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SHORT NOTE

MODELING WHITE-TAILED DEER *Odocoileus virginianus* POPULATION CONTROL BY CONTRACEPTION

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Abstract

Large populations of white-tailed deer Odocoileus virginianus *present conservation problems in suburban landscapes because of limited population control options. We used the GAPPS II modeling system to simulate temporal effects of contraception on deer population control and the interaction between contraception and uncertain immigration rates. Contraception rates less than 50% of female deer curbed population growth with a long (30 year) planning horizon, but did not reduce the size of the population. A minimal contraception rate of 50% was necessary to reduce population size, but even with contraception rates > 50% a 5–10 year planning horizon was necessary to see significant population declines in a closed population. Variability among simulations with the same contraception rate was high and suggests difficulty in detecting population changes in the field. This difficulty could pose management problems because contraception is most economically applicable for smaller populations. For an open population, population size was a non-linear function of contraception and immigration rates. Contraception does not seem a viable option for an open population unless a landscape-level conservation strategy is implemented to control metapopulation growth.*

Keywords: white-tailed deer, contraception, population dynamics, immigration, simulation, landscape.

INTRODUCTION

White-tailed deer *Odocoileus virginianus* populations have increased dramatically throughout the Eastern United States over the last several decades (McCabe & McCabe, 1984) and occur in a variety of landscapes, including suburban areas with a mixture of open fields and small forest patches in a matrix of commercial or residential development. In addition to state and municipal parks, industry and government facilities within suburban landscapes often become foci for deer activity by providing refugia from human activity and relatively large forest fragments for browse and cover. Many facilities require security fencing that, to varying degrees, can isolate a deer population. Suburban deer can thus be characterized as metapopulations, with suburban landscape structure determining local subpopulation isolation, extinction, and immigration from surrounding subpopulations.

Curtailed hunting in suburban areas can promote large deer populations with detrimental impacts. Browsing damage to tree regeneration and forest composition by white-tailed deer populations has been documented for a variety of forest types and regions (Ross *et al.*, 1970; Anderson & Loucks, 1979; Bratton, 1979; Kroll *et al.*, 1986; Storm *et al.*, 1989; Tilghman, 1989; Bratton & Kramer, 1990; Warren & Ford, 1990). Thus conservation of forest structural heterogeneity and forest advanced regeneration are often contingent on control of browsing. In addition, Decker and Connelly (1989) have documented many of the accident risks that large suburban deer populations pose for humans and the serious economic damage to ornamental plants in suburban areas.

It is important that measures be considered for stabilization or reduction of deer populations in some suburban areas. Despite its cost-effectiveness, hunting is usually prohibited for safety reasons in suburban areas (Decker & Connelly, 1989). One common alternative is chemical contraception (Kirkpatrick & Turner, 1985) for wildlife. Development and testing of remotely delivered immunocontraception for white-tailed deer (Turner *et al.*, 1992) has generated much interest because it seems well-suited for confined populations, such as those within fenced commercial or government reservations, and minimizes animal handling expenses. Unfortunately many of these deer populations occur on private lands or institutions whose missions are not related to population ecology, and little quantitative information on the population can be expected. It is thus difficult for managers to project the success of population control measures. Our objective

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was to simulate contraceptive control of white-tailed deer populations under the conditions of information uncertainty likely to exist for populations within suburban areas. To accomplish this we focused on the Goddard Space Flight Center in Greenbelt, MD, as an example of such conditions. Specifically, we (1) explored effective contraceptive delivery rates and planning horizons for reducing populations of these long-lived organisms, and (2) examined the inherent uncertainty associated with implementing such a procedure for populations without locally-known demographic characteristics, particularly immigration.

METHODS

The study site

Characteristics of the US National Aeronautics and Space Association's Goddard Space Flight Center (GSFC), Greenbelt, MD, were used for this simulation study. GSFC's main campus is approximately 165·5 ha in area and is surrounded by a 2·4 m fence topped with barbed wire. Of this area, approximately 55 ha consist of woodlots with mature hardwood or mixed pine–hardwood forest, most of which is found in three fragments. Small saplings and seedlings are uncommon in these woodlots because of heavy browsing. The remaining area consists largely of lawns, buildings, roads, and parking lots. One small pond is located on the campus and provides an abundant year-round water supply.

During September–October 1992, estimates were made of the deer population size on GSFC (M. Hille, pers. comm.). Multiple (9) direct counts along a set auto route (Kinningham, 1980) were carried out in late evening when deer were foraging on the lawns and along woodlot edges. For comparison, three strip counts were carried out in the woodlots by an individual during midday when deer were seeking cover. These techniques resulted in population and age structure estimates. Safety and Security Department personnel from GSFC have recorded deer deaths from occasional poaching and regularly-occurring vehicle collisions for several years, thus allowing annual accident mortality rates to be calculated.

Simulation software

Given the multiple sites that may eventually be interested in assessing the usefulness of contraceptive techniques for deer population control, we chose a commercial software package, the Generalized Animal Population Projection System (GAPPS II, Version 1.2), for our population simulations. GAPPS II (Applied Biomathematics, 1993) is a modular, individual-based population simulation system designed for relatively small populations. The model simulates the age, reproduction, survival, migration, and death of individuals. By simulating each individual in a population, GAPPS II is particularly appropriate for small populations in which management activities, such as contraception, can be applied to known individuals. Rates for life history characteristics, which can vary with age, sex, etc., are applied to individuals rather than cohorts and are implemented stochastically for annual iterations of the model.

Population parameters and simulations

Many population parameters for the simulation were derived from an intensively studied, enclosed deer population at the George Reserve (McCullough, 1979). These parameters included the proportion of the population that breeds each year (by age class), number of offspring, annual probability of death from natural causes, and age of weaning such that parents breed again. At GSFC, direct roadside counts resulted in a mean population estimate of 30 (SE = 6·8) individuals, a buck:doe ratio of 1:2, and a fawn:doe ratio of approximately 1. The less intensive strip censuses resulted in a population estimate of 33. Our simulations were carried out with an initial population of 30 because of the greater number of roadside censuses. Proportions of animals in fawn (36%), yearling (15% female, 4% male) and adult (29% female, 16% male) age classes were derived from the roadside count with the largest number of animal observations and assumed not to change over the short time period of the population counts. The exact white-tailed deer carrying capacity (K) of GSFC is unknown. Observations by security personnel, who patrol all areas of the campus, indicate no obvious changes in deer numbers and the frequency of deer–vehicle collisions between 1989 and 1992 showed no pattern of increase or decline. Based on this information and the degraded nature of woodlot vegetation we assume the population is at or near K. For all simulations we used the hunting module of GAPPS II to simulate the death of animals by road accidents (13%). Individuals killed on nearby roadways outside the fenced perimeter were not included in calculation of this rate because it was unknown whether they actually belonged to the GSFC population. The data on road kills within GSFC did not indicate a sex or age bias. We thus assumed that the annual probability of being killed by a vehicle was equal for all members of the simulated population.

We first simulated deer populations with different proportions of does receiving contraceptive treatment. This model experiment focused on temporal rates of population decline with different treatment levels and assumed a closed population without immigration or emigration. Despite fencing, deer commonly move onto and from GSFC through open traffic gates and mature individuals have been observed to jump the fence where soil mounds from uprooted trees are near the fence to provide assistance. Thus, secondly, we simulated population sensitivity to immigration during contraceptive treatment. Specifically, we examined the interaction between contraception and immigration by simulating different combinations of each. Contour plots were developed (Anon., 1993) to display population size as a function of these two variables. All simulations were run for 30 years. Simulated contraception scenarios

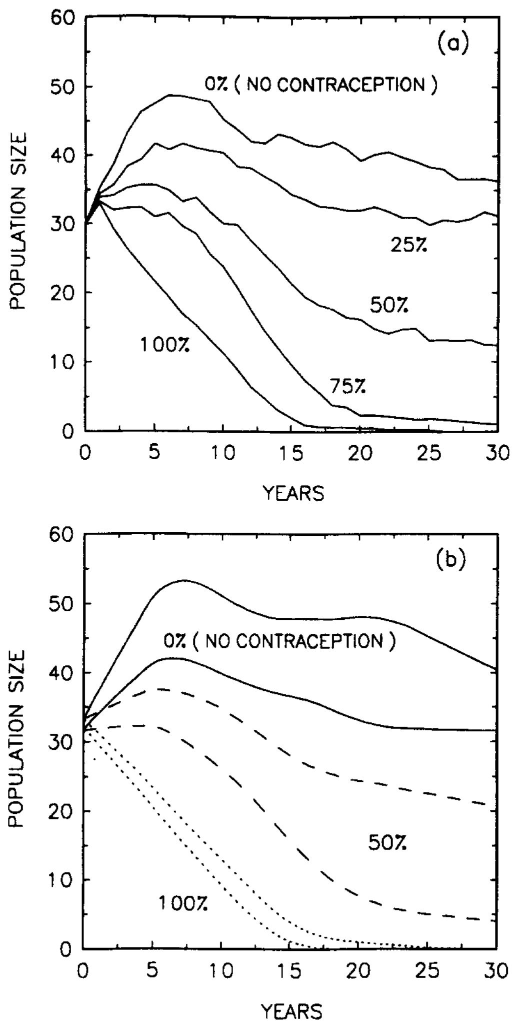

Fig. 1. Temporal trends of a white-tailed deer population exposed to different delivery rates of contraceptive (a), and variation of population size among simulations having the same contraception rate (b). Each population line in (a) is the mean of 10 model simulations, starting with an initial population of 30 animals. Variation in (b) is represented by ± 1 SD around the mean for each model time step. Variation for only 0%, 50%, and 100% contraception are shown.

assumed that contraception was effective 95% of the time. For all simulation scenarios, population sizes from 10 model runs were averaged and the mean used to represent population trends.

RESULTS

Percent contraception

Our control simulation (Fig. 1(a)), having no contraception, resulted in the mean deer population size increasing over the first 6 years of the simulation from 30 to approximately 48 individuals. This increase was followed by a gradual decline toward the carrying capacity of 30 individuals. This population trend resulted from two factors. First, the initial population has a large number of individuals with a high probability of breeding. Secondly, in this model, a population size above K decreases the probability of breeding for each individual. The impact of 25% contraception was apparent (Fig. 1(a)); however, the temporal mean population trend was similar to the control with an average 11% reduction in size from control levels. When an average of 50% of the females did not breed, a steep mean population decline occurred between 5 and 20 years, followed by a slower population decrease for the remainder of the simulation (Fig. 1(a)). Thus, between 25% and 50% contraception there exists a threshold of population susceptibility to this treatment. Seventy-five and 100% contraception increased the rate of mean population decline and resulted in small stable populations at 20 and 16 years, respectively (Fig. 1(a)).

Despite distinct rates of mean population decline with different contraception levels (Fig. 1(a)), there is considerable variation among simulations having the same contraception rate (Fig. 1(b)). In fact, changes in a contraception rate of ≥ 50% are necessary to make a clear distinction among contraception impacts (Fig. 1(a),(b)). This variation among simulations decreased with 100% contraception. Variation is maintained across all contraception levels because contraception was considered only 95% effective and because stochastic effects can be pronounced in small populations.

Immigration–contraception interaction

Intuitively, immigration should decrease the effectiveness of contraception in lowering deer population sizes, although the degree of this effect is not clear. In our simulation results, this decrease in effectiveness is evidenced by diagonal population contours as a function of interacting immigration and contraception rates (Fig. 2). As the population planning horizon increased from 5 to 20 years (Fig. 2(a)–(c)), population contours became closer, reflecting the greater reduction in population size at high contraception and low immigration as well as the greater increase in population size with low contraception and high immigration rates. Different planning horizons and degrees of population isolation will certainly call for different percentages of contraception delivery to reduce or stabilize population size. More importantly, the interaction between immigration and contraception was nonlinear, with the contour lines becoming steeper at contraception rates less than 25–50%. This effect was most evident over longer planning horizons. Thus deer population management using contraception delivery rates lower than 50% may be ineffective at either curbing growth or decreasing population size even at low immigration rates.

DISCUSSION

The cost of estimating population size, population age structure, and immigration rate is highly dependent on the detail of information desired. Estimating population size and age structure by the methods used here are seldom exact, but do provide an index by which to gauge the temporal success of population control and are relatively inexpensive. We believe that our population estimate for GSFC is probably low. However, we

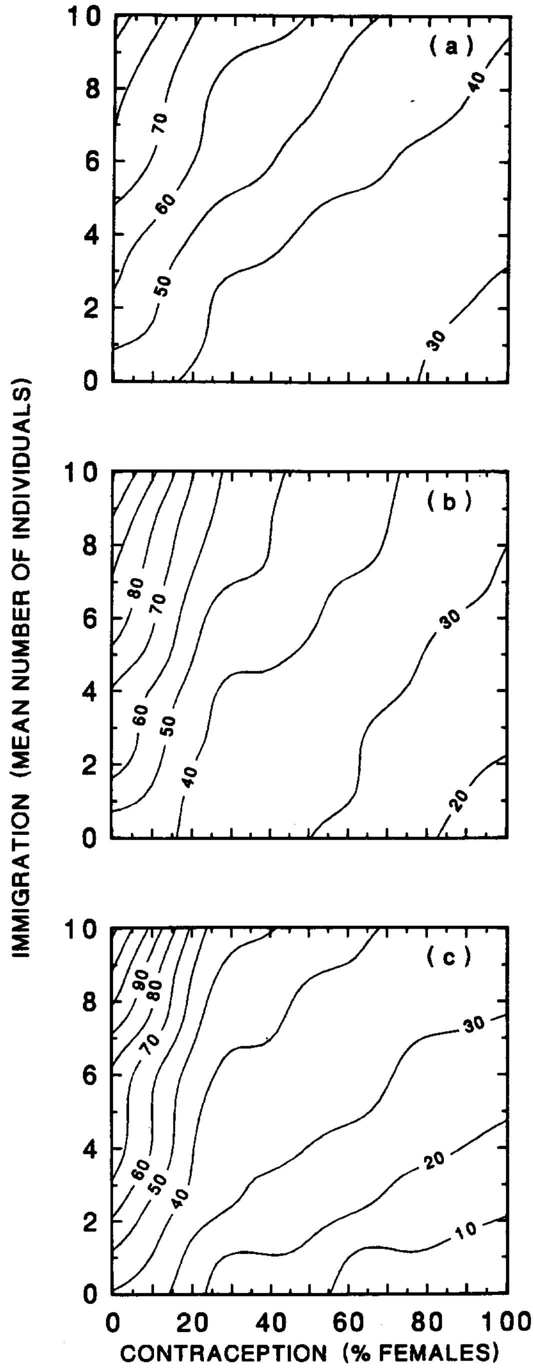

Fig. 2. White-tailed deer population size as a function of contraception rate and immigration rate for 5 year (a), 10 year (b), and 20 year (c) planning horizons. Population sizes are the mean of 10 simulations.

suggest that simple population size indices are acceptable for monitoring success of contraception within areas where intensive population management for a maximum sustainable harvest is not a priority. Nonetheless, at low to moderate levels of contraception, variability among simulations suggests potential difficulty in quantifying population changes in the field, especially if population sizes are very low in which case errors in estimating population indices can be inflated. Immigration rate is an important parameter to consider in planning population control and, as shown by our simulations, immigration has strong ramifications for control of small populations. Unfortunately, reliable estimates of immigration rates probably require extensive efforts of marking and tracking animals.

Generally, our simulations suggest a planning horizon of at least 5–10 years for significant deer population reduction even with 100% delivery of contraceptives. The feasibility of a 10-year planning horizon depends on the objectives for population control. For example, conservation of endangered plant species susceptible to browsing may dictate shorter term planning and adoption of other population management methods. Alternatively, accumulation of advanced regeneration saplings for forest/woodlot succession may withstand longer term planning, unless regeneration has already been prohibited for a substantial time period and/or overstory (seed tree) mortality is high due to other factors. Planning horizons will also obviously be dependent on current population level with respect to desired population levels. Whatever the initial planning horizon, contraceptive programs will need to be maintained as long as habitat and food conditions are conducive to deer population growth. However, initially high contraceptive rates used to reach a target population level might be replaced by lower rates to maintain that level.

As indicated by our simulations of immigration–contraception interactions, with an increasingly open population the effectiveness of contraceptive control decreases quickly. Management of mobile wildlife is, in reality, a landscape-level problem dealing with metapopulations where immigration and emigration occur among semi-isolated subpopulations. Quantitative planning at the landscape scale would be the most effective means to determine where concurrent contraception and other management techniques should be implemented to achieve the most cost-effective and spatially extensive conservation result.

We have focused on the population effects of contraception. Although increasingly attractive to local managers because of species-specificity, we doubt that many private and government institutions wishing to employ contraception will be interested in long-term studies to parameterize models and assess migration. Our simulations reflect these conditions and draw heavily on published literature for population parameters. With this limited data approach site-specific model inaccuracies will always exist. Thus the temptation simply to 'deliver as high a contraceptive rate as possible until a noticeable population decline is observed' will exist. As demonstrated, this strategy can easily fail. Assessment of site characteristics, such as population size and isolation, and understanding site characteristics in a landscape context, provide the greatest opportunity for cost-effective conservation of both vegetation and wildlife resources.

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REFERENCES

Anderson, R. C. & Loucks, O. L. (1979). White-tailed deer (*Odocoileus virginianus*) influence on the structure and composition of *Tsuga canadensis* forests. *J. Appl. Ecol.*, **16**, 855–61.

Anon. (1993). AXUM: technical graphics and data analysis. TriMetrix, Inc. Seattle, Washington.

Applied Biomathematics (1993). GAPPS II: generalized animal population projection system. Version 1.2. Applied Biomathematics, Setauket, NY.

Bratton, S. P. (1979). Impacts of white-tailed deer on the vegetation of Cades Cove, Great Smoky Mountains National Park. *Proc. Ann. Conf. SE Assoc. Fish & Wildl. Agencies*, **33**, 305–12.

Bratton, S. P. & Kramer, E. A. (1990). Recovery of live oak sprouts after release from browsing on Cumberland Island National Seashore, Georgia. Research on Mid-Atlantic Coastal Barrier Islands, National Park Service and The Nature Conservancy. Nags Head, NC (unpublished report).

Decker, D. & Connelly, N. A. (1989). Deer in suburbia — pleasures and pests. *Conservationist*, **43**, 46–9.

Kinningham, M. J. (1980). Density and distribution of white-tailed deer (*Odocoileus virginianus*) in Cades Cove, Great Smoky Mountains National Park, Tennessee. MS thesis, University of Tennessee.

Kirkpatrick, J. F. & Turner Jr, J. W. (1985). Chemical fertility control and wildlife management. *BioScience*, **35**, 485–91.

Kroll, J. C., Goodrum, W. D. & Behrman, P. J. (1986). Twenty-seven years of over-browsing: implications to white-tailed deer management on wilderness areas. In *Wilderness and natural areas in the Eastern United States: a management challenge*, ed. D. L. Kulhavy & R. N. Conner. Center for Applied Sciences, School of Forestry, Stephen F. Austin University, Nacogdoches, TX, pp. 294–303.

McCabe, R. E. & McCabe, T. R. (1984). Of slings and arrows: an historical retrospective. In *White-tailed deer: ecology and management*, ed. L. K. Halls. Stackpole, Harrisburg, PA, pp. 19–72.

McCullough, D. (1979). The George Reserve deer herd: populations ecology of a K-selected species. University of Michigan Press, Ann Arbor, MI.

Ross, B. A., Bray, J. R. & Marshall, W. H. (1970). Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. *Ecology*, **51**, 1088–93.

Storm, G. L., Yahner, R. H., Cottam, D. F. & Vecellio, G. M. (1989). Population status, movements, habitat use, and impact of white-tailed deer at Gettysburg National Military Park and Eisenhower National Historic Site, Pennsylvania. US National Park Service Project Report. University Park, PA (unpublished report).

Tilghman, N. G. (1989). Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J. Wildl. Manage.*, **53**, 524–32.

Turner, J. W., Jr, Liu, I. K. M. & Kirkpatrick, J. F. (1992). Remotely-delivered immunocontraception in white-tailed deer. *J. Wildl. Manage.*, **56**, 154–7.

Warren, R. J. & Ford, C. R. (1990). Population and ecological characteristics of white-tailed deer on Catoctin Mountain Park. Final Report. National Park Service, Washington, DC (unpublished report).