

TIME TO REDUCTION: FACTORS INFLUENCING MANAGEMENT EFFICACY IN STERILIZING OVERABUNDANT WHITE-TAILED DEER

JOHN A. MERRILL,¹ Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA
EVAN G. COOCH, Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA
PAUL D. CURTIS, Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA

Abstract: In managing overabundant white-tailed deer (*Odocoileus virginianus*), fertility control frequently is regarded as a viable alternative to lethal strategies. However, little information is available concerning expected duration of fertility control. Our objectives were to create a flexible model for application in a diverse array of environmental conditions, determine the extent to which various parameters contributed to population growth, and assess the time necessary to reduce a population to a given level. The modeled population was assumed geographically closed without density dependence. Using prospective perturbation analysis on a linear time-invariant Lefkovich matrix model, survival rates contributed to overall population growth nearly twice that of birth rates. Using numerical analysis, a general relationship between annual sterilization rate, desired population reduction, and time to that reduction was determined. This relationship was nonlinear and showed decreased efficiency per unit effort. Depending on local parameter values, we determined that a population could be reduced by 30% to 60% in 4–10 years if a manager could sterilize 25–50% of available fertile females annually. Thus, sterilization may be a viable option for communities with the financial resources and political will to sterilize.

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Effective control of species regarded as overabundant, such as white-tailed deer, is of increasing concern to conservation biologists and wildlife managers. White-tailed deer populations have reached unprecedented levels throughout the eastern United States as aesthetic preference for forested suburban landscapes have created large areas of virtually predator-free habitat (Diamond 1992, McCollough et al. 1997). Tolerance for deer in many areas has been exceeded due to automobile collisions and damage to residential vegetation and local ecosystems (Decker and Connelly 1989, Diamond 1992, McCollough et al. 1997, Curtis et al. 1998). In an increasing number of communities, however, hunting, culling, and other lethal management strategies have become impractical for legal and ethical reasons (Decker and Connelly 1989, Wright 1993, McCollough et al. 1997), fostering interest in alternatives. However, most nonlethal strategies have proven ineffective. Deer adapt to deterrence measures (e.g., noise and fencing) by becoming increasingly desensitized (Decker and Connelly 1989, McCollough et al. 1997). Translocation is rarely feasible due to limited release sites and stress suffered on transport and arrival (Waas et al. 1999). Predator reintroduction is unacceptable to most stakeholders for safety reasons (Diamond 1992).

Fertility control has been proposed as an alternative to lethal techniques (Tyndale-Biscoe 1991, Wright 1993). Duration can vary from transient (e.g., immunocontraception, in which the effects of treatment may last less than the lifetime of the individual) to permanent sterilization. Immunocontraception has shown potential under some circumstances, but may be unsuitable in a number of communities. For instance, long-term costs of immunocontraception may be prohibitive due to expected time horizons (defined here as the time between initially sterilizing a population and reaching an a-priori reduction objective), uncertainty in identifying treated individuals, and the need for a regular boosting schedule (Kirkpatrick et al. 1997, Muller et al. 1997, Pech et al. 1997, Rudolph et al. 2000). Additionally, dart rifles used for immunocontraception invoke legal and safety concerns, which stakeholders may wish to avoid. Therefore, we limited the scope of our study exclusively to permanent sterilization.

The relative efficacies of lethal control and sterilization have been compared theoretically under certain assumptions (Knipling and McGuire 1972, Garrott 1991, Pech et al. 1997, Bromley and Gese 2001). For deer, Boone and Wiegert (1994) identified sterilization as a viable alternative to lethal control when used to supplement hunting pressure but concluded that a massive initial effort was needed. Seagle and Close (1996) looked at the effects of various sterilization pro-

¹ E-mail: jam82@cornell.edu

portions, but did not explicitly examine uncertainty in survival and birth rates (although they did model these parameters stochastically). Barlow et al. (1997) found that modeled populations with density-dependent adult mortality were reduced by sterilization earlier than those regulated by density-dependent recruitment.

Hobbs et al. (2000) showed that fertility control of varying duration could regulate ungulate populations under some circumstances (e.g., a closed population [here, meaning only without immigration or emigration], infinite time horizon, and the ability to identify treated individuals) and that, in some cases, sterilization may be more effective in maintaining desired population sizes than lethal control. Hobbs et al. (2000), however, evaluated sterilization using asymptotic equilibrium assumptions calculated over infinite time horizons and did not consider the relative efficiency for finite, fixed time horizons. Therefore, the effectiveness of sterilization is uncertain if stakeholders want a given reduction within 5 or 10 years—time scales over which local communities often make their decisions.

In addition, the role of uncertainty in population demographics has not been adequately evaluated for fertility control. While the effects of changing survival or birth rates have been noted (Boone and Wiegert 1994, Barlow et al. 1997, Hobbs et al. 2000), no clear relationship has been shown between specific demographic parameters and management goals.

Managers must evaluate 2 aspects of using sterilization as a management tool: (1) whether reducing the population through sterilization is biologically possible, and (2) whether sterilization can be practically implemented. Here, we address the former, because the inquiry of whether population reduction by sterilization is biologically possible logically precedes questions regarding its application. In reality, managers must assess implementation questions such as cost. However, conditions and available resources could vary dramatically between communities, so we examined the relationship between various biological parameters of a deer herd and management effort. Management effort (hereafter effort) is defined in our study as the number of sterilizations over a particular time horizon. Effort is related to but not synonymous with cost.

We assessed the dynamics of a hypothetical deer population subjected to sterilization. We considered the proportion of the population that would need to be sterilized annually to achieve a target

reduction under various conditions and time horizons. In addition, we examined the consequences of uncertainty concerning parameter estimates, the initial composition of the population, and the ability to selectively sterilize fertile females.

METHODS

Base Model

We examined the effects of sterilization on the dynamics of a hypothetical white-tailed deer population using a linear time-invariant female-based matrix model:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \quad (1)$$

where $\mathbf{n}(t)$ was a vector giving abundances of each stage in the population at time t and \mathbf{A} was the population projection matrix where the ij^{th} entry, a_{ij} , indicated the average contribution of an individual in stage j to stage i over one time step. The projection interval (from t to $t+1$) was 1 year.

Our base population model (only females without sterilization) consisted of 3 age classes, which corresponded to: fawns (0–1 years old, class 0), yearlings (1–2 years old, class 1), and adults (≥ 2 years old, class 2). Our base model was entirely specified by the birth and survival rate of age class i , B_i and S_i , respectively, and has the following structure:

$$\mathbf{A} = \begin{bmatrix} S_0 B_1 & S_1 B_2 & S_2 B_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{bmatrix}. \quad (2)$$

This model made several simplifying assumptions. First, we assumed density-independence. Although density-dependence ultimately is a logical necessity for all populations, our initial interest focused on urban deer populations currently experiencing rapid growth, where density feedback on survival or fertility was small (Decker and Connelly 1989, Curtis et al. 1998). Second, we assumed a population under conditions of geographic closure. Because female deer generally inhabit small ranges with high site fidelity (Labisky and Fritzen 1998, Grund et al. 2002), we considered this assumption reasonable. Additionally, because our primary purpose was to gauge the relative influence of various factors on the time needed to reach a desired population reduction, we considered examining the dynam-

ics under ideal (i.e., simple) conditions as instructive. Third, we assumed that the population was not male-limited and that we could accurately assess dynamics from only females. Fourth, we assumed age-class homogeneity (i.e., every individual in each class had identical parameters and behavior). Finally, the base model assumed a post-breeding census, which advanced the birth rate contributions by 1 age class (i.e., 1 year passes between censuses). For instance, a yearling at time t (N_{1t}) contributed to fawns at time $t + 1$ at rate B_2 because it survived to breed as an adult (N_{2t+1}) before the census at time $t + 1$. Fawns contribute to fecundity because they became yearlings between censuses. The number of fawns at time $t + 1$ is given by

$$N_{0,t+1} = \sum_{i=0}^2 N_i S_i B_{i+1} \quad (\text{where } B_3 = B_2) \quad (3)$$

Model Development: Addition of Sterilization

We modified our base model to reflect the sterilization of females in our hypothetical deer population. The sterilization rate of age class i is represented by θ_i . In effect, this served to create a second gender classification of sterilized females. For a fertile female to produce offspring, she must survive and avoid sterilization ($1 - \theta_i$). Conversely, the sterilized age class was the sum of newly sterilized and surviving sterilized females. For example, in a given year, $t + 1$, the 1 year-old (yearling) age class would consist of $N_{f1,t+1}$ fertile individuals: the number of fertile female fawns surviving from t ,

$$N_{f1,t+1} = N_{f0} S_{f0} (1 - \theta_1), \quad (4)$$

and $N_{s1,t}$, the number of sterile females who were newly sterilized or survived from the previous year

$$N_{s1,t+1} = N_{f0} \theta_0 + N_{s0} S_{s0}, \quad (5)$$

(where the subscript, s , indicated sterilized individuals, and the subscript, f , indicated fertile individuals). Similarly, the number of fertile fawns at time t was the cumulative product of net fertility from females that had not been sterilized (eq. 7).

$$N_{f0,t+1} = \sum_{i=0}^2 N_{fi} S_{fi} B_{i+1} (1 - \theta_i) \quad (\text{where } B_3 = B_2). \quad (6)$$

The modified projection matrix including sterilization is

$$A = \begin{bmatrix} S_0 B_1 (1 - \theta_0) & S_1 B_2 (1 - \theta_1) & S_2 B_1 (1 - \theta_2) & 0 & 0 & 0 \\ S_0 (1 - \theta_0) & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 (1 - \theta_1) & S_2 (1 - \theta_2) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ S_0 \theta_0 & 0 & 0 & S_0 & 0 & 0 \\ 0 & S_1 \theta_1 & S_2 \theta_2 & 0 & S_1 & S_2 \end{bmatrix}. \quad (7)$$

This modified model makes the same assumptions as the base model. In addition, the model assumes the following ordering of life events: mortality, births, census, and sterilizations. Hence, sterilized fawns became yearlings by the next census, so we had no observable sterilized fawns.

Our modified model was female-based and assumed that only females are sterilized. We made this assumption because practically all males would need to be sterilized to reduce the population even under conditions of geographic closure (Garrott and Siniff 1992). Conversely, the benefits of sterilizing females, in theory, are additive (Hobbs et al. 2000). Nevertheless, although males were not directly sterilized, they are inherently affected by female sterilization. By sterilizing females, we changed the overall birth rate and altered the recruitment of male fawns. Therefore, we had to include males in the model if we were to use total population size as an indicator of the progress of sterilization as a management tool. We can still accurately say that this model is not male-limited, however. While sterilization affects male numbers, we assume that reproductive limitations are compensatory in male deer. For instance, few mature male deer can impregnate many receptive female deer. Thus, we do not need a maternity function that relates the total number of mature male deer to recruitment.

Thus, we further modified the model to include males (Fig. 1). This modified model was entirely specified by the survival rate (S_{xi}) of age class i and gender classification x , the birth rate (B_{fi}), the sterilization rate (θ_{fi}) of fertile female age class i , and the probability of a fawn being female (ω). We now had 9 classifications: 3 age classes in each of 3 gender classifications. Because we were no longer concerned with only female fawns, the birth rate was now the average number of total fawns produced per fertile female in an age class. For example, the number of male fawns is

$$N_{m0,t+1} = (1 - \omega) \sum_{i=0}^2 N_{fi} S_{fi} B_{i+1} (1 - \theta_i) \quad (\text{where } B_3 = B_2), \quad (8)$$

which is the equivalent of equation 6 multiplied by the probability that the fawn is not a female.

The projection matrix corresponding to our final model is

$$\mathbf{A} = \begin{bmatrix}
 0 & 0 & 0 & S_{f_0}(1-\varpi)B_{f_1}(1-\theta_0) & S_{f_1}(1-\varpi)B_{f_2}(1-\theta_1) & S_{f_2}(1-\varpi)B_{f_3}(1-\theta_2) & 0 & 0 & 0 \\
 S_{m_0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & S_{m_1} & S_{m_2} & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_{f_0}\varpi B_{f_1}(1-\theta_0) & S_{f_1}\varpi B_{f_2}(1-\theta_1) & S_{f_2}\varpi B_{f_3}(1-\theta_2) & 0 & 0 & 0 \\
 0 & 0 & 0 & S_{f_0}(1-\theta_0) & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & S_{f_1}(1-\theta_1) & S_{f_2}(1-\theta_2) & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_{f_0}\theta_0 & 0 & 0 & 0 & S_{s_0} & 0 \\
 0 & 0 & 0 & 0 & S_{f_1}\theta_1 & S_{f_2}\theta_2 & 0 & S_{s_1} & S_{s_2}
 \end{bmatrix} \quad (9)$$

This matrix is reducible and is therefore affected by initial conditions (Grant and Benton 2000, Caswell 2001). We varied the starting population composition using 3 initial population vectors: all adults, all fawns, and a vector where the age distribution matched the equilibrium standard stage distribution (SSD).

To assess how each parameter impacted the growth rate of the population, we used prospective perturbation analysis (sensitivity and elasticity; sensu Benton and Grant 1999, Caswell 2001,

McLeod and Saunders 2001) and numerical simulation. The projected growth rate of the model was derived as the dominant eigenvalue λ of the matrix. Perturbation analysis was followed by numerical projection to demonstrate specific effects of variation (uncertainty) in survival and fertility. Numerical analysis allowed us to observe the effects of sterilization on population abundance under numerous conditions (Grant and Benton 2000) and calculate the time necessary, under the assumptions of the model, to reach a given population reduction under all possible θ s.

We parameterized our models using values from Boldgiv (2001) based on a recent study of a small urban population of white-tailed deer in upstate New York. The range of values, denoted as low, medium, and high (Table 1), encompasses most conditions encountered in urban deer habitat. All analyses used medium parameter values unless otherwise noted.

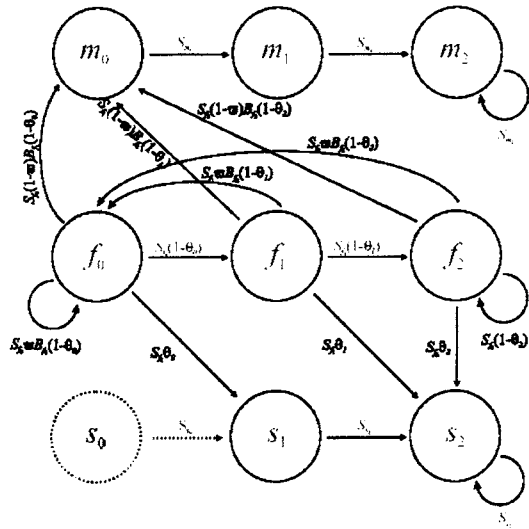


Fig. 1. Life-cycle graph for final model with both males and sterilized females. Node y_x refers to age class x in gender classification y . We included 3 gender classifications (unsterilized females [f], sterilized females [s], and males [m]), and three age classes (fawns [0], yearlings [1], and adults [2]). The dashed node, s_0 , represents sterilized fawns. The timing of our model (post-breeding census) implies surviving sterilized fawns become yearlings by the next census (i.e., sterilized fawns are never observed at time of census). Within the model, and represent the survival and birth rates, respectively, of age class x in gender classification y ; θ represents the annual sterilization rate of fertile females in age class t ; and ϖ represents the probability of a newborn fawn being female. Model assumes a geographically closed population that is not male-limited (i.e., males do not directly contribute to the fawn age class via a maternity function).

RESULTS

Model Results—Prospective Perturbation Analysis

Using medium values for all parameters (Table 1), the projection matrix \mathbf{A} corresponding to Fig. 1 was

$$\mathbf{A} = \begin{bmatrix}
 0 & 0 & 0 & 0.451 & 0.672 & 0.792 & 0 & 0 & 0 \\
 0.55 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0.3 & 0.45 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0.451 & 0.672 & 0.792 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0.55 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0.7 & 0.825 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0.55 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.7 & 0.825
 \end{bmatrix} \quad (10)$$

For this matrix \mathbf{A} , the projected growth rate $\lambda = 1.274$ (for matrices with low birth and survival

rates, $\lambda = 1.091$; with high rates, $\lambda = 1.484$), with the corresponding elasticity matrix **E**,

$$\mathbf{E} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \sim 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.125 & 0.08 & 0.148 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.228 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.148 & 0.271 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sim 0 \end{bmatrix} \quad (11)$$

Note that survival elasticities are nearly twice those of birth rates, indicating that a given change in survival will have twice the impact on projected growth as would an equivalent change in birth rate. For an explanation of why non-zero matrix elements have zero elasticity values, see Appendix A.

We partitioned contributions of each matrix element a_{ij} to population growth into contributions from lower-level elements of the matrix, $e(x)$. Fertile female survival rates had the largest lower-level elasticity values [$e[S_{f_2}] = 0.4188$, $e[S_{f_1}] = 0.2280$, $e[S_{f_0}] = 0.3529$], and birth rates had a smaller influence [$e[B_{f_2}] = 0.2280$, $e[B_{f_1}] = 0.1249$]. Additionally, the sex ratio, ω , has a large impact [$e[\omega] = 0.3529$] on the growth of the population. The elasticities for the survival rates of male and sterilized females equaled zero, consistent with the results of the above elasticity analysis.

Model Results—Numerical Projection

The time to reach a specified reduction level varied nonlinearly with sterilization fraction, θ (Fig. 2), consistent with Hone (1992). An increase in the fraction sterilized produced a diminishing

Table 1. Parameter values used in analytical and numerical analysis. Unless otherwise noted, we used medium birth and survival rates as mean predictions. Parameter estimates were obtained from Boldgiv (2001).

Stage (parameter)		Low	Medium	High
Birth rates	Yearlings (B1)	1.53	1.70	1.87
	Adults (B2)	1.74	1.92	2.10
Survival rates	Female fawns (S_{f_0}, S_{s_0})	0.45	0.55	0.65
	Female yearlings (S_{f_1}, S_{s_1})	0.65	0.70	0.75
	Female adults (S_{f_2}, S_{s_2})	0.75	0.825	0.90
	Male fawns (S_{m_0})	0.45	0.55	0.65
	Male yearlings (S_{m_1})	0.15	0.30	0.45
	Male adults (S_{m_2})	0.40	0.45	0.50

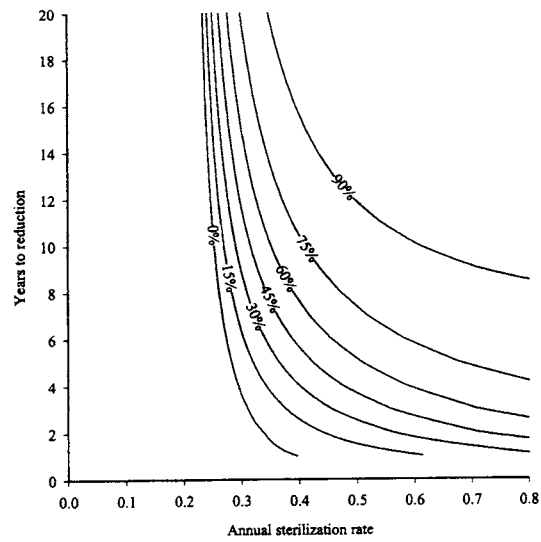


Fig. 2. Population reduction (percent reduction of the current deer abundance) as a function of time (in years) and annual sterilization rate assuming medium survival and birth rates ($B_1 = 1.70$, $B_2 = 1.92$, $S_{f_0} = S_{s_0} = 0.55$, $S_{f_1} = S_{s_1} = 0.70$, $S_{f_2} = S_{s_2} = 0.825$, $S_{m_0} = 0.55$, $S_{m_1} = 0.30$, $S_{m_2} = 0.45$). Sterilization rates represent a constant proportion of fertile females rendered sterilized each year. Contour shifts up or to the right indicate increased management effort.

marginal gain in time to desired reduction. For instance, with a 3-year time frame, an increase from a zero percent reduction (stable, nongrowing population) to a 30% reduction, required the sterilization fraction to be increased from 0.3 to 0.5. However, an increase from a 30% reduction to a 60% reduction required the proportion sterilized to be increased from 0.45 to 0.75. An increase in desired reduction produced a similar diminishing marginal gain. Reaching a 75% reduction instead of a 60% reduction, at $\theta = 0.5$, required an additional 2-year wait. Reaching a 90% reduction instead of a 75% reduction required an additional 6 years.

A minimum sterilization fraction was required to achieve any given reduction level, regardless of time (graphically interpreted as vertical asymptotes in Figs. 2 through 5). This reflects positive growth of an unregulated, density-independent population in the absence of sterilization. These asymptotic values were close together for small sterilization fractions over long time intervals, thus errors at lower sterilization levels could have large impacts in the reduction achieved, consistent with Seagle and Close (1996) and Pech et al. (1997).

Birth Rate.— As we increased birth rates, management effort (in time and sterilizations) increased, but only moderately (Fig. 3a). Effects

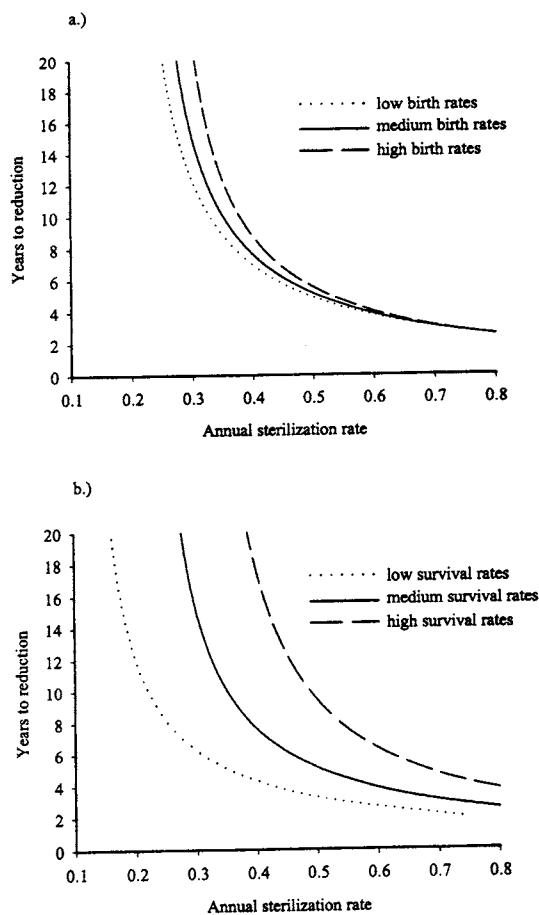


Fig. 3. Effects of variation in (a) births and (b) survival rates on the time to 60% reduction in initial deer abundance. In (a), survival rates are held constant and, in (b), birth rates are held constant, at medium levels. Low levels: $B_1 = 1.53$, $B_2 = 1.74$, $S_{f0} = S_{s0} = 0.45$, $S_{f1} = S_{s1} = 0.65$, $S_{f2} = S_{s2} = 0.75$, $S_{m0} = 0.45$, $S_{m1} = 0.15$, $S_{m2} = 0.40$. Medium levels: $B_1 = 1.70$, $B_2 = 1.92$, $S_{f0} = S_{s0} = 0.55$, $S_{f1} = S_{s1} = 0.70$, $S_{f2} = S_{s2} = 0.825$, $S_{m0} = 0.55$, $S_{m1} = 0.30$, $S_{m2} = 0.45$. High levels: $B_1 = 1.87$, $B_2 = 2.10$, $S_{f0} = S_{s0} = 0.65$, $S_{f1} = S_{s1} = 0.75$, $S_{f2} = S_{s2} = 0.90$, $S_{m0} = 0.65$, $S_{m1} = 0.45$, $S_{m2} = 0.50$.

of birth rate tended to be more pronounced at lower sterilization rates, which is consistent with the elasticity analysis. Lower elasticity values indicate that any policy affecting fertility will impact the system, but secondarily compared with survival rates.

Survival Rate.—Increasing survival rates dramatically increased management effort (Fig. 3b). This means that uncertainty about survival rates could substantially impact management outcomes, consistent with the elasticity analysis. High elasticity values indicate that any policy affecting survival rates will create the largest and fastest impact on the system.

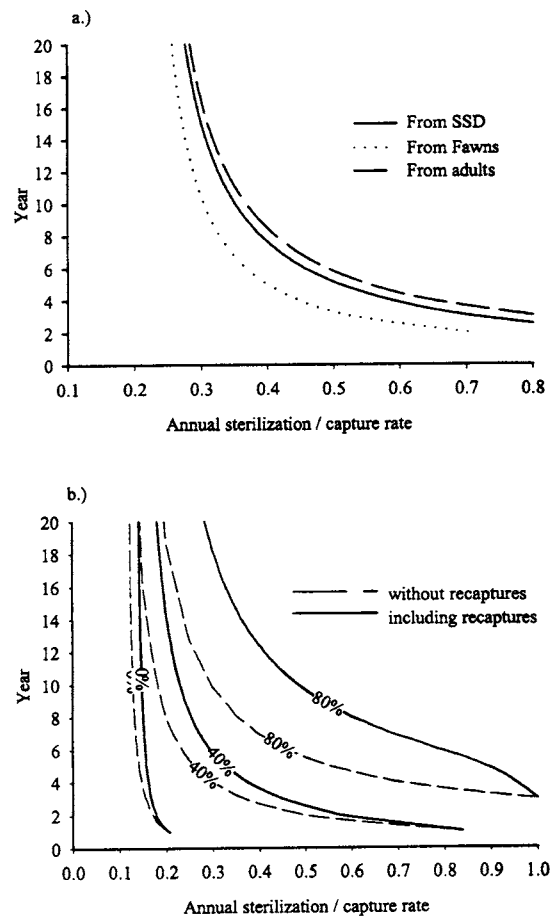


Fig. 4. (a) Effects of variation in the age structure of the initial population on time to 60% reduction in initial deer abundance. All survival and birth rates were set at medium levels ($B_1 = 1.70$, $B_2 = 1.92$, $S_{f0} = S_{s0} = 0.55$, $S_{f1} = S_{s1} = 0.70$, $S_{f2} = S_{s2} = 0.825$, $S_{m0} = 0.55$, $S_{m1} = 0.30$, $S_{m2} = 0.45$). Where starting populations were either all fawns or all adults, the initial vector contained equal numbers of male and females. (b) Effect of variation in the rate of recapturing sterilized individuals. Dashed lines assume a population where a constant proportion of fertile females can be captured and sterilized. Solid lines represent a population where the proportion of sterilized individuals recaptured is equal to the overall proportion of sterilized individuals within the female population as a whole.

Starting Age Structure.— When the starting population vector was biased toward adults, the time required to reach a given reduction relative to the standard stage distribution (SSD) increased (Fig. 4a). This reflected the comparatively higher survival and reproductive capacity of adult females. For instance, in a population of 100 adult females with 20% sterilization, 80 fertile adult females breed—59 more than at SSD. Therefore, before sterilization could take effect,

the population grew rapidly while it equilibrated proportionately to SSD, slowing the time to desired reduction. In contrast, when the starting age vector was skewed toward younger individuals, the time to reduction decreased relative to SSD, reducing management effort. In a population of all fawns, even in the absence of sterilization, the population declined initially as individuals died before breeding. Additionally, when sterilizing a population of fawns, we would have sterilized for 2 years before individuals reached their highest reproductive capacity, giving sterilization a head start and greater impact.

Any proportional increase in the number of males in the starting composition reduces the time to reduction because males have zero reproductive capacity in the model. This confirms our lower-level elasticity analysis that showed $e(\omega) = 0.3529$.

Partial Controllability.—As more females are sterilized, the probability of recapturing a sterilized individual increases, and the net efficiency of capturing and sterilizing fertile female deer decreases (Frank and Sajdak 1993, Boone and Wiegert 1994, Hobbs et al. 2000). To assess the magnitude of this potential effect, we modeled the population assuming that we would capture female deer proportionately to their frequency in the population (θ becomes c , the capture rate). As desired reduction increases, recapturing increasingly influences the results (Fig. 4b). At low reduction levels, the effect is minimal. However, at desired reduction levels of $\geq 66\%$, recaptures would substantially increase the necessary c and the time required to get to a desired reduction level.

DISCUSSION

We explored the efficacy of permanent sterilization to control overabundant urban deer. Our approach differed in 3 basic ways from previous models that explored the viability of fertility control for white-tailed deer (Boone and Wiegert 1994, Barlow et al. 1997, Hobbs et al. 2000, Seagle and Close 1996). First, we analytically assessed the relative influence of model parameters on population dynamics of a hypothetical deer population. While other researchers have considered the effects of varying 1 or more parameters to some degree (Boone and Wiegert 1994, Seagle and Close 1996, Barlow et al. 1997, Hobbs et al. 2000), we considered the contributions of survival and fertility rates of all gender classifications to our results. As such, we were able to create an important tool that clearly compared various control strategies.

Second, we focused on the impacts of uncer-

tainty in birth and survival rates across all possible sterilization levels. Our model provides an indication of population responses over a wide range of conditions, making the model applicable to many situations. We also considered uncertainty concerning stage structure of the initial population, which must be evaluated to determine management effort and the composition of a population as it moves to a new equilibrium.

Finally, and perhaps most practically from the perspective of assessing the utility of sterilization, we considered the relationship between annual sterilization rates and the expected time to the desired level of population reduction. Time horizons may be the most important factor in appraising fertility control because they largely determine treatment costs.

Efficacy of Sterilization

Fertility control has been attempted on several species of mammals and birds (Fayrer-Hosken et al. 1997, Pech et al. 1997, Hundgen et al. 2000, Bromley and Gese 2001). Many basic results in other species including nonlinearity are analogous to ours. Most studies agree, in theory, that fertility control might reduce and maintain populations at desired levels, empirically demonstrated in some closed experiments (Sturtevant 1970, Knipling and McGuire 1972, Chambers et al. 1999, Twigg and Williams 1999). However, implementation becomes increasingly difficult with larger organisms, and considerable disagreement exists as to the actual feasibility of fertility control in deer (Seagle and Close 1996, Barlow et al. 1997, Hobbs et al. 2000, Rudolph et al. 2000). The argument has been made that fertility control may be more efficient than culling because sterilized individuals, while removed from the population reproductively, are able to contribute to resource limitation and density-dependence (*sensu* Knipling and McGuire 1974, Boone and Weigart 1994). In contrast, others (Nielsen et al. 1997, Hobbs et al. 2000) argue that culling will always be a more effective strategy and must be included as part of fertility control for a program to be effective. Hobbs et al. (2000) and Nielsen et al. (1997) concluded that fertility control is an effective way to maintain a population at a given size, but lethal control generally is required to initially reduce a population to that level.

While the comparison between lethal and fertility control is a nonissue here because culling was not considered, in our prospective perturbation analyses, survival (elements $a_{5,4}$, $a_{6,5}$, and $a_{6,6}$ of

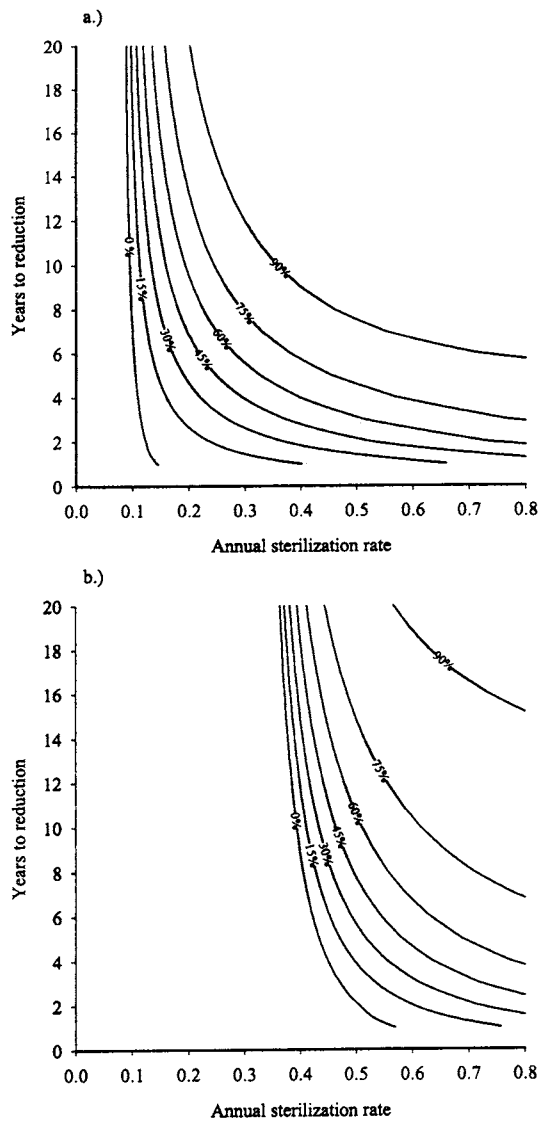


Fig. 5. Reduction in population size as a function of time and yearly sterilization rate assuming (a) low birth and survival rates ($B_1 = 1.53$, $B_2 = 1.74$, $S_{f_0} = S_{s_0} = 0.45$, $S_{f_1} = S_{s_1} = 0.65$, $S_{f_2} = S_{s_2} = 0.75$, $S_{m_0} = 0.45$, $S_{m_1} = 0.15$, $S_{m_2} = 0.40$) and (b) high birth and survival rates ($B_1 = 1.87$, $B_2 = 2.10$, $S_{f_0} = S_{s_0} = 0.65$, $S_{f_1} = S_{s_1} = 0.75$, $S_{f_2} = S_{s_2} = 0.90$, $S_{m_0} = 0.65$, $S_{m_1} = 0.45$, $S_{m_2} = 0.50$).

the projection matrix, eq. 9) made a much larger proportional contribution to projected population growth than did fertility (elements $a_{4,4}$, $a_{4,5}$, and $a_{4,6}$), consistent with Barlow et al. (1997) and Hobbs et al. (2000). Elasticities from the lower-level elements showed a similarly dramatic difference between survival and birth rates. Thus, we anticipate that management actions affecting survival rates should have a relatively large impact on

population growth while events varying birth rates are expected to have a more moderate influence. Thus, sterilization should require a longer period to achieve a given reduction than lethal control, assuming that sterilization exclusively affects birth rates. Additionally, the sex ratio, ω , has a relatively large impact ($e[\omega] = 0.3529$) on the growth of the population. Therefore, we anticipate any alteration in fawn sex ratio to have a large influence on population growth rate. Skewing ω toward females ($\omega > 0.5$) slowed sterilization progress.

Our results support the Hobbs et al. (2000) finding that sterilization requires a substantial effort to achieve a desired reduction, which is shown by the nonlinear relationships and vertical asymptotes in Figs. 2, 5a, and 5b. For instance, in Fig. 5a, to achieve a 60% reduction in 4 years, a 40% reduction of available fertile females must be achieved each year. To maintain this level of reduction, however, 13% of the available females must be continually sterilized each year.

Model Assumptions

Our results are conditional on the various assumptions in the models we analyzed. First, we assumed homogeneity among all individuals within a category (any individual within a category has an equal chance of dying, leaving the system, or being captured for sterilization). If an individual moves between categories, it immediately shares all qualities held by other individuals in its category. These assumptions could have impacted the results in a variety of ways. Some deer may be more likely to be captured than others, and these deer may or may not contribute as much to the reproductive capacity of the population. Tamer deer may be more easily captured but may also have a higher incidence of automobile collisions (therefore higher mortality), which reduces the effectiveness of sterilization. Alternatively, tamer deer may teach such behavior to their fawns, thereby making sterilization a successful way to target problem individuals. Such predictions are speculative, however.

We assumed that mortality and sterilization are independent: if a fertile female yearling dies after sterilization, she would have died regardless of the procedure. In all likelihood, some deer will die from the stress of the sterilization procedure, and this may be undesirable to stakeholders who selected sterilization as a humane alternative to lethal control. However, animals released from the energetic costs of reproduction may have higher survival rates.

We also assumed that survival and birth rates are density-independent. While rapid growth of urban populations in many locales suggests that these populations are considerably below local carrying capacities (Curtis et al. 1998, Boldgiv 2001), limited density-driven effects may skew results negatively (Boone and Wiegert 1994), and density-dependence may produce misleading elasticity values (Grant and Benton 2000). If density-dependence were operational, even to a limited degree, it would increase the effectiveness of sterilization, as the reproductive removal (but not physical removal) of some animals from the herd would intensify density-dependent feedback. Populations in which density-dependence affects adult mortality will be reduced by sterilization earlier than those regulated by density-dependent recruitment (Barlow et al. 1997), consistent with our perturbation analyses.

Further, we assumed geographic closure. Urban and suburban female deer demonstrate small ranges and high site fidelity (Labisky and Fritzen 1998, Grund et al. 2002). In addition, it is not known what drives immigration into a deer population. Movement may be driven by resource limitation in bordering areas, and thus population reduction within the local area may free resources for immigrants. Migration may be a function of the total population size, population size within a particular category, territorial distribution, or other factors. Seagle and Close (1996) made some initial immigration models by adding a given number of deer to the population annually and showed projected population size over time varied nonlinearly with annual deer supplement (i.e., diminishing marginal reduction, analogous to our birth rate and survival rate simulations). However, P. D. Curtis (Cornell University, personal communication) indicated that deer tend to move from areas of high density to lower density. While this tendency needs to be quantified, it provides an optimistic outlook to the efficacy of female-based sterilization, rendering geographic closure a reasonable assumption. Geographic closure remains valid in fenced-in systems such as government reservations (Seagle and Close 1996). Further work must be done assessing the possible effects of immigration.

We also assumed a yearly cycle with discrete time units. Deer give birth around May, and some properly nourished fawns may have matured sexually by early winter at age 0.5. More likely, however, fawns do not become sexually mature until the following year, at age 1.5. While our life-cycle diagram is thus slightly inaccurate, by using an

average birth rate for B_{fj} , we largely alleviated this problem (Curtis et al. 1998, Boldgiv 2001). We also assumed that survival was simply a series of independent Bernoulli trials. While this assumption is unrealistic because it creates the possibility a deer could live indefinitely, it remains useful for discussing age classes as units.

We assumed that hormonally stable sterilization (e.g., tubal ligation) does not dramatically alter a doe's behavior (Muller et al. 1997, Chambers et al. 1999, Miller et al. 2000). Nevertheless, once sterilized by tubal ligation or ovariectomy, we are uncertain of the behavioral consequences. Nettles (1997) describes a large number of possible side-effects, including behavioral, physiologic, and ecological consequences. For instance, a fertile female deer goes into estrus in November and usually remains so until she becomes pregnant. We do not know how long a hormonally unchanged sterilized deer will remain in estrus. If a sterilized female is in estrus for several months, she may attract more males into the area, increasing the likelihood of automotive collisions.

Our model was essentially additive, with any reduction in fertility having an immediate effect on the population, without a compensatory buffer. Studies with mice and rabbits (Chambers et al. 1999, Twigg and Williams 1999) noticed compensatory responses through increased recruitment in fertile age classes. However, recruitment was not sufficient to offset the desired effects of sterilization. A deer population exhibiting compensatory behavior would decrease the efficiency of sterilization. Managers must consider the behavioral and demographic consequences of both sterilization and reduction.

Finally, we included no environmental uncertainty in our model. Factors such as rainfall, severe winters, and food abundance were not accounted for, but could influence various parameters. However, elasticity values for the mean projection matrix are accurate even in the presence of large stochastic environmental fluctuations (Grant and Benton 2000). Therefore, our elasticity analyses should indicate the potential impacts of environmental uncertainty without sacrificing insights about mean population dynamics.

MANAGEMENT IMPLICATIONS

An effective management strategy for control of overabundant urban deer populations will likely require 2 stages. The first is to reduce the population to a given level. The second is to maintain that level. In the first stage, sterilization

will be less effective compared to culling (Hobbs et al. 2000), and stakeholders using sterilization should be prepared to invest considerable time and effort. As noted by Hobbs et al. (2000), the most practical approach typically will require an initial population reduction using methods that directly reduce adult survival (e.g., lethal control). However, in our models, we sterilized a certain proportion of females each time period, so the number of sterilized females accumulated in the population over time. By using such a recursive model, we applied a more efficient approach by incrementally reaching an optimal proportion of sterilized deer, lessening the effort problem in reducing a herd.

The extent and speed with which sterilization yields results in the first stage depends on uncertainty concerning the model parameters and in the assumptions inherent in the model. Comparing Figs. 5a and 5b provides a contrast of the best- and worst-case scenarios, respectively, for time to reach the objective. These should also be compared with Fig. 2 to show how possible outcomes may differ from mean projections.

In the second stage, managers should note that the contours in Figs. 2 and 5 are considerably close together. Thus, error in sterilization rate could have considerable consequences for the population (Seagle and Close 1996). Sterilization is a viable management option in both management stages if a target proportion of fertile females can be sterilized annually.

We used population reduction as a proxy for relief of the problems associated with an overpopulated herd. Vegetation damage and car collisions have risen with deer populations over the previous 2 decades (Boldgiv 2001). However, we do not know if reducing the deer herd to former numbers will consequently lower damages to previous levels. For instance, our elasticity analysis exposes an interesting policy trap. One assumption of the model was constant survival rates, and if survival increases as fecundity declines, the effects of sterilization on the population growth rate will be reduced (Hone 1992). In urban and suburban environments, however, mortality largely is a result of automobile collisions. Therefore, sterilization should work if car collisions occur at the same rate. If survival rates increase due to a decline in automotive collisions, the effect of sterilization would be mitigated. Nonetheless, this also would indicate that sterilization was effective to some degree. The exact opposite may be true, however. For instance, from the perspec-

tive of the deer, the probability of a collision while crossing a road is a function of the density of cars on the road (along with weather conditions, posted signs, speed limits, etc.). A reduced deer population should not influence the abundance of automobiles; the survival rate of any individual deer remains unchanged. From the perspective of a driver, however, the probability of a collision likely is a function of the density of deer. A reduced deer population, therefore, would reduce the probability of any individual vehicle colliding with a deer without changing vital rates within the system. Policymakers should be aware of these possible circumstances.

We did not explicitly examine cost. Managers must study cost while evaluating sterilization as an option. However, management effort and cost are likely related, so our inferences concerning parameter uncertainty can reasonably be extended to speculate what will influence costs. Cost probably is a function of start-up (likely a constant), surgeries (may be approximated as a linear function of cost per deer), and capture (probably a nonlinear function as recaptures increase). Initially a large number of animals may have to be sterilized (Boone and Wiegert 1994), probably carrying substantial costs. A community would need to maintain this maximum effort for only a few years, gradually tapering off as the proportion of sterile females increased, before shifting to a maintenance program (Nielsen et al. 1997). Therefore, we anticipate that surgery costs should decline to a minimum maintenance level. Capture and handling cost should be initially high due to a large number of animals handled. However, capture costs will be directly related to behavioral response. If sterilized animals become trap adverse, managers would recapture fewer deer, allowing them to more easily target unsterilized animals. Conversely, if sterilized animals become "trap happy," perhaps because of the use of baited trapping stations, capture costs should increase. If all deer remained equally likely to be captured, capture costs should decline and then level off once sterilized individuals comprised a large enough segment of the population. Due to this uncertainty, it is unknown whether capture costs would overtake surgery costs. Hypothetically, costs probably should either decline and then stabilize at a minimum value, or decline to a minimum value, increase to some extent, and then stabilize. This question deserves further consideration.

Translocations and short-duration contraceptives have proven ineffective, and new methods

must be found to deal with overabundant deer. While sterilization may require a substantial initial effort relative to hunting, it may reduce a deer population if stakeholders are prepared to endure time horizons of approximately 10 years. However, after a population is reduced, sterilization may be more efficient than lethal control in maintaining populations at desired levels. Lacking natural sources of mortality, sterilization may be a viable nonlethal option for population reduction in communities where hunting is infeasible.

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APPENDIX A

Component Prospective Perturbation Analysis of a Reducible Lefkovich Matrix

The overall projection matrix (eq. 9) can be conceptualized as nine 3×3 submatrices, where each of the submatrices represents the relation of one gender classification to another (Fig. A1).

Each 3×3 submatrix can be seen as an independent matrix with its own growth rate (its dominant eigenvalue), λ . The following are the submatrices with non-zero components for our model without sterilization with medium birth and survival rates substituted.

$$\mathbf{A}_{M \rightarrow M} = \begin{bmatrix} 0 & 0 & 0 \\ S_{m_0} & 0 & 0 \\ 0 & S_{m_1} & S_{m_2} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 \\ 0.55 & 0 & 0 \\ 0 & 0.3 & 0.45 \end{bmatrix}, \quad \lambda = 0.45 \quad (A1)$$

$$\mathbf{A}_{F \rightarrow M} = \begin{bmatrix} S_{f_0}(1-\varpi)B_{f_1}(1-\theta_0) & S_{f_1}(1-\varpi)B_{f_2}(1-\theta_1) & S_{f_2}(1-\varpi)B_{f_2}(1-\theta_2) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad \lambda = 0.451 \quad (A2)$$

$$= \begin{bmatrix} 0.471 & 0.672 & 0.792 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

$$\mathbf{A}_{F \rightarrow F} = \begin{bmatrix} S_{f_0}\varpi B_{f_1}(1-\theta_0) & S_{f_1}\varpi B_{f_2}(1-\theta_1) & S_{f_2}\varpi B_{f_2}(1-\theta_2) \\ S_{f_0}(1-\theta_0) & 0 & 0 \\ 0 & S_{f_1}(1-\theta_1) & S_{f_2}\varpi B_{f_2}(1-\theta_2) \end{bmatrix}, \quad \lambda = 1.274 \quad (A3)$$

$$= \begin{bmatrix} 0.471 & 0.672 & 0.792 \\ 0.55 & 0 & 0 \\ 0 & 0.7 & 0.825 \end{bmatrix}$$

$$\mathbf{A}_{S \rightarrow S} = \begin{bmatrix} 0 & 0 & 0 \\ S_{s_0} & 0 & 0 \\ 0 & S_{s_1} & S_{s_2} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 \\ 0.55 & 0 & 0 \\ 0 & 0.7 & 0.825 \end{bmatrix}, \quad \lambda = 0.825 \quad (A4)$$

In a reducible matrix, the subpopulation that grows the fastest will dominate the matrix overall, and its growth rate becomes the overall growth rate of the modeled population (Caswell 2001). All com-

ponent submatrices showed a decline in growth ($\lambda < 1$) except for the contribution of fertile females to themselves where projected growth was $\lambda = 1.274$ with medium birth and survival rates. Because males and sterilized females did not contribute to this submatrix (and thus, did not contribute to the projected growth of the matrix overall; since the population was assumed not to be male-limited, no mechanism existed in the matrix to relate male numbers to fawn production), their elasticity values within the complete matrix were effectively zero. Thus non-zero matrix components had zero elasticity values (i.e., only gender classes that fed back into the fawn age class had non-zero values in the elasticity matrix; Fig. 1; eq. 11). Males and sterilized females merely accumulate and do not directly contribute to population growth (but do contribute to overall abundance at a particular point in time).

		from								
		Males			Females			Sterilized		
to	Males	0	0	0	$S_{f_0}(1-\varpi)B_{f_1}(1-\theta_0)$	$S_{f_1}(1-\varpi)B_{f_2}(1-\theta_1)$	$S_{f_2}(1-\varpi)B_{f_2}(1-\theta_2)$	0	0	0
		S_{m_0}	0	0	0	0	0	0	0	0
		0	S_{m_1}	S_{m_2}	0	0	0	0	0	0
	Females	0	0	0	$S_{f_0}\varpi B_{f_1}(1-\theta_0)$	$S_{f_1}\varpi B_{f_2}(1-\theta_1)$	$S_{f_2}\varpi B_{f_2}(1-\theta_2)$	0	0	0
		0	0	0	$S_{f_0}(1-\theta_0)$	0	0	0	0	0
		0	0	0	0	$S_{f_1}(1-\theta_1)$	$S_{f_2}(1-\theta_2)$	0	0	0
	Sterilized	0	0	0	0	0	0	0	0	0
		0	0	0	$S_{f_0}\theta_0$	0	0	S_{s_0}	0	0
		0	0	0	0	$S_{f_1}\theta_1$	$S_{f_2}\theta_2$	0	S_{s_1}	S_{s_2}

Fig. A1. Component submatrices within overall model, corresponding to Fig. 1. Relationship of each gender classification (columns) to itself (rows) divided by lines. Within the model, and represent the survival and birth rates, respectively, of age class x in gender classification y ; θ_i represents the annual sterilization rate of fertile females in age class i ; and ϖ represents the probability of a newborn fawn being female.