Research Article

Managing an Overabundant Deer Population by Sterilization: Effects of Immigration, Stochasticity and the Capture Process

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Abstract

Fertility control is an alternative to lethal removal for managing overabundant populations. This approach invokes several simplifying assumptions; in particular, that specific individuals can be targeted for sterilization. We evaluated the influence of relaxing this assumption on the likelihood of achieving population control by considering potential sources of variation in the capture and sterilization process in an overabundant white-tailed deer (Odocoileus virginianus) population in Cayuga Heights, New York, USA. Using numerical analysis of an individually based seasonal projection model, including demographic stochasticity, we found that heterogeneity in both sampling, and response to trapping, increased the effort required to achieve population reduction within some acceptable degree of certainty. The inability to precisely control the demographic structure of captured deer required increased capture effort to achieve a given reduction. Trap-aversive behavior following capture improved the efficacy of sterilization while trap affinity reduced it. The efficacy of sterilization as a management tool was reduced dramatically by the presence of net immigration and emigration from the population. We found that sterilization could reduce growth rates of overabundant populations under some conditions, but it is unlikely to be a viable means for reducing populations in general, where there is significant net movement of individuals into the population, and where there is imprecise control over the capture process. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):268–277; 2006)

Key words

Wildlife managers are increasingly challenged with controlling species regarded as overabundant. One conspicuous example of this in North America involves white-tailed deer (*Odocoileus virginianus*) populations that have exceeded historical levels as increasing suburbanization, and concurrent decreases in agricultural land use (resulting in significant increases in rates of forest regeneration), have created large areas of predator-scarce habitat (Diamond 1992, McCullough et al. 1997). Increased deer-related vegetation, ecosystem, and automobile damage in these areas frequently exceed the tolerance of local communities (Decker and Connelly 1989, Diamond 1992, McCullough et al. 1997). In some areas, local legal statutes prevent the use of lethal removals (Wright 1993, McCullough et al. 1997, Chase et al. 2002). Traditional nonlethal alternatives have also proven ineffective. Deer become increasingly habituated to deterrent measures such as repellents and fencing (Decker and Connelly 1989). Translocation is rarely feasible due to limited release sites and stress suffered during transport (McCullough et al. 1997, Waas et al. 1999, Beringer et al. 2002). Reintroduction of predators evokes safety concerns for many stakeholders (Diamond 1992).

Fertility control has been suggested as an alternative to lethal strategies (Tyndale-Biscoe 1991, Frank and Sajdak 1993, Kennelly and Converse 1997). While transient fertility control (e.g., immunocontraception, where the effects of treatment may last less than the lifetime of the individual) has shown potential under some circumstances, it may be impractical due to high costs of identifying treated individuals, the need for repeated immunocontraceptive dosing on a regular schedule, and unacceptable time-to-reduction (Kirkpatrick et al. 1997, Muller et al. 1997, Miller et al. 2000, Rudolph et al. 2000). Here, we focus on sterilization (i.e., permanent fertility control) as the mechanism of population control, with particular reference to overabundant ungulate populations (although many of the considerations we address are general).

While previous model-based analysis has suggested that sterilization might reduce overabundant ungulate populations (Barlow et al. 1997, Hobbs et al. 2000), there are potential impediments to successful use of sterilization as a management tool. First, a successful sterilization program is likely to require substantial effort to achieve population reduction (Boone and Wiegert 1994, Seagle and Close 1996, Barlow et al. 1997), particularly if the timeline for reaching a population goal is short (<5 years; Merrill et al. 2003). Second, the results of these earlier studies, which focused primarily on the plausibility and efficacy of sterilization as a management strategy, were generally strongly conditioned on several simplifying assumptions, which may limit their generality: 1) complete control in targeting and sterilizing segments of the population, 2) that deterministic models reliably predict outcomes, 3) no behavioral changes occur due to sterilization, and 4) population (demographic) closure.

The first assumption, that managers exercise precise control over sampling, is largely unrealistic because of complex issues surrounding deer capture. For example, a manager needs to capture and sterilize a substantial number of fertile females, but fertile females are only a fraction of deer encountered; typically males and previously sterilized females are also captured and subsequently released (therefore wasting capture effort).

The assumption that deterministic models reliably predict outcomes has not been adequately examined. Complex effects of

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environmental and demographic stochasticity could persist in a population. A particularly productive breeding year could generate a cohort with more individuals than usual. These animals would have the potential to breed and exacerbate overabundance problems for several years. Further, temporal variation in vital rates would increase uncertainty for managers in the ability to sample specific individuals in the population.

The assumption that treatment does not affect future capture rate (i.e., probability that an individual deer is captured on a given trapping occasion) is also problematic. For example, stress from capture, handling, and sterilization may render a sterilized female partially or totally trap-averse (Waas et al. 1999, Haulton et al. 2001). This could reduce the number of recaptures, skew captures towards previously uncaptured individuals, and affect the estimated effort required to achieve management goals. If deer exhibit trap affinity due to baited stations (Haulton et al. 2001), recaptures could increase, and a manager might sterilize an insufficient number of deer.

Finally, most efforts to date model efficacy of sterilization programs have assumed "demographic closure." While Seagle and Close (1996) examined the effect of a limited number of deer jumping into an enclosed area, the more general issue of net movement into or out of an arbitrarily defined population (e.g., political boundary) has not been adequately addressed; such movements could dramatically impact capture effort. Fertility-control strategies assume that population growth can be inhibited if birth rates can be reduced. This always would be true in a closed population in which recruitment is a function of new births exclusively. In an open population, recruitment consists of both newborns and immigrants, but sterilization only reduces births from resident mothers (sensu Twigg et al. 2000).

Using numerical analysis of a series of models for a hypothetical deer population (Merrill et al. 2003), we consider the effect of relaxing these assumptions on the projected efficacy of sterilization as a means for controlling population size of a hypothetical deer population subjected to permanent sterilization. We extend Merrill et al. (2003) by addressing the degree to which each factor may potentially influence the efficacy of the capture process, and subsequently, the success of sterilization as a management strategy. We consider the number of deer that would need to be captured annually to achieve satisfactory probability of a desired reduction under a variety of fairly typical conditions and timelines.

Methods

Population Model

Merrill et al. (2003) used asymptotic results from analysis of a time-invariant, female-based model to explore the efficacy of sterilization for a population assumed to be closed to emigration and immigration. In most real situations, the dynamics of the population and sampling are likely to be strongly influenced by both demographic and environmental stochasticity. To better accommodate stochasticity, particularly in terms of sampling, we restructured the model to an analogous individual-based model. That is, instead of using expected numbers of individuals making particular transitions, we followed the fate of each individual, as an independent realization (Boolean trial) of an underlying set of stochastic processes. This introduced simple (demographic)

stochasticity and also allowed us to consider the interaction of stochastic demographic and sampling events simultaneously.

In addition to adoption of an individual stochastic model, we modified the age-structure of the model to account for 1) the potential reproduction by fawns at <1 year of age (Curtis et al. 1998), and 2) age-specific differences in the pregnancy probability of fertile females. We assume a gravid female of age class x can be sterilized at rate θ_x; following Merrill et al. (2003), we assumed that sterilization occurred between the fall and winter seasons (although relaxing this assumption did not strongly influence our general results). We parameterized survival, birth rates, pregnancy rates, and fawn sex ratio using literature values (Merrill et al. 2003), and parameter estimates from a companion study of a local deer population in Cayuga Heights, New York, USA (C. Jennelle et al., unpublished data; Table 1). We used SAS (release 9) for our simulations.

Capture process.—To account for limited capacity to capture deer for sterilization, we converted sterilization rates to absolute number captured, C, of which only the fertile females were sterilized (sensu Merrill et al. 2003). Thus, the capture of a fertile female became the realization of a stochastic event, which will be conditional on the sampling fraction, and the proportion of the sample comprised of fertile females. We modeled capturing C deer (with replacement) for sterilization once annually, between fall and winter. Except for our analysis of behavioral effects on capture probability, we assumed that all animals were equally likely to be captured. Unless otherwise noted, all simulations were performed using an initial population size of $N_0 = 100$; this allowed us to easily refer to percentage growth or reduction from N_0 using a common scaling.

To examine the consequences of possible behavioral changes in response to the trapping process, we varied the probability of recapture to simulate a range of projected levels of trap aversion and trap affinity. Assuming homogeneity of encounter rates among individuals and no behavioral response to capture and surgical sterilization, the likelihood of recapturing (encountering) sterile females of a particular age class is

$$P(N_{s_Y}) = \frac{N_{f_X}}{N_{total}}$$

or simply the proportion of the sterile female age class (N_f) to the

Table 1. Parameter values used in numerical analysis of hypothetical deer population. Parameter estimates were obtained from Boldgiv (2001), and estimates from the local Cayuga Heights, New York, USA, population (C. Jennelle et al., Cornell University, unpublished data).

	Stage (parameter)	Parameter value
Pregnancy rates	Fawns (P_0)	0.59
	Yearlings (P_1)	0.94
	Adults (P_2)	0.97
Birth rates	Fawns (B_0)	0.67
	Yearlings (B_1)	1.70
	Adults (B_2)	1.92
Survival rates	Female fawns (S_{f_0}, S_{s_0})	0.55
	Female yearlings (S_{f_1}, S_{s_1})	0.75
	Female adults (S_{f_2}, S_{s_2})	0.75
	Male fawns (s_{m_0})	0.40
	Male yearlings (S_{m_1})	0.35
	Male adults (S_{m_2})	0.40

total population (N_{total}), where X represents the age class. Due to sampling with replacement and discrete seasonal life events, $P(N_{f_x})$ is constant within a season.

If there is a behavioral response to surgery, the probability of recapturing a sterilized female, $P(N_{s_x})$, becomes skewed and $P(N_{m_x})$ and $P(N_{f_x})$ compensate so that

$$\sum_Y \sum_X P(N_{Y_X}) = 1 \qquad (2)$$

Thus, if deer exhibit a behavioral response to capture (and surgery),

$$P^*(N_{f_X}) = \frac{N_{f_X}}{\sum_X (N_{m_X} + N_{f_X}) + \rho \sum_X N_{s_X}} \qquad (3)$$

$$P^*(N_{s_X}) = \frac{\rho N_{s_X}}{\sum_X (N_{m_X} + N_{f_X}) + \rho \sum_X N_{s_X}} \qquad (4)$$

where $\rho = 0$ if a captured female becomes completely trap-averse, $0 < \rho < 1$ if a captured female becomes partially trap-averse, $\rho = 1$ if there is no effect, and $\rho > 1$ if a captured female exhibits trap affinity (e.g., if $\rho = 2$, a sterilized female is twice as likely to be recaptured than if $\rho = 1$). By examining the relationship between ρ and population size over time, we determined the effect of behavioral response on sterilization efficacy. In our models, we assumed that encounter probabilities were constant across gender and age classes within a particular level of ρ; given the strong sociality of deer, there is the potential for relatively constant encounter rates among females, at least seasonally (although there is some potential for capture of 1 individual deer from a family group to influence the capture probability of other family members; see Discussion).

Movement.—Finally, we added immigration and emigration to the model (i.e., relaxed the demographic closure assumption). We used 2 basic models for movement (see below); in each case, movements of individuals into or out of the population occurred as discrete events between spring and summer (consistent with observations from the local Cayuga Heights population), involving a specified number (or proportion) of deer at the end of the spring season (thus, movement in our models was not individually stochastic). In all cases, the age distribution of immigrating/ emigrating individuals reflected the age/gender specific movement rates estimated for our local population (C. Jennelle et al., Cornell University, unpublished data). Since considerable uncertainty exists regarding net movement functions for deer populations in general (and for Cayuga Heights, specifically), we considered 2 contrasting yet plausible models. First, we considered models in which both a constant number of individuals either entered or exited the population, independent of current population size, under 2 different scenarios: 1) immigration without emigration, and 2) *net* immigration with emigration (i.e., immigration > emigration > 0); we considered the latter situation because emigration of sterilized individuals may influence overall population reproductive capacity and because it best reflected the dynamics of the local Cayuga Heights population (C. Jennelle et al., Cornell University, unpublished data).

Second, although we did not have sufficient data to test for density-dependent movements, to assess the potential impact of such dependence on our results we also modeled immigration and emigration as a density-dependent process. We considered 2 different response functions: 1) additive linear density-dependence, where immigration declined and emigration increased linearly as overall population size increased, and 2) a compensatory density-dependent immigration function, where immigration remained constant over low population densities (i.e., the first immigration model), and then, declined as a saturation level was approached (analogous to the additive model). For both compensatory and additive models, we set saturation level (N_{sat}) at 154 deer per km^2 (Boldgiv 2001). For all analyses of movement, we assumed that the age structure of the sample of individuals entering (or leaving) the population was proportional to the stable age distribution. While clearly an unrealistic assumption for many deer populations (e.g., Porter et al. 2004), we desired to minimize the complexity of our models (as would be required if we wanted to precisely characterize various scenarios in which movement rates differed in specific ways among age- and sex-classes), using the stable-age distribution as a null model.

While we did consider density-dependent effects on net movement rates, we assumed density-independence of both survival and birth rates. We did not have sufficient data from the Cayuga Heights population to test this hypothesis, but we feel it is reasonable. Many urban deer populations (including the Cayuga Heights population) are currently far enough below carrying capacity that density-dependent survival and fertility effects are likely minimal. In addition, our model assumed that encounter probabilities were constant across gender and age classes, for a given level of ρ.

Assessing Efficacy of Sterilization

Because our models were stochastic, results from our projections were probabilistic. Therefore, we determined mean population size as a function of N_0, C, and time (year), bounded by 95% confidence intervals (calculated as the 2.5% and 97.5% tails of the numerically generated distribution of population sizes). We also determined probability of success for a given set of conditions. Success refers to the probability of achieving a specified objective, determined in advance by relevant stakeholders, to reduce the population to a specific goal within a specified time. The probability of success was calculated as the frequency of simulations reaching the desired objective (success). A manager may be interested in the probability of reaching an objective given the unique conditions of a local system. For illustrative purposes, we defined success as a 60% reduction (i.e., $0.4 \cdot N_0$) on a specific timeline. However, this criterion for success is obviously arbitrary.

Analysis of Sensitivity of Model Projections to Sources of Variation

For deterministic, annual projection matrix models (sensu Merrill et al. 2003), analytic methods for assessing relative sensitivity of model outputs to variation in one or more parameters are available (Caswell 2001). However, in the present case, our models are individual stochastic. While methods have been described for analysis of individual demographically stochastic models (Caswell 2001), these methods are complex and not easily extrapolated to the simultaneous consideration of both demographic stochasticity

and sampling heterogeneity. Instead, we used simple comparative numerical projection analysis (which is functionally equivalent) to compare the relative impact of different sources of variation on our results.

Results

Numerical Simulation Results

Stochasticity, sampling variation, and probability of success.—Using parameter values derived for a typical urban deer population (Table 1), we were able to project population size as a function of the number of deer captured annually (C). Within a simulated closed population where $N_0 = 100$ at stable stage distribution (SSD), values of $C < 30$ did not produce a population decline, although it slowed growth. A capture number of $C = 30$ resulted in a mean population decline of ~60% within 13 years (Fig. 1a). In contrast, a value of $C = 45$ produced a mean decline of 60% within 7 years (Fig. 1b). Additionally, there was generally a lag in population decline before sterilized animals died from natural mortality. When $C = 30$, the mean population size increased approximately 10% within 2–3 years before declining. If $C = 45$, the mean population increased approximately 2% within 2–3 years before declining. Increasing C increased the certainty of management outcome, indicated by narrower 95% confidence intervals (Fig. 1b). We note that the 95% confidence limits to population size bound zero in both cases at some point, indicating that extirpation is a potential outcome. This is an artifact of the use of a constant sampling number, regardless of the size of the population at a particular time; in practice, it is likely that the preferred (optimal) strategy would be to make C an annual management decision conditional on population size. Moreover, in the presence of net immigration into the population, extirpation is only a transient possibility.

The interaction of stochasticity and sampling uncertainty increased the variance in our results over time, as indicated by wider 95% confidence intervals (Fig. 4a). For instance, if $N_0 = 100$ and $C = 30$, the mean population declined, but a possibility existed of the population growing to approximately 140% of N_0 levels. This variability was constrained as C increased. For instance, if C was increased to 45, the mean population and the lower and upper confidence intervals all showed a decline and remained relatively close (Fig. 1b).

To ensure success (here, a 60% reduction) with 90% confidence, C must be greater than 40 (Fig. 2). Longer timelines (i.e., greater time to achieve a particular reduction) resulted in higher probabilities of success with less effort. Approximately 30 deer ($C = 30$) would need to be captured annually to have a 90% expectation of success over periods of 20 to 40 years ($N_0 = 100$). For time-to-reductions approximating 10 years, about 40 deer would have to be captured annually to have a 90% expectation of success (400 captures total over 10 years). There was a very small probability of success for short timelines. For example, there was only a 10% chance of success within 5 years at $C = 40$.

Trap aversion and trap affinity.—Simulated behavioral response to surgery and trapping contributed substantially to the rate of population decline. Permanent trap aversion ($\rho = 0$) increased the rate of population reduction because sterilized individuals were not recaptured, and, thus, C was skewed towards
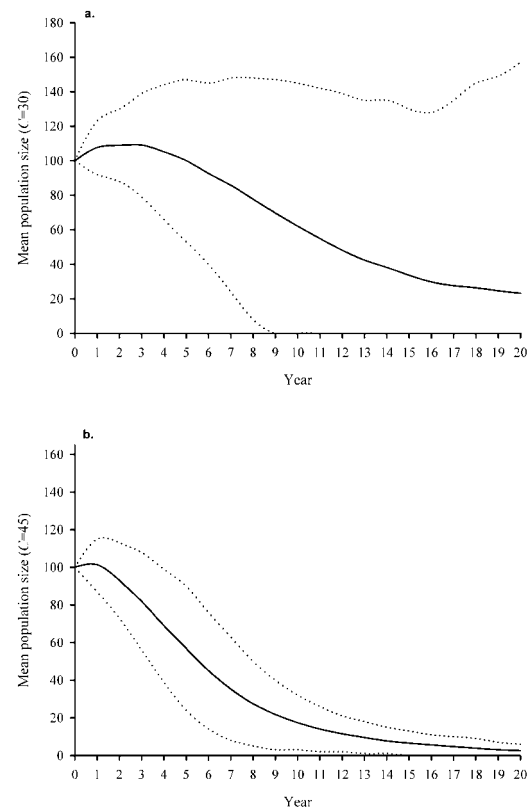

Figure 1. Change in population size over time as a function of capturing (a) $C = 30$, or (b) $C = 45$ deer, and sterilizing those that are fertile females ($N_0 = 100$). Lines are spline fits to means calculated across 200 replications, shown with numerically estimated 95% confidence intervals (dotted lines).

fertile animals. On the other hand, trap affinity ($\rho = 2$) significantly interfered with sterilization progress as recaptures became a significant proportion of animals captured (Fig. 3). For instance, over a 10-year time horizon where $N_0 = 100$ and $C = 30$, if sterilized females were captured proportionately to their numbers in the population as a whole, mean N_t declined to 50. However, if sterilized females became permanently trap-averse, mean N_t declined to 20. If sterilized females become twice as likely to be recaptured, mean N_t declined to 80 within 10 years, and never declined below 60 animals within 20 years.
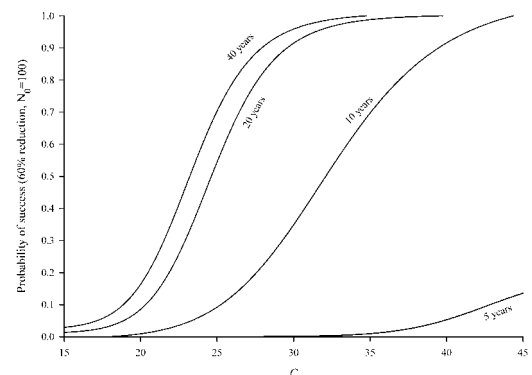

Figure 2. Probability of success in reaching management objective (defined as population size 60% lower than starting point) as a function of yearly capture sample C. Lines are spline fits to mean probabilities calculated over 200 repetitions; each line shows mean probabilities for different numbers of years needed to reach objective

Movement.—Immigration into the population dramatically impacted the rate of population growth, even when numerous deer were sterilized. Sterilization reduced the population growth rate, but not enough to stop or reverse growth. Field data from Cayuga Heights indicated that approximately 65 animals (15–20% of current population size) entered the population annually (C. Jennelle et al., Cornell University, unpublished data). We assessed the sensitivity of our model to rates of movement by contrasting results using our estimated base value with those obtained by increasing or decreasing rates of movement by some proportion ϕ (i.e., $\phi = 0.5$ if absolute immigration and emigration were half of our local estimates). If movement levels were constant, sterilization failed to reduce the population (Fig. 4). However, sterilization did reduce the growth rate; the population grew to 1,110 animals after 10 years if $C = 30$, but only to 665 animals if $C = 60$. Sterilization led to a population reduction only when 1) the net movement rates were 25% of our observed base values, and 2) $C > 45$. There was no difference between absolute immigration (without emigration) and absolute net immigration (with emigration). This indicates that emigration has a minimal impact on the efficacy of sterilization (relative to a model with no emigration) if immigration and emigration are constant.

If movement levels were additive (linearly density-dependent), sterilization did not lead to a reduction of the population (Fig. 5). Nevertheless, sterilization did influence equilibrium and delay the necessary time for a population to reach that equilibrium; the population grew to 380 animals at $C = 45$, but only to 329 animals at $C = 60$ after 20 years. At higher capture levels ($C = 60$), decreasing ϕ decreased the equilibrium level of the population after 20 years. Also, using $C = 45$, the population reached equilibrium in 15 years, whereas at $C = 60$, the population reached this equilibrium after 20 years. Sterilization reduced the population only when net movement rates were reduced to 25% of our observed base values and the number captured increased to $C > 45$. The presence of emigration substantially decreased the effectiveness of sterilization. For instance, if $\phi = 0.25$ and $C = 45$, the mean population declined to 74 animals after 20 years without emigration but grew to 200 animals in the presence of emigration. This indicates that emigration of sterilized individuals can alter results considerably, if immigration and emigration are additive.
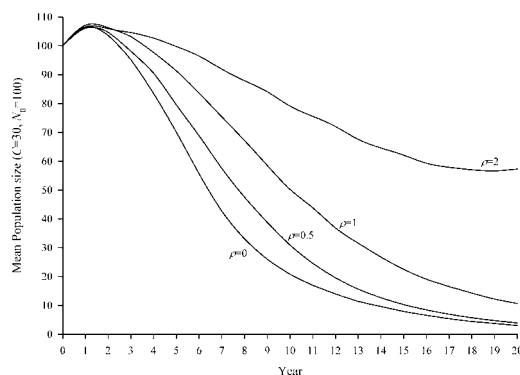

Figure 3. Influence of trapping effect ρ (capture probability; $\rho = 1$ indicates no trapping effect, $\rho < 1$ indicates trap aversion, and $\rho > 1$ indicates trap "happiness") on change over time in mean population size. Lines are spline fits to means calculated over 200 replications assuming an annual capture of $C = 30$ individuals. Initial population size is 100.

If movement levels were compensatory, sterilization did not reduce the population when $\phi = 1$ (Fig. 6). Similar to the additive model, sterilization did influence equilibrium population levels and delayed the necessary time for a population to reach the equilibrium level. Sterilization was found to reduce the population size only when $\phi < 0.25$ and $C > 45$. The presence of emigration in the model reduced the effectiveness of sterilization, but not to the degree evidenced in the additive model. Overall, the compensatory model affected outcomes quite similarly to the additive model because the models were identical for populations above N_{dens}.

Discussion

We determined that in a closed population, permanent fertility control (sterilization) could begin to reduce a population after 2–3 years, and a population reduction of approximately 60% could be achieved within 10 years (sensu Merrill et al. 2003), but this would require capturing approximately 30–45 animals out of each 100 annually. In a population with considerable immigration, however, sterilization would not likely reduce the population size regardless of management effort. In general, any factor contributing to variation in the sampling fraction decreased the likelihood of success.

Our results differ from previous work in 3 ways. First, we determined that stochasticity in both the system and the sampling fraction decreased the probability that sterilization would be successful. The sampling fraction had to be increased to reduce a population with confidence because random increments to productivity could linger in the population for 3–4 years, reducing the likelihood that sterilization would be successful. However, a random decrease in survival might be likely due to severe winters, increasing the likelihood sterilization would be successful. Our approach assumed constant effort expended annually (e.g., if $C = 30$, then 30 deer were always captured annually). This assumes that such efforts are attainable. In reality, if the population were reduced, trapping success would likely decline. While a reduced population reflects management success and less sterilization would reduce cost, the effort exerted capturing each fertile female would increase (Porter et al. 1991). In application, effort could be reduced using an optimized adaptive management strategy (Nielsen et al. 1997) that explicitly accounts for sources of both structural (model) uncertainty, and uncertainty in both the structure of the population at any point in time, and lack of precise control of the sample of deer captured (Williams et al. 2002).

Second, we determined that in some cases, trap aversion improves the probability of success while trap affinity considerably limits it. Our model only considered recapture effects for sterilized individuals and assumed that the capture rate of untrapped individuals did not change. If males became trap-averse, the positive effects of trap aversion would increase further. However, we assumed homogeneity in catchability among males and previously uncaught females. If some deer were considerably more difficult to capture than others, then the population could maintain a reproductive reserve that sterilization could not influence. This would reduce the efficacy of sterilization and may require extra trapping effort. Additionally, we did not assume
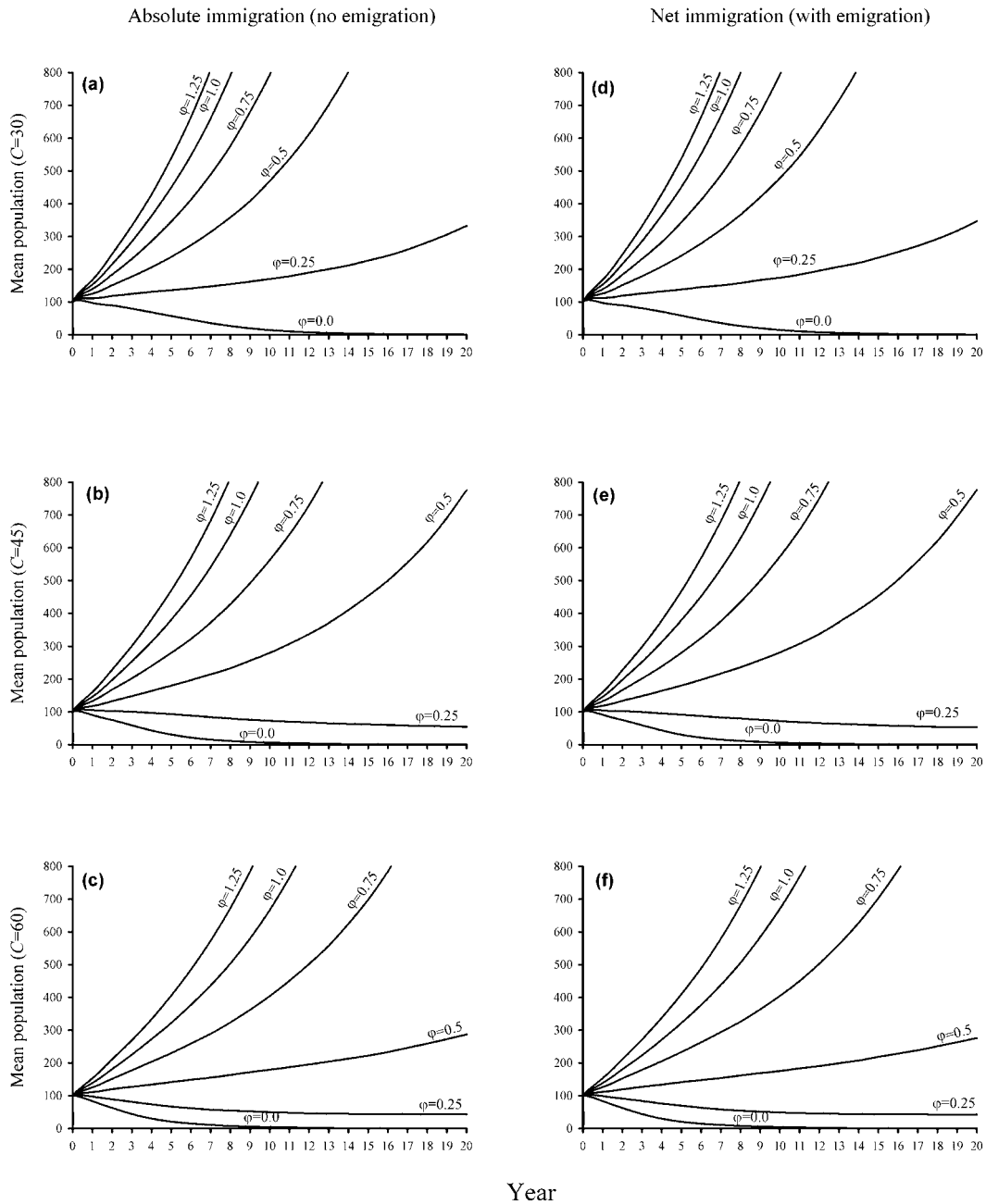
Figure 4. Influence of constant immigration on change over time in mean population size. Annual mean population size calculated across 200 replications for 3 levels of capture effort (*C* = 30, *C* = 45, *C* = 60) assuming a constant number (65) of only immigrants annually (a–c) and a constant number of both immigrants (101) and emigrants (36) annually (d–f). Magnitude of immigration was varied as a proportion φ of the base value. Immigration assumed to occur between spring and summer. Lines are spline fits to means calculated over 200 replications.

a social-structure effect in trap affinity. Capture of 1 individual in a family group might increase trap aversion among remaining individuals in that family group, For instance, if a fertile female mother with 2 nursing fawns was captured and became permanently trap-averse, her fawns could become similarly wary of traps. If social structure influences catchability, there may be a fertile segment of the population that would be extremely difficult to capture, reducing the effectiveness of sterilization. This would suggest a possible advantage to methods that allow for capture of complete family (or other social) groups (e.g., rocket nets or drop nets).

Finally, we demonstrated that sterilization would probably not reduce a truly open population. There are at least 3 reasons for this. First, for a closed population to have no growth (i.e., $\lambda = 1$), absolute births must equal absolute deaths. However, in an open population with net influx, the absolute number of deaths must equal the absolute number of births plus the absolute net gain of immigrants. Therefore, there must be enough absolute deaths to overcome net immigration, regardless of birth rates. In Cayuga Heights, the number of deaths is currently insufficient to outnumber new immigrants, although immigration rates have been observed to vary considerably from year to year. Therefore, fertility control—which affects only birth rates—might slow population growth, but it is unlikely to reduce the population
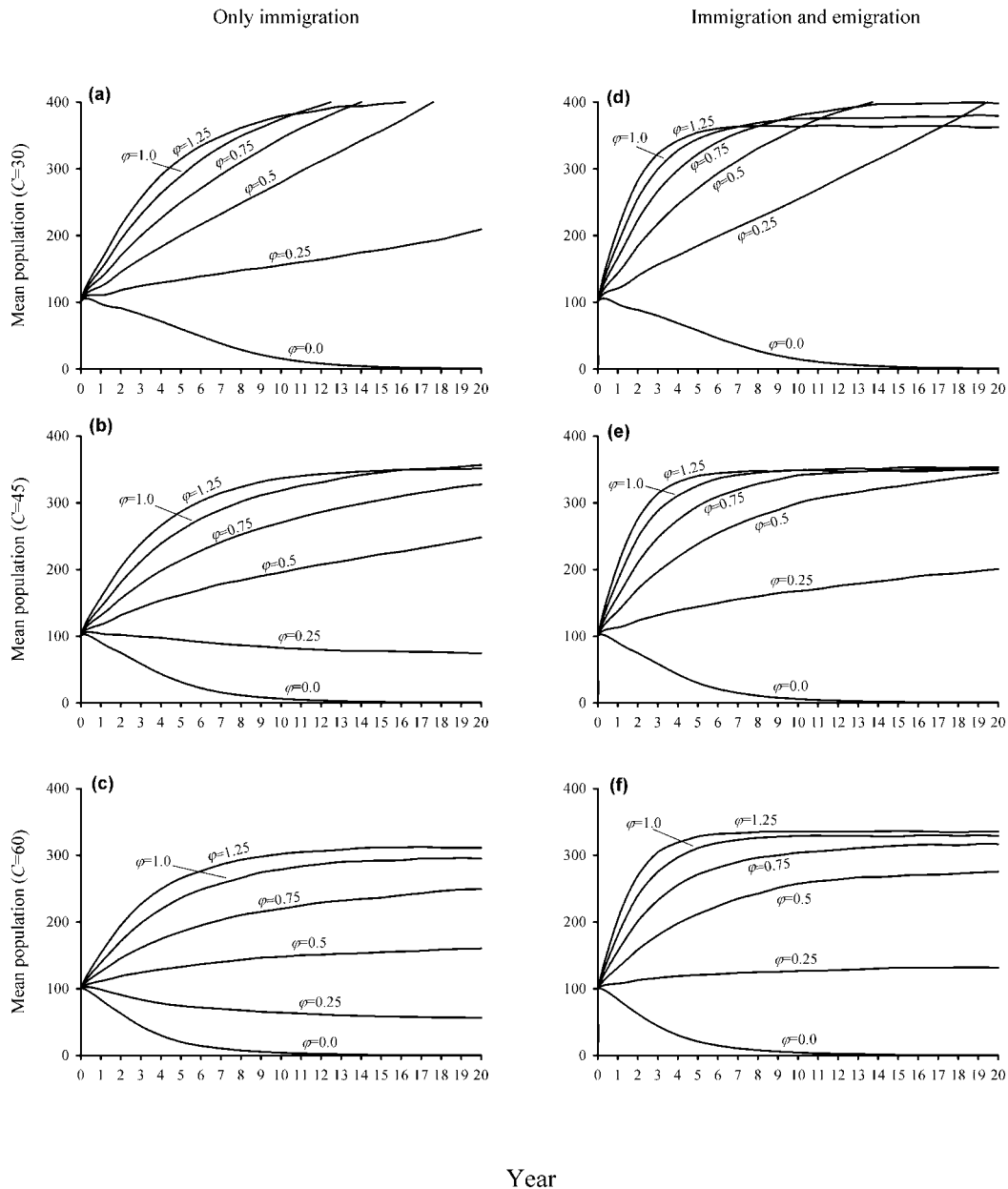
Only immigration

Immigration and emigration

Figure 5. Influence of additive immigration on change over time in mean population size. Immigration and emigration rates were linearly density-dependent functions of population size where population saturation ($\Delta N_t = 0$; see text) occurred at $N_t = 400$. Annual mean population size calculated across 200 replications for 3 levels of capture effort ($C = 30$, $C = 45$, $C = 60$) assuming an absolute number of only immigrants annually (a–c) and a constant number of both immigrants and emigrants annually (d–f). Magnitude of immigration was varied as a proportion ϕ of the base value. Immigration assumed to occur between spring and summer. Lines are spline fits to means calculated over 200 replications.

unless immigration rates are also low. The problem becomes exacerbated when immigration increased as population size decreased, which is the equivalent of an ecological sink. If immigration declined as population size increased, the population grew to equilibrium, and although sterilization may reduce this equilibrium population size, there was still positive net growth from N_0.

Second, in a closed population, fawns (which have minimal reproductive capacity relative to older individuals) are the only new individuals annually recruited to the population. However, in an open population, some new immigrant individuals will be yearling and adult females reproducing at near maximum capacity.

However, the influx of these individuals is not directly affected by sterilization. Therefore, a highly productive immigrant reserve exists regardless of sterilization.

Third, in a population with sterilized individuals, the possible emigration of sterilized females may open space for fertile female immigrants, wasting the resources expended in sterilizing the emigrant. In our simulations, we assumed that hormonally stable surgical sterilizations did not alter female behavior. If this assumption is violated and sterilized individuals were more likely to leave the system, they could be increasingly replaced with fertile individuals from outside the system, wasting the effort in sterilizing the exiting individual. However, this emigration would
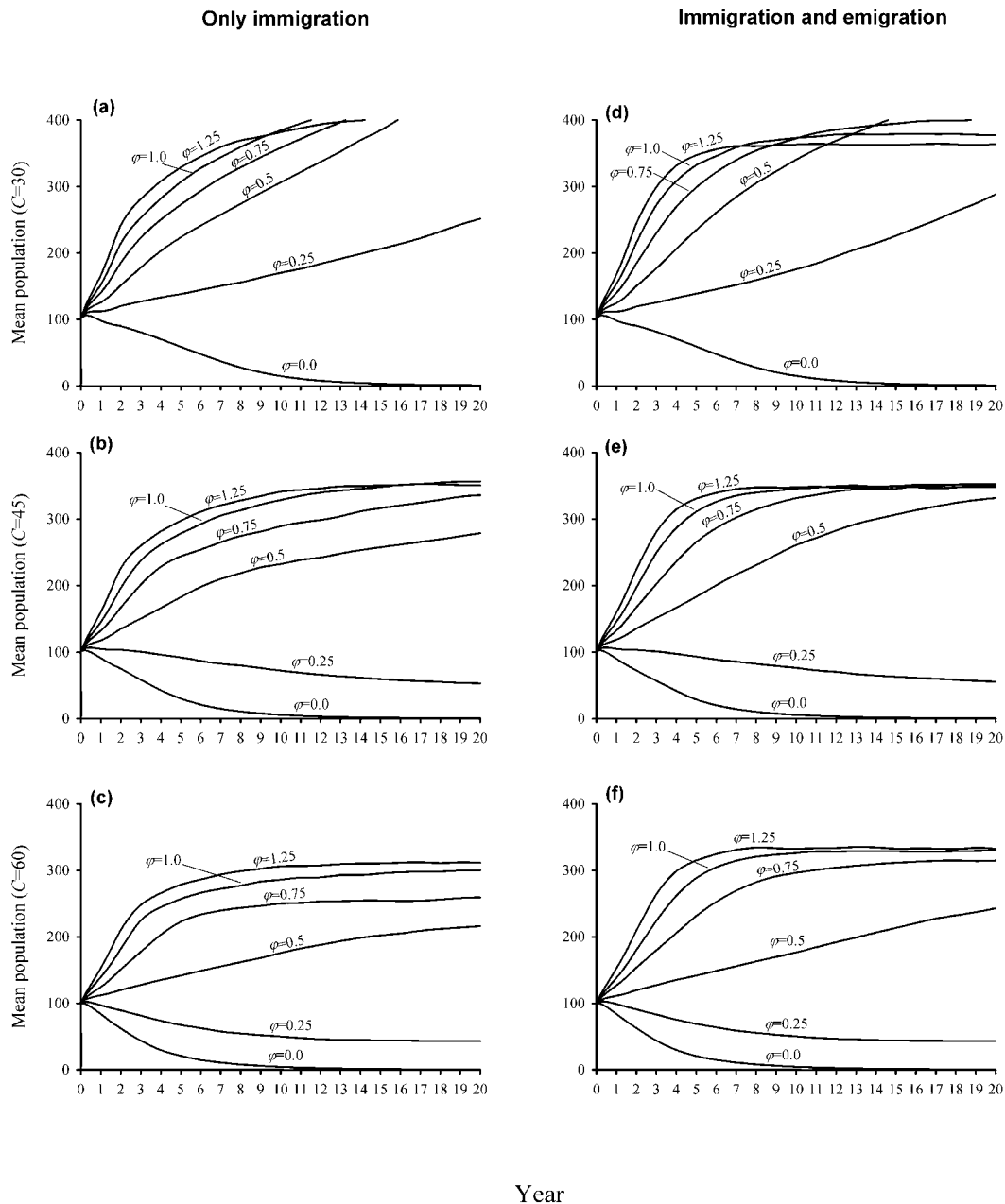
Figure 6. Influence of compensatory immigration on change over time in mean population size. Immigration and emigration were linearly density-dependent functions of population size when $N_t > 225$, population saturation ($\Delta N_t = 0$; see text) occurred at $N_t = 400$; immigration and emigration rates were constant when $N_t < 225$. Annual mean population size calculated across 200 replications for 3 levels of capture effort ($C = 30$, $C = 45$, $C = 60$) assuming an absolute number of only immigrants annually (a–c) and a constant number of immigrants and emigrants annually (d–f). Magnitude of immigration was varied as a proportion ϕ of the base value. Immigration assumed to occur between spring and summer. Lines are spline fits to means calculated over 200 replications.

offset immigration pressure to some extent (i.e., net immigration would be reduced).

Although immigration into the population is probably a function of demographic, social, and habitat characteristics of both the population and the adjoining areas, we assumed immigration was simply a function of characteristics within the population. Additionally, in our calculations of density-dependent immigration rates, we assumed a saturation level (i.e., a population size in which immigration would stop) of 154 deer per km² (Boldgiv 2001). If the saturation level were lower, the population size would level off at lower values. We modeled immigration as

additive and compensatory functions of abundance simply to demonstrate how structural assumptions would change the result. Preliminary analyses of data from the local Cayuga Heights population indicated substantial immigration (C. Jennelle et al., Cornell University, unpublished data). If such immigration is constant (i.e., not density-dependent), then it is unlikely that sterilization will work for this population. If immigration is density-dependent, either additive or compensatory, then sterilization may slow the population growth but is unlikely to reduce the population (which requires negative population growth).

Fertility versus Lethal Control

Reducing survival rates, particularly of adult individuals, is the most effective means of control of deer populations. However, when comparing the relative importance of immigration and birth rates on deer population dynamics, controlling immigration is potentially more effective than controlling birth rates in populations similar to Cayuga Heights. Twigg et al. (2000) showed that in the absence of control of net movement into or out of a rabbit population, fertility control would likely provide only a partial—and temporary—solution to population control. While controlling immigration (e.g., erecting fences and other barriers) may be difficult to implement, it would be a useful adjunct to a sterilization strategy. Hobbs et al. (2000) and Merrill et al. (2003) suggested that culling the population to an acceptable size and then using sterilization to maintain that size would be more effective than using fertility control alone to reduce a population. However, both methods assume a closed population. In an open population, a cull would not necessarily be sufficient to reduce a population to an acceptable size because in any of the 3 immigration models discussed here, a population reduction would create an ecological sink, resulting in new, fertile individuals filling the void. However, Porter et al. (1991) also proposed a spatial "rose-petal" model of overlapping deer territories in which offspring move to areas adjacent to the area of the mother. In a rose-petal model, periodic culls may be more effective because of the time necessary for several generations to spread from the ranges of surviving mothers. Alternatively, the use of control agents not restricted to specific geographic locations and that are able to self-apply by means of spreading through the population (e.g., infection by a released virus that has lethal or sublethal effects on the host; Twigg et al. 2000), may be effective in some cases.

Management Implications

Most research to date on the efficacy of sterilization to control deer populations has focused on biological feasibility. We have shown in this and our earlier analysis (Merrill et al. 2003) that potential for successful application of in situ sterilization to control deer populations will be strongly conditioned by several factors. First, sterilization is most likely to be effective if the population is demographically closed, or nearly so; for open populations, we have shown clearly that the chances for successful reduction and control of a typical deer population are significantly reduced, although predicting the impact of movement on the likelihood of achieving success will also be influenced by whether or not movements into and out of the population are density-dependent, and the functional form of any such dependence. This necessarily reduces the spatial scale at which sterilization is an option. Thus, evaluating sterilization as a management option would require preliminary assessment of whether or not the target population was effectively closed or could be rendered so by a companion action (e.g., fencing) and the pattern and process of movements of individuals for more open populations (sensu Porter et al. 2004).

Second, even for closed populations, assessment of the behavioral response of deer to both trapping and sterilization will be needed. Our analysis shows that trap response can significantly influence both the probability of achieving a particular population reduction and the time needed to achieve that objective. Further, trap response may be strongly influenced by capture methods used in the field; the effect of different capture methods on post-capture behavior is not well studied.

In summary, we believe that sterilization may require a substantial effort to reduce a population within an acceptable time-span, even one that is demographically closed. In an open population, sterilization alone probably will not be effective at controlling deer overabundance, especially if immigration increases as population size decreases. While stakeholders may be averse to hunting, consistent lethal control—either alone or in combination with fertility control (e.g., sterilizing most easily captured individuals, followed by lethal removal of remaining, more trap-averse individuals)—may be the only way to sustainably reduce a local deer herd below current levels.

Acknowledgments

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Associate Editor: McCorquodale.