

Population-level effects of immunocontraception in white-tailed deer (*Odocoileus virginianus*)

Allen T. Rutberg^{A,C} and Ricky E. Naugle^B

^ADepartment of Environmental and Population Health, Tufts–Cummings School of Veterinary Medicine, 200 Westboro Road, North Grafton, MA 01536, USA.

^BThe Humane Society of the United States, 700 Professional Drive, Gaithersburg, MD 20879, USA.

^CCorresponding author. Email: allen.rutberg@tufts.edu

Abstract. In North America, dense populations of white-tailed deer (*Odocoileus virginianus*) in suburbs, cities and towns have stimulated a search for new population-management tools. Most research on deer contraception has focused on the safety and efficacy of immunocontraceptive vaccines, but few studies have examined population-level effects. We report here results from two long-term studies of population effects of the porcine zona pellucida (PZP) immunocontraceptive vaccine, at the National Institute of Standards and Technology (NIST), Gaithersburg, Maryland, USA, and at Fire Island National Seashore (FIIS), New York, USA. Annual population change at NIST was strongly correlated with population fertility ($r_p = 0.82$, $P = 0.001$); when population fertility at NIST dropped below 0.40 fawns per female, the population declined. Contraceptive treatments at NIST were associated with a 27% decline in population between 1997 and 2002, and fluctuated thereafter with the effectiveness of contraceptive treatments. In the most intensively treated segment of FIIS, deer population density declined by ~58% between 1997 and 2006. These studies demonstrate that, in principle, contraception can significantly reduce population size. Its usefulness as a management tool will depend on vaccine effectiveness, accessibility of deer for treatment, and site-specific birth, death, immigration, and emigration rates.

Introduction

In the last three decades, conflicts with white-tailed deer (*Odocoileus virginianus*) have proliferated in North America. This proliferation has arisen from the confluence of several historical, environmental, and biological trends. Following near-extirpation in the 18th and 19th centuries, North American deer populations began to recover in the first half of the 20th century through a combination of strongly enforced regulatory restrictions on hunting, habitat protection and enhancement, and aggressive relocation programs (Tober 1981; Gilbert and Dodds 1992). The growth of deer populations accelerated in the second half of the 20th century due to the introduction of high-yield crops in rural areas, and the post-war growth of suburbs, which proved to be excellent deer habitat. In many rural and suburban districts, the rising deer population swamped the capacity of hunters to control the population; both hunter numbers and access to hunting land have diminished (Rutberg 1997; Brown *et al.* 2000). Moreover, the state agencies that are responsible for managing deer populations are hampered by a history of policies and programs structured to increase deer populations, and by inexperience in dealing with stakeholders other than hunters and farmers.

Dense populations of deer in suburbs and towns have proven to be particularly challenging, especially along the mid-Atlantic coast and in urban fringes of midwestern cities such as Chicago, Minneapolis and St Louis (Brown *et al.* 2000; DeNicola *et al.* 2002). Deer in these suburbs routinely

reach densities of 30–100 km⁻² and higher (Swihart *et al.* 1995; Palmer *et al.* 1997; Peck and Stahl 1997; Underwood and Porter 1997; this study). At these elevated densities, motorists face increased risks of deer–vehicle collisions, deer aggravate homeowners by stripping ornamental plantings and gardens, and shrubs and wildflowers vanish from public parks (Conover *et al.* 1995). Perceptions that deer spread tick-borne diseases such as Lyme disease and ehrlichiosis also raise public alarm (Barbour and Fish 1993). The public demands action, often with a focus on deer population control.

Often, however, traditional hunting practices are obstructed in densely settled areas by safety concerns, legal restrictions, limited land access, and public opposition (although highly structured, intensely managed hunts are sometimes successful for reducing circumscribed suburban deer populations) (Hansen and Beringer 1997; Brown *et al.* 2000; Kilpatrick *et al.* 2002). Together with burgeoning interest in animal welfare among suburbanites, practical and legal limitations on hunting have spawned considerable public and professional interest in the application of contraceptives to deer management (Stout *et al.* 1997; Lauber and Knuth 2000; Fagerstone *et al.* 2002; Kirkpatrick 2005).

Although attempts to use contraceptives to stop deer from breeding date back to the 1960s, none showed management promise until the emergence of immunocontraceptive vaccines in the late 1980s (Kirkpatrick and Rutberg 2001; Naugle *et al.* 2002). The initial studies showed only that pregnancy could be blocked in captive deer with multiple-shot vaccines (Turner *et al.*

1992, 1996; Miller *et al.* 1999). These were followed by studies showing that these vaccines could be delivered effectively to deer in the field (Kirkpatrick *et al.* 1997; Curtis *et al.* 2002; Naugle *et al.* 2002). However, the requirement for repeated initial shots and annual boosters was widely understood to limit management application, and research turned to formulating vaccines that would be effective for several years with a single treatment (Muller *et al.* 1997; Turner *et al.* 2001). Three technologies now appear to have achieved this capacity: Spay-Vac (ImmunoVaccine Technologies Ltd, Halifax, Nova Scotia), GonaCon (USDA National Wildlife Research Center, Fort Collins, Colorado), and porcine zona pellucida (PZP) in timed-release pellets (Fraker *et al.* 2002; Hernandez *et al.* 2006; Killian *et al.* 2006; Turner *et al.* 2007, 2008). The technical challenges that remain comprise improving remote delivery, scaling up production, and reducing costs.

At the same time, prospects for USA regulatory approval have brightened considerably. Federal jurisdiction over wildlife contraceptives is being transferred from the Food and Drug Administration (FDA) to the Environmental Protection Administration (EPA), and the EPA has already conferred two provisional registrations on a novel bird contraceptive (OvoControl-G for Canada geese and OvoControl-P for pigeons: Innolytics, LLC, Rancho Santa Fe, California). Although the process of obtaining EPA registration for wildlife contraceptives is expected to be highly rigorous, EPA's testing, manufacturing, labelling, and record-keeping requirements are likely to be far better suited to the evaluation and production of wildlife contraceptives than are FDA's procedures, which are scaled to testing, production, and revenue expectations that exceed those of wildlife contraceptives by several orders of magnitude.

Thus, it is timely to begin considering the problems of management application of contraceptives to white-tailed deer and other species: what can we expect of, or hope for, deer contraception? Among the immediate questions are:

- How deep a population reduction can we obtain from deer contraception alone?
- How fast can such a reduction be accomplished?
- What kinds of social and biological landscapes are best suited to the use of contraception as a management tool?
- How much is contraception likely to cost?

In this paper, we describe our experience with the control of white-tailed deer populations at a suburban study site, the National Institute of Standards and Technology, Gaithersburg, Maryland, USA, and provide supplementary information on a second suburban study site, Fire Island National Seashore, New York, USA. From these experiences, we draw some conclusions about the prospects for immunocontraception as a tool for managing white-tailed deer in suburban environments.

The National Institute of Standards and Technology,
Maryland

In the early 1990s, the managers of the 233-ha fenced research campus of the National Institute of Standards and Technology (NIST) in Gaithersburg, Maryland, USA, were facing the prototypical suburban deer-management dilemma. Established

nearly 30 years earlier in what was then farm country, NIST and its resident herd of wild white-tailed deer had become engulfed by the sprawling suburbs of Washington DC. With ~145 ha of lawn and 16 ha of mixed hardwood forest, NIST also received a steady stream of immigrant deer whose home ranges had been disrupted by development. As its deer population swelled, deer-vehicle collisions became more common, ornamental azaleas were stripped to 2 m in height, and the floors of its two small woodlots became utterly barren. Nearly surrounded by highway, shopping centres, and high-density housing, and used continuously by researchers, technicians, and maintenance workers, the NIST campus is unhuntable.

After a few years of provisioning the deer with corn, which probably exacerbated its problem, NIST's managers sought other alternatives for coping with its deer. In 1993, NIST signed a Memorandum of Agreement with The Humane Society of the United States to cooperate to mitigate the impacts of deer on the NIST campus.

Methods

Beginning in 1994, we captured deer using three methods: trapping with solid-sided Stephenson-style box traps baited with corn; chemical immobilisation with mixtures of Telazol or Ketaset and Xylaject delivered in barbed self-injecting 2–3-cc darts fired from a Pneu-dart cartridge-powered dart rifle; and hand-capture of fawns less than one week old. All captured deer were fitted with a uniquely numbered plastic eartag and a metal eartag bearing a matching number (Rutberg *et al.* 2004).

Adult, yearling, and fawn females were hand-injected or remotely darted with PZP, prepared as described in Liu *et al.* (1989). Between November 1995 and October 2006, we administered a variety of vaccine formulations, including seven different adjuvants: Freund's Complete Adjuvant (FCA) and Freund's Incomplete Adjuvant (FIA) (Sigma-Aldrich, St Louis, Missouri); Modified Freund's Adjuvant (MFA) (CalBiochem, LaJolla, California), Carbopol 934P (B.F. Goodrich, Cleveland, Ohio); Montanide ISA 50 and Montanide ISA 206 (Seppic, Paris); and synthetic trehalose dicorynomycolate (Corixa, Hamilton, Montana). PZP doses ranged from 100 to 400 mg. These preparations varied widely in effectiveness (Rutberg 2005). Approximately 61% of all females treated received an initial vaccination of 100 mg PZP emulsified in FCA or MFA, and subsequent boosters of 100 mg PZP emulsified in FIA (after Kirkpatrick *et al.* 1990). For the purposes of this paper, females were classified as 'treated' if they had received an initial PZP primer and one or more subsequent boosters, including a booster administered 2–10 weeks before the onset of the autumn breeding season.

To monitor reproduction, the campus was searched intensively for fawns by vehicle and on foot 2–3 times per week in May and June, and 1–2 times per week in July, August and September. Fawns were matched with their mothers via observations of nursing and close spatial associations, as well as female udder condition. We estimated the number of fawns per female among PZP-treated females by dividing the number of fawns associated with treated females by the number of treated females, and estimated overall population fertility by

dividing the total number of fawns observed by the number of yearling and adult females in the population. Because some stillbirths and neonatal mortality were probably missed, all estimates of fawning rate represent minimums.

We used three methods of direct, complete counting to estimate population size (Davis and Winstead 1980): counts by vehicle, combination vehicle and drive counts, and, beginning in 2000 (when >90% of all deer on campus were ear-tagged), complete inventories of ear-tagged (and untagged) individuals (Rutberg *et al.* 2004). Tag inventories were also used to note disappearances of tagged animals, and identify new animals that had entered the site. Deaths and identification numbers of tagged deer were reported to campus police, NIST project staff, and investigators. Because timing of disappearances was difficult to determine, only the cumulative number and annual averages are reported for disappearances.

Until 90% of the deer population was ear-tagged (2000), it was difficult to produce even crude estimates of the number of immigrant deer. Estimates are reported only for 2003–06.

Relationships between change in population size and other variables were described using Pearson correlations. All statistical analysis was carried out on SPSS 13.0 for Windows.

Windows Excel was used to create a simple deterministic model to predict population trends at NIST over 10 years. Starting with the observed population size in 2005, the model used successive annual iterations of

$$N_{t+1} = N_t \times L \times \delta I + PF \times M \times \beta I;$$

where L = overall annual survival probability, PF = proportion of yearling and adult females in the population, M = number of fawns/adult and yearling female, and I = number of immigrants. The proportion of adult and yearling females in the population was estimated from the 1994–2006 averages; annual survival was estimated from 2001–06 data on deaths and disappearances; and number of immigrants was estimated from 2003–06 data. Number of fawns produced per female was varied to suit the purposes of the model.

Results

Between March 1994 and December 2006, we captured and ear-tagged 747 deer (357 males and 390 females). We spent an average of 11.0 person-hours per deer captured (s.d. = 5.9) via chemical immobilisation, with no linear trend over the years ($r = -0.37$, $P = 0.17$). It was not possible to estimate effort required for other capture techniques, because they were carried out simultaneously with other field tasks. We administered 1630 PZP treatments to 311 females, spending an average of 1.8 h per treatment (s.d. = 0.8) for dart delivery. As with chemical capture, there was no linear trend over the years ($r = 0.27$, $P = 0.21$).

Annual fertility of PZP-treated females varied between 0.12 and 0.59 (Fig. 1). Females treated with PZP/FCA or PZP/MFA primers and PZP/FIA boosters averaged 0.19 fawns per doe; other preparations typically showed poorer results. Between 1994 and 1999, untreated females (those that had never received any PZP treatments) averaged 0.77 (s.d. = 0.16) fawns per year. (After 1999, almost all females that had never been treated with PZP were yearlings, skewing fertility

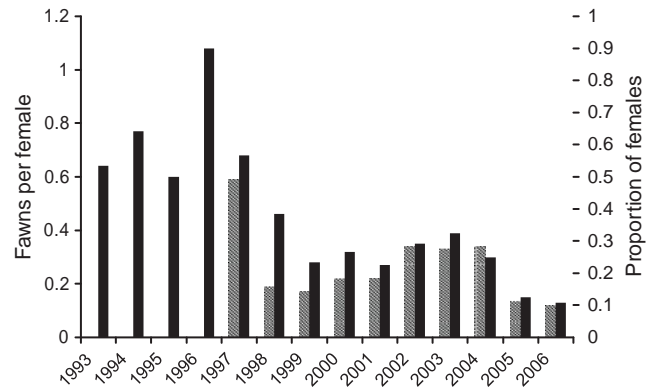


Fig. 1. At National Institute of Standards and Technology (NIST), annual fertility in fawns per female in porcine zona pellucida (PZP)-treated females (hatched bars) and the total population (solid bars), and proportion of females treated (line).

rates downward.) Total population fertility decreased as vaccine efficacy and the proportion of females treated increased (Fig. 1).

Deer population size at NIST grew at ~10–12% per year from 185 in 1993 to a peak of ~300 in 1997, in the first year of contraception. The population then declined at ~6–8% per year to just above 200 in 2002, rose slightly during 2003–04, and then resumed declining through 2007 (Fig. 2). Between 1993 and 2006, population sex ratios (adults and yearlings) averaged 0.54 males per female (s.d. = 0.08), and did not change with time ($r = 0.02$, $P = 0.477$). Changes in population size closely tracked changes in population fertility, and annual population change was highly correlated with the number of fawns born per female the previous year ($r = 0.82$, $n = 13$, $P = 0.001$) (Fig. 3). The value of population fertility at the x-intercept (=0.40) estimates the point at which the population should be stable, i.e. zero population growth.

Between 1994 and 2006, 431 deer, including 323 ear-tagged deer, were found dead on or adjacent to the NIST campus, averaging 14% annual minimum mortality (s.d. = 5.2, c.v. = 0.37). Of the 297 deaths for which cause of death was known, 59.9% were caused by collisions with vehicles. In addition, 107 ear-tagged deer disappeared from 2001 through

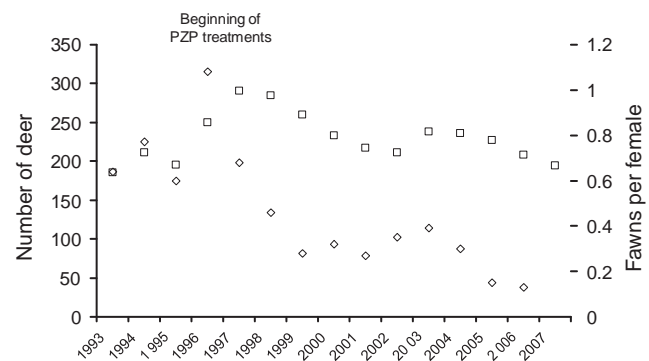


Fig. 2. Autumn population size (squares and dashed line) and population fertility in fawns per female (diamonds and solid line) at National Institute of Standards and Technology (NIST).

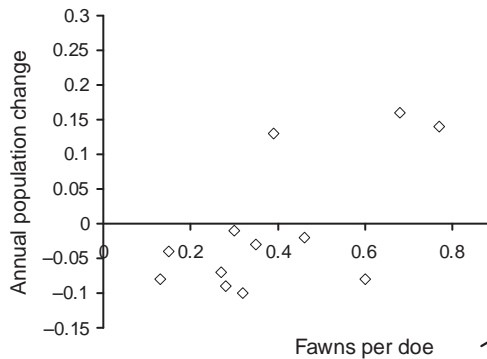


Fig. 3. Annual population change versus population fertility in fawns per female in the preceding year at National Institute of Standards and Technology (NIST) ($r_p = 0.82$, $P = 0.001$).

2006, or ~8% of ear-tagged deer per year (although the proportions varied widely, in part because of difficulties in pinpointing the time of disappearance). The combined death and disappearance rate for 2001–06 was thus ~22% per year.

Approximately 5–12 immigrants entered the NIST deer population annually between 2003 and 2006. However, the development of adjacent land may have been responsible for an influx of as many as 30 deer in 1996–97.

Using the data-derived estimates of 78% annual survival, 58% adult and yearling females, and 8 immigrants per year, we modelled the expected NIST deer population trajectory for 2005–17. As predicted by Fig. 3, a fertility rate of 0.40 fawns per female yields a stable population. A fertility rate of 0.15 fawns per female, which was achieved in 2005 and further reduced in 2006 (Fig. 1), predicts a population decrease of ~50% in 6 years, and asymptotes towards a stable population of 60–70 deer.

Discussion

Changes in deer population size impressively tracked the effectiveness of contraception effort, as measured by the number of fawns produced per female across the population. The increases in population fertility in 2002 and 2003, and the subsequent increases in population size in 2003 and 2004, were associated in 1999 and 2001 with tests of vaccine reversibility, in which we stopped administering boosters to 27 females, and to treatment of 25 females during 2000–02 with several vaccine preparations that proved to be ineffective. Starting in 2004, we resumed treating a high proportion of females with our best available vaccine (PZP emulsified in MFA followed by PZP/FIA boosters), which resulted in decreased population fertility and resumption of the population decline. This short-term rise in population fertility and population size observed at NIST in 2003 and 2004 emphasises the roles that vaccine efficacy and treatment effort play in successful population-control efforts (see General Discussion and Conclusions, below).

Inspection of Fig. 3 suggests, for the NIST population, a threshold value of ~0.40 fawns per doe above which population increased, and below which population decreased. This estimate is supported by the simple spreadsheet population

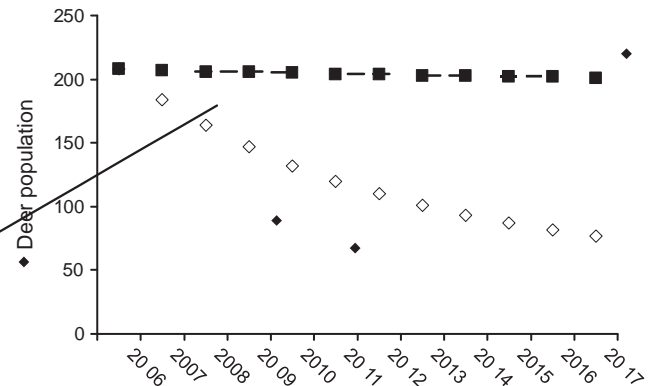


Fig. 4. Projected population trends over the next 10 years at National Institute of Standards and Technology (NIST) at fertility rates of 0.4 fawns per female (squares and dashed line) and 0.15 fawns per female (diamond and solid line).

model, which yields a stable population over 10 years at that level. The value of this threshold depends on the rate at which resident deer die and disappear and on the number of new immigrants entering the campus each year.

Because there is so much variability in annual rates of death and disappearance, it is difficult to determine whether there is density-dependent mortality over the population range observed. The predominance of deer–vehicle collisions as a mortality source suggests that density dependence, if any, may be weak. The model results displayed in Fig. 4 assume continued density-independent mortality. However, if the number of deer at NIST continues to drop as predicted, it is possible that survivorship would improve. Female survivorship might also improve because of the direct effects of the vaccine itself, as demonstrated in wild horses and suggested by improvements in body condition in contraceptive-treated deer at other sites (McShea *et al.* 1997; Kirkpatrick and Turner 2007). We have no data that directly address that question at NIST; however, because vehicle collision risk is unrelated to contraceptive treatment status at NIST, it is unlikely that longevity at NIST will be much affected by contraception (Rutberg and Naugle 2008). Improvement in survivorship would diminish the effectiveness of contraception in reducing population size.

Because nearly all the land near NIST has either been developed or protected at this writing, no large influx of immigrants is anticipated in the future, and in the predictive model the number of immigrants is fixed at 8 per year. Any decrease in the rate of immigration would tend to reinforce contraceptive efforts. Of course, population dynamics are also susceptible to stochastic variations of weather, food production, and changes in environment; in addition, population age structure and differential mortality by age and sex were not taken into account by the model.

Overall, however, our model indicates that if (1) population fertility rates can be maintained through continued application of contraceptives at the values recorded for 2005 and 2006, (2) the rate of mortality does not decrease sharply, and (3) no major immigration events occur, the NIST deer population should continue to drop steadily, with an additional 50% reduction achieved in approximately 6 years.

Fire Island National Seashore, New York

Fire Island is a barrier island 51 km long and 0.2–1.0 km wide running approximately east–west off the southern coast of Long Island, New York, USA. The island is a habitat mosaic supporting salt marsh, meadow, interdune, maritime forest, and dune vegetation communities, as well as 19 villages, heavily used beachfront recreation areas, and small patches of relatively undisturbed habitat between the villages. The island is likewise a complex administrative mosaic, comprising a state park, a county park, and the 48-km-long Fire Island National Seashore (FIIS) administered by the National Park Service (NPS). Within FIIS lie a federal wilderness area as well as the self-governed communities, and two different New York State county jurisdictions. A diverse mix of non-native ornamental plants dominates the island in and near the communities (Naugle *et al.* 2002; Underwood 2005).

Records of white-tailed deer on Fire Island go back to at least the beginning of the 20th century, and deer are presumed to be native there (Underwood 2005). Aerial counts conducted in 1983–98 and distance sampling conducted in 1997–2003 indicate that deer densities in the wilderness area are high but relatively stable. However, persistent and dramatic increases in deer densities were documented in the developed, western end of the island beginning in the mid-1980s (O'Connell and Sayre 1988; Underwood 2005). These increases were associated with heavy artificial feeding of deer by residents and visitors, which was widely observed by, and reported to, NPS staff (as well as the authors). The sharp increases in deer numbers raised NPS concerns about deer impacts on native vegetation, and the deer were also increasingly perceived by some island residents as a nuisance and a public safety threat. In 1988–89, the NPS and the New York State Department of Environmental Conservation held a limited archery/firearms hunt in the western part of the island. However, the hunt proved intensely controversial among residents, was the subject of a lawsuit, and was not repeated (O'Connell and Sayre 1988; Underwood 2005).

In 1993, our research team was invited to begin a large-scale PZP field trial by a group of residents who opposed the hunt but recognised that continued growth of the deer population was unacceptable (Kirkpatrick *et al.* 1997; Naugle *et al.* 2002). The initial goal of the study was to test the effectiveness of PZP when delivered in the field. This was accomplished, and in 1998 we began to examine population trends in the test areas (Naugle *et al.* 2002). At the same time, the NPS began an aggressive outreach program to discourage feeding of deer by island visitors and residents (Underwood 2005).

Methods

PZP preparation followed the methods described above, and in Naugle *et al.* (2002). Deer received an initial autumn treatment of 100 mg PZP emulsified in either FCA or Montanide ISA-50 adjuvants, and subsequent boosters of 100 mg PZP emulsified in either FIA or Montanide ISA-50. Deer were neither captured nor tagged. In the initial five years of the study, individual deer were recognised by resident deer monitors, who maintained files containing physical descriptions and associations, and cooperated with investigators in identifying animals for

treatment and recording the appearance of fawns. These deer were treated remotely but generally within 10 m with 1-cm³ darts delivered by blowpipes. Beginning in 1998, deer were no longer individually identified; rather, they were darted with combination 1-cm³/3-cm³ vaccination/marketing darts (Pneu-Dart, Williamsport, Pennsylvania), using red Sharp-Mark livestock marker concentrate (NASCO, Fort Atkinson, Wisconsin) as a dye. This enabled us to determine which animals had been vaccinated during the darting season, but did not allow reidentification during the subsequent spring/summer fawning season. Vaccination/marketing darts were delivered via Dan-Inject CO₂ Blo-jectors at distances not exceeding 15 m.

NPS staff and investigators and students from the US Geological Survey and the College of Environment and Forestry at the State University of New York, Syracuse, used distance-sampling methods to estimate deer densities and group composition in different segments of Fire Island (Burnham *et al.* 1980; Buckland *et al.* 1993; Naugle *et al.* 2002; Underwood 2005). We report here only the results from the most intensively and longest-treated segment of the island, Kismet–Lonelyville (K–L), comprising ~1.3 km² near the western end of the island.

For each year, we calculate the number of fawns per doe in autumn as the highest value reported in monthly surveys of group composition conducted between August and October.

Results

Between 1993 and 2004, 958 PZP vaccinations were remotely delivered to female deer in K–L. At all Fire Island sites, we spent 1.4 h per treatment (s.d. = 0.5), with no linear trend across the years ($r = 0.250$, $P = 0.63$) (data from 2001–06). Between 1993 and 1998, 17.6% of females receiving their first treatments as adults, and 21.0% of females receiving their first treatments as yearlings had fawns versus 83.5% in the year before treatment (Naugle *et al.* 2002); because individual reproduction was not systematically monitored after 1998, no later data on efficacy are available.

Between 1995 and 2002, the number of fawns per doe in autumn ranged between 0.09 and 0.25. Population density increased by 11% per year between 1995 and 1998 (Naugle *et al.* 2002), then trended downward at an average rate of ~10% per year between 1998 and 2006 (Naugle *et al.* 2002; H.B. Underwood, pers. comm.) (Fig. 5). Population density in 2006 was ~42% of that in the peak years of 1996–97.

Discussion

Although gradual, the reduction in deer densities in the K–L portion of FIIS has been very marked and very consistent. However, at least two factors other than contraception may have contributed to the reduction in densities in K–L. First, deer in K–L could move freely to other portions of the island. Because we did not monitor individual deer after 1998, however, we cannot exclude movements away from the study site as a source of population reduction. In addition, the National Park Service, The Humane Society of the United States, and our research team engaged in a collaborative island-wide effort to discourage feeding of deer by island residents and visitors, an

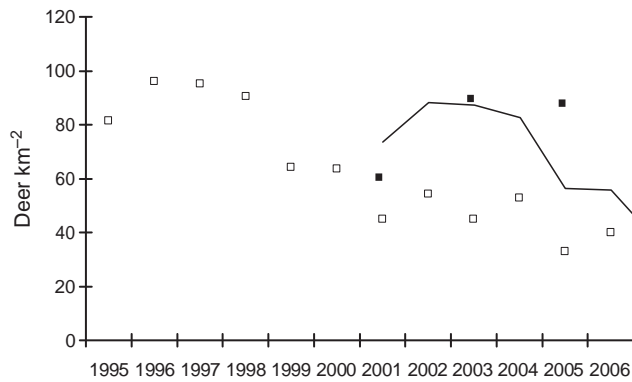


Fig. 5. Population density trends in the Kismet–Lonelyville segment of Fire Island National Seashore (FIIS), 1995–2005. Contraception began in autumn 1993, but no population data are available before 1995.

effort that intensified after 1998 and proved highly successful. The contraception program was integral to this effort; by sharply reducing fawning and stopping deer population growth, we provided some reassurance to heavily-feeding residents that the deer they cared about would not starve. Many of the residents who fed deer were also incorporated into the project by allowing them to maintain ‘bait stations’ to attract the deer for darting. We then gradually limited the amount and seasonal occurrence of feeding to the minimum needed to facilitate darting.

Less success at population control has been seen in other portions of FIIS. While there is evidence that the eastern communities on FIIS have also experienced significant reductions in deer population densities, the ‘mid-island’ communities have not (Underwood 2005). In those communities, access to deer for darting has been more restricted; feeding of deer is believed to be continuing; and deer may be more mobile. These issues mirror those that have been raised in connection with efforts to control deer by hunting (Brown *et al.* 2000).

General Discussion and Conclusions

Our experiences at both NIST and FIIS indicate that, with persistence and steady effort, very marked reductions in suburban white-tailed deer populations can be obtained using contraception alone. These reductions have occurred over time scales of ~10 years, which is not short. In this context, it is worth noting that many communities coping with deer conflicts spend 2–3 or more years sorting out possible solutions, with multiple municipal deer committees, heated political controversies, lawsuits, and election campaigns delaying the actual implementation of deer-management plans for many years (Curtis and Hauber 1997; Kohn 1998). Should contraception prove an effective and relatively non-controversial management tool, it might shorten the time to implementation, and gain a head-start over more controversial alternative techniques. Moreover, both of these field studies used multiple-shot, single-year PZP vaccines, and had multiple objectives (including vaccine efficacy testing) which diminished the impacts of contraception on population dynamics. Presumably, a long-acting, single-shot vaccine could produce more dramatic population effects in a shorter period.

More powerful contraceptive tools will also face more challenging environments than are offered by NIST and the Kismet–Lonelyville portion of FIIS. Neither of these environments is simple; although they may be portrayed as ‘confined’ or ‘isolated,’ both sites experience ingress and egress of deer, sometimes considerably so.

The effort and cost of applying contraception will also play a crucial role in determining where contraception will be adopted as a deer-management tool. The population-control achievements at NIST and FIIS rested on the physical accessibility of the sites and on the behaviour of the resident deer, which were highly habituated to human activities (to a remarkable and somewhat disturbing degree at FIIS). These traits are reflected in the relatively high efficiency of darters at both sites (1.4 h per treatment at FIIS and 1.8 h per treatment at NIST). Nevertheless, deer at both sites became significantly warier as time passed, and the fact that this growing wariness is not reflected in increases in darting and capture effort over time is due largely to a compensatory improvement in the skill of the darters, and on the increasing reliance on delivery systems with greater range. However, the ability to compensate for changes in deer behaviour may not be endless, further highlighting the importance of introducing longer-acting vaccines that eliminate the necessity to treat deer every year, as well as reducing the number of deer that need to be treated each deer to effect population control.

The specifics of deer population dynamics aside, it is well worth pointing out that at both NIST and FIIS, community concerns with deer conflicts have fallen off considerably. At NIST, the frequency of deer–vehicle collisions has declined, both because of a decline in deer population and an aggressive public education campaign (Rutberg and Naugle 2008). At both sites, public complaints to government agency personnel have dropped considerably, and media attention to deer conflicts has waned. From the viewpoint of solving social problems, contraception has been a great success in both locations.

Thus, the applicability of contraception as a deer-management tool will also depend heavily on the objectives of the community or landowner weighing the options. Although professional wildlife managers are inclined to focus on specific deer density targets, the issue dynamics that guide management actions are more subtle. In some communities, deer conflicts may be more a matter of public perception than of substantive impacts, and contraception may suffice to take deer off the community’s issue agenda simply by easing fears of perpetual population growth. In contrast, communities in which, for example, deer pose a serious threat to public safety may desire faster, more dramatic, population reduction than contraception can offer (e.g. DeNicola and Williams 2008).

Much ink has been spilled attacking and defending deer contraception in professional journals and popular media (Kirkpatrick 2005). Most of these arguments have been founded on hypotheticals: what might contraception accomplish, or not accomplish, if it were tried? The final technical details of safe, effective, long-acting contraceptive vaccines are being worked out, and we have proved the principle that deer contraception can significantly reduce suburban deer populations. The time has come to stop arguing

the hypotheticals: let's take contraception into the field to see where, when, and how we can make it work.

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