

THESIS

FORECASTING THE EFFECTS OF FERTILITY CONTROL ON OVERABUNDANT
UNGULATES

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ABSTRACT

FORECASTING THE EFFECTS OF FERTILITY CONTROL ON OVERABUNDANT UNGULATES

Overabundant populations of native vertebrates can cause environmental degradation and loss of biological diversity. Culling or regulated harvest is often used to control overabundant species. These methods become infeasible in residential areas and national parks. White-tailed deer populations on the eastern coast of the United States have grown exponentially during the urbanization of the 20th century causing severe environmental and economic damage. Managers of National Parks in the Washington, D. C. area seek to reduce densities of white-tailed deer from the current average (50 deer per km²). It has been shown theoretically that fertility control is not an effective way to reduce an overabundant populations, but these conclusions have not be verified with empirical models. Here, we present a Bayesian hierarchical model using 13 years of distance sampling data from 10 National Parks in the National Capital Region Network to forecast the effects of fertility control on overabundant ungulates. We estimated a survival probability for adult female deer that was the same as what we found in previous literature (adult female = 0.74). However, our estimation of adult male and juvenile probabilities were different than what has been found in past studies (adult male = 0.39, juvenile = 0.67). This may be because of the high densities of white-tailed deer in our study area. Our posterior predictive checks show that our model does adequately represent the data ($P_\beta = 0.419$). Our model experiments found that fertility control is not capable of rapidly reducing deer abundance unless a high relative effort over no action is feasible. However, it can be combined with culling to maintain a population below carrying capacity with a high probability of success. This gives managers confronted with problematic overabundance a framework for implementing management actions with a realistic assessment of uncertainty.

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FORECASTING THE EFFECTS OF FERTILITY CONTROL ON OVERABUNDANT UNGULATES

Introduction

Worldwide increases in urbanization have caused a global decline in biodiversity (Lovejoy 2006; Sala et al. 2000) as habitat for native species has been developed for human uses. However, there are also many cases where the effects of urbanization have allowed generalist species to proliferate. Invasion ecology has developed into a vital area of research (Simberloff et al. 2013), but typically focuses on non-native species. Some populations of native vertebrates resemble “invaders” when they become excessively abundant and cause environmental harm (Garrott et al. 1993; Carey et al. 2012). These populations thrive in response to increased foraging options and decreased predation pressure arising from extensive landscape change and development (Côté et al. 2004).

Overabundant species are problematic when they threaten human life or livelihoods, depress densities of other species, or cause ecosystem dysfunction (Jewell et al. 1981; Van Der Peet 2007). Wildlife managers often seek to mitigate these harmful effects by reducing the size of the problem population, traditionally by using regulated hunting or culling. Although hunting can provide recreational and economic benefits, lethal methods can be unpopular with the public or logistically infeasible because wildlife live in residential areas or in areas that prohibit hunting, for example in national parks and other types of conservation reserves (Wright 1993). Density dependence can make it difficult to control species by lethal means because reproductive rates can increase dramatically as population numbers decline (Knowlton 1972). Consequently, non-lethal methods, especially fertility control, have become more attractive to wildlife managers as a way to control wildlife populations (Malcolm et al. 2010; Kirkpatrick et al. 1997).

Analytical and simulation models cast doubt on the idea that fertility control can be used to efficiently achieve reduction goals for overabundant species or maintain populations within acceptable limits (Hobbs et al. 2000; Hone 1992; Barlow et al. 1997). However, these

models have been entirely deterministic and have rarely been combined with data. The ostensible certainty of the predictions of these models might create false confidence about decisions on fertility control. Thus, a first step in evaluating the efficacy of fertility control is to develop population models that are reliably assimilated with data to provide a statistically coherent assessment of uncertainty (Ransom et al. 2014). These models can provide an honest assessment of the feasibility of management alternatives by forecasting the effects of alternative actions on populations. Bayesian hierarchical models of population dynamics are a particularly promising tool for evaluating management alternatives because they support true forecasts – predictions accompanied by proper estimates of uncertainty.

White-tailed deer (*Odocoileus virginianus*) were once considered endangered and are now recognized as overabundant (Diamond 1992; Garrott et al. 1993; Jewell et al. 1981; Martin et al. 2013). In the late 19th century, there were fewer than 500,000 white-tailed deer in the entire United States. The Lacey Act of 1900 regulated interstate trade and established penalties for hunting endangered species. These regulations solved the issue of white-tailed deer under-abundance. Today, there are over 30 million white-tailed deer nationwide with high concentrations on the east coast of the United States (McCabe and McCabe 1997). Their feeding retards forest regeneration and harms biological diversity of vegetation by causing local extinction of many palatable understory plants (Russell et al. 2001; Knight et al. 2009). Overabundant deer threaten human safety by increasing traffic hazards and by providing a reservoir for ticks that carry lyme disease (*Lyme borreliosis*). Furthermore, human economies are harmed by damage to crops caused by deer (Côté et al. 2004).

Managers of National Parks in the eastern U.S. are especially concerned about the effects of overabundant wildlife on biological diversity because these effects are inconsistent with the mission of the parks, to preserve natural resources for the enjoyment, education and inspiration of the people. Those concerns motivate an improved understanding of alternatives for population control. Here, we describe a Bayesian hierarchical model to inform decisions on managing overabundant white-tailed deer. The objective of our work was to forecast

the effect alternative actions on white-tailed deer populations using a model that includes uncertainty.

Materials and methods

Census and classification data

We analyzed observations of white-tailed deer population density, white-tailed deer group composition, and white-tailed deer harvest from ten National Parks in the National Capital Region Network (NCRN) near Washington, D.C during 2001-2013. The NCRN parks have collaborated using standardized distance sampling methods (Buckland et al. 1993) to annually obtain density estimates of white-tailed deer populations in each park (Figure 1).

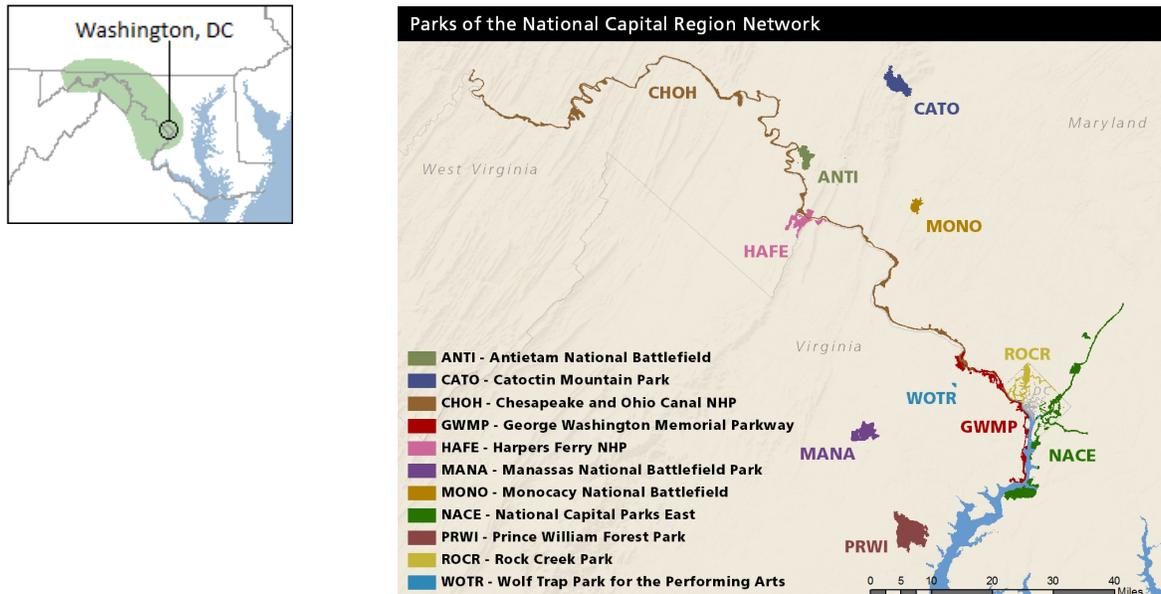


Figure 1: The study area included ten parks in the National Capital Region Network in the area surrounding Washington D.C. Each park used standardized distance sampling methods which produced a time series from 2000 to 2011 of regional estimates of white-tailed deer abundance.

Distance sampling is a widely used approach for estimating the abundance of wildlife populations (Buckland et al. 1993). A standard operating procedure for distance sampling of deer was used for all ten parks in the NCRN (Bates 2006). Censuses were conducted after leaf-fall and before hunting season for three consecutive nights in each park. Three observers drove specified transect roads with a spotlight to locate groups of deer. After

the deer were counted, the distance from observers was determined with a laser rangefinder positioned perpendicular to the transect. Observers also classified each deer in every group as buck, doe, fawn, or “unknown.” Program Distance (Thomas et al. 2010) was used to convert these distance sampling counts to estimates of mean population densities with an associated standard error for each park each year. We used data from 10 parks over 13 years to support our analyses.

Analysis

We used a fully Bayesian, hierarchical model to obtain posterior distributions of parameters, latent states, and derived quantities of interest. A model of ecological processes, models linking the processes to data, and models for parameters Berliner (1996) provided a unified framework for inference,

$$[\boldsymbol{\theta}_p, \mathbf{n}_t, \mathbf{n}_{t-1} | \mathbf{Y}_t] \propto \underbrace{[\mathbf{n}_t | \boldsymbol{\theta}_p, \mathbf{n}_{t-1}]}_{\text{process}} \prod_{l=1}^2 \underbrace{[y_{lt} | \boldsymbol{\theta}_{dl}, \mathbf{n}_t]_l}_{\text{data}} \underbrace{[\boldsymbol{\theta}_p]}_{\text{parameters}} . \quad (1)$$

The notation $[a | b, c]$ reads the distribution of a conditional on b and c . The quantity $\boldsymbol{\theta}_p$ is a vector of parameters in the process model; $\boldsymbol{\theta}_{d,l}$ is a vector of parameters in data model l ; \mathbf{n}_t is a vector representing the true, unobserved demographic and disease state of the population at time t , and $\mathbf{y}_{(t)}$ are vectors of observations of the true state at time t . There are two data models (also called likelihoods), one each for census observations and classifications. In the sections that follow, we describe these models.

Process model

We used a Lefkovitch matrix to predict the median number of individuals in three stages at census juveniles of both sexes aged 0 to 6 months (n_1), adult females, aged ≥ 1.5 years and older (n_2), and adult males aged ≥ 1.5 years and older (n_3). Model census (Caswell

2006) occurs six months after the birth pulse. The deterministic difference equations are.

$$n_{1it} = s_2 f_{it} n_{2it-1} \quad (2)$$

$$n_{2it} = s_1 m n_{1it-1} + s_2 n_{2it-1} \quad (3)$$

$$n_{3it} = s_1 (1 - m) n_{1it-1} + s_3 n_{3it-1} \quad (4)$$

Parameters are survival probabilities for juveniles (s_1), females (s_2), and males (s_3), fecundities f_{it} for each park (i) and year (t), and sex ratio (m). These survival probability parameters include harvest. Survival probabilities in equation 2 were not raised to the one half power (Noon and Sauer 2001) because the preponderance of mortality occurs before birth pulse due to the combined effects of winter severity and harvest. Fecundities implicitly include survival of juveniles from the birth pulse to census. We accounted for effects of population density on fecundity (McCullough 1979) using

$$f_{it} = e^{r_f - \frac{r_f}{K_f} (\sum_{j=1}^3 n_{jit-1} / \text{area}_i)} \quad (5)$$

where r_f is the maximum number of fawns surviving to census produced per doe when population size is zero and K_f is the density of animals when fecundity equals zero.

The deterministic model is an abstraction of the underlying mechanisms that control annual variation in deer abundance every year. We can recast the system of deterministic, difference equations as

$$\mathbf{A}_{it} = \begin{bmatrix} 0 & s_2 e^{r_f - \frac{r_f}{K_f} (\sum_{j=1}^3 n_{jit-1} / \text{area}_i)} & 0 \\ s_1 m & & s_2 & 0 \\ s_1 (1 - m) & & 0 & s_3 \end{bmatrix}_{it} \quad (6)$$

$$\mathbf{n}_{it} = \mathbf{A}_{it} \mathbf{n}_{it-1} \quad (7)$$

We make the model stochastic to account for influences on the true state that are not

represented in our process model:

$$\log(\mathbf{n}_{it}) \sim \text{multivariate normal}(\log(\mathbf{A}_{it-1}\mathbf{n}_{it-1}), \sigma_p^2\mathbf{I}) \quad (8)$$

Where σ^2 is the process variance parameter that represents all sources of variation in deer abundance that are not included in our deterministic model. We assumed a single process variance for all stages and park.

Parameter models

We assumed that parameters representing vital rates were the same across parks. Survival probabilities for each stage $s_{ji} \sim \text{beta}(1, 1)$. We also assumed that juvenile deer survived to the adult stage with a 1:1 sex ratio (m) with a variance of .02 such that by moment matching

$$m \sim \text{beta}(312, 312)$$

We assumed this because there will be no preferential harvest during a juvenile's first year. We chose a variance of .02 because it is less than 5% of 0.5 and allowed a small amount of variation.

We use an allometric equation for the scaling of birth rate of Artiodactyls (Western 1979) to inform the prior distribution of r_f (Eqn. 5),

$$r_f \sim \text{normal}(2 \cdot 3.09W^{-0.33}, 0.1304^2)$$

We assumed a mean body mass (W) of 65 kg for white tailed deer (McCullough 1979) and calculated a residual standard error of 0.1304. We multiplied Western's equation by 2 because his model is offspring per individual in the population including males and females. To ensure that our use of Western's equation was reasonable, we used it in a simple, deterministic 2 x 2 matrix model with adult survival set at 0.90. We then compared the prediction of population growth rate (λ_{Western}) based on this matrix model with the prediction of λ obtained from

the scaling relationship of Sinclair (2003) ($\lambda_{\text{Sinclair}}$). There was close agreement between the two predictions ($\lambda_{\text{Western}} = 3.09W^{-0.33}$, $\lambda_{\text{Sinclair}} = 1.375W^{-0.315}$).

Dynamic models require estimating initial conditions as parameters. The initial conditions of the state vector \mathbf{n}_{i1} were informed by both types of data using

$$\boldsymbol{\gamma}_{i1} \sim \text{Dirichlet}(\mathbf{y}_{\boldsymbol{\alpha}_{i1}} + 1) \quad (9)$$

$$n_{i1} \sim \text{normal}(y_{d_{i1}}, \hat{\sigma}_{i1}^2) \quad (10)$$

$$\mathbf{N}_{i1} = n_{i1} \times \boldsymbol{\gamma}_{i1} \times \text{area}_i \quad (11)$$

where $\mathbf{y}_{\boldsymbol{\alpha}_{i1}}$ are the categorical data for each park at year 1, $y_{d_{i1}}$ are the density data for each park at year 1 with associated standard error ($\hat{\sigma}_{i1}$) from Program Distance (Thomas et al. 2010), and N_{i1} represents the initial conditions for each park at year 1.

Data models

The data are observations of sex and age structure ($\mathbf{y}_{\boldsymbol{\alpha}_{it}}$) as well as density data ($y_{d_{it}}$) for each park (i) at each year (t). It is important to estimate group composition, so that we can make correct inferences about the age and sex structure of the population. The vectors $\mathbf{y}_{\boldsymbol{\alpha}_{it}}$ give the number of animals classified as juvenile, adult female and adult male for park i at time t , and N_{it} is the total number of animals categorized. Our data model for the classification observations was

$$\mathbf{y}_{\boldsymbol{\alpha}_{it}} \sim \text{multinomial}(N_{it}, \boldsymbol{\pi}_{it})$$

where $\boldsymbol{\pi}_{it}$ is a vector of proportions from the process model

$$\boldsymbol{\pi}_{it} = \left[\frac{n_{1it}}{\sum_{j=1}^3 n_{jit}}, \frac{n_{2it}}{\sum_{j=1}^3 n_{jit}}, \frac{n_{3it}}{\sum_{j=1}^3 n_{jit}} \right]. \quad (12)$$

We estimated the population density for each park by dividing the estimate total deer

abundance for each park by the parks area (Eqn. 13). Distance sampling methods allowed managers to calculate animal density y_{dit} and a standard error $\hat{\sigma}_{it}$ for each park and year. We used these data in the likelihood

$$y_{dit} \sim \text{normal} \left(\frac{\sum_{j=1}^3 n_{jit}}{\text{area}_i}, \hat{\sigma}_{it}^2 \right) \quad (13)$$

where area_i is the total area of park i . The standard error ($\hat{\sigma}_{it}$) was provide to us by Program Distance (Thomas et al. 2010). We square the standard error provided to represent the variance of the normal distribution. We show the full posterior and joint distributions in the appendix.

Estimation

Marginal posterior distributions of states, parameters, and model predictions were calculated using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.3.0 (Plummer 2003, 2012) called from the R computing environment (R Core Team 2013) using the rjags package (Plummer 2013). Initial values of chains were chosen to vary 20% in either direction relative to the means of the prior distributions (Brooks and Gelman 1998). We accumulated 10,000 samples from each chain and 2,000 iterations as burn-in. Convergence was assured by inspection of trace plots and by the diagnostics of Brooks and Gelman 1998 and Heidelberger and Welch 1983.

Model Evaluation

We tested for lack of fit using posterior predictive checks. This approach compares data simulated from the model to real data used to estimate the model parameters. If the simulated data is not distributed like the real data, there may be structural deficiencies in the process or the data models. We calculated a test statistic from the observed data (T^{obs})

and from the simulated data sets (T^{rep}),

$$T^{obs} = \sum_{i=1}^I \sum_{t=1}^T (y_{d_{it}} - \mu_{it})^2 \quad T^{rep} = \sum_{i=1}^I \sum_{t=1}^T (y_{d_{it}}^{rep} - \mu_{it})^2$$

where \mathbf{y}_d^{rep} is drawn from the posterior predictive distribution and μ_{it} is the model prediction of the median of the distribution of the density of white-tailed deer in each park, each year.

We then calculated a Bayesian P value, P_B

$$P_B = Pr [T^{rep}(y^{rep}, \theta) \geq T^{obs}(y, \theta) \mid y]$$

A model shows lack of fit if P_B is close to 0 or 1.

Model Experiments

We conducted model experiments with four treatments: culling, sterilization, one-year duration contraceptives, and three year average duration contraceptives. We assumed that 20%, 40%, 60% or 90% of adult females were treated to allow comparison among treatments type and treatment intensity. Fawns were not given contraceptive in the model experiments because they are ineffective for fawns (McShea et al. 1997). We assumed that culling, sterilization, or contraceptives were administered immediately after census. In the culling experiment c represents the proportion of adult females that were culled. The projection matrix for the culling experiment was

$$\begin{bmatrix} 0 & s_2 f(1-c) & 0 \\ s_1 m & s_2(1-c) & 0 \\ s_1(1-m) & 0 & s_3 \end{bmatrix} \cdot \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1} \quad (14)$$

We created an additional state including infertile females (n_4) to represent treatment with fertility control agents. The parameter c represents the proportion of fertile adult females annually treated. The model for sterilization (permanent infertility) was

$$\begin{bmatrix} 0 & s_2 f(1-c) & 0 & 0 \\ s_1 m & s_2(1-c) & 0 & 0 \\ s_1(1-m) & 0 & s_3 & 0 \\ 0 & s_2 c & 0 & s_2 \end{bmatrix} \cdot \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_{t+1} \quad (15)$$

Treatment with single year contraceptives was modeled using

$$\begin{bmatrix} 0 & s_2 f & 0 & 0 \\ s_1 m & s_2(1-c) & 0 & s_2(1-c) \\ s_1(1-m) & 0 & s_3 & 0 \\ 0 & s_2 c & 0 & s_2 c \end{bmatrix} \cdot \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_{t+1} \quad (16)$$

The fecundity term for adult females (n_3) was not influenced by this treatment because it does not affect the viability of a current pregnancy.

For fertility control with longer efficacy than one year, we represented a hypothetical contraceptive agent that on average renders animals infertile for three years. Let α be the average duration of a fertility control agent. It follows that the probability that a treated female becomes fertile during each year following treatment is ψ , where $\psi = 1 - e^{-\alpha \Delta t}$, $\alpha^{-1} = 3$. Thus, the model for the three year treatment was

$$\begin{bmatrix} 0 & s_2 f & 0 & 0 \\ s_1 m & s_2(1-c) & 0 & s_2(1-c)(1-\psi) \\ s_1(1-m) & 0 & s_3 & 0 \\ 0 & s_2 c & 0 & s_2 c + s_2(1-c)\psi \end{bmatrix} \cdot \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_{t+1} \quad (17)$$

Eigenanalysis

The equivariance property of MCMC means that quantities that are calculated from random variables are random variables with their own posterior distributions. We sought inference on the effects of treatment on the long-term population growth rate. The domi-

nant eigenvalue describes the ergodic properties of population growth (Caswell 2006). We calculated the posterior distributions of asymptotic growth rate (λ) by performing a classic eigenanalysis using the MCMC output— a single estimate of λ was calculated from the projection matrix at each iteration in the chain. Because our model includes a non-linear term for density dependence, we performed the eigenanalysis under the assumption of no density dependence by setting $N_{it-1} = 0$ in equation 5. This allows us to calculate the upper bound of each management action’s effectiveness by using the estimated maximum possible fecundity in the analysis. The population growth rate calculated this way is very useful for comparison between model experiments because it will use the same scale to show the effect of management on population growth. The eigenanalysis was implemented with package popbio.R (Stubben and Milligan 2007) in the R computing environment (R Core Team 2013).

Evaluating Management Action

We calculated posterior predictive process distributions for future states using

$$[\mathbf{n}_{T+1}|y_1, \dots, y_T] = \int \int \dots \int [\mathbf{n}_{T+1}|\mathbf{n}_T, \boldsymbol{\theta}_m, \sigma_p^2] \\ [\mathbf{n}_1, \dots, \mathbf{n}_T, \mathbf{n}_{T+1}, \boldsymbol{\theta}_1, \dots, \boldsymbol{\theta}_m, \sigma_p^2|y_1, \dots, y_T] d\theta_1, \dots, d\theta_m, d\sigma_p^2 dn_1, \dots, dn_{T+1}$$

where \mathbf{n}_{T+1} is the true state of the population in the future given the data (y_1, \dots, y_T) . To assess the effectiveness of different management actions (Hobbs 2014 *in revision*) and to calculate the probability of reaching an objective, we obtain the posterior predictive process distribution of the true state of the population at a point in the future and use Monte Carlo integration to approximate the probability that the goal will be met *given no action*. (Figure 2 A). The posterior predictive process distribution of the true state of the population at the same point in the future and the probability of achieving the same goal *given a management action* (Figure 2 B). The ratio of the probability that an objective will be realized given implementation of a management action over the probability that an objective will be realized

given no action provides assessment of the net effect of the management action in the face of uncertainty. (Figure 2 C). The net effect of management can be reported to a manager in terms such as, “Taking this action is ten times more likely to achieve the goal relative to not taking this action.”

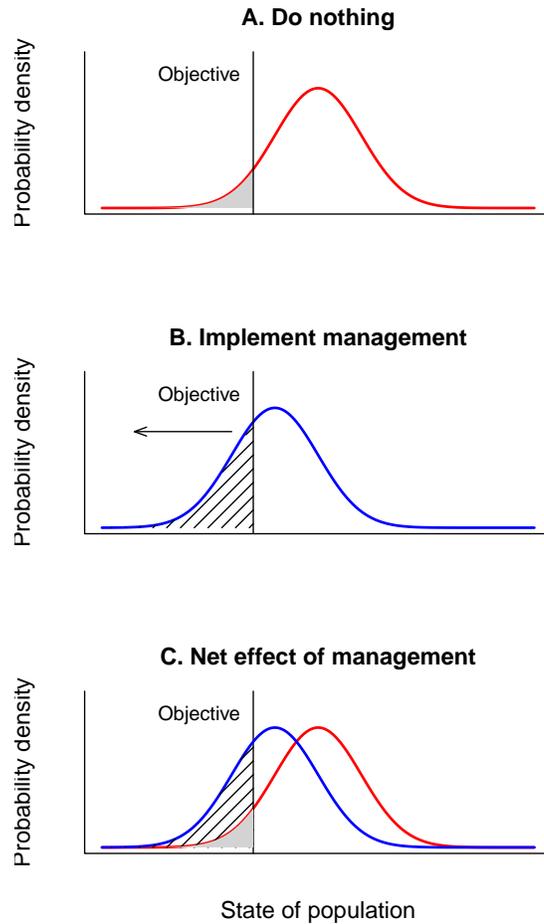


Figure 2: A. The posterior predictive process distribution of a forecasted density of a population. The vertical line indicates a manager’s objective for the population. The area that is shaded gives the probability that an objective will be met given no action. B. The Posterior distribution conditional on a management action, for example, culling or delivering contraceptives. The stippled area under the curve is the probability that a manager will reach their objective given this action. C. The net effect of management is the ratio of the stippled area to the shaded area.

Results

Model checking and parameter estimation

We verified the MCMC algorithm by recovering parameters used to simulate data. The verified MCMC algorithm converged after 20,000 iterations using real data. The upper quantile of Gelman diagnostics (Gelman and Rubin 1992) was less than or equal to 1.01 for all parameters. Posterior predictive checks showed no evidence of lack of fit (Figure 5).

Median survival probability for adult females was greater than adult males or juveniles (Table 1, Figure 3). We estimated that 0.61 fawns surviving to census would be produced per adult female at low population density. This is much lower than our prior with a mean of 1.56 and a standard deviation of 0.1304. However, we did detect a density dependence feedback (Figure 4).

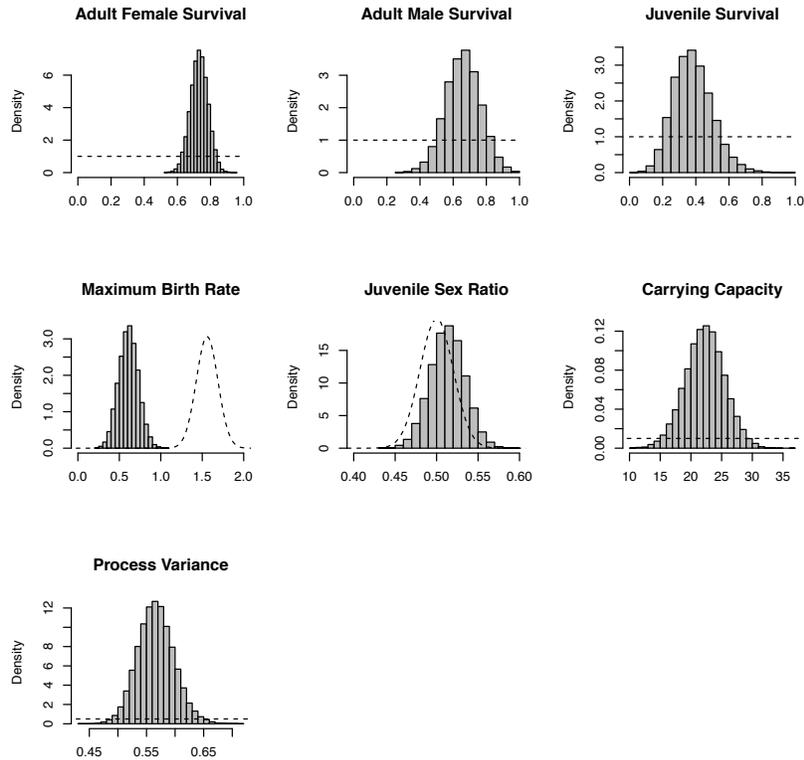


Figure 3: Posterior distributions for the vital rate parameters. One set of parameters was estimated for all parks. The dotted line indicates the prior distribution given for each parameter.

Table 1: Estimates of model parameters and 95% equal tailed Bayesian credible intervals (BCI).

	Mean	Median	SD	2.5% BCI	97.5% BCI
Carrying capacity (K_f)	22.12	22.12	3.06	16.11	28.17
Maximum fecundity (r_f)	0.61	0.61	0.11	0.39	0.84
Juvenile sex ratio (m)	0.51	0.51	0.02	0.47	0.55
Female survival (s_2)	0.74	0.74	0.05	0.63	0.83
Male survival (s_3)	0.67	0.67	0.10	0.47	0.87
Juvenile survival (s_1)	0.37	0.37	0.11	0.17	0.61
Process variance (σ^2)	0.56	0.56	0.03	0.51	0.63

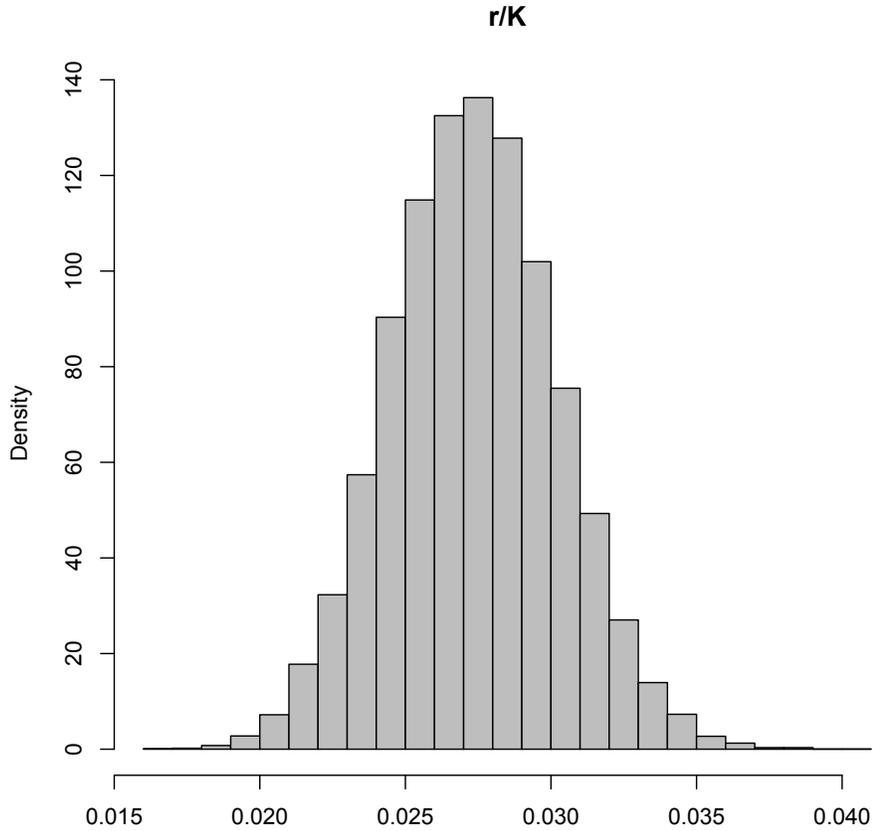


Figure 4: The posterior distribution for the slope of the density dependent function. Since this does not overlap 0, we can confirm that density dependence is present in this population.

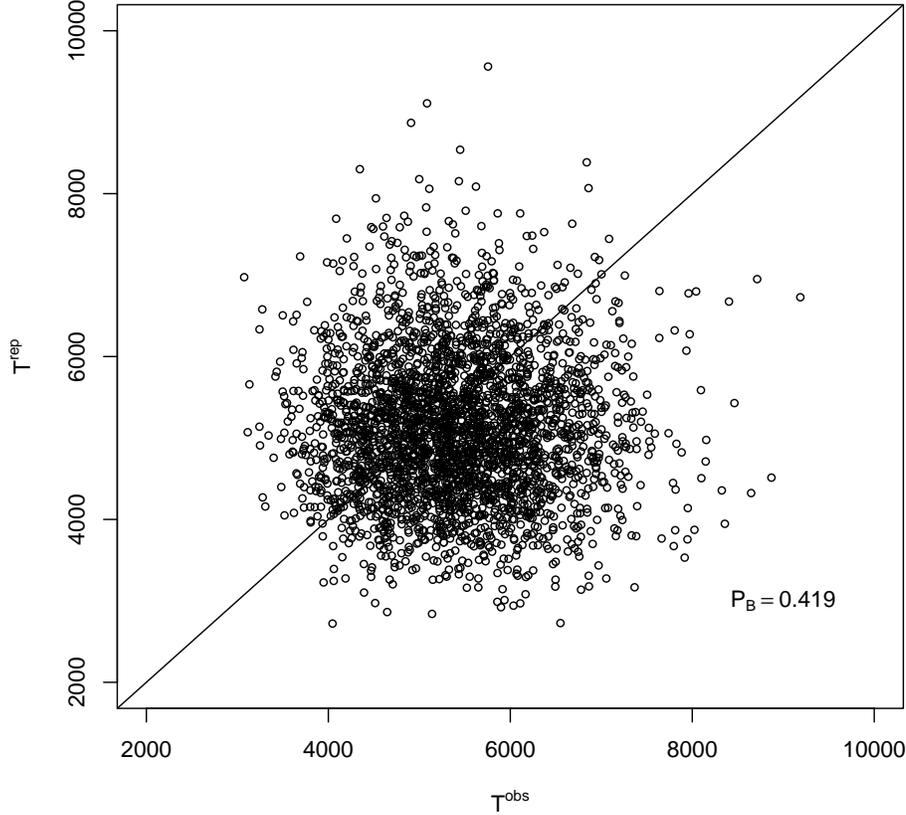


Figure 5: Test statistics for posterior predictive checks were calculated from observed data ($T^{obs} = \sum_{i=1}^I \sum_{t=1}^T (y_{dit} - \mu_{it})^2$) and from simulated data ($T^{rep} = \sum_{i=1}^I \sum_{t=1}^T (y_{dit}^{rep} - \mu_{it})^2$) where \mathbf{y}_d^{rep} is a dataset drawn from the posterior predictive distribution at each iteration of the MCMC algorithm and μ_{it} is the model prediction of the median of the distribution of the density of white-tailed deer in each park, each year. The Bayesian P value is $P_B = Pr [T^{rep}(y^{rep}, \theta) \geq T^{obs}(y, \theta) | y]$. This image was thinned by 10 to enhance clarity of the plot.

Forecast without management action

We made regional forecasts for white-tailed deer density from 2014 to 2018 (Figure 6) as well as forecasts for each park (See Appendix: Figure 11). Assuming no action to control the population, the model predicted that white-tailed deer density is decreasing with a population growth rate of 0.883 (95% equal tailed Bayesian credible interval, BCI = 0.8, 0.971) (Figure 7). However, the wide credible intervals on forecasts indicate substantial uncertainty about the growth of the population in the future (Figure 6).

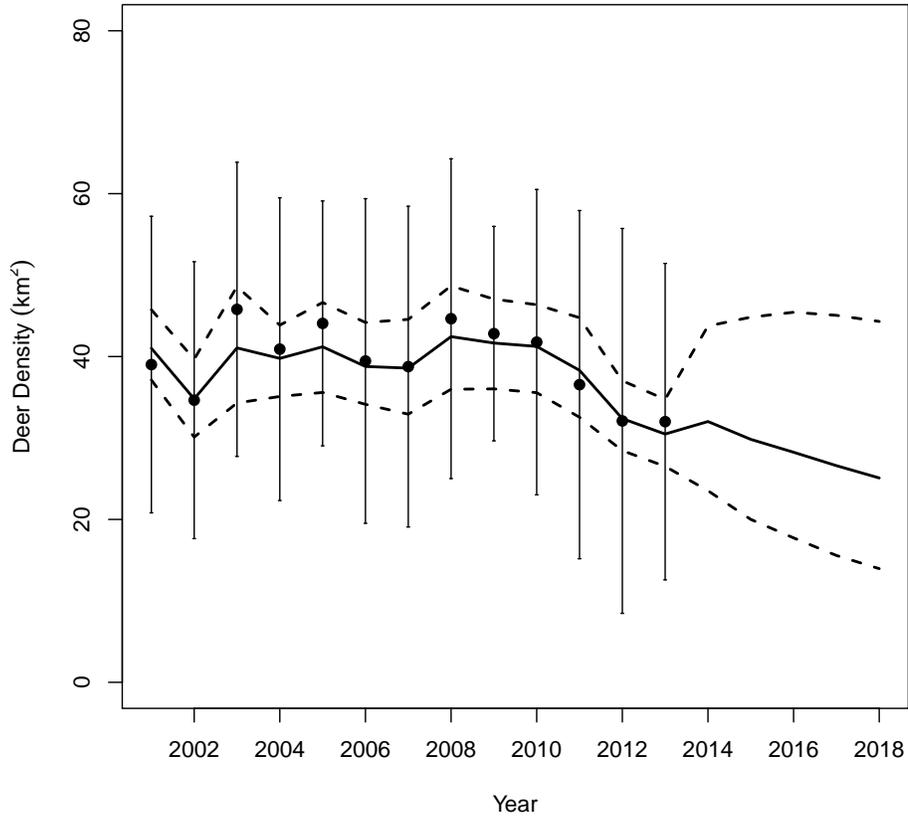


Figure 6: Estimate of the true population density of white-tailed deer in the National Capital region during 2001 to 2013 and forecasts of density from 2014 to 2018. The solid line represents the median of the posterior distribution while the dotted lines show the 95% equal-tailed Bayesian credible intervals. The vertical lines are the \pm one standard deviation of the medians of the density data.

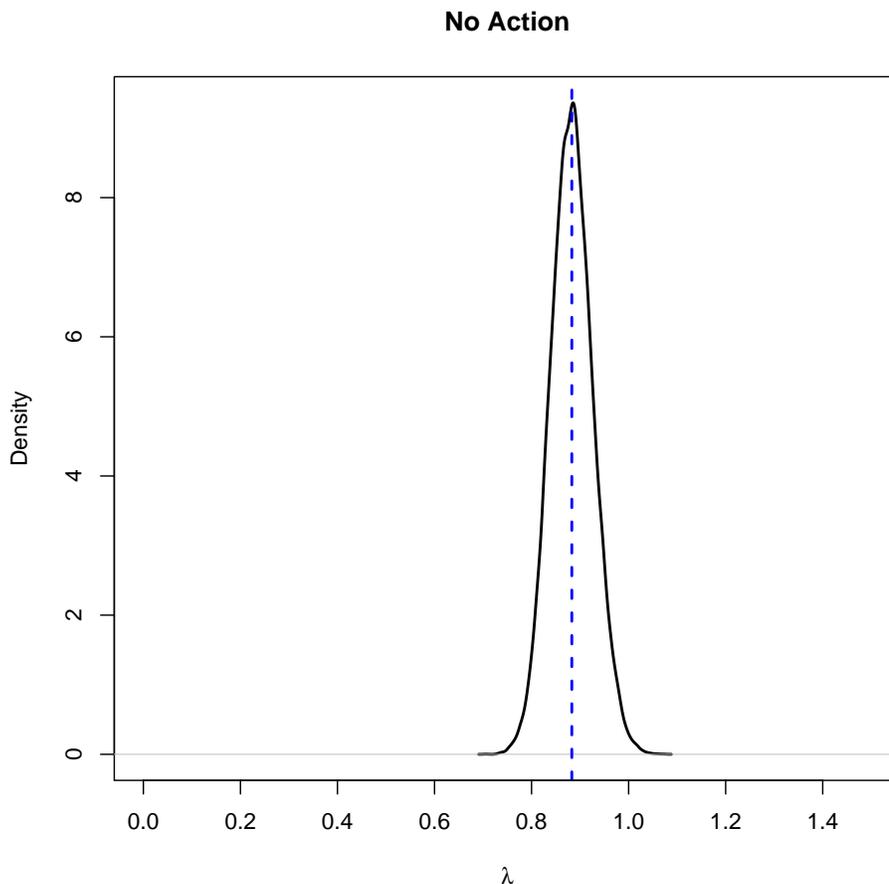


Figure 7: The population growth rate (λ) of the white-tailed deer in the National Capital Region without any management action has a median of 0.883 (95% equal tailed Bayesian credible interval, BCI = 0.8, 0.971). Although the median suggests that the population will decrease, the distribution overlaps one indicating that the population may increase.

Results of model experiments

We report the effects of different fertility control regimes on population growth rate and the probability of achieving a hypothetical management objective. We also show the estimated number of adult female deer that would need to be treated over five years in the region in order to achieve the reported effect on population growth rate which we will refer to as “number treated” or “treatment numbers.”

Growth Rate

All actions reduced the population growth rate compared no action (Table 2). Culling adult females decreased the population growth rate more than the fertility control regimes. Culling 90% of adult female deer (~ 4500 over 5 years) reduced the population growth rate ($\lambda = 0.15$, 2.5% BCI = 0.12, 97.5% = 0.19). Culling and sterilization had very similar treatment numbers, but culling reduced the population growth rate more as the proportion of adult females culled increased while sterilization of any proportion of adult females caused a median population growth rate of 0.73. Because λ is the ergodic growth rate of the population, all females will eventually become sterile no matter what proportion are sterilized each year. Treating 40% (~ 7600 adult female deer over 5 years) of the regional adult female population with contraceptives that lasts an average of 3 years decreased the population growth rate ($\lambda = 0.83$, 2.5% BCI = 0.75, 97.5% = 0.91). Contraceptives when 90% of the adult female population were treated (~ 16000 over 5 years) that last 3 years or 1 year yielded almost the same growth rate as sterilization. This is because the population growth rate will asymptotically approach sterilization as all the adult females become infertile. The short duration contraceptives had the smallest effect of any treatment when 20% are treated each year ($\lambda = 0.86$, 2.5% BCI = 0.78, 97.5% = 0.94).

Table 2: Population growth rate for different fertility control regimes.

Treatment	Percent Treated	2.5% BCI	Median	97.5% BCI
No Action	0	0.82	0.90	0.99
Cull	20	0.66	0.73	0.81
Sterilize		0.67	0.75	0.84
1 Year		0.78	0.86	0.94
3 Year		0.75	0.83	0.91
Cull	40	0.52	0.58	0.64
Sterilize		0.63	0.73	0.84
1 Year		0.76	0.84	0.92
3 Year		0.72	0.80	0.88
Cull	60	0.37	0.42	0.47
Sterilize		0.64	0.74	0.84
1 Year		0.73	0.81	0.89
3 Year		0.69	0.77	0.86
Cull	90	0.12	0.15	0.19
Sterilize		0.63	0.74	0.84
1 Year		0.67	0.76	0.85
3 Year		0.64	0.74	0.84

Probability of achieving a management objective

We selected a hypothetical management objective based on advice from National Park Service collaborators. We then computed the probability that the treatment would cause the population to be below, within, or above the objective (Table 3). There was a 0.04 probability that the population would be within the objective in 5 years because the forecasted population decreased. The only management regimes that had a probability $> .01$ of achieving the objective the first year was culling 60% or 90% of the adult female population (Figure 8). However, continuing to cull at these levels each year had a high probability of pushing the population below the lower bound of the objective (Table 3). Culling 40% of the population for 5 years had a high probability of being within the objective (Probability in = 0.8) while culling only 20% for 5 years had a lower probability of being within the objective (Probability in = 0.6). Culling reduced the population most quickly followed by sterilization. Sterilization had the highest probability of meeting the management objectives when 60%

of the adult females were treated for 5 years (Probability in = 0.8). The contraceptives had the smallest probabilities of meeting the objective (Probability in ≤ 0.7 for all proportions). However, treating 90% with 3 year contraceptives for five years was 20 times more likely to achieve the objective than no action.

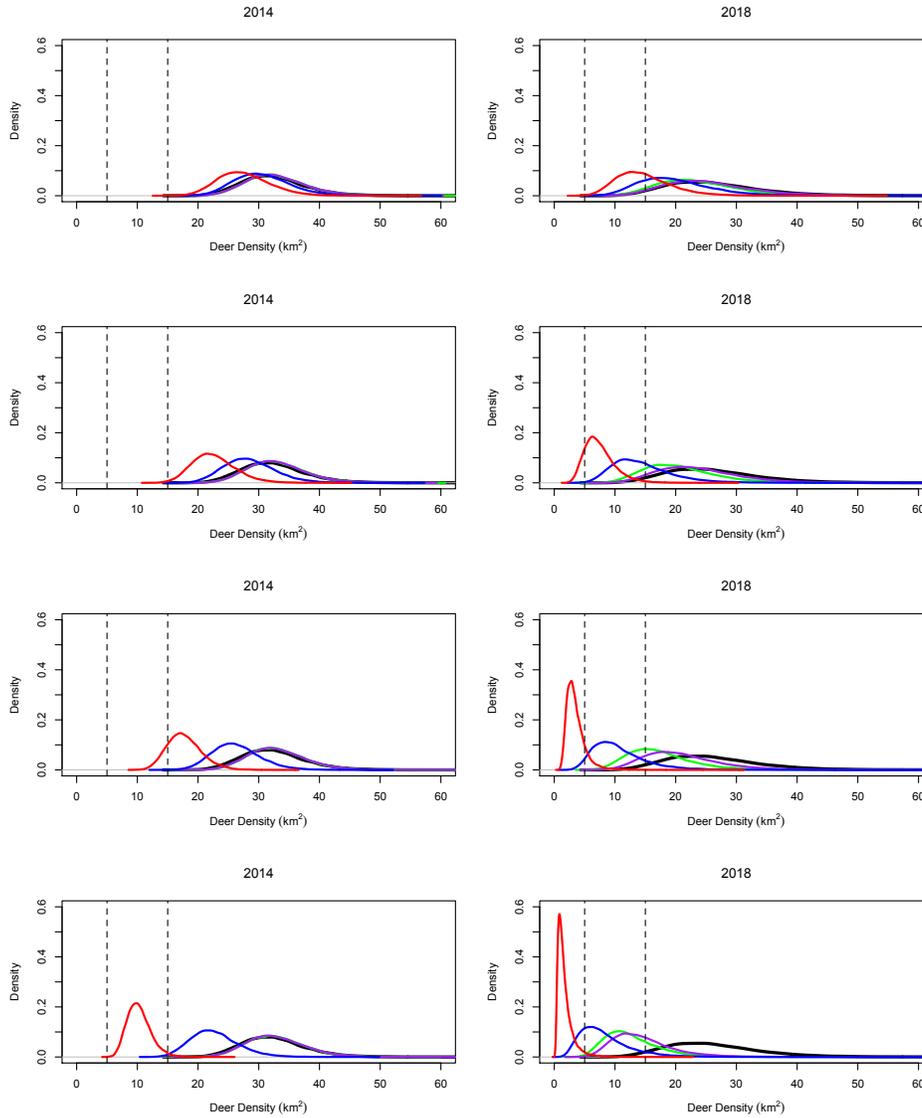


Figure 8: Effects of fertility control treatments on white-tailed deer population densities forecasted for 2014 and 2018 with plot rows corresponding to percent treated from top to bottom: 20%, 40%, 60%, and 90%. The black distribution represents the change in population with no action to show that the population may decrease without any management action. The purple distribution represents the population effect of contraceptives with one year effectiveness. The green distribution represents the population effect of contraceptives with three year effectiveness. The blue distribution represents sterilization. Sterilization reduced the population at a faster rate than contraceptives and may be worth further investigation. Culling (the red distribution) had the most dramatic effect on population density. The dotted vertical lines represent the bounds of the hypothetical management objective.

Table 3: We report the effects of four management actions (culling, sterilization, 1 year contraceptives, and 3 year contraceptives) at four different levels (20%, 40%, 60%, and 90% treated). For each treatment, we calculated the probability that the population will be below the objective (P <), within the objective (P in), and above the objective (P >). We also show the median number of adult females that would need to be treated throughout all parks.

Treatment	Percent Treated	Year	P <	P in	P >	Number Treated
No Action		2014	0.00	0.00	1.00	0
		2015	0.00	0.00	1.00	0
		2016	0.00	0.00	1.00	0
		2017	0.00	0.02	0.98	0
		2018	0.00	0.04	0.96	0
3 Year	20	2014	0.00	0.00	1.00	827
		2015	0.00	0.00	1.00	771
		2016	0.00	0.00	1.00	780
		2017	0.00	0.03	0.97	743
		2018	0.00	0.07	0.93	705
	40	2014	0.00	0.00	1.00	1652
		2015	0.00	0.00	1.00	1551
		2016	0.00	0.01	0.99	1574
		2017	0.00	0.06	0.94	1462
		2018	0.00	0.17	0.83	1363
60	2014	0.00	0.00	1.00	2481	
	2015	0.00	0.00	1.00	2333	
	2016	0.00	0.03	0.97	2361	
	2017	0.00	0.17	0.83	2127	
	2018	0.00	0.37	0.63	1927	
90	2014	0.00	0.00	1.00	3722	
	2015	0.00	0.01	0.99	3447	

		2016	0.00	0.14	0.86	3466
		2017	0.00	0.50	0.50	2970
		2018	0.00	0.73	0.26	2584
1 Year	20	2014	0.00	0.00	1.00	827
		2015	0.00	0.00	1.00	772
		2016	0.00	0.00	1.00	775
		2017	0.00	0.02	0.98	734
		2018	0.00	0.05	0.95	706
	40	2014	0.00	0.00	1.00	1652
		2015	0.00	0.00	1.00	1547
		2016	0.00	0.01	0.99	1567
		2017	0.00	0.03	0.97	1456
		2018	0.00	0.07	0.93	1389
	60	2014	0.00	0.00	1.00	2481
		2015	0.00	0.00	1.00	2328
		2016	0.00	0.01	0.99	2362
		2017	0.00	0.07	0.93	2144
		2018	0.00	0.16	0.84	1997
	90	2014	0.00	0.00	1.00	3722
		2015	0.00	0.01	0.99	3453
		2016	0.00	0.10	0.90	3495
		2017	0.00	0.40	0.60	3000
		2018	0.00	0.61	0.39	2660
Sterilize	20	2014	0.00	0.00	1.00	827
		2015	0.00	0.00	1.00	627
		2016	0.00	0.02	0.98	518
		2017	0.00	0.09	0.91	414

		2018	0.00	0.21	0.79	332
	40	2014	0.00	0.00	1.00	1652
		2015	0.00	0.01	0.99	980
		2016	0.00	0.11	0.89	645
		2017	0.00	0.36	0.64	410
		2018	0.00	0.61	0.39	269
	60	2014	0.00	0.00	1.00	2481
		2015	0.00	0.06	0.94	1060
		2016	0.00	0.36	0.64	504
		2017	0.00	0.69	0.31	236
		2018	0.04	0.81	0.15	115
	90	2014	0.00	0.01	0.99	3722
		2015	0.00	0.32	0.68	665
		2016	0.00	0.68	0.32	112
		2017	0.06	0.79	0.15	23
		2018	0.22	0.71	0.08	11
Cull	20	2014	0.00	0.00	1.00	827
		2015	0.00	0.02	0.98	626
		2016	0.00	0.14	0.86	519
		2017	0.00	0.36	0.64	420
		2018	0.00	0.57	0.43	345
	40	2014	0.00	0.01	0.99	1652
		2015	0.00	0.32	0.68	982
		2016	0.00	0.79	0.21	644
		2017	0.02	0.93	0.05	424
		2018	0.14	0.84	0.01	289
	60	2014	0.00	0.16	0.84	2481

	2015	0.00	0.93	0.07	1060
	2016	0.09	0.91	0.00	505
	2017	0.57	0.43	0.00	252
	2018	0.87	0.13	0.00	131
90	2014	0.00	0.98	0.02	3722
	2015	0.55	0.45	0.00	664
	2016	0.89	0.11	0.00	111
	2017	0.95	0.05	0.00	27
	2018	0.97	0.03	0.00	12

Culling to a desirable level followed by fertility control

Culling caused the highest reductions in the forecasted deer population, but culling more than 40% each caused the population to decrease < 5 deer per km^2 . Some managers seek a plan to reduce population by culling first then maintaining the population with an alternative management plan. We present the results from culling 90% the first year then administering 20%, 40%, 60%, and 90% of alternative management strategies that include sterilization, hypothetical 3 year contraceptives, and 1 year contraceptives (Figure 9 and Table 4). Contraceptives of 1 and 3 year efficacy had high probabilities of maintaining the population within the management objective. Sterilization had a high probability of maintaining the population the first few years but then had an increasing probability of decreasing the population below the management objective. Culling 90% the first year then implementing a fertility control regime greatly reduced the number of adult female deer that needed to be treated every year (Table 4).

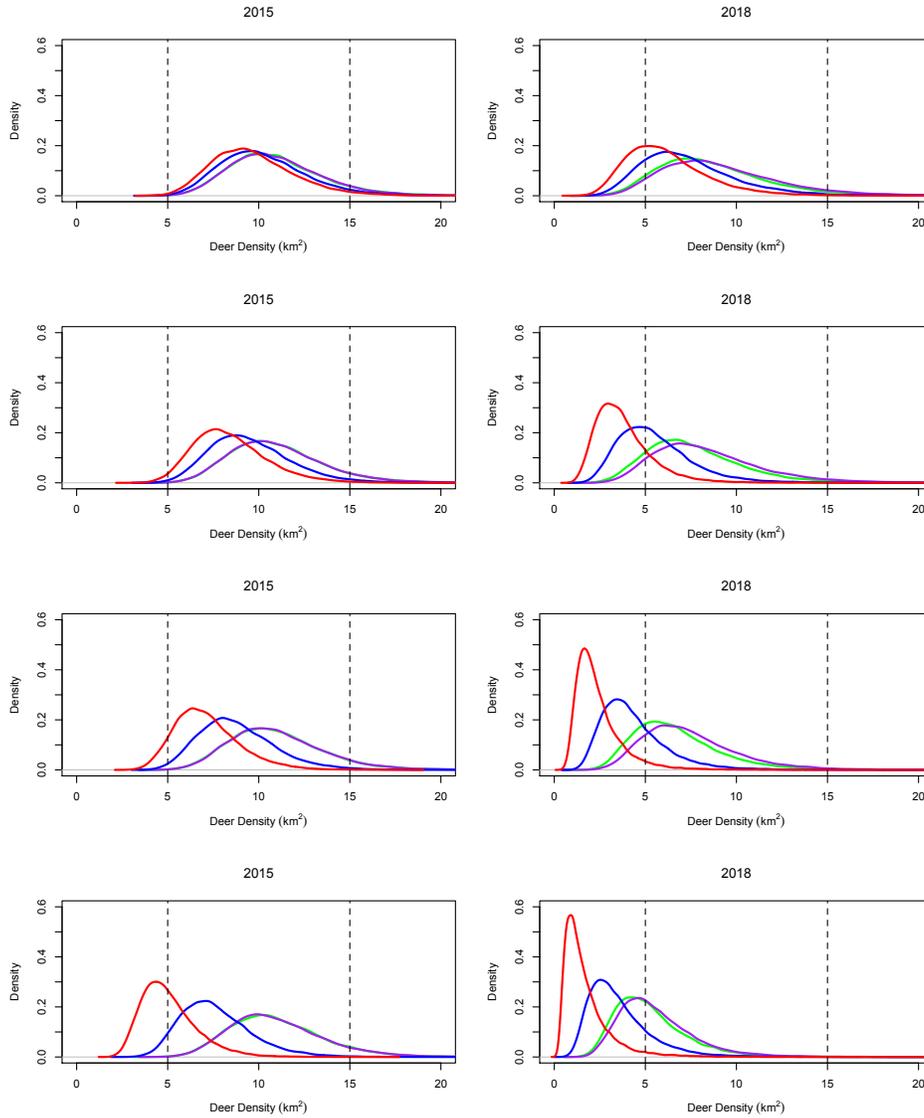


Figure 9: Effects of fertility control treatments on white-tailed deer population densities forecasted for 2015 and 2018 after culling to a management objective in 2014 followed by fertility control treatment. The rows corresponding to the percent of adult females treated from top to bottom: 20%, 40%, 60%, and 90%. The black dotted vertical line represents population density after culling in 2014 to give a baseline for population growth. The purple distribution represents the population effect of contraceptives with one year effectiveness which has the potential to maintain the population. The green distribution represents the population effect of contraceptives with three year effectiveness which has a similar effect to the 1 year contraceptives. The blue distribution represents sterilization. Sterilization reduced the population at a faster rate than contraceptives. The red distribution represents culling. Continuing to cull after an initial cull of 90% of the population further decreases the population beyond the management objective. The dotted vertical lines represent the bounds of the hypothetical management objective.

Table 4: We implemented four management actions (culling, sterilization, 1 year contraceptives, and 3 year contraceptives) at four different levels (20%, 40%, 60%, and 90% treated) after culling 90% of the adult female population. For each treatment, we calculated the probability that the population will be below the objective ($P <$), within the objective ($P \text{ in}$), and above the objective ($P >$). We also show the median number of adult females that would need to be treated throughout all parks.

Treatment	Percent Treated	Year	$P <$	$P \text{ in}$	$P >$	Number Treated
3 Year	20	2015	0.00	0.93	0.07	291
		2016	0.01	0.95	0.04	272
		2017	0.03	0.92	0.04	304
		2018	0.07	0.88	0.04	298
	40	2015	0.00	0.93	0.07	291
		2016	0.01	0.96	0.03	272
		2017	0.06	0.92	0.02	304
		2018	0.13	0.85	0.02	298
	60	2015	0.00	0.93	0.07	443
		2016	0.03	0.96	0.02	413
		2017	0.10	0.89	0.01	463
		2018	0.25	0.74	0.01	437
	90	2015	0.00	0.93	0.07	660
		2016	0.07	0.92	0.01	609
		2017	0.21	0.79	0.00	685
		2018	0.52	0.48	0.00	599
1 Year	20	2015	0.00	0.93	0.07	148
		2016	0.01	0.95	0.04	136
		2017	0.03	0.92	0.05	152
		2018	0.06	0.89	0.06	154
	40	2015	0.00	0.93	0.07	291
		2016	0.02	0.96	0.03	272

		2017	0.04	0.93	0.04	304
		2018	0.09	0.88	0.03	299
	60	2015	0.00	0.93	0.07	443
		2016	0.03	0.96	0.02	414
		2017	0.07	0.91	0.02	465
		2018	0.16	0.83	0.01	437
	90	2015	0.00	0.93	0.07	660
		2016	0.07	0.93	0.01	610
		2017	0.18	0.82	0.01	686
		2018	0.46	0.54	0.00	603
Sterilize	20	2015	0.00	0.96	0.04	148
		2016	0.02	0.96	0.02	111
		2017	0.08	0.91	0.02	104
		2018	0.17	0.81	0.01	90
	40	2015	0.00	0.98	0.02	291
		2016	0.07	0.93	0.01	171
		2017	0.23	0.77	0.00	129
		2018	0.46	0.54	0.00	90
	60	2015	0.01	0.98	0.01	443
		2016	0.16	0.83	0.00	185
		2017	0.47	0.53	0.00	107
		2018	0.72	0.28	0.00	55
	90	2015	0.05	0.94	0.00	660
		2016	0.39	0.61	0.00	111
		2017	0.69	0.31	0.00	27
		2018	0.83	0.16	0.00	12
Cull	20	2015	0.00	0.97	0.02	148

	2016	0.05	0.94	0.01	110
	2017	0.17	0.82	0.01	104
	2018	0.34	0.66	0.00	91
40	2015	0.02	0.98	0.01	291
	2016	0.25	0.75	0.00	171
	2017	0.60	0.40	0.00	129
	2018	0.82	0.18	0.00	91
60	2015	0.09	0.91	0.00	443
	2016	0.63	0.37	0.00	185
	2017	0.88	0.12	0.00	106
	2018	0.95	0.05	0.00	56
90	2015	0.55	0.45	0.00	660
	2016	0.89	0.11	0.00	111
	2017	0.95	0.05	0.00	27
	2018	0.97	0.03	0.00	12

Discussion

Parameters in Context

We estimated vital rate parameters and forecasted deer abundance into the future giving probabilistic inference to managers seeking to reduce populations of overabundant ungulates. Our estimate of adult female survival (0.74, SD = 0.051) matches results we calculated from published literature (0.74, SD = 0.14) (Brinkman et al. 2004; Campbell et al. 2005; DePerno et al. 2000; Dusek et al. 1992; Fuller 1990; Grovenburg et al. 2011; Van Deelen et al. 1997; Whitlaw et al. 1998). Our estimate for juvenile survival (0.37, SD = 0.11) was much lower than the average from previous literature (0.67, SD = 0.20) (Brinkman et al. 2004; Burroughs et al. 2006; Campbell et al. 2005; Fuller 1990; Van Deelen et al. 1997; Vreeland et al. 2004;

Whitlaw et al. 1998; Wickham et al. 1993). This difference in survival could be due to the higher than average deer densities found in our study area resulting in overgrazing leading to poor body condition. In addition, the adult male survival probability estimated in our model (0.67 SD = 0.1) is higher than the adult male survival probabilities found in the literature (0.39, SD = 0.19) (Bowman et al. 2007; Campbell et al. 2005; Fuller 1990; Van Deelen et al. 1997). This could be due to lower harvest rates in the National Capital Region compared to the study areas of previous research.

It is important to represent density dependence in this population model of white-tailed deer because culling a population may elevate recruitment (Diamond 1992). We did detect density dependence but our parameter estimates are much lower than expected. Our model estimated the maximum birth rate of white-tailed deer to be $r_f = 0.61$ with an SD = 0.11. The number of juvenile per adult female at low densities has typically been reported to be near 0.98 (McCullough 1979) or 1.30 (Fuller 1990). Our estimate for carrying capacity was also lower than the current regional median ($K_f = 22$, SD = 3.1). There are three reasons why this may have happened. First, the birth rates reported by McCullough (1979) and Fuller (1990) do not include neonatal survival. Second, our model estimated a lower than expected maximum birth rate to account for low numbers of births observed in the data. Finally, our model does not differentiate between female adults and yearlings, and yearlings are known to produce fewer fawns (Vreeland et al. 2004).

Our model also does not have an explicit term for immigration/emigration because we do not have data to support an estimate for that parameter. This information gap can be justified because white-tailed deer exhibit high site fidelity, and it has also been shown that reduction in deer density does not lead to increased immigration (Kilpatrick et al. 2001). That may not be the case in our situation because of the small size of the parks in our study area. The reduction of white-tailed deer in a small area may be trivial because they will soon be replaced by surrounding deer. What we have presented here is the ideal situation for use of fertility control. We assume that any immigration/emigration that may occur

becomes part of the process variance of our model. Further improvement to the model could be implemented by placing GPS or VHF tracking devices which would inform an immigration/emigration parameter.

Assessing Relative Effort

Our model provides an estimate of population growth rate and probabilities that specific management regimes will achieve and/or maintain a reduction in a white-tailed deer population below carrying capacity. It has been shown, theoretically, that culling a population to a certain level followed by introducing contraceptive methods may maintain a population at a level below carrying capacity (Hobbs et al. 2000; Hone 1992; Barlow et al. 1997). Our results suggest that all types of fertility control, including culling, will accelerate the decline in the population. However, the number of individuals that need to be treated in order to reach a stated objective (i.e., relative effort) differs greatly between contraceptives (1 or 3 year efficacy) and culling/sterilization.

The white-tailed deer population in the Washington, D.C. area will decrease with no action ($\lambda = 0.883$, BCI = 0.8, 0.971). This decline depends on harvest outside of the National Parks. If harvest remains constant causing the survival probabilities to stay the same, the population will decrease by 50% in 10 years. Therefore, encouraging harvest outside of the parks may be a sufficient management strategy. When the projection matrix was subjected to any fertility control regime, the population decrease accelerated. Contraceptives with an average of three year effectiveness had a slightly larger effect on population growth rate than contraceptives with an average of one year effectiveness, causing the population to decrease by 50% in 6 years if survival probabilities remain constant. Using contraceptives alone has a higher variance and a slower effectiveness than sterilization unless a large fraction of the population can be treated with contraceptives ($> 90\%$). Sterilization also decreased the population growth rate (0.73). Culling had the most dramatic effect on population growth rate causing the population to decrease by more than 50% in 1 year if 90% of the adult female population were culled.

Managers may seek to reduce a population more rapidly than the population is currently decreasing with a low relative effort. It is possible to rapidly accelerate population reduction of white-tailed deer with contraceptives, but only if 90% are treated for several sequential years. The number of adult female deer that would need to be given contraceptives to reduce the population quickly would exceed 16200 over 5 years throughout all parks. The cost per doe for non-surgical fertility control is estimated to be \$750. Implementing this management regime would cost over \$12,000,000 with a low probability of achieving the objective (1 year contraceptives Probability in = 0.61, 3 year contraceptives Probability in = 0.73). Sterilization has a high probability of success if between 60% (Probability in = 0.81) and 90% (Probability in = 0.71) of adult females are treated each year, but the costs would be more than double contraceptives. Culling, on the other hand, has a low relative effort. The cost per doe for culling is estimated to be \$370. Only 3990 adult females (40%) need to be culled over 5 years (\$1,480,000) to have a probability of 0.84 of being within the management objective. With our hypothetical management objective, it would be 91% more efficient to cull 40% of females each year than it would be to administer 90% of females each year with contraceptives. These results highlight that using contraceptives alone to control a population is not a viable option for managers seeking to reduce the deer population rapidly with low relative effort.

Each of the management strategies has its own set of undesirable effects. For instance, culling alone can cause a population to fall below a desirable management objective and in extreme cases cause the population to become extinct. Regulated harvests can be unpopular with the public or logistically complicated due to proximity to urban areas. However, reducing the survival of a population decreases the relative effort of reducing the population by contraceptives or sterilization. Using contraceptives after culling to a desired management objective may be a very effective way to maintain a population below carrying capacity because fewer animals need to be culled and fewer animals need to be treated with contraceptives (Table 4). If 90% adult females were culled the first year followed by 1 year

contraceptives administered to 20% for 5 years, the probability that the population would be within the management objective is 0.89. A hypothetical treatment plan may be as follows: 0.98 adult females would need to be culled the first year (\$1,380,000) and 590 would need to be administered contraceptives over the next four years (\$590,000). This type of management plan reduces the relative effort 88% compared to using only fertility control and increases the probability that the population will remain below carrying capacity but will not become endangered.

Conclusion

Management of overabundant ungulates has become a point of contention in several ecosystems around the world because of the excessive amount of environmental and economic damage (Pimentel et al. 2005; Garrott et al. 1993). Managers need an approach that balances goals of conservation as well as wildlife wellbeing. In this study, we have described a framework for forecasting the effects of different fertility control regimes and comparing possible management actions. The robustness of the dataset allowed for the use of statistically rigorous methods for estimating white-tailed deer abundance.

We have provided evidence confirmed with 13 years of data that contraceptives alone will reduce the population growth rate more than no action but will not reduce the population rapidly unless $> 90\%$ can be treated. Sterilization has the potential to decrease the population and maintain it below carrying capacity if 60% of adult females can be treated each year. However, if the objective is to reduce the population rapidly, the relative effort of implementing these fertility control regimes outweighs the probability that the management objective will be achieved unless there is an initial cull. Culling to a predetermined level followed by administering lower amounts of fertility control, rather than implementing a contraceptive program alone, would be an efficient way to achieve management objectives below carrying capacity with low relative effort. We suggest that managers of overabundant ungulates estimate vital rate parameters with associated uncertainty to assess which management regime will balance relative effort with a population objective in their ecosystem.

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APPENDIX

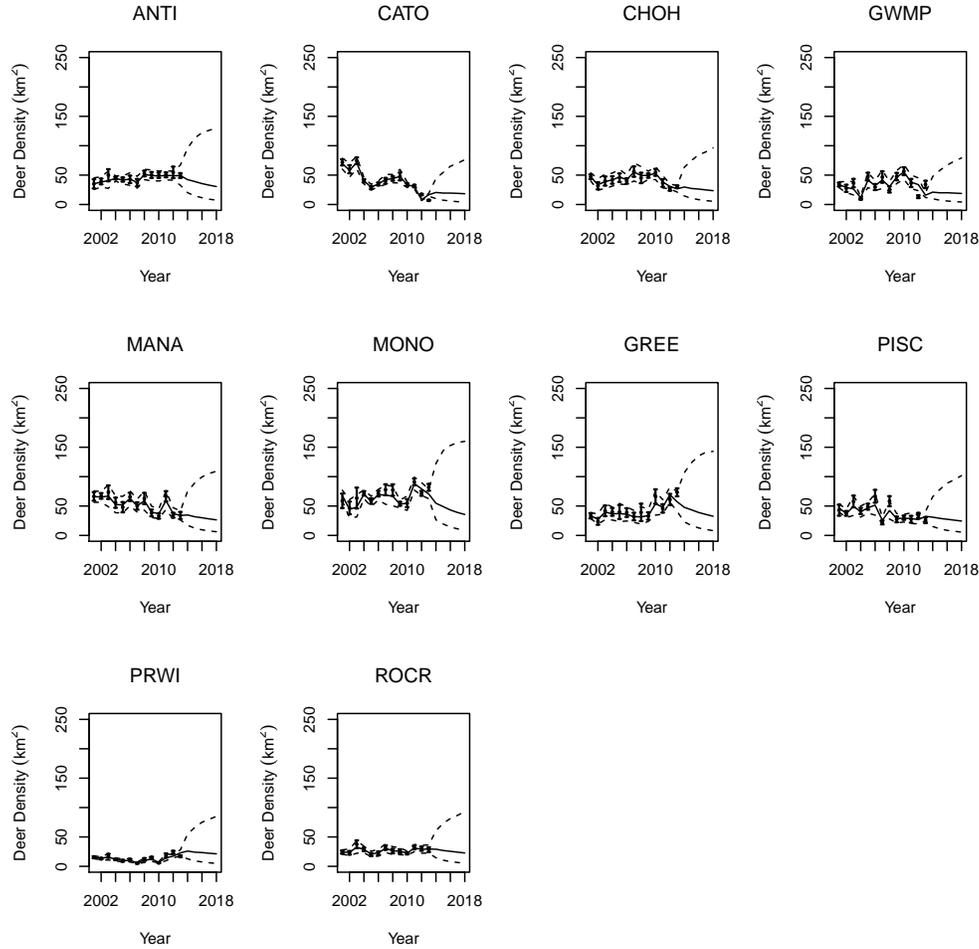


Figure 11: Forecast by park for the years 2001 to 2018. The solid line is the median of the estimate. The dashed lines are the 95% Bayesian credible intervals (BCI) of the estimate. The dots with vertical lines are the medians of the data with standard deviation error bars. The abbreviations for each park are in the titles of each plot. ANTI: Antietam National Battlefield, CATO: Catoclin Mountain Park, CHOH: Chesapeake and Ohio Canal NHP, GWMP: George Washington Memorial Parkway, MANA: Manassas National Battlefield Park, MONO: Monocacy National Battlefield, GREE: Greenbelt Park as part of the National Capital Parks East, PISC: Piscataway as part of the National Capital Parks East, PRWI: Prince William Forest Park, ROCR: Rock Creek Park

$$\begin{aligned}
& \left[\boldsymbol{\theta}, \mathbf{n}_{it}, \sigma^2 \mid \mathbf{y}_{\boldsymbol{\alpha}_{it}}, y_{d_{it}}, \hat{\sigma}_{it}, y_{N_{it}} \right] \\
& \propto \prod_{i=1}^{10} \prod_{t=1}^{13} \left(\left[\mathbf{y}_{\boldsymbol{\alpha}_{it}} \mid y_{N_{it}}, \boldsymbol{\pi}_{it} \right] \right) \\
& \times \prod_{i=1}^{10} \prod_{t=1}^{13} \left(\left[y_{d_{it}} \mid \frac{\sum_{j=1}^3 n_{jit}}{area_i}, \hat{\sigma}_{it}^2 \right] \left[\log(\mathbf{n}_{it}) \mid \log(\mathbf{A}_{it-1} \mathbf{n}_{it-1}), \sigma_p^2 \right] \right) \\
& \times \prod_{i=1}^{10} \left(\left[n_{i1} \mid y_{d_{i1}}, \hat{\sigma}_{i1}^2 \right] \left[\gamma_{i1} \mid \mathbf{y}_{\boldsymbol{\alpha}_{i1}} + 1 \right] \right) \\
& \times \prod_{j=1}^3 \left[s_j \mid 1, 1 \right] \left[r_f \mid 2 \cdot 3.09W^{-0.33}, .1304^2 \right] \left[K_f \mid 0, 100 \right] \left[m \mid 312, 312 \right] \left[\sigma^2 \mid 0, 2 \right]
\end{aligned}$$

Figure 10: The full posterior and joint distributions. The distributions and definitions of parameters are given in the methods section.