day in the fawn pregnancy sub-model and in the yearling and adult Deer Removal sub-models based on dSep test results (Tables S5-S7). We calculated Standardized Path Coefficients, which allow for comparison between paths within the same SEM, by scaling model coefficients using the ratio of the variance of the predicted values to the variance of the observed values following the observation-empirical approach as described by (Lefcheck 2021). We considered effects to be statistically significant using a cutoff of $p < 0.05$.

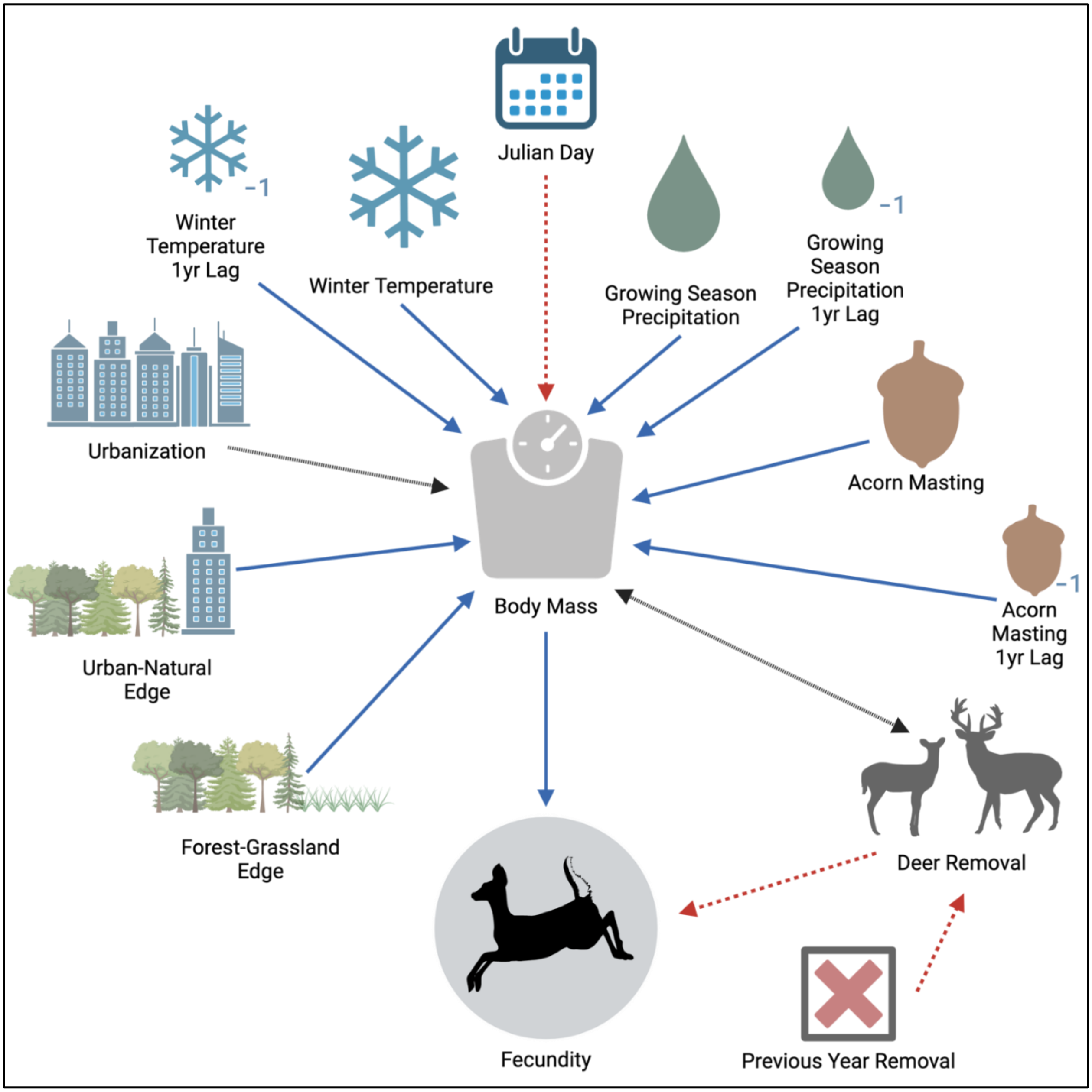

Figure 2. Conceptual diagram of expected causal relationships between white-tailed deer body mass, fecundity, and biotic and abiotic covariates. Solid, blue arrows indicate an expected positive effect, dashed, red arrows indicate an expected negative effect, and dotted, black arrows indicate an expected effect for which there is conflicting evidence. Pathways from environmental covariates to the Deer Removal response variable are excluded from this diagram for clarity. Diagram created with BioRender (biorender.com) and white-tailed deer silhouettes created by Gabriela Palomo-Munoz and made available via PhyloPic (phylopic.org).

## Results

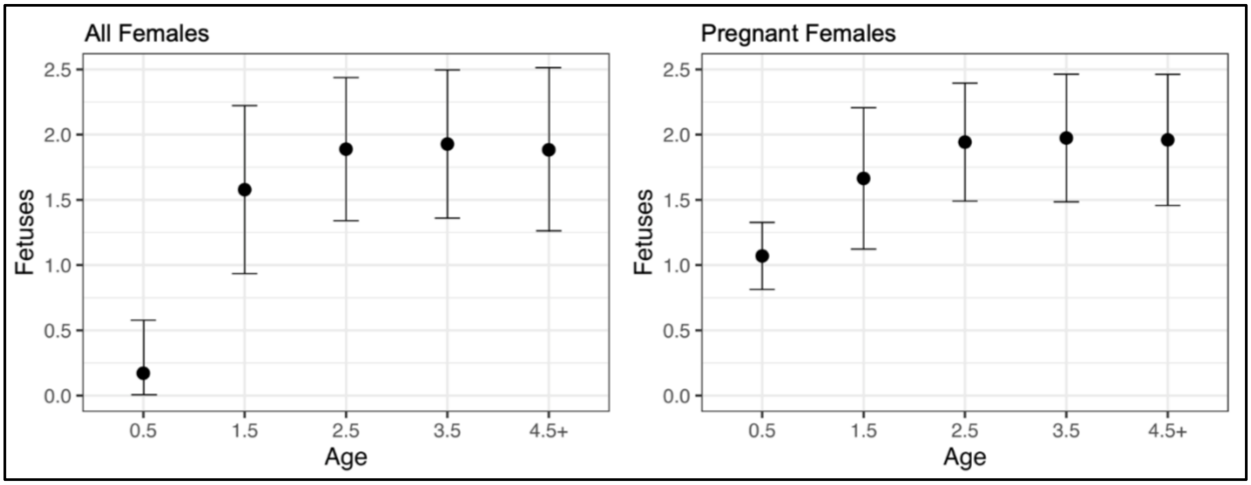

Figure 3. Average number of fetuses *in utero* by age for all female white-tailed deer (left) and for only pregnant does (right). Fawns were 0.5 years old, yearlings were 1.5 years old, and all other ages were classified as adults. Results based upon a dataset of removed female deer between 2000 and 2021 in Cleveland, Ohio, USA.

Fecundity varied significantly with deer stage ($p < 0.01$; Figure 3; Table S1). Fawns were pregnant less often than yearlings or adults; only 16% of fawns were pregnant while 95% of yearlings and 97% of adults were pregnant. Fawn fecundity rate across all individuals (i.e., including fawns that were not pregnant) was 0.17 fetuses/doe (95% Confidence Interval [CI]: 0-0.97; Figure 3). Pregnant fawns carried an average of 1.08 fetuses/doe (95% CI: 0.54 - 1.62; Figure 3). Yearlings and adults had pregnancy rates near 1.0 (yearlings = 0.95; adults = 0.97; Figure 3). Yearlings carried an average of 1.59 fetuses/doe (95% CI: 0.35 - 2.83) while adults averaged 1.88 fetuses/doe (95% CI: 0.75 - 3.00; Figure 3). The average body mass of fawns was 78.4 lbs (95% CI: 57.2 - 99.5 lbs; 35.6 kg; 95% CI: 25.9 - 45.1 kg), yearlings 120.6 lbs (95% CI: 93.1 - 148.1; 54.7 kg; 95% CI: 42.2 - 67.2 kg), and adults 135.8 lbs (95% CI: 106.3 - 165.3; 61.6 kg; 95% CI: 48.2 - 75.0 kg; also see Table S1).

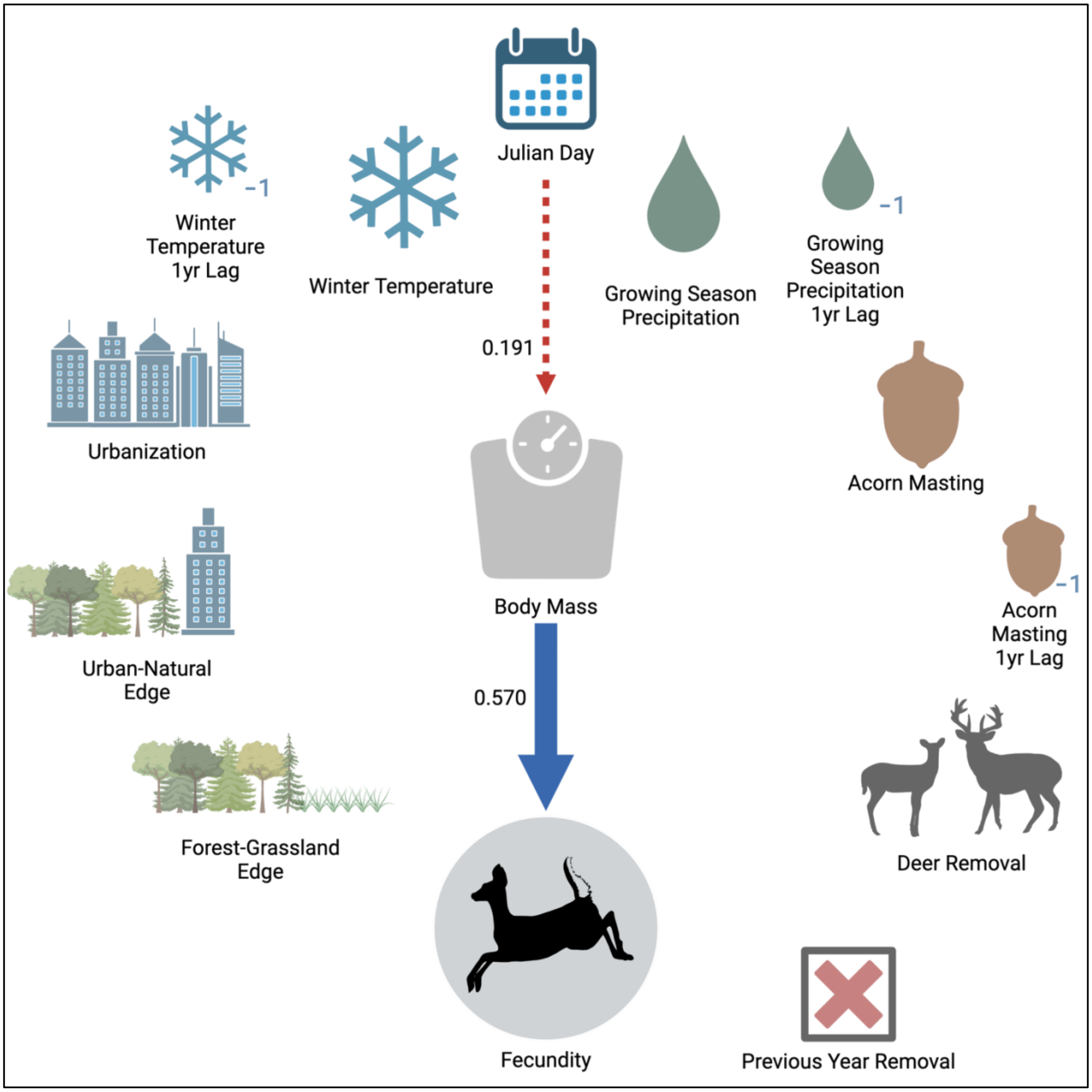

Figure 4. Fawn structural equation model results based upon a dataset of removed female white-tailed deer between 2000 and 2021 in Cleveland, Ohio, USA. Blue and red dashed arrows indicate significant positive and negative effects, respectively. Numbers next to each arrow indicate the Standardized Path Coefficient. Pathways from environmental covariates to the Deer Removal response variable are excluded from this diagram for clarity. Diagram created with BioRender (biorender.com) and white-tailed deer silhouettes created by Gabriela Palomo-Munoz and made available via PhyloPic (phylopic.org).

*Fawns*

Deer body mass and Julian day were significant predictors of pregnancy in fawns, with larger fawns more likely to be pregnant (Standardized Path Coefficient = 0.570; $p < 0.001$; Figure 4; Figure 5a; Table S5) and fawns removed later in the year more likely to be pregnant (Standardized Path Coefficient = 0.191; $p=0.011$; Figure 4; Figure 5b; Table S5). No management, habitat, winter severity, or forage covariates significantly affected fawn body mass (Figure 4; Table S5).

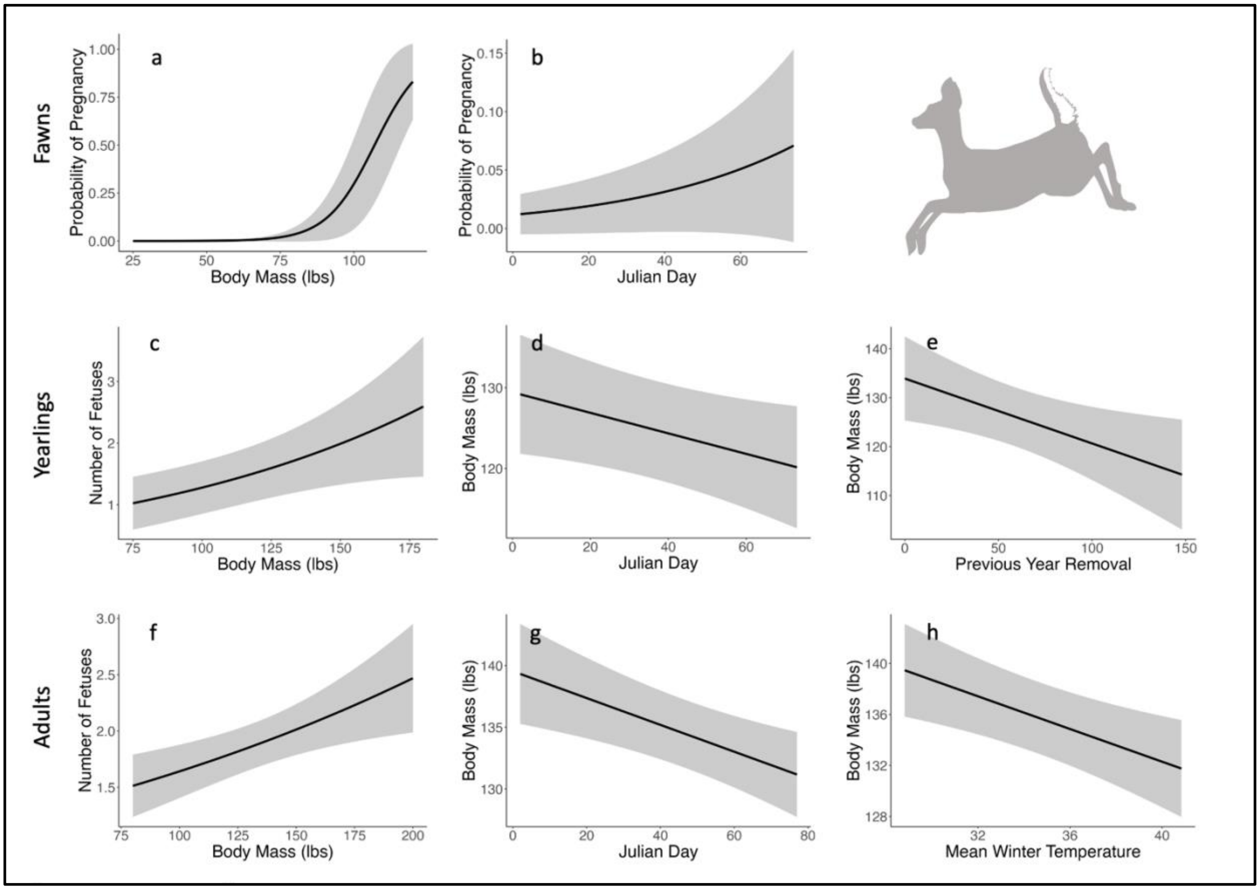

Figure 5. Significant effects of model covariates from structural equation models based upon a dataset of removed female white-tailed deer between 2000 and 2021 in Cleveland, Ohio, USA. White-tailed deer silhouette created by Gabriela Palomo-Munoz and made available via PhyloPic (phylopic.org).

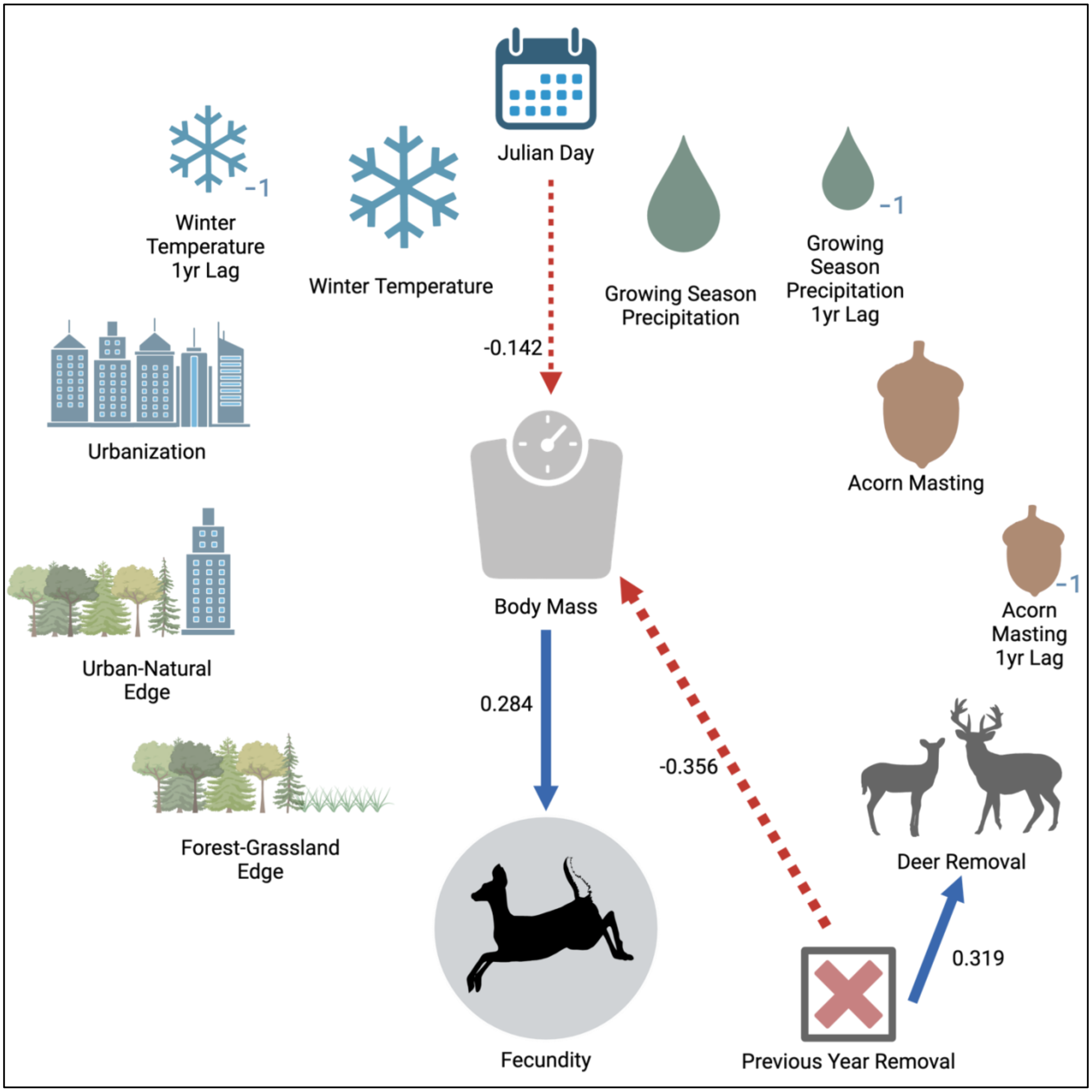

Figure 6. Yearling structural equation model results based upon a dataset of removed female deer between 2000 and 2021 in Cleveland, Ohio, USA. Blue and red dashed arrows indicate significant positive and negative effects, respectively. Numbers next to each arrow indicate the standardized path coefficient, which allows for comparison between paths within the same structural equation model. Pathways from environmental covariates to the Deer Removal response variable are excluded from this diagram for clarity. Diagram created with BioRender (biorender.com) and white-tailed deer silhouettes created by Gabriela Palomo-Munoz and made available via PhyloPic (phylopic.org).

*Yearlings*

We found that deer body mass significantly predicted the fecundity of yearlings (Standardized Path Coefficient = 0.284; p = 0.003; Figure 6; Figure 5c; Table S6). Higher removal in the previous year and later Julian day of removal significantly decreased yearling body mass (previous year removal Standardized Path Coefficient = -0.356; p = 0.014; Julian day Standardized Path Coefficient = -0.142; p=0.041; Figure 5d; Figure 5e; Figure 6; Table S6). Higher removal in the previous year also significantly increased current year removal within a reservation (Standardized Path Coefficient = 0.319; p < 0.001; Table S6), but this did not significantly impact yearling body mass or fecundity (Figure 6; Table S6). Contrary to our predictions, no other management, habitat, winter severity, or forage covariates in our model significantly affected yearling body mass or fecundity (Figure 6; Table S6).

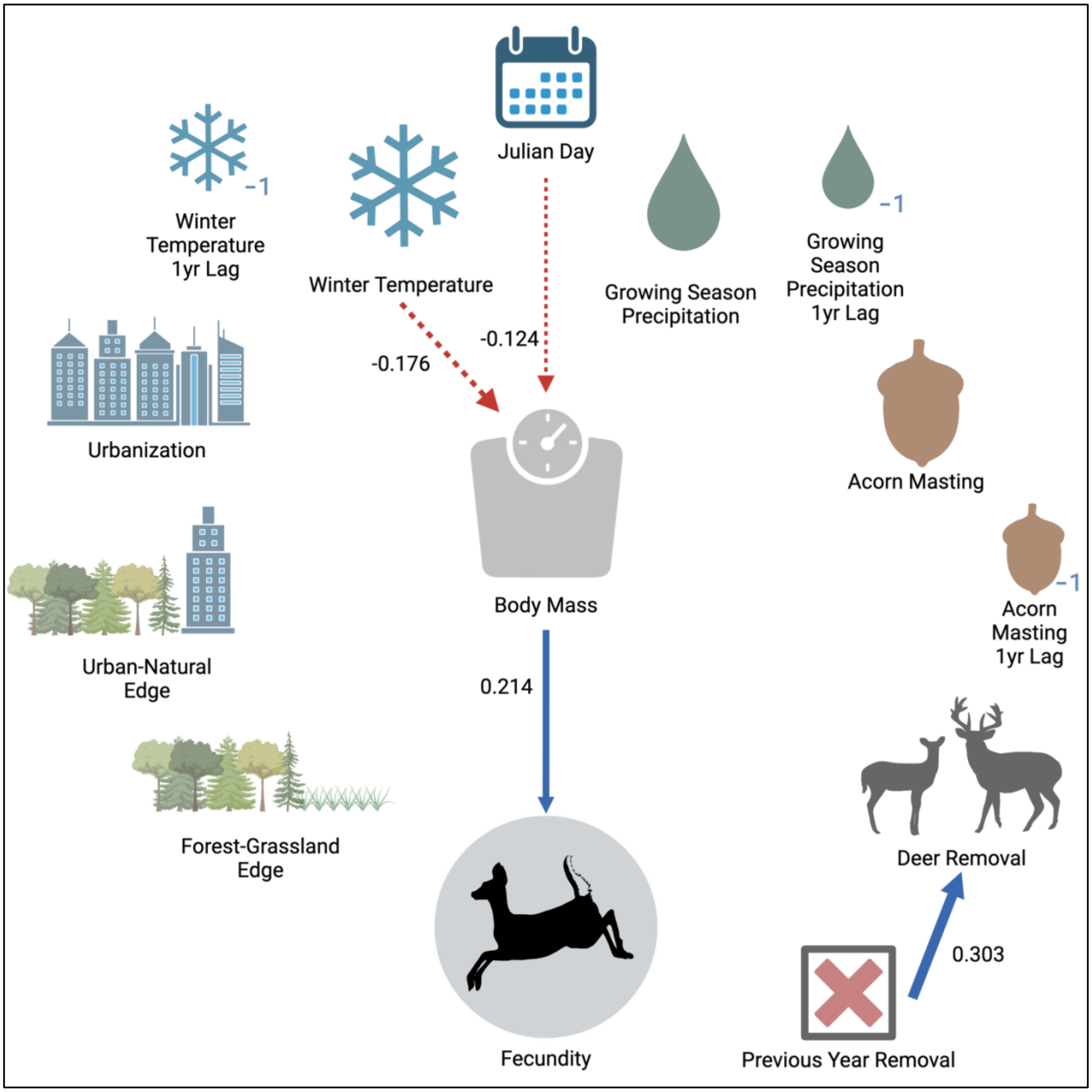

Figure 7. Adult structural equation model results based upon a dataset of removed female deer between 2000 and 2021 in Cleveland, Ohio, USA. Blue and red dashed arrows indicate significant positive and negative effects, respectively. Numbers next to each arrow indicate the standardized path coefficient, which allows for comparison between paths within the same structural equation model. Pathways from environmental covariates to the Deer Removal response variable are excluded from this diagram for clarity. Diagram created with BioRender (biorender.com) and white-tailed deer silhouettes created by Gabriela Palomo-Munoz and made available via PhyloPic (phylopic.org).

*Adults*

Higher body mass increased adult fecundity (Standardized Path Coefficient = 0.214; p = 0.002; Figure 5f; Figure 7; Table S7). Like yearlings, Julian day negatively affected adult body mass; adults removed later in the winter had lower body masses (Standardized Path Coefficient = -0.124; p=0.002; Figure 5g; Figure 7; Table S7). Unlike fawns and yearlings, adult body mass was significantly affected by winter severity. Contrary to our predictions, warmer winters corresponded with lower adult doe body masses (Standardized Path Coefficient = -0.176; p = 0.002; Figure 5h; Figure 7; Table S7). No other management, habitat, winter severity, or forage covariates directly affected adult fecundity or body mass (Figure 7; Table S7). Higher deer removal in the previous year increased current year deer removal, but that removal did not affect adult body mass or fecundity (Standardized Path Coefficient = 0.303; p<0.001; Figure 7; Table S7).

## Discussion

Using a dataset of 3,986 female deer removed over a 20-year period in a large urban park system, we found that deer fecundity was almost completely decoupled from environmental drivers (including winter severity, growing season precipitation, and acorn mast) that have high predictive power in areas of lower human impact (i.e., natural and rural areas; Morton and Cheatum 1946; Verme 1969; Stoll and Parker 1986; Mech et al. 1987; Feldhamer et al. 1989; Wentworth et al. 1992; Ford et al. 1997; Patterson and Power 2002). Specifically, we found that urban deer fecundity was not directly impacted by management, habitat, forage, or winter severity. We also surprisingly found that urbanization failed to affect fecundity directly or via an indirect pathway mediated by body mass. Instead, we found that fecundity was strongly determined by doe stage and body mass, with larger and older individuals more likely to be pregnant and carrying more offspring (Figures 3-7). Overall, these patterns are suggestive that a carefully planned and consistent urban deer management program over many years may promote stable demographic rates and that in such a herd, the level of urbanization has little or no effect on fecundity or body mass.

Studies on urban mammals often highlight differences in body masses, densities, and stressors between urban and rural populations (Hoffmann and Gottschang 1977; Riley et al. 1998; Wright et al. 2012). Urban deer populations frequently reach higher densities than populations in other habitats (McAninch et al. 1993; Conover et al. 1995; Bowman 2011). Access to food resources in urban areas (e.g.: garden plantings, bird feeders, and direct supplemental feeding) can increase deer fecundity by elevating nutritional levels and contribute to overabundance (Nielsen and Porter 2011). High deer densities can in turn lead to increased nutritional stress and competition resulting in lower deer body masses (McCullough 1985; Ashley et al. 1998; Keyser et al. 2005). Urban deer tend to have higher hair cortisol concentrations than rural populations (Potratz et al. 2019) and may be at higher risk for hosting parasites (Ballash et al. 2019). Together, this myriad of interacting factors suggests uncertain influences of urbanization on deer population health and density. In our study, habitat (including urbanization and urban-natural edge) did not drive differences in deer body mass or fecundity across an urban gradient (Figures 4-7). Individuals in highly urban locations were indistinguishable from deer in reservations bordered by more contiguous forests or rural reservations adjacent to more agricultural land, and there were no differences in fecundity across these habitat gradients. More broadly, within the context of other findings, our results suggest continued management to reduce or maintain local deer densities can help achieve management objectives such as the reduction of vegetation damage due to over-browsing, which was a motivating factor at the inception of this deer management program.

In this study, fawn, yearling, and adult fetus counts averaged 0.17 (1.08 for pregnant fawns), 1.59, and 1.88 fetuses/doe, respectively. These fecundity rates are lower than statewide fecundity estimates from Ohio from 1951-1967 (pregnant fawns: 1.29, yearlings: 1.87, adults: 2.01) when deer densities were much lower than today (Nixon 1971). Current fecundity is also lower than estimates for deer from farmland regions during 1981-1983 when Ohio deer populations were rapidly growing (fawns: 0.85, yearlings: 1.96, adults: 1.91; Stoll and Parker 1986). In contrast, our fecundity rates were higher than those reported in nearby Sandusky, Ohio in the 1960s in an area with an enclosed, problematically high-density herd (fawns: 0, yearlings: 1.29, adults: 1.82; Harder and Peterle 1974). Therefore, current fecundity rates across life-stages are suggestive of a population that is not over carrying capacity and is not experiencing a reduction in reproductive output due to crowding throughout the Cleveland Metroparks (see DeNicola et al. 2008 for additional comparison data). These rates also imply the necessity of continued management efforts by Cleveland Metroparks and surrounding municipalities to avoid population sizes approaching carrying capacity.

Contrary to our predictions, warmer winters correlated with a significant decrease in adult deer body mass. People engage in direct supplemental feeding more often when winter weather conditions are perceived as severe (Thompson et al. 2008). Urban residents sometimes spread high calorie foods (e.g. corn) for deer during periods of severe weather out of perceived concern for animal welfare (Thompson et al. 2008). These practices could result in increased deer body mass due to increased caloric intake despite more severe winter weather conditions (Tarr and Pekins 2002). Despite these perceived benefits, wildlife management agencies generally discourage supplemental feeding due to the potential negative impacts including deer habituation to humans, increased competition, and potential for disease transmission when deer occur at high densities around feeding sites (Ozoga and Verme 1982; Tarr and Pekins 2002; Thompson et al. 2008). Additionally, in warmer winters with less snow accumulation, urban deer in our study system may also have more access to grass lawns and golf courses as a food source as these areas are not always covered in snow (E. Shaffer pers. comm.). However, deer do not digest grass efficiently compared with forage from woody browse plants and a diet high in grass may actually decrease deer fitness in the current season (Gray and Servello 1995). It is possible that during warmer winters, the deer in our study were provided with less supplemental food by the public and had access to more grasses due to reduced snow cover, leading to a lower nutritional plane during warmer winters.

In our yearling and adult models, management activity during the previous year affected the current year’s deer removal within each reservation, but these changes in removal did not directly affect fecundity. The previous year's removal significantly increased current removal in both the yearling and adult deer models (Figures 5-7) but were not significant in our fawn model (Figure 4). This difference could have been driven by one reservation where no fawns were removed, meaning it was not included in our fawn model but was included in the yearling and adult models (Table S1). There are various mechanisms that could drive the positive relationship between current deer removal and higher removal during the previous year, including immigration from surrounding populations, increased habituation to bait sites for animals that were not removed, and/or lower avoidance or fear of management activities due to a naïve deer population (Kilpatrick and Spohr 2000; Grund et al. 2002; Little et al. 2016; Schuttler et al. 2017). Management activities vary in the communities surrounding the Cleveland Metroparks, with some municipalities actively managing deer with sharpshooter programs or allowing public hunts, while others do not manage deer populations (J. Cepek pers. comm.). Deer from surrounding areas with higher population densities (especially communities that do not manage deer populations) could therefore immigrate into the Cleveland Metroparks as local deer abundances decrease due to management activities. More practically, areas with observed higher deer activity were sometimes targeted with greater removal across years, meaning that this association could have resulted from strategic management decision-making rather than from ecological mechanisms. Untangling the details of these patterns requires further research with more specific techniques such as population-level genetic analyses and/or GPS tracking.

Interestingly, deer body masses were not affected by current deer removal but yearling body masses decreased with higher removal during the previous management season (Figure 5e; Figure 6). Higher previous year's removal in a reservation might indicate higher deer densities during the previous year, which could negatively impact yearling body masses due to increased competition during the year when they were fawns. Results from other studies of suburban and urban deer similarly indicate that higher deer densities can decrease nutritional condition and fecundity (Swihart and DeNicola 1993; Keyser et al. 2005; Bowman 2011). Our results suggest that urban deer populations in the Cleveland region are not resource-limited, but that higher densities during an animal's first year may have impacts on body condition into the subsequent year. As expected, yearling and adult body masses declined through the winter, likely because access to browse decreased and fat reserves were depleted (Figure 5d; Figure 5g; Figure 6; Figure 7; Mautz 1978; Nicholson et al. 2008; Parker et al. 2009). Unexpectedly, fawn body masses did not significantly change with Julian day (Figure 4; Table S5). It is possible that fawns have less fat in reserve than adults (Nordan et al. 1970; Moen 1976), resulting in a lesspronounced change in body mass over the season. Alternatively, fawns may lose their body fat more quickly than adults (Nordan et al. 1970; Moen 1976). If fawns lose body mass early in the winter, a linear relationship with Julian day is less likely. In contrast to our results, Taillon et al., (2006) found that fawn body masses progressively declined over winter in Quebec, Canada. Winters in Quebec are harsher than in our study system (Ohio, USA) and active management likely maintains the population in our study below carrying capacity. Therefore, the fawns in our study may not experience intense competition for resources, may have access to adequate forage (even during winter), may benefit from supplemental food sources in the urban environment (e.g., garden plantings, bird feeders, or direct supplemental feeding), or may not be breeding and thus conserving more resources during fall than adults. Future work on fawn winter body condition in urban environments could bring clarity to this issue.

None of the other covariates in our models had strong direct effects on deer fecundity, and few covariates affected deer body masses (Figures 4-7). In many widespread ungulate species, adult fecundity is robust to annual variation in environmental conditions (Gaillard et al. 2000; Eberhardt 2002; Bonenfant et al. 2009). It is possible that variation in winter severity in this region is not extreme enough to cross the threshold at which winter would impact adult deer fecundity (as in Campbell and Wood 2013). Many of the studies on the impacts of winter severity on deer occur at higher latitudes than this study, where winter weather can be much more severe (e.g., Verme 1969; Mech et al. 1987; Patterson and Power 2002). Forage availability has been shown to impact fecundity in some rural deer populations. Wentworth et al. (1992) found that deer populations in southern Appalachia were strongly, positively influenced by increased acorn availability. Similarly, in rural deer populations in Tennessee, high acorn yields increased deer body mass and spring deer densities (Feldhamer et al. 1989). It is possible that growing season precipitation is not an appropriate proxy for primary productivity in this region, especially if the system is not water limited and is impacted by decreased sunshine during wetter years (Mohamed et al. 2004; Fang et al. 2005; Zhang et al. 2009) or due to the high landscape heterogeneity (Wang et al. 2006, 2009) throughout the Cleveland Metropolitan area. Additionally, we did not have data on beech (*Fagus grandifolia*) mast to include in our models, and it is possible that beech mast is an important food source in this system. Beech mast is influential for small mammals (Zwolak et al. 2016) but is not frequently included in studies on deer (see Ryan et al. 2004 for an exception that included beech mast). We found no significant impact of our measures of forage availability (growing season precipitation and acorn masting) or winter severity (winter temperature) on deer fecundity, indicating that the fecundity of the deer population in this study is unrelated to environmental variation, potentially because overall forage availability could have effects that were not adequately captured by growing season precipitation or acorn masting.

Like many other urban-dwelling wildlife species, white-tailed deer living in developed systems present unique management challenges while potentially having large impacts on local ecosystem characteristics such as vegetative health. Our findings suggest that fecundity in urban deer populations under active management is likely not driven by the environmental factors that commonly affect rural populations. Therefore, stable fecundity rates are expected in such systems, perhaps because populations do not exceed carrying capacity. The results from this study fill an important knowledge gap regarding urban deer fecundity across an urban gradient by revealing that a consistently managed herd can exhibit strong and stable reproductive rates while experiencing few environmental or urban-related limiting factors. Given that urban deer management is a relatively young discipline (McAninch et al. 1993; Bowman 2011), this work can help shape management approaches to urban deer herds aimed at simultaneously minimizing the deleterious effects of deer overabundance while supporting individual animal health in free-living populations. In cities, alternative forage availability and reduced impacts of winter severity (e.g., higher temperatures due to urban heat islands or snow removal allowing for increased winter movement) may dampen the effects of environmental drivers on deer fecundity, but an active management program is likely the primary factor in maintaining an urban deer population with consistent fecundity. More broadly, our results emphasize how certain forms of human influence (e.g., active management to maintain a population below carrying capacity) may overpower others (e.g., urban development, winter severity, and forage availability), emphasizing the crucial role of management programs in urban contexts.

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## Supplemental Information

Table S1: Summary of female fecundity from a dataset of female deer removed between 2000 and 2021 in Cleveland, Ohio, USA.

| | | | **Fawns** | | **Yearlings** | | **Adults** | |
|---|---|---|---|---|---|---|---|---|
| **Reservation** | **Years With Deer Removal** | **Total Female Deer Removed** | **Average Body Mass (lbs)** | **Average Fecundity (fetuses/ doe)** | **Average Body Mass (lbs)** | **Average Fecundity (fetuses/ doe)** | **Average Body Mass (lbs)** | **Average Fecundity (fetuses/ doe)** |
| BC | 1 | 8 | NA | NA | 98.3 | 1.0 | 128.0 | 1.8 |
| BE | 19 | 611 | 77.3 | 0.1 | 120.5 | 1.6 | 135.8 | 1.9 |
| BR | 20 | 391 | 77.0 | 0.1 | 114.4 | 1.4 | 132.0 | 1.88 |
| BW | 19 | 363 | 78.9 | 0.3 | 124.7 | 1.8 | 141.2 | 2.0 |
| HI | 17 | 207 | 79.4 | 0.2 | 120.7 | 1.7 | 135.6 | 2.03 |
| HU | 2 | 16 | 76.3 | 0.3 | 125.0 | 2.0 | 161.7 | 2.67 |
| MS | 21 | 1124 | 78.1 | 0.1 | 121.1 | 1.5 | 134.6 | 1.83 |
| NC | 19 | 363 | 78.7 | 0.2 | 120.1 | 1.6 | 136.4 | 1.93 |
| RR | 19 | 618 | 80.2 | 0.3 | 120.6 | 1.7 | 137.8 | 1.96 |
| SC | 14 | 83 | 81.2 | 0.4 | 129.1 | 1.7 | 138.4 | 1.91 |
| WC | 9 | 202 | 76.9 | 0.1 | 118.4 | 1.3 | 132.4 | 1.71 |

Table S2: Descriptions, rationales, and supporting references for expected relationships depicted in Figure 1 regarding white-tailed deer demography in the Cleveland Metroparks, Cleveland, Ohio, USA.

| **Expected relationship** | **Rationale** | **References** |
|---|---|---|

| | | |
|---|---|---|
| Positive effects of body mass on fecundity | Larger does with higher nutritional condition, especially fawns and yearlings, tend to have higher pregnancy rates and more offspring | (Verme 1969, DelGiudice et al. 2007, DeYoung 2011) |
| Negative effects of deer removal (as a proxy for deer densities) on fecundity | Higher local deer densities can increase competition leading to decreased body mass and fecundity, especially of fawns | (Kie and Bowyer 1999, Keyser et al. 2005, Patterson and Power 2002) |
| Negative effects of previous removal on current-year deer removal | Higher removal in the previous year could decrease local deer populations or decrease local densities as deer avoid hunting pressure | (Kie and Bowyer 1999, Little et al. 2016, Patterson and Power 2002) |
| Positive effects of winter temperatures on body condition | More severe winters can limit movement and foraging, while warmer winters allow for increased movement and foraging | (Morton and Cheatum 1946, Mech et al. 1987) |
| Positive effects of forage quantity or quality (measured with growing season precipitation and acorn masting) on body mass | Increased quantity or quality of forage linked to increased weight gain in summer/fall | (Morton and Cheatum 1946, Stoll and Parker 1986, Feldhamer et al. 1989, Wentworth et al. 1992, Ford et al. 1997) |
| Uncertain effects of urbanization on body mass | Local densities tend to be higher in more fragmented urban areas which could lead to lower body masses; Resource provisioning from urban/suburban areas might increase food availability | (Hansen and Beringer 1997, Bowman 2011) |
| Positive effects of edge habitats (forest-grassland or urban-natural edges) on body mass | Edge habitats are associated with greater forage availability and higher deer densities | (Ford et al. 1997, Kie and Bowyer 1999, Kilpatrick and Spohr 2000) |
| Positive effects of forest-grassland edge on deer removal | Forest edges are associated with increased deer densities and edge habitat can increase removal success for sharpshooters | (Hansen and Beringer 1997, Little et al. 2016, Kie and Bowyer 1999, Kilpatrick and Spohr 2000) |
| Potential significance of 1 – 3yr lag effects for forage availability and winter severity | Current deer fecundity and populations may reflect 1-3yr lags in forage availability or winter stressors | (Campbell and Wood, 2013) |

Table S3: Covariates considered in Structural Equation Models of deer fecundity using a dataset of removed female deer between 2000 and 2021 in Cleveland, Ohio, USA.

| **Covariate** | **Description** | **Data source** |
|---|---|---|
| Urbanization | 22-low, 23-medium, and 24-high development land use at 30 m resolution | NLCD; multiple years |
| Forest | 41-deciduous, 42-evergreen, and 43-mixed forest land use at 30 m resolution | NLCD; multiple years |
| Urban-natural edge | Calculated edge density between urban (21-open, 22-low, 23-medium, and 24-high development) and natural (forest, scrub/shrub, woody wetland, and grassland) land cover types within a 1000m buffer | NLCD; multiple years; *landscapemetrics* |
| Forest-grassland/shrubland edge | Calculated edge density between forest (41-deciduous, 42-evergreen, and 43-mixed) and grassland (52-scrub/shrub and 71-grassland) land cover types within a 1000m buffer | NLCD; multiple years; *landscapemetrics* |
| Snow accumulation | Cumulative seasonal snowfall (Nov-Mar) | Hopkins International Airport weather station |
| Days with >1 inch snow depth | Cumulative days (Nov-Mar) | Hopkins International Airport weather station |
| Winter temperature | Mean seasonal temperature (Nov-Mar) | Hopkins International Airport weather station |
| Acorn masting | Annual statewide estimation of proportion white and red oak trees with acorns calculated across 38 wildlife areas | Ohio Department of Natural Resources |
| Growing season precipitation | Cumulative seasonal precipitation (Apr-July) | Hopkins International Airport weather station |
| Deer Removal | Number of individuals removed via sharpshooting annually at each site | Cleveland Metroparks |
| Previous year removal | The number of deer removed within each reservation during the previous management season | Cleveland Metroparks |
| Stage | Fawn (0.5 yr), yearling (1.5 yr), and adult (2.5+ yr) stages | Cleveland Metroparks |
| Body mass | Whole body mass for each individual doe | Cleveland Metroparks |
| Fecundity | Number of fetuses *in utero* (yearlings and does) | Cleveland Metroparks |
| Pregnant | Binary variable 1 = pregnant and 0 = not pregnant (fawns only) | Cleveland Metroparks |

| | | |
|---|---|---|
| Julian date | Day in the year that doe was collected | Cleveland Metroparks |
| Year | Year of study | Cleveland Metroparks |
| Reservation | Reservation in which deer removal took place | Cleveland Metroparks |

Table S4. Closest NLCD year assigned to each year of deer removal.

| Year | NLCD Year |
|---|---|
| 2000 | 2001 |
| 2001 | 2001 |
| 2002 | 2001 |
| 2003 | 2001 |
| 2004 | 2004 |
| 2005 | 2004 |
| 2006 | 2006 |
| 2007 | 2006 |
| 2008 | 2008 |
| 2009 | 2008 |
| 2010 | 2008 |
| 2011 | 2011 |
| 2012 | 2011 |
| 2013 | 2013 |
| 2014 | 2013 |
| 2015 | 2013 |
| 2016 | 2016 |
| 2017 | 2016 |
| 2018 | 2016 |
| 2019 | 2019 |
| 2020 | 2019 |
| 2021 | 2019 |

Table S5. Structural equation model output for the final fawn pregnancy model fit to a dataset of removed female deer between 2000 and 2021 in Cleveland, Ohio, USA. Model selection included comparisons of Fisher’s C, Chi-square goodness-of-fit tests, $R^2$ values, and ΔAIC, as recommended for piecewise SEMs that include generalized linear models (Lefcheck 2021).

Covariates included in our final model incorporate the results of tests of directed separation (DSep tests) which indicated additional significant pathways between environmental covariates (current and previous year winter temperature, growing season precipitation, and acorn mast) and the Deer Removal response variable. Bold text indicates statistical significance.

Fawns

(combined AIC = 4113.19; Chi-squared = 790.72; Fisher's C = 15.28)

Deer Removal sub-model (marginal $R^2 = 0.12$; conditional $R^2 = 0.69$)

| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
|---|---|---|---|---|
| urbanization | 0.1108 | 0.1402 | 0.0358 | 0.4330 |
| urban-natural edge | -0.0003 | 0.0008 | -0.0113 | 0.6880 |
| forest-grassland edge | 0.0002 | 0.0036 | 0.0016 | 0.9602 |
| previous year removal | -0.0002 | 0.0008 | -0.0207 | 0.7483 |
| **winter temperature** | **0.0496** | **0.0059** | **0.3705** | **<0.0001** |
| **winter temperature 1-yr lag** | **-0.0158** | **0.0070** | **-0.1149** | **0.0239** |
| **growing season precipitation** | **-0.0226** | **0.0105** | **-0.1999** | **0.0318** |
| **growing season precipitation 1-yr lag** | **-0.0336** | **0.0119** | **-0.2902** | **0.0051** |
| acorn mast | 0.0057 | 0.0054 | 0.1721 | 0.2931 |
| **acorn mast 1-yr lag** | **-0.0065** | **0.0028** | **-0.1786** | **0.0202** |

Body Mass sub-model (marginal $R^2 = 0.08$; conditional $R^2 = 0.20$)

| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
|---|---|---|---|---|
| urbanization | 7.5794 | 4.1945 | 0.1038 | 0.0904 |
| urban-natural edge | 0.0019 | 0.0316 | 0.0028 | 0.9523 |
| forest-grassland edge | 0.0169 | 0.1395 | 0.0063 | 0.9046 |
| winter temperature | -0.5291 | 0.4347 | -0.1676 | 0.3292 |
| winter temperature 1-yr lag | -0.1720 | 0.4571 | -0.0530 | 0.7426 |
| growing season precipitation | -0.5674 | 0.4613 | -0.2126 | 0.3404 |
| growing season precipitation 1-yr lag | -0.0956 | 0.3744 | -0.0350 | 0.8193 |
| acorn mast | 0.1006 | 0.1697 | 0.1284 | 0.6116 |
| acorn mast 1-yr lag | 0.1437 | 0.1908 | 0.1672 | 0.5273 |
| deer removal | -2.7691 | 1.6241 | -0.1173 | 0.1019 |
| Julian day | -0.0563 | 0.0350 | -0.0912 | 0.1421 |

Pregnancy sub-model (marginal $R^2 = 0.32$; conditional $R^2 = 0.36$)

| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
|---|---|---|---|---|
| **weight** | **0.1186** | **0.0148** | **0.5698** | **<0.0001** |
| deer removal | -0.3917 | 0.3812 | -0.0797 | 0.3042 |
| previous year removal | -0.0001 | 0.0049 | -0.0019 | 0.9818 |
| **Julian day** | **0.0245** | **0.0096** | **0.1905** | **0.0109** |

Table S6. Structural equation model output for the final yearling fecundity model fit to a dataset of removed female deer between 2000 and 2021 in Cleveland, Ohio, USA. Model selection included comparisons of Fisher's C, Chi-square goodness-of-fit tests, $R^2$ values, and ΔAIC, as recommended for piecewise SEMs that include generalized linear models (Lefcheck 2021). Covariates included in our final model incorporate the results of tests of directed separation (DSep tests) which indicated additional significant pathways between environmental covariates (current and previous year winter temperature and acorn mast) and the Deer Removal response variable. Bold indicates statistical significance.

| Yearlings<br>(combined AIC = 3832.42; Chi-squared = 458.84; Fisher's C = 152.61) | | | | |
|---|---|---|---|---|
| Deer Removal sub-model ($R^2$ = 0.429; conditional $R^2$ = 0.411) | | | | |
| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
| **urbanization** | **0.9687** | **0.1214** | **0.3734** | **<0.0001** |
| **urban-natural edge** | **-0.0030** | **0.0011** | **-0.1254** | **0.0063** |
| **forest-grassland edge** | **0.0152** | **0.0045** | **0.1526** | **0.0008** |
| **previous year removal** | **0.0031** | **0.0005** | **0.3192** | **<0.0001** |
| **winter temperature** | **0.0381** | **0.0052** | **0.4378** | **<0.0001** |
| **winter temperature 1-yr lag** | **-0.0209** | **0.0050** | **-0.2432** | **<0.0001** |
| **acorn mast** | **-0.0169** | **0.0034** | **-0.4669** | **<0.0001** |
| **acorn mast 1-yr lag** | **-0.0210** | **0.0035** | **-0.7659** | **<0.0001** |
| **Julian day** | **0.0029** | **0.0012** | **0.1210** | **0.0141** |
| Body Mass sub-model (marginal $R^2$ = 0.169; conditional $R^2$ = 0.1104) | | | | |
| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
| urbanization | -4.756 | -1.071 | -0.0482 | 0.6573 |
| urban-natural edge | -0.0645 | 0.0552 | -0.0704 | 0.2438 |
| forest-grassland edge | -0.2447 | -0.2295 | -0.0647 | 0.2871 |
| winter temperature | -0.6226 | 0.5720 | -0.1877 | 0.2773 |
| winter temperature 1-yr lag | 0.0659 | 0.7177 | 0.0202 | 0.9269 |
| growing season precipitation | -0.0277 | 1.2460 | -0.0083 | 0.9823 |
| growing season precipitation 1-yr lag | 0.3902 | 1.3560 | 0.1169 | 0.7738 |
| acorn mast | 0.0080 | 0.6695 | 0.0058 | 0.9904 |
| acorn mast 1-yr lag | 0.0556 | 0.3667 | 0.0532 | 0.8796 |
| deer removal | -6.0810 | 3.6120 | -0.1597 | 0.0933 |
| **previous year removal** | **-1.3270** | **0.0539** | **-0.3561** | **0.0143** |
| **Julian day** | **-0.1273** | **0.0622** | **-0.1419** | **0.0415** |

| Fecundity sub-model (conditional $R^2$ = 0.1167) | | | | |
|---|---|---|---|---|
| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
| **weight** | **0.0088** | **0.0030** | **0.2836** | **0.0029** |
| deer removal | -0.1182 | 0.1407 | -0.1002 | 0.4010 |
| previous year removal | -0.0015 | 0.0020 | -0.1335 | 0.4496 |

Table S7. Structural equation model output for the final adult fecundity model fit to a dataset of removed female deer between 2000 and 2021 in Cleveland, Ohio, USA. Model selection included comparisons of Fisher's C, Chi-square goodness-of-fit tests, $R^2$ values, and ΔAIC, as recommended for piecewise SEMs that include generalized linear models (Lefcheck 2021). Covariates included in our final model incorporate the results of tests of directed separation (DSep tests) which indicated additional significant pathways between environmental covariates (current and previous year winter temperature, growing season precipitation, and acorn mast) and the Deer Removal response variable. Bold indicates significance.

| Adults<br>(combined AIC = 12485.6; Chi-squared = 3080.01; Fisher's C = 395.38) | | | | |
|---|---|---|---|---|
| Deer Removal sub-model ($R^2$ = 0.413; conditional $R^2$ = 0.405) | | | | |
| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
| **urbanization** | **1.0770** | **0.0736** | **0.4057** | **<0.0001** |
| urban-natural edge | -0.0007 | 0.0007 | -0.0287 | 0.2914 |
| forest-grassland edge | 0.0038 | 0.0026 | 0.0403 | 0.1497 |
| **previous year removal** | **0.0030** | **0.0003** | **0.3027** | **<0.0001** |
| **winter temperature** | **0.0698** | **0.0059** | **0.7761** | **<0.0001** |
| **winter temperature 1-yr lag** | **-0.0539** | **0.0077** | **-0.6014** | **<0.0001** |
| **growing season precipitation** | **-0.0858** | **0.0143** | **-1.0521** | **<0.0001** |
| **growing season precipitation 1-yr lag** | **-0.0969** | **0.0158** | **-1.0592** | **<0.0001** |
| **acorn mast** | **0.0353** | **0.0083** | **0.9467** | **<0.0001** |
| acorn mast 1-yr lag | 0.0087 | 0.0047 | 0.3160 | 0.0606 |
| **Julian day** | **0.0016** | **0.0007** | **0.0731** | **0.0164** |
| Body Mass sub-model (marginal $R^2$ = 0.0809; conditional $R^2$ = 0.0625) | | | | |
| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
| urbanization | 5.9687 | 5.9017 | 0.0557 | 0.3121 |
| urban-natural edge | -0.0207 | 0.0347 | -0.0203 | 0.5498 |
| forest-grassland edge | -0.1464 | 0.1240 | -0.0382 | 0.2383 |

| | | | | |
|---|---|---|---|---|
| **winter temperature** | **-0.6413** | **0.2068** | **-0.1764** | **0.0020** |
| winter temperature 1-yr lag | 0.1188 | 0.1863 | 0.0316 | 0.5239 |
| growing season precipitation | -0.3189 | 0.2337 | -0.0963 | 0.1726 |
| growing season precipitation 1-yr lag | 0.1560 | 0.2122 | 0.0444 | 0.4624 |
| acorn mast | 0.0387 | 0.1139 | 0.0314 | 0.7342 |
| acorn mast 1-yr lag | 0.1668 | 0.1115 | 0.1471 | 0.1352 |
| deer removal | 1.4622 | 1.8704 | 0.0436 | 0.4345 |
| **Julian day** | **-0.1087** | **0.0344** | **-0.1243** | **0.0016** |
| Fecundity sub-model (conditional $R^2 = 0.0696$) | | | | |
| Covariate | β Estimate | Std. Error | Std. Estimate | p-value |
| **weight** | **0.0041** | **0.0013** | **0.2137** | **0.0021** |
| deer removal | -0.0652 | 0.0630 | -0.0924 | 0.3004 |
| previous year removal | -0.0001 | 0.0010 | 0.0193 | 0.8892 |