FINE-SCALE GENETICS, POPULATION DYNAMICS, AND MANAGEMENT OF SUBURBAN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

by

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Abstract

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Advisor: Robert Rockwell

Overabundant populations of white-tailed deer *Odocoileus virginianus* can cause broad declines in native biodiversity, the lack of advanced woody regeneration, and shifts in successional trajectories. These problems are especially pronounced in the suburbs of the Northeastern U.S. In the northern suburbs of New York City, land managers have begun implementing small scale (< 20 km^2), bow-only hunts to reduce overabundant deer herds. The success of these controlled hunts will depend on deer socio-population dynamics, the efficacy of bow hunting, and the sustained participation of bow hunters. I used a multi-disciplinary approach to address these issues and to evaluate the utility of bow hunting as a tool for managing suburban deer.

I used surveys to evaluate why hunters from Westchester, NY and Fairfield, CT participated in controlled hunts. Members were primarily motivated by the chance to see wildlife, opportunities for recreation, and a passion for archery. Most (71%) reported that their enjoyment had increased since first joining their controlled hunt. Nevertheless, I documented several trends that threaten the long-term sustainability of these programs. First, 78.2% of survey respondents were over the age of 40, possibly suggesting few young recruits. Second, the opportunity to hunt previously unhunted land, a transitory incentive, was the most common

reason for participating in controlled hunts. Third, respondents whose doe harvest was limited by choosing to spend time hunting outside of the controlled hunts were also more likely to have seen fewer deer when participating in those controlled hunts (G-test = 13.2, df = 4, P = 0.01). This suggests that if herd reduction is successful, and opportunities for seeing and harvesting deer become fewer, that hunter participation and effort may decline as well.

To evaluate the impact of deer management activities, land managers need accurate measures of deer abundance. I proposed modifications to Jacobson et al.'s (1997) camera trap method to estimate the abundance of the Mianus River Gorge Preserve (MRGP; Westchester County, NY) deer herd. This method uses photographs to provide a minimum count of distinctive branch-antlered males, and then uses the photographic rate of males, females, and fawns to estimate demographic ratios. These ratios are used to extrapolate from the number of individual branched-antlered males to the number of females, fawns, and spike males. I modified this technique to 1) generate measures of uncertainty for parameter estimates via bootstrapping camera stations, and 2) address the concern that demographic ratios will be biased if groups of animals differed in their probability of being photographed. For each demographic group, I standardized photographic rates by a measure of detection probability using linear regression. I evaluated the performance of using standardized vs. raw photographic rates by estimating female abundance using both sets of ratios. I compared the results to an independent estimate of MRGP female abundance based on mark-resight methods. Using standardized rates generated a female estimate ($\bar{x}$ = 60.43 44, 95% PI = 44.78–77.38) closest to the mark capture estimate ($\bar{x}$ = 49.50, 95% PI = 38.70–63.40), although precision intervals were wide regardless of whether raw or standardized ratios were used.

The concept that deer can be successfully managed at fine-scales (<20 sq km) is based on the rose-petal hypothesis (RPH). Under this theory, female deer are believed to exist in spatially exclusive, matrilineal social-units whose members are philopatric and exhibit low rates of dispersal. In theory, repopulation of the removal area should be slow as immigration is low and because deer immediately adjacent to the removal area will not shift their movements towards the void. Previous studies have demonstrated that the RPH model leaves a genetic fingerprint such that female deer separated by short distances (< 1.0 km) are genetically related. I used molecular techniques and Moran I's spatial autocorrelation analyses to evaluate whether an overabundant deer herd in suburban Westchester County was structured following the RPH. At the MRGP, tissue collected from deer that were sampled at the same spatial coordinate were genetically similar (r^2=0.21). However, Moran's I index of genetic relatedness became non-significant (e.g. no different from 0) by 230 m. High deer densities may have resulted in overlapping ranges of non-related social units thus weakening a broader genetic signature.

To evaluate the short and long-term impact of bow hunting, I used projection models to simulate harvests on deer herds exhibiting density-dependent growth and survival across a range of carrying capacities and immigration rates. For scenarios believed to be representative of the MRGP (low immigration, ~ 7%, and carrying capacity = 13.8 female km^{-2}), maximum herd reduction was modest (~20%) when simulated harvest rates approximated those observed at the MRGP. Sustaining harvests over multiple decades is the biggest challenge facing bow-only hunts. Hours per female harvest increased rapidly as population declined ($C_F(t) = 0.0031 N_F(t)$; R^2=0.56). As controlled bow hunts are executed by volunteer sportsman, realized reductions will be contingent hunters' incapability or unwillingness to increase effort. Consequently, bow hunting will likely result in deer densities lower than historical peak values, yet higher than is currently assumed necessary for forest regeneration.

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My work would not be possible without the financial support of the Conservation Fund of the Camp Fire Club of America. Special thanks to Jeff Gronauer. I also want to thank the NYS Department of Environmental Conservation, specifically Jeremy Hurst and Kevin Clarke.

Dedication

To my family, my wife, and the deer.

Scratch the deer. One of them hit my car.

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Chapter 5

Chapter 1: Introduction

White-tailed deer (*Odocoileus virginianus*) are a testament to the success of the early 20th century conservation movement. By the late 1800s, deer populations had plummeted across the Northeastern United States owing to unrestricted harvests and habitat loss (Foster et al. 2002). However, through reintroductions, increased hunting regulations, the reforestation of agricultural areas, and the extirpation of wolves and cougars, deer populations had rebounded by the mid 20th century (Rooney 2001). By the 1980s and 90s, the once threatened species reached very high densities, especially in suburban areas of the Northeast where conditions were ideal for rapid and sustained growth. Owing to shifts in cultural norms, there are fewer hunters in suburban areas and consequently hunting pressuring is generally lower (McDonald et al. 2002). The largest non-human predator is the coyote; however, such predators are not believed capable of regulating prey that exists near carrying capacity (Mech and Nelson 2000, Rooney 2001). Suburban forests are heavily fragmented creating edge habitat, a preferred deer cover type (Waller and Alverson 1997). Furthermore, suburban lawns and ornamental plantings provide supplemental food sources (Conover and Kania 1988). These conditions have resulted in high annual survival rates (Etter et al. 2002), an old-age structure (DeNicola et al. 2008), and subsequently the development of "overabundant" deer herds with densities in excess of 20 deer km^{-2} (DeNicola et al. 2008). Overabundant deer have been linked to reduced woody regeneration (Anderson and Loucks 1979), a decrease in biodiversity (Rooney and Waller 2003), increased rates of Lyme disease (Daniels et al. 2009), and are estimated to cause over 1 billion dollars a year in deer-automobile collisions (Conover et al. 1995).

In response, many suburban communities are looking to reduce the size of these deer herds. In the United States, wildlife populations have been traditionally been managed through hunting (Geist et al. 2001). This approach is challenged in suburban ecosystems where dense human populations preclude the use of firearms (Kilpatrick and Walter 1999). In suburban Westchester County, only bow hunting is allowed. However, bow hunting has been criticized as being ineffective owing to its short projectile range (Hansen and Beringer 1997). In addition, in suburban areas such as Westchester, the landscape is fractured politically as it is ecologically. There are few large properties on which to conduct management activities and adjacent landowners may have different opinions on the use of lethal management strategies.

In the 1990s, a new hypothesis of deer population growth and expansion was posited that provided a new avenue for suburban deer management. The rose-petal hypothesis (RPH) suggested that female deer are organized in spatially explicit, matriarchal social groups whose members exhibit high philopatry and low dispersal (Porter et al. 1991). Experimental removal of social units generated a pocket of lowered density that lasted for a minimum of 5 years (Oyer and Porter 2004). Adjacent, unmanaged deer did not shift their movements towards the reduction area owing to a high fidelity to their natal range. The RPH, therefore, was the basis for the idea of localized management suitable to suburbia (Porter et al. 1991) where local deer social units could be targeted for removal on small landholdings ranging from 7 – 20 km^2 (Oyer and Porter 2004).

Between 2004 and 2012, over 10,000 acres of land have been opened to bow hunting in Westchester County. This land is not contiguous, rather is owned by several different non-governmental organizations, state and town agencies. Each has implemented independent, bow-only deer management programs (DMP) to locally reduce deer populations to promote advanced woody regeneration. While most do not openly cite the RPH as justification for their management activities, the success of these programs depends, in part, on the predictions of low dispersal and high philopatry holding true. The success of these DMPs is also contingent on the efficacy of the principle management tool, the bow, and the sustained participation of volunteer sportsmen, the bow hunters. As the problems of suburban deer management are multi-faceted, I have taken a multi-disciplinary approach to better understand the population dynamics of white-tailed deer and the ecology of suburban hunters.

In chapter 2, I explore the attitudes, motivations, and satisfaction of hunters participating in controlled bow hunts. The success of any hunting program relies on the action of these hunters. However, reducing deer by hunting presents a seemingly intractable paradox. Managers want to use hunters to dramatically reduce deer herds to levels that may not be enjoyable to hunters. What are the motivations of hunters participating in DMPs? What harvest decisions do they make and why? How can DMP managers design programs satisfactory to hunters while still attempting to drive down deer densities?

In chapter 3, I propose modifications to a non-invasive camera technique for estimating deer abundance. Abundance estimates are important both for modeling the impact of bow hunting and for describing the functional response of bow hunters (Chapter 4). They are also important for deer managers who need to quantify the results of lethal management activities. Camera traps are an increasingly popular tool for population monitoring (Kays et al. 2009); however, they can be limited when used to make inferences on animals lacking distinctive marks (e.g. female deer). Often researchers make the assumption that photographic rates and abundance correlate 1-to-1; however, differences in detection probability based on species, age, sex, time, or place will also impact photographic rates (McCoy 2010) and thus bias abundance estimates. I propose using a measure of detection probability to standardize photographic rates when generating relative abundance estimates. These standardized photographic rates are used to estimate demographic ratios (e.g. female-to-male ratio) that are then used to estimate the abundance of bucks, does, and fawns.

In chapter 4, I use molecular techniques to indirectly evaluate whether Westchester female deer are structured following the RPH model. Matrilineal organization coupled with high philopatry in deer has been shown to produce genetic spatial autocorrelations over very fine scales (<1000m, Laseter 2004, Miller 2008) owing to substantial genetic structuring between adjacent social units (Matthews 1989). I use spatial-autocorrelation analysis on genetic samples collected from hunter-killed and live-captured deer to test for this putative signal.

In chapter 5, I use projection modeling to predict the impact of bow hunting on population growth under a range of conditions reflecting a plausible range of deer survival, fecundity, and immigration rates. I also explore the functional response of hunters to examine how harvest rates change as a function of deer density and time. Based on these modeling exercises, I discuss the likely impact of bow hunting on deer population growth in suburban ecosystems.

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Chapter 2: The sustainability of controlled archery programs: the motivation and satisfaction of suburban hunters

Abstract

Over the last decade, wildlife professionals in the New York City (NY, USA) metropolitan area have increasingly turned to controlled archery hunts to reduce overabundant suburban deer populations. The success of these deer management programs (DMPs) depends on a willing pool of hunters motivated to meet harvest goals. This requires maintaining hunter satisfaction both now, and in the future when successful herd reduction will result in fewer opportunities for deer harvest. With the goal of providing local deer managers with feedback from hunters partaking in DMPs, we used surveys designed to evaluate why members hunted, why they joined DMPs, members' views on deer management, and ultimately, their satisfaction with controlled hunts. Members were primarily motivated to hunt by the chance to see wildlife, opportunities for recreation, and a passion for archery. Most (71%) reported that their enjoyment had increased since first joining a DMP and satisfaction was not linked to harvest opportunity or success. Nevertheless, we documented several trends that threaten the long-term sustainability of DMPs. First, 78.2% of survey respondents were over the age of 40, possibly suggesting fewer younger recruits into DMPs. Second, the opportunity to hunt previously unhunted land, a transitory incentive, was the most common reason for participating in DMPs. Third, respondents whose DMP doe harvest was limited by choosing to spend time on private, non-DMP land were also more likely to have seen fewer deer on DMP lands (G-test = 13.2, df = 4, P = 0.01). This suggests that effort will decline as deer herds decline.

Weckel, M., R. F. Rockwell, A. Wincorn. 2011. The sustainability of controlled archery programs: the motivation and satisfaction of suburban hunters. Wildlife Society Bulletin 35: 330-337.

Introduction

Over the past 2 decades, overpopulation of white-tailed deer (*Odocoileus virginianus*) has been a persistent ecological and public safety concern in the suburban Northeast, where densities in excess of 20 deer/km^2 have been reported (Kilpatrick and Walter 1999, DeNicola and Williams 2008, Daniels et al. 2009). At high densities, deer cause increased car accidents (Conover et al. 1995, Etter et al. 2002), declines in biodiversity (Rooney and Waller 2003, Côté et al. 2004), increased threat of Lyme disease transmission (Wilson et al. 1985), and destruction of landscaping (Sayre et al. 1992). In response, suburban land managers have implemented deer management programs (DMPs) in an effort to reduce overabundant populations. Unlike purely recreational hunts, suburban DMPs come with their own set of rules and regulations (McDonald et al. 1998) such as the requirement that hunters take a certain number of antlerless deer before they can harvest an antlered buck. In the New York metropolitan area (NY, USA), these DMPs provide new opportunities for recreational hunters.

Successful deer management requires a reliable pool of hunters who enjoy participating in these highly regulated hunts, and who are motivated to reach the goals set by managers (Brown et al. 2000). However, the goal of drastic population reduction may not be an attractive prospect for deer hunters (deCalesta and Stout 1997). In a statewide study of Pennsylvania, USA hunters, most did not see current herd densities as detrimental to forests and were reluctant to harvest adequate numbers of antlerless deer despite documented browse damage to forest vegetation (Diefenbach et al. 1997). There is evidence that hunters are more accepting of herd reduction in suburban settings (Responsive Management 2004) where deer overpopulation and its impact on human health and safety may be more apparent. Regardless, hunters often do not view themselves as instruments of deer management, and it is unknown to what degree hunters are willing to alter their hunting effort and strategy to meet the goals set by managers (Brown et al. 2000). Furthermore, if herd reduction is successful, hunters may lose interest in participating in DMPs as deer numbers decline and harvesting deer becomes more difficult, which would threaten DMP sustainability. To remedy this problem, managers need to design DMPs that cater to all aspects of the hunting experience (Hendee 1974).

Studies have shown that hunters have a diverse set of motivations and goals that determine their satisfaction with the hunting experience (Hendee 1974). However, there has been little research on the motivations and satisfaction of suburban hunters participating in DMPs (Brown et al. 2000). In this paper, we examine the attitudes, motivations, and satisfaction of bow hunters participating in archery-only DMPs in Westchester County, New York and Fairfield County, Connecticut, USA. Specifically, we surveyed DMP hunters (hereafter, members) to determine 1) their demographics, 2) their primary motivations for hunting, 3) their views on deer management and how they view their role in DMPs, 4) where they get their information about deer, 5) their opinions on possible management strategies (e.g., fawn harvest, antler restrictions), 6) whether and to what extent they enjoy participating in DMPs, and 7) limitations on their ability to successfully harvest does in DMPs. The DMPs included in this study are less than a decade old, so we initiated this survey to provide managers with information that could be useful in adapting programs to maintain hunter participation over time.

Methods

Study Area

Westchester County (1,121 km^2) and Fairfield County (1,621 km^2) are part of the greater metropolitan New York area and are located directly north of New York City (Fig. 1).

Westchester County is a slightly more densely populated ($\bar{x}$ = 846.7 people/km^2) than Fairfield ($\bar{x}$ = 565.6/km^2; U.S. Census Bureau 2010). Both counties are characterized by a strong south-to-north urban–rural gradient with dense urban centers such as Yonkers, New York (4,203.7 people /km^2) and Stamford, Connecticut (1,279.8 people/km^2). Deer management programs are concentrated in more forested areas to the north where population densities are well below county averages.

In 2009, we distributed a voluntary, anonymous survey prior to the hunting season and asked that surveys be completed by 31 January 2010. We created a website (www.urbanwhitetail.com) and recruited respondents by distributing advertisements at DMP meetings. Surveys could be filled out by hand or on-line. We made an effort to enlist respondents from all DMPs active in 2009 in Westchester County and Fairfield County. These DMPs involved bow hunting only, relied on recreational hunters, operated during the regular New York and Connecticut hunting seasons, and had forest regeneration as a primary management objective. Deer management programs differed with regard to organizational structure, regulations, and harvest quotas.

Questions addressed basic demographics and employment, information on hunting history, motivations for hunting, reasons for participating in controlled archery programs, overall satisfaction with specific DMPs, and factors that limited the number of antlerless deer each hunter harvested. Respondents were allowed to skip questions and submit partially completed surveys. When % of respondents is indicated, sample size *n* represents the number of survey takers who provided an answer and did not leave a question blank. On questions asking for opinions, we asked respondents to choose from a 5-point scale (from 1 = strongly disagree to 5 = strongly agree). For motivational questions, we asked respondents to rate the overall importance of each variable on a 4-point scale (very important = 4 to not important = 1). In an attempt to identify a few motivational types, we used factor analysis to extract latent composite factors explaining variation in respondents' motivation following the methods outlined in Decker and Connelly (1989). We used a Catell's scree, a graphical test plotting eigenvalues (describing variance extracted by each factor) against the number of factor components to determine the appropriate number of latent factors to extract (McGarigal et al. 2000).

To evaluate the degree of nonreporting bias, we examined the age distribution of survey respondents compared to that of registered members from 3 DMPs where such data were made available. Agreement between respondents (sampled population) and registered DMP members (parent population) would suggest the sample is representative, at least with regard to age (Filion 1975). Age is an important statistic because previous studies have shown strong correlations between hunter age, motivation, satisfaction, and response rate (Filion 1975, Decker and Connelly 1989). All analyses were performed in R (R Development Core Team, Vienna, Austria). Surveys were carried out under Institutional Review Board protocol 09-0031C approved by the City College of the City University of New York.

Results

Surveys were completed by 89 hunters of 7 Westchester DMPs (Bedford Audubon, BA; Butler Sanctuary, BS; Mianus River Gorge Preserve, MRGP; Rockefeller State Park, RF; Town of Pound Ridge, TRP; Westchester County Parks, WCP; and Westmoreland Sanctuary, WMS; and 2 Fairfield DMPs (Town of Redding, TR; and Greenwich Audubon, GA). Return rates expressed as a percentage of eligible 2009 DMP participants ranged from a low of 11.8% (Town of Pound Ridge) to a high of 100.0% (Bedford Audubon), with a mean of 50.87% (SE = 9.92).

The mean age of survey respondents (*n* = 86) was 48.0 (SE = 1.08; Fig. 2), while the mean age of 120 registered DMP members from WCP, TPR, and MRGP (representing DMPs with high and low response rates) was 44.1 (SE = 0.95). The distribution of hunters across age classes was not different between the 2 groups (*G*-test = 8.93; df = 11, *P* = 0.63) minimizing the potential problem of nonreporting bias based on age.

Of 87 respondents, 71.0 % answered that they hunted as children, and the mean age at first hunt was 17.4 (*n* = 77, SE = 0.87). Nearly all respondents (99.0%) who provided the age of their first hunt (*n* = 77) had their first hunting experience before the mean age of DMP hunters, and 88% began hunting at an age younger than the youngest DMP participant (Fig. 2). Of those who hunted as children and completed questions regarding the locale of such hunting (*n* = 47), 72% indicated they hunted in suburban and/or urban areas in their youth. Fifty-four percent of respondents (*n* = 78) held white-collar jobs, followed by 36% blue collar, 9% retired, and 4% students. Using U.S. Census classifications, the top 4 jobs were management (18.2%), construction (16.7%), sales (12.12%), and financial services (9.09%).

The majority of respondents assigned a high degree of importance to most motivation variables, making our factor analysis of hunting motivation largely inconclusive. Examining Catell's scree plot, we found that each extracted component explained an equal portion of the variance and, therefore, did not suggest the existence of a few explanatory latent factors. However, factor loadings grouping the motivation variables 'Hunt for recreation' and 'Hunt to see wildlife' were consistently high (>0.5) for all component numbers. These variables, along with 'Archery is a passion,' ranked as the most important motivating variables among all participants (Table 1).

The majority (64.5%) of respondents (*n* = 76) in DMPs believed that deer had a negative impact on human safety and forest health (81.6%). Nevertheless, 71.0% of those respondents who thought deer negatively impacted people and the forest (*n* = 62) believed that there were 'a good number' of does in the DMPs in which they participated, and only 4.8% believed there were too many. Nearly all (98.6%) of respondents (*n* = 73) agreed that archery could lower deer populations and reduce negative impacts on forest regeneration, destruction to ornamental plantings (95.9%), deer–automobile collisions (73.2%), and Lyme disease (71.2%). Respondents obtained information on deer biology and management from a variety of media and institutional sources. Overall, DMP staff were the most common source of deer information, with >86% of respondents (*n* = 77) indicating this was an important source in contrast to blogs (33%). Magazines and state agencies were equally relevant, with 76% of hunters claiming them as important, followed by 65% who also relied on Quality Deer Management Associations (QDMA) and 54% who relied on scientific literature.

Nearly all (93.4%) respondents (*n* = 76) indicated that the opportunity to hunt previously unhunted land was an important factor in participating in DMPs. The second most commonly cited reason was the opportunity to harvest a trophy buck (89.5%), and the third was population control (87.2%). Only 23.7% of respondents relied on DMPs for their only hunting spot, even though 55% of all respondents (*n* = 77) indicated that they were unable to hunt their own property.

Overall, 86.7% of respondents (*n* = 75) were satisfied with the rules and regulations of their individual DMPs. Eighty-two percent of respondents (*n* = 73) agreed that managers took participants' input into consideration in the design and implementation of controlled hunts. Only 4.1% disagreed. For those respondents who participated in ≥1 season prior to taking the survey (n = 53), the mean years in their DMP was 2.53 (SE = 0.24). The majority of these returning respondents reported that their enjoyment in their DMP had increased since they started (71%). Responses on whether harvesting a buck was more difficult since they joined their DMPs were split (38.9% agreed, 37.0% disagreed, 24.1% had no opinion). Discounting respondents who had no opinion, respondents' level of enjoyment of participating in DMPs was not dependent on the perceived level of difficulty in harvesting a buck (*G*-test = 0.03; df = 1, $P = 0.86$). Regarding does, nearly 48.1% of respondents believed harvesting a doe had become more difficult (37.0% disagreed, 12.3% had no opinion). As with bucks, hunter enjoyment was not dependent on perceived difficulty of harvesting does (*G*-test = 1.17; df = 1, $P = 0.28$).

Most (79%) of the respondents ($n = 74$) supported antler restrictions that would protect bucks under a certain antler size from harvest. Nearly 64% of all respondents ($n = 74$) believed that the antler size of remaining bucks would increase by allowing controlled hunts. Twenty-three percent believed antler size would decline. The majority of respondents supported earn-a-buck initiatives (60%, $n = 74$) that allow hunters to harvest a bucks only after they harvest a certain number of antlerless deer. However, a sizeable minority opposed them (24%). Nearly all (98.0%) of the respondents ($n = 80$) agreed that it is ethical to harvest adult does and adult bucks; however, there was considerably less support among respondents (n = 78) for the harvest of fawns (34% ethical, 52% unethical). Of those respondents who believed it is unethical (n = 41), 54% would harvest a fawn if required and 41% would harvest a fawn if it counted as an antlerless harvest where earn-a-buck restrictions are in place.

When asked what variables limit the hunters' doe harvest in DMPs (Table 2), the reason most frequently reported (55.8%) by respondents ($n = 52$) was choosing to spend time hunting non-DMP land. Choosing to spend time on non-DMP land was related to a lack of deer observations (*G*-test = 13.2, df = 4, $P = 0.01$) and few shot availabilities (*G*-test = 13.7 df = 4, *P*-value = 0.008). In addition, 37.3% of respondents ($n = 51$) indicated that hunting in multiple DMPs influenced their deer harvest in any one program. Selective avoidance of does when hunting bucks was important to 33.3% of all respondents ($n = 51$), while 21.2% of respondents ($n = 52$) indicated that a lack of state hunting tags or no additional need for venison played a role in their doe harvest.

A large majority (82.0%) of respondents ($n = 61$) believed the opportunity to hunt in DMPs would be available for the foreseeable decade; however, this number declined to 69.4% ($n = 62$) and 64.6% ($n = 65$) at 15 yr and 20 yr, respectively. Fifty-one respondents indicated why they thought DMPs would or would not be available in the future. For those who thought DMPs would survive ≥15 yr and provided a reason ($n = 31$), the majority (93.5%,) believed their services would be needed to maintain herd levels or for further herd reductions. Among those who expressed skepticism and voiced an opinion ($n = 20$), 50.0% believed DMPs would decline due to anti-hunting sentiment, 35.0% believed the success and subsequent cessation of controlled hunts would make their services unnecessary, and 10.0% believed there were too few hunters to maintain DMPs.

Discussion

The immediate challenge facing urban deer managers is meeting their mandate to reduce deer herds to levels that may be frustrating or unacceptable to those recreational hunters enlisted to get the job done. Suburban DMP members appear to support the goals of DMPs and share the perspective that the size of the current deer population in Westchester and Fairfield is detrimental to human and ecological health. Nevertheless, regarding the DMPs they hunt, the majority of members were satisfied with current deer densities and few believed that there were either too many or too few deer. Members know that wildlife professionals are employing them as management tools to reduce deer populations, and currently there does not appear to be a conflict, with only 15% of those surveyed claiming that their enjoyment in DMPs has diminished over time.

Nevertheless, Westchester and Fairfield DMPs are young, and long-term adaptive management of suburban DMPs requires that managers identify and plan for potential impediments to long-term sustainability. The first, and perhaps most pressing, concern is that hunters in the Westchester–Fairfield are a mature population. The majority of DMP members first started hunting before the age of 25, yet there is a paucity of DMP members of this age group, thus representing a nearly 2–3-decade gap in hunter recruitment. Although this is not of immediate concern, this can threaten the sustainability of DMPs in the relatively near future, and there is no obvious reason to expect a reversal in this trend. First, hunting is not a widespread component of the NYC metropolitan suburban culture. Second, informal interviews of several DMP members found that few of their children choose to hunt. Without tradition and peer-group interest, youth are unlikely to pick up recreational hunting owing to competing recreational activities such as video games and organized sports (Schulz et al. 2003). Recruiting older age adults is a possibility, but studies have suggested that individuals that start hunting later in life are more likely to abandon the activity (Purdy and Decker 1986). It is possible that DMPs attract only older hunters from the general (and a younger) hunting population and our findings consequently exaggerate this recruitment gap. However, surveys of 2009 New York state hunters showed the state-wide mean hunter age, similar to this study, was 49.5 (J. Hurst, New York state Department of Environmental Conservation, personal communication) and has been increasing since the 1980s (Enck and Brown 2008).

If hunting is to be an important element in a long-term regional solution to suburban deer overpopulation, then dealing with this recruitment gap is paramount. The decline in hunter recruitment is a national issue (Brown et al. 2000), and the causes and solutions are well beyond the capabilities and purview of local DMP managers. Aside from the issue of scale, managers may be constrained in advocating for policies or programs that could increase the number of hunters and, therefore, DMP recruits. Many managers of suburban DMPs walk a fine line between maintaining support for controlled archery and inciting anti-hunting activism. There is a risk of having public hunts shut down due to anti-hunting opposition, as was the case for the 2010 controlled hunts in the Town of Croton and Teatown Lake Reservation in Westchester (F. Koontz, Teatown Lake Reservation, personal communication). There is also a general concern among some hunters that supporters of DMPs tolerate hunting only as a necessity and would prefer nonlethal control methods if they were feasible (M. Weckel, personal observation). This atmosphere reinforces the idea of hunters as tools of management: local wildlife professionals support hunting out of necessity while avoiding support for hunting as a sport or pastime. Thus, some DMP members believe controlled hunts will be dismantled either because hunters are successful and no longer necessary or because political support will swing the other way.

In addition to a limited pool of hunters, DMP members have alternative options for hunting other than DMPs. Only 23.7% of respondents relied on DMPs for access to land, and the top driver for participating in a DMP (accessing unhunted land) is short-lived. This might give new DMPs an initial boost; but it suggests that DMP participants might be a highly mobile resource. For example, 37% of respondents indicated that the need to hunt across multiple DMPs limited their doe harvest in any one DMP. This competition for DMP members may serve to redistribute hunting effort across the region, but may not translate into overall increases in regional harvests (Brown et al. 2000). Furthermore, 55% of respondents also expressed that their desire to hunt private, non-DMP land limited their antlerless harvest on DMP land. These same respondents also were more likely to cite few deer sightings and few shot opportunities on DMP land as reasons explaining their antlerless take. Although DMP members may not report that they are dissatisfied by seeing fewer deer, they did respond to perceived fewer deer sightings by deciding to hunt on private parcels and/or different DMP land.

Overall harvests may also be limited by individual decisions made by hunters. Over a quarter of respondents indicate that they do not harvest does either during the rut or while hunting a buck. Bow hunting has been criticized for being relatively inefficient (Hansen and Beringer 1997), producing slow, moderate, or incomplete declines (Ellingwood and Spignesi 1986, Krueger et al. 2002); and passing up shots of does will only further limit the success of bow hunters. Faced with the prospect of a highly mobile pool of hunters, some of whom may curtail their maximum potential doe harvest, managers should consider rules that require a minimum amount of hunter effort for retention in the program. For example, respondents were mixed with regard to the ethics of harvesting fawns. Nevertheless, even those opposed to harvesting fawns were willing to do so if they counted toward a buck or if managers required them to take fawns. Rules that incentivize extra effort or larger harvests should not be so complicated or onerous as to frustrate hunters or discourage future participation (Enck and Decker 1990, Heffelfinger and Olding 1997); however, they should be stringent enough to ensure that hunters meet harvest quotas of individual programs.

Overall, hunters did not express that a perceived increase in the difficulty of harvesting a deer was linked to hunter satisfaction, supporting previous research where killing deer was not the most important reward for hunting (Hammitt et al. 1990). In fact, respondents demonstrated a broad variety of motivating factors. This presents managers with the opportunity to tailor their programs in a broad variety of ways to keep hunters engaged (Hendee 1974, Decker et al. 1980, Hammitt et al. 1990), even in the face of declining deer populations. Suburban hunters in this study were a fairly cohesive group that could not be subdivided into any preconceived category. They shared many characteristics with appreciative (Decker and Connelly 1989), or nature-loving (Kellert 1978) hunters, such as the importance they placed on viewing wildlife, their fairly advanced age and level of experience (Decker and Connelly 1989), and the relative unimportance to them of hunting as a source of food (Burt 1980). This supports previous research that suggested that urban–suburban hunters were dominated by 'nature'-oriented hunters (Kellert 1976, Burt 1980). However, DMP participants also identified the chance to socialize (affiliative-oriented; Decker and Connelly 1989), performance-based measures (achievement-oriented; Decker and Connelly 1989), and the ability to have solitude while hunting as highly important motivating factors. In follow-up studies, forcing respondents to rank motivating variables may clarify the relative importance of these factors and help managers prioritize strategies to maximize hunter participation, satisfaction, and ultimately, efficiency.

With regard to the desire for solitude, suburban deer managers can arrange DMP members throughout the landscape in a way that minimizes interaction between other members while hunting. This is in contrast to state-run hunts in which (in many cases) there are no individually assigned hunting spots and hunters share the woods with other registered hunters. Both the MRGP DMP and the TPR DMP currently assign members permanent spots. That the use of assigned spots caters to an important hunter motivation is a fortuitous coincidence. Managers assigned hunting spots in response to a high level of controversy over hunting on DMP land. By assigning areas, managers were aware, often several days in advance, of which members were in which locations at what times. This procedure satisfied concerns over public safety and DMP accountability. Participants of both the MRGP and TPR DMP have expressed that having assigned spots is a favorite perk because it maximizes the feeling of remoteness and solitude while hunting (Chief D. Ryan, Town of Pound Ridge, personal communication).

Another step managers can take to optimize the DMP experience is to integrate members into the design and implementation of DMPs. This both assures a certain level of buy-in on the part of hunters and caters to their desire for opportunities to socialize. Integrating members into the management of the program can be done in 2 ways. The first is to allow hunters to participate in the leadership of the DMP. For example, the MRGP DMP participants elect a representative council every 2 yr. Council members are responsible for assessing how many new members are needed for the program, member retention and recruitment, and the development of new rules for the program. A second way of involving members in the administration of DMPs is by capitalizing on existing hunting communities. Managers can seek out existing hunting organizations to help run DMPs. A number of regional DMPs have implemented this approach. The RS DMP has enlisted Westchester Bow Association for help, GA DMP uses the Greenwich Sportsmen Landowners Association, and BP DMP uses the Westchester–Putnam chapter of QDMA to help administer their programs. In theory, hunters will be more likely to follow rules they have developed themselves. They will also likely take a more active role in building and maintaining the DMP if they feel that they are part of a community that can influence the future of the program, rather than just serve as ‘management tools.’

If individual members are to share in the responsibilities of running DMPs, they need to know in what ways the program has succeeded and where it needs work. Hunters from programs throughout the region have shown themselves to be avid consumers of deer information stemming from a variety of sources, the most important being DMP managers. Managers should, therefore, openly share information on hunting statistics, such as the number, gender, and size of animals harvested or observed, to justify potential changes to DMP rules and regulations. In addition, sharing information with members encourages socialization between managers and hunters, which was an important motivating factor for the hunters in this study. To that end, managers of many DMPs maintain an open-door policy and try to be present for hunts. Managers of the WC DMP often greet hunters daily at sign-in kiosks to motivate hunters and to facilitate the sharing of deer sightings (D. Aitchson, Curator of Wildlife Westchester County Parks, personal communication). Numerous DMP members have expressed that they enjoy hunting Westchester and Fairfield DMPs for the connection between research, conservation, and deer management (M. Weckel, personal observation). Furthermore, this sharing of information and ideas on management will become important in addressing members' reluctance to harvest does while buck-hunting, and members' perceived declines in deer density. Ultimately, the goal is to create policies that meet the needs of managers without alienating hunters.

Management Implications

Schulz et al. (2003) suggested that the challenge facing urban wildlife professionals was finding a balance between the goals of increasing hunter opportunity while minimizing the artificiality of the hunt experience. Suburban DMP managers must attend to this dichotomy in addition to the political reality that support for deer hunting is not universally shared among all stakeholders.

As a result, it is important that wildlife professionals make it clear to hunters, land owners, preserve patrons, and politicians that the decision to open preserve land to bow hunting is only the first step toward herd reduction. What comes next is an ongoing and evolving discussion that is necessary to designing sustainable DMPs that acknowledge the limitations of archery and the conflicting motivations of hunters and managers. Notwithstanding the inherent limitation of archery, bow hunters will need to demonstrate substantial declines in deer populations if they want public support for hunting to continue. In turn, managers should design programs that satisfy other non-tangible motivations for hunting in preparation for the day when bow hunters appreciably reduce local deer herds.

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Table 1. Reasons for hunting cited by participants in deer management programs of Westchester, New York and Fairfield, Connecticut (USA), 2009.

Category	*n*	Important[a]	Not important	No opinion
To see wildlife	83	100	0.0	0.0
Recreation	77	98.7	0.0	1.3
Passion for archery	79	97.5	1.3	1.3
To harvest a buck	82	90.3	6.1	3.7
To test one's skill	75	89.3	5.3	5.3
To control deer populations	83	86.7	2.4	10.8
Solitude	81	84.0	12.4	3.7
Opportunity to socialize	81	79.0	9.9	11.1
For food	83	71.1	19.3	9.6
Tradition	82	64.6	15.9	19.5
Nostalgia	80	60.0	18.8	21.3+

[a] Very important and important responses were combined.

Table 2. Hunter's reasons explaining the number of does harvested in deer management programs, Westchester, New York and Fairfield, Connecticut, USA, 2009.

Category	*n*	Important[a]	No opinion	Not important
Chose to hunt private lands	52	55.8	19.2	25.0
No further ethical shot opportunities	52	44.2	15.4	36.5
Participation in other deer management programs	51	37.3	23.5	31.4
Pass up shots of does while hunting bucks	51	33.3	13.7	58.8
Pass up shots of does during the rut	51	32.7	13.5	51.9
Did not see any more does	52	26.9	21.2	50.0
Enough food for personal use	52	21.2	13.5	65.4
No more doe tags	52	21.2	21.2	55.8

[a] Very important and important responses were combined.

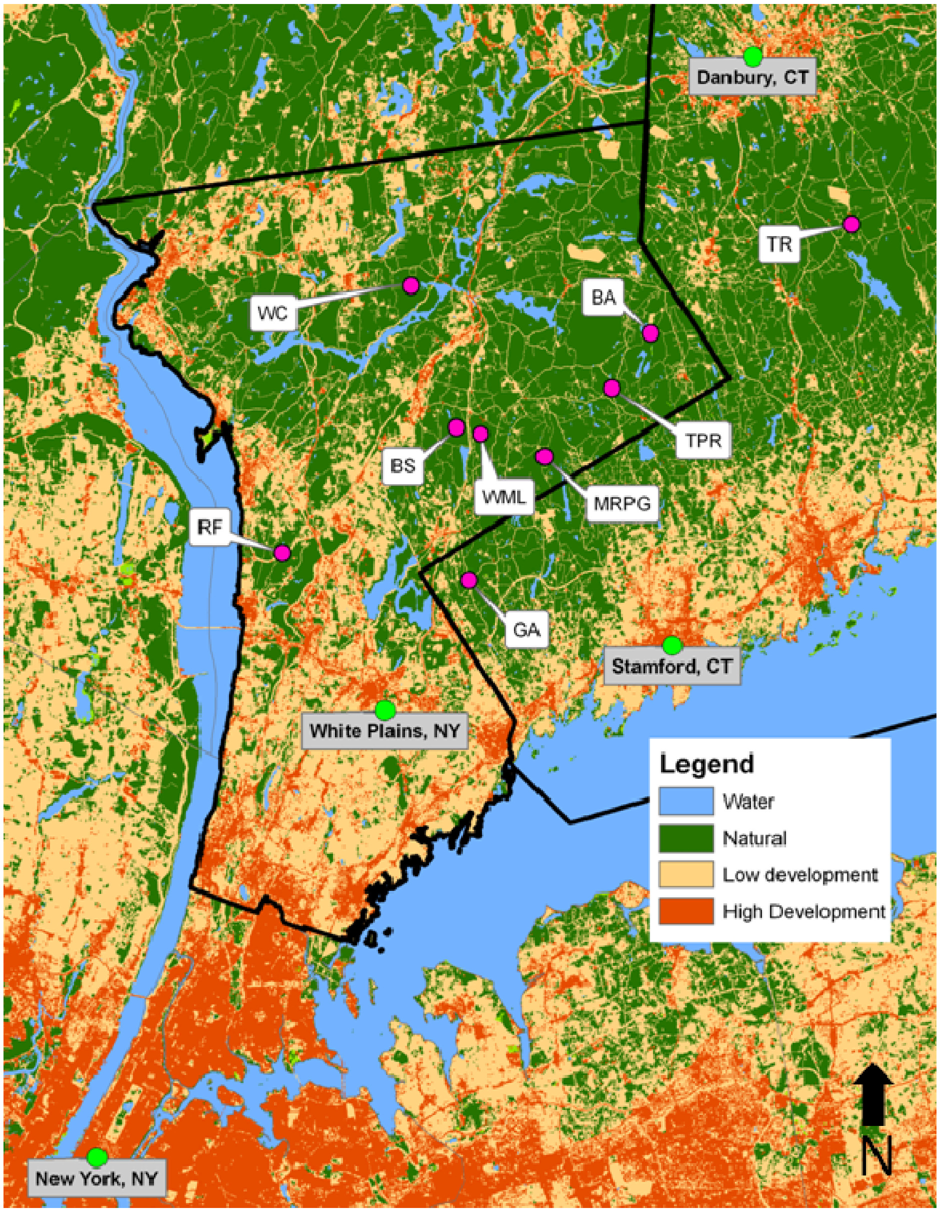

Figure 1. Map of Westchester County, New York and Fairfield County, Connecticut (USA) showing land use and location of deer management programs (DMPs) included in this study. DMPs and year of first hunt: Greenwich Audubon (GA, 2003); Mianus River Gorge Preserve (MRGP, 2004); Rockefeller State Park (RSP, 2005); Town of Pound Ridge (TPR, 2006),Town of Redding (TR, 2006); Bedford Audubon (BA, 2008); Butler Sanctuary (BS, 2009); Westchester County (WC, 2009); Westmoreland Sanctuary (WML, 2009).

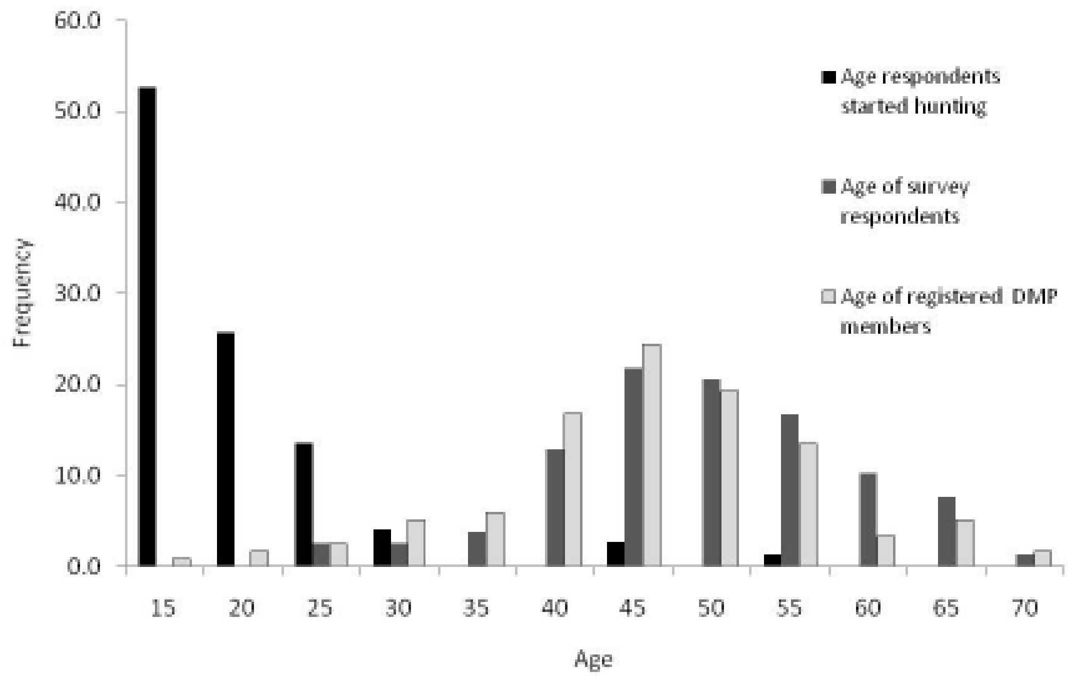

Figure 2. Histogram describing the age of survey respondents (*n* = 81), and members (*n* = 120) of 3 deer management programs (Mianus River Gorge Preserve, Town of Pound Ridge, and Westchester County Parks), and the age at which respondents began hunting (*n* = 74), Weschester, New York, and Fairfield, Connecticut (USA), in 2009.

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Chapter 3: A modification of Jacobson et al.'s (1997) individual branch-antlered male method for censusing white-tailed deer

Abstract

Jacobson et al.'s (1997) individual branch-antlered male (IBAM) method is a popular camera technique for estimating white-tailed deer (*Odocoileus virginianus*) abundance. Demographic ratios are estimated from raw photographic occurrences (RPO) of males, females, and fawns. Point abundance estimates of each group are estimated by using said ratios to extrapolate from a count of uniquely identifiable males. In 2009, using camera trap data from the Mianus River Gorge Preserve (NY), we modified the IBAM technique to 1) generate measures of uncertainty for parameter estimates via bootstrapping camera stations, and 2) address the concern that RPO ratios may be biased if groups of animals differ in their probability of being photographed (e.g., trap success [TS]). For each sex–age group, we evaluated RPO as a function of TS using linear regression to generate photographic counts standardized by TS (standardized photographic occurrences [SPO]). We generated estimates of sex–age ratios and abundances using both RPO and SPO. To evaluate the accuracy of using SPO in conjunction with the IBAM method, we independently estimated the abundance of a marked group of female deer using a Poisson log normal (PNE) mark–resight estimator. Abundance estimates across sex–age classes were most similar between PNE and IBAM when SPO demographic ratios were used. Owing to the greater trap success of females, using SPO discounted the relative abundance of females and, thus, lowered the female:male ratios and raised the fawn:female ratio. Uncertainty was broad across all approaches, yet accounting for trap success reduced the confounding variability owing to

differences in detection probability and generated more accurate parameter estimates.

Weckel, M., R. F. Rockwell, F. Secret. 2011. A modification of Jacobsen et al. (1997) individual branch-antlered male method for censusing white-tailed deer. Wildlife Society Bulletin 35: 445-451.

Introduction

Population estimation techniques, such as aerial inventories, thermal infrared sensing, or spot-light surveys, provide useful metrics for monitoring white-tailed deer (*Odocoileus virginianus*) abundance (Fafarman and DeYoung 1986, Naugle et al. 1996), but may not be appropriate for the scale of smaller management areas characteristic of fragmented suburban and urban environments. Here, deer management can be highly localized (Porter et al. 2004, McDonald et al. 1998) and wildlife professionals need accurate abundance estimates specific to individual properties to plan harvest goals and track population trends. This is especially important where lethal means to reduce overpopulated suburban deer herds are subject to political pressure and public accountability.

Jacobson et al.'s (1997) individual branch-antlered male (IBAM) abundance estimator is a popular method suitable to this scale. The method uses camera-trap data to enumerate a minimum number of uniquely identifiable adult males and to estimate sex and age-class ratios (hereafter, demographic ratios). The abundance of all males, females, and fawns is calculated by way of extrapolation. However, there are 2 major drawbacks to the IBAM estimator that limit its broad application. First, the method does not provide error terms for parameter estimates (Curtis et al. 2009). Without a measure of precision, comparing abundance across time and place is limited. Second, the method estimates the relative abundance of males, females, and fawns using raw photographic occurrences (RPO), which assumes that the different groups have equal detection probabilities (McCoy 2010, O'Brien 2011). Failing to meet this assumption will bias abundance estimates in favor of those groups whose individuals are more frequently photographed.

In this paper, we propose modifications to Jacobson's IBAM method that generate measures of uncertainty for parameter estimates and that standardize photographic occurrences (SPO) by detection to minimize bias. By evaluating RPO as a function of detection, researchers can quantify differing detection rates among demographic groups and then standardize photographic captures, thus providing less-biased estimates of nonmale abundances. To evaluate the accuracy of the IBAM method using both RPO and SPO demographic ratios, we used McClintock et al.'s (2008) mark–resight estimator on a marked population of female deer to generate an independent deer-abundance estimate.

Method

Study Area

We conducted our camera survey at the Mianus River Gorge Preserve (MRGP; 309 ha or 764 acres), located in suburban Westchester (NY) and Fairfield (CT) counties, USA. The MRGP was established to protect an old-growth Eastern hemlock (*Tsuga canadensis*) forest and 70–100-yr-old mixed hardwood forest. Dominant overstory species included black birch (*Betula lenta*), yellow birch (*B. alleghaniensis*), black oak (*Quercus nigra*), red oak (*Q. rubra*), red maple (*Acer rubrum*), and sugar maple (*A. saccharum*). The MRGP lay along the Mianus Greenway and was surrounded by large estates, smaller suburban developments, and protected reservoir land. Since 2004, the deer population has been managed using controlled archery. Exact prehunt deer densities for the MRGP were unknown. However, in 2002, 2 independent aerial inventories were conducted adjacent to the preserve in unmanaged areas of Bedford, New York and Greenwich, Connecticut. Daniels et al. (2009) estimated the Bedford deer population to be 22 deer/km^2. More forested areas of Greenwich (which were contiguous with the MRGP via the Mianus Greenway) had densities of 23.6 deer/km^2 (Brash et al. 2004). From 2002 to 2008, 160 deer were harvested from the MRGP, with female deer comprising 72% of the total harvest.

Deer Capture

We captured adult female deer (>1.5 yr old) between June and September of 2008 and 2009 using immobilizing drugs remotely delivered by cartridge-powered darts (Pneu-Dart, Williamsburg, PA). Deer were targeted for capture by driving roads bordering the MRGP. Darts contained a 1.0–1.5-mL solution of butorphanol (50mg/mL), azaperone (100mg/mL), and medetomidine (40mg/mL) in a ratio of 6:2:3 (Wildlife Pharmaceuticals, Inc., Fort Collins, CO). Deer were revived by intramuscular injections of 3 mL antisedan (5 mg/mL), 1 mL naltrexone (50 mg/mL), and 1 mL tolazoline (200 mg/mL). In 2008, each deer received a uniquely color-coded ear tag embedded with a 14.7-g, 433-MHz active radiofrequency identification transponder (RF Code, Austin, TX). In 2009, transponders were embedded in radiocollars (Sirtrak, North Liberty, IA) rather than ear tags. Transponders actively broadcasted over an average range of 131 m at the MRGP (M. Weckel, unpublished data), allowing authors to determine whether animals were alive and within the study area during the camera survey. Immobilization and tagging were carried out under Institutional Animal Care and Use Committee protocol 0715 approved by the City College of the City University of New York.

Camera Monitors

We conducted the camera survey from 16 August to 16 October 2009 at unbaited camera stations. We chose this 2-month period following fawning and prior to the NYS Region 3S hunting season because we assumed the population was closed, but also because antler growth was approaching full development. At each camera station, we deployed a Reconyx RC55 (Reconyx, Holmen, WI) camera affixed to a tree between 0.5 m and 0.75 m off the ground and 0.5–1.0 m off the trail. These cameras use an infrared flash and are passively triggered by heat and motion. Cameras were programmed to take 5 successive photos when triggered and had no delay between successive trigger events, allowing for near continuous photographic captures at the rate of 1 photograph/sec. For each event we recorded the age, sex, and number of deer seen.

We sampled the MRGP in 2 contiguous blocks of 12 cameras, each with each camera operational for an average of 29 days. (Twenty-three cameras stations were included in the final analysis because one camera failed). Initial camera-station locations were randomly chosen, but they were slightly adjusted in the field so that well-used trails were sampled. Also, because mark–recapture procedures assume that no animal has a zero probability of being photographed, camera stations were separated by no more than 500 m. This configuration was based on the average summer home range (21.4 ha) of suburban female deer documented by Porter et al. (2004). We felt our camera stations were conservatively spaced because Porter et al.'s (2004) estimate was equal to or smaller than many other female suburban-deer home ranges (Kilpatrick and Spohr 2000, Etter et al. 2002, Grund et al. 2002, Storm et al. 2006).

Estimating RPO, SPO, and Demographic Ratios

Following Jacobson et al. (1997), we estimated 3 demographic ratios based on RPO: spike males:branch-antlered males (rP_s), females:all males (rP_d), and fawns:females (rP_f). For example, $rP_d = N_d / N_b$, where N_d = total number of antlerless adult deer occurrences in photographs and N_b = total number of male occurrences in photographs. We used 1,000 nonparametric bootstrapped resamples of camera-station data to generate 95% percentile intervals (PI) of the demographic ratios as a measure of parameter uncertainty (Efron and Tibshirani 1993). These 95% PI rely on variability among bootstrap samples and are distinct from confidence intervals for a Neyman–Pearson assessment of significance, which rely on data meeting assumptions of normality (Efron and Tibshirani 1993).

Jacobson et al.'s (1997) method assumed that the ratio of RPO to abundance is constant across demographic groups. Violations of this assumption would inflate or deflate the relative abundance of sex–age classes based on differences in detection among males, females, and fawns (e.g., if F deer are more likely to be photographed, then their relative abundance would be biased high). We sought to compute SPO that corrected RPO for any potential inequalities in detection rates among the sex–age classes. To do so, we first estimated trap success (TS [the proportion of trap-nights with ≥1 deer photograph]) for each sex–age class at each camera station. For each sex–age class, we examined the relationships between RPO and TS using linear regression (Fig. 1). We forced a structural y-intercept of zero because the number of photographs must always be zero if TS equals zero. We estimated parameters using least-squares regression techniques and estimated SPO as the model beta, β. The model β, or slope, can be interpreted as the number of photographs per unit of TS; see Fig. 1). We used 1,000 nonparametric bootstraps of our camera stations to estimate uncertainty for SPO. We visually inspected standardized residual plots to check for any obvious departures from normality. We then used SPO estimates for each demographic group to generate standardized spike:branch-antlered male ratio (sP_s), female:male ratio (sP_d) and the standardized fawn:female ratio (sP_f). We again used nonparametric bootstrapping at this step, sampling from the distribution of SPO observed in each demographic group, to generate percentile intervals for demographic ratios.

Estimating Abundance Using IBAM and a Mark–Resight Estimator

We identified branch-antlered males based on antler size and configuration, as well as additional identifying characteristics such as relative body size and pelage patterns. This minimum number of unique branch-antlered males (B) was the starting point for calculating the number of spikes (M with unbranched antlers), spikes:all males, males:females, and females:fawns using both RPO and SPO ratios (e.g., where S = spike abundance; $S = B \times rP_s$ or

$S = B \times sP_s$). We used 1,000 nonparametric bootstraps drawing from the observed frequency distribution of demographic ratios and abundances to estimate the abundance of successive age-classes. We refer to estimates generated by Jacobson et al.'s (1997) method either as IBAM + RPO or IBAM + SPO depending on whether raw or standardized photographs were used.

We used the mark–resight Poisson log normal estimator (PNE; McClintock et al. 2008) in Program Mark (White and Burnham 1999) to analyze capture data of female deer. This estimator uses individual capture histories of marked animals and the number of photographs of unmarked animals to estimate total abundance. We used the mean female estimate generated by the PNE analysis as a starting point to extrapolate from females to all males, and from females to fawns using both RPO and SPO ratios. As with the above analysis, we estimated uncertainty in our parameter estimates in successive abundance calculations using nonparametric bootstrapping. We refer to estimates generated by McClintock et al.'s (2008) method either as PNE + RPO or PNE + SPO depending on whether raw or standardized photographs were used.

Generating estimates of males and females by extrapolating from females (PNE) and male estimates (IBAM), respectively, provided a cross-validation and allowed us to evaluate the relative accuracy of using RPO versus SPO. Ideally, an unbiased demographic ratio (either RPO or SPO) would yield agreement between estimated and extrapolated male and female abundances.

Results

Estimating RPO, SPO, and Demographic Ratios

Camera stations were operated for 662 trap-nights. During this time, we collected 130, 66, 480, and 112 RPO of branch-antlered males, spikes, females, and fawns, respectively. Across camera stations, female deer had a higher TS ($\bar{x}$ = 0.31, SE = 0.02) than branch-antlered males

($\bar{x}$ = 0.14, SE = 0.01), spikes ($\bar{x}$ = 0.08; SE = 0.01), and fawns ($\bar{x}$ = 0.12, SE = 0.01). Using camera data on trap success to standardize photographic occurrences via linear regression, we predicted the mean SPO for each sex–age class: spike males (β = 27.86, 95% PI = 19.64–33.98), branch-antlered males (β = 42.65, 95% PI = 33.58–54.04), all males (β = 40.02, 95% PI = 31.28–48.70), for females (β = 60.57, 95% PI = 49.16–72.99), and fawns (β = 42.02, 95% PI = 35.85–47.54).

Using SPO to estimate demographic ratios, the mean female:male ratio was 24% smaller as compared to RPO-derived ratio estimates (Fig. 2). The converse was true for the fawn:female ratio and spike:branch-antlered male ratios, which were 223% and 34.7% higher, respectively, when using SPO versus RPO. Nevertheless, owing to broader uncertainty, we found considerable overlap in demographic ratios computed from RPO and SPO for female:male and spike:branch-antlered male ratios (Table 1).

Estimating Abundance Using IBAM and a Mark–Resight Estimator

Using Jacobson's criteria, we identified 19 distinct branch-antlered males. We found that 51.5% of photographs of branch-antlered males were of too poor quality to attempt individual identification. Average capture rate for these 19 branch-antlered males was 3.32 photos (SE = 0.48). Fourteen female deer were marked and remained alive within the study area during the entire camera survey. All 14 marked female deer were photographed, with a mean capture rate of 7.86 photos (SE = 1.52). Twenty-two percent of marked female photographs could not be identified to an individual. Using the PNE mark–resight method of McClintock et al. (2008), we estimated the MRPG female herd at 49.5 females (95% PI = 38.7–63.4).

In comparing total male abundance estimates across all methods, there was similar agreement except for that generated using the PNE + RPO. Here, only 19 males were estimated, a likely underestimate considering that 19 individual branch-antlered males were identified from photographs. Regarding females, agreement between mean abundance estimates was closest for IBAM + SPO and PNE + SPO analyses (Table 2). Using SPO ratios, the IBAM-method female estimate was 22% higher than the mark–recapture female estimate, as compared to 43% higher when RPO was used. Regarding fawns, there was again most agreement between the IBAM + SPO and PNE + SPO estimates. Overall, mean total deer estimates were closest between the PNE + SPO and IBAM + SPO; nevertheless, there was considerable overlap among PI across methods, obscuring this difference.

Discussion

In our study, we used cross-validation to evaluate the relative accuracy of demographic ratios derived from RPO and SPO. We used a mark–resight analysis (PNE) to estimate the number of females, the IBAM method to estimate the number of branch-antlered males, and demographic ratios derived from photographs (RPO vs. SPO) to extrapolate the abundances of other demographic groups. Only unbiased demographic ratios should converge on the same estimate of deer abundance, regardless of whether the starting point for extrapolation was branch-antlered males (IBAM) or marked females (PNE). In our study, we found estimates of total deer, females, males, and fawns were most similar between IBAM and PNE methods when SPO were used for extrapolation.

Jacobson et al.'s (1997) approach is a creative way of using natural markings of adult male deer to estimate a minimum number of branch-antlered males. If there are no biases due to different sex–age probabilities of being photographed, Jacobson's use of RPO would be suitable for extrapolating from branch-antlered males to females and fawns. However, we did document differences in TS with females being the most frequently photographed group, on average twice as often as males and fawns. Subsequently, using information on TS to generate SPO, the relative abundance of females was discounted, describing a deer herd with fewer females, more males, and more fawns.

At the MRGP and at nearby Westchester preserves, controlled hunts can be controversial and subject to political pressure to demonstrate declines in female abundance. A difference between 71 and 60 females generated by IBAM + RPO and IBAM + SPO, respectively, can mask whether or not herd reduction is occurring. Similarly, using RPO measures as an indication of recruitment would suggest a slower growing population and would strongly influence any attempt to model harvest scenarios. Based on RPO, the MRGP herd has an unlikely 5 females for every 1 fawn during our study's late-summer camera survey, compared to the SPO estimate of 1.4 females for every fawn. With the knowledge that mean fertility rates among suburban adult females are safely in excess of 1.0 (Witham and Jones 1992, Swihart et al. 1995) and suburban fawn survival at 6 months has been found to be >80% (Witham and Jones 1992, Swihart et al. 1995, Etter et al. 2002), the RPO fawn:female ratio of 0.22 is dubious. Using RPO to estimate demographic ratios may produce greater disparities in sex–age distributions where differences in TS are more extreme. For example, Curtis et al. (2009) documented a female:male ratio of 3.7 in comparison to 0.94 reported by Jacobson et al. (1997). Curtis et al. (2009) attributed this disparity to differing management strategies affecting the density of males and females; however, it can also be due to differences in male and female TS across study sites.

Several confounding variables, including sex–age–based differences in home range (Jacobson et al. 1997), baiting (McCoy 2010), social status (Séquin et al. 2003), and even the model of camera (Kelly and Holub 2008) can influence the rate and number of photographic captures. These factors ultimately bias relative abundance indices, making comparative use of camera data across groups (sex, age, or species) difficult to interpret. For example, our greater female trap success may be an artifact of our camera density. We intentionally designed our camera array around a small female home range to maximize female captures and improve our mark–resight estimates. Likewise, Jacobson et al. (1997) observed a higher rate of female capture as camera density increased, which they attributed to smaller female home ranges and an increased likelihood of photographing a female's core area. Although comparative studies of male and female movement are lacking for suburban areas, there is evidence that male home ranges are considerably larger than those of females (Gaughan and DeStefano 2005). In addition, MRGP hunters, as well as the authors, have noted that it is not uncommon to see the same marked female deer multiple times per week in the same location; while repeat visits by any branch-antlered male are less frequent (e.g., M. Weckel, personal observation). Consequently, knowing that our camera placement produced a positive bias in favor of female photographs and that female deer may have smaller home ranges, discounting female RPO by female TS facilitated a more conservative use of photographic data in estimating demographic ratios. This approach of using SPO can also extend the utility of camera traps as a multispecies monitoring tool and generate more accurate relative abundance indices of entire communities of species.

Accounting for TS may also renew the discussion surrounding the use of bait in conjunction with Jacobson et al.'s (1997) method. Several authors have warned against baiting due to differences in bait use by different sex–age classes (Koerth and Kroll 2000, Roberts et al. 2006, McCoy 2010). However, by standardizing photographs by differences in trap success, one could potentially control for these differences. Bait could improve the initial enumeration of branch-antlered males by keeping animals within the frame and generating numerous photographs at many angles, ultimately facilitating identification. In our study, approximately half of branch-antlered photographs were eliminated from this analysis because they were of too poor quality to permit identification. These pictures were of males who walked perpendicularly to the camera, providing blurred photographs of only one flank. With that said, accounting for differences in the use of bait does not address the concern that baiting can shift deer ranges, thereby violating the assumption of geographic closure (Kilpatrick and Stober 2002, Curtis et al. 2009).

Standardizing photographs as a function of TS generated more accurate and biologically reasonable parameter estimates, yet is subject to meeting the assumptions of linear modeling. Although we did not observe any gross departures from linearity or homoscedasticity, parameter estimates of SPO are strongly influenced by the distribution and inherent variability in the data set. For example, we estimated the SPO of branch-antlered males (42.65) to be greater than that that of all males (42.02). Clearly, the ratio of branch-antlered males to all males is not 1:1. Rather, this results from aggregating spike and branch-antlered males. Spikes generally produced fewer RPO at a lower TS, which served to depress the β in the all-male analysis. This provides a cautionary note that extreme RPO values (RPO larger or smaller than expected from the model), especially at low or high TS, can strongly influence parameter estimates. Extreme RPO values may occur where cameras are placed in hotspots of activity (e.g., a scent station frequented daily by M bachelor groups, or a wildlife corridor funneling movement between fenced human developments). Cameras with low RPO at high TS can be expected if cameras are placed on or near bed sites of a solitary individual or of a small female social unit. Here, camera stations may have frequent visitation (high TS), but photograph only 1 or 2 individuals. Using purely randomly generated camera stations may help in minimizing variability caused by the researcher's camera-site selection (Kays et al. 2009); however, doing so can only increase the chance of surveying sub-par habitat and underestimating the count of individually branch-antlered males, violating an assumption of Jacobson et al's. (1997) IBAM method; this problem needs to be further addressed.

Whether one uses RPO or SPO with Jacobson et al.'s (1997) IBAM method, large uncertainty in parameter estimates can obscure detection of changes in deer abundance over time. Our exercise in bootstrapping camera traps demonstrated that the variability in RPO among camera stations alone can contribute to large uncertainty. As long as the study animal is not uniformly distributed in space, variability among camera traps will remain. Increasing sample size via additional camera stations may help decrease variability to the benefit of both the RPO and SPO approach; however, there is a limit to how densely cameras can be deployed before autocorrelation will become a concern (Koenig 1999, Silveira et al. 2003). Furthermore, large PI are compounded by the very nature of Jacobson et al.'s (1997) method, where uncertainty in each ratio estimate and uncertainty in each abundance estimate is compounded in calculating final total deer abundance. The basic technique relies on multiplication to extrapolate from the branch-antlered male abundance; therefore, wide PI will be hard to avoid.

Management Implications

Accurate estimation of deer herds, especially the abundance of females, is key to the long-term success of urban and suburban deer management programs. Jacobson's IBAM estimator offers a promising method by capitalizing on the natural markings of adult males to generate total deer abundance, including female abundance. However, as with any method that compares raw photographic captures across sex, age, space, time, or species, the use of camera data will be limited where the assumption of equal detection is not tested or supported (Cutler and Swann 1999, Séquin et al. 2003, Larrucea et al. 2007, O'Brien 2011). The method of standardizing RPO by TS acknowledges that TS is a complicated variable, contingent on a variety factors that may be difficult to control. Our solution uses measurable differences in TS as a means of standardizing RPO delivering a more conservative interpretation of camera data. Furthermore, when using camera-based methods to census and monitor white-tailed deer, wildlife professionals need to consider the level of precision necessary for the question at hand and the magnitude of population change one needs to discern. These concerns should be considered along with the benefits of using camera traps, which include the ability to simultaneously and noninvasively monitor activity period (Carthew and Slater 1991), spatial distribution (Atwood and Weeks 2002), sex and age structure (Jacobson et al. 1997), and to sample remote areas (Roberts et al. 2006) where vegetation cover (Anderson and Lindzey 1996) or prohibitive cost (Koerth et al. 1997) may preclude traditional methods such as aerial surveys.

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Table 1. Comparing demographic ratios computed using raw photographic occurrences (RPO) and standardized photographic occurrences (SPO), in Mianus River Gorge Preserve, Westchester County, New York, USA, 2009.

Sex–age ratio	Standardized or raw photographs	Symbol[a]	Mean	95% PI
Spike:branch-antlered M	RPO	rP_s	0.49	0.29–0.88
	SPO	sP_s	0.66	0.43–0.90
F:M	RPO	rP_d	2.52	1.67–3.91
	SPO	sP_d	1.92	1.50–2.40
Fawns:F	RPO	rP_f	0.22	0.14–0.34
	SPO	sP_f	0.71	0.52–0.95

[a] Demographic ratios based on RPO (r): spike males:branch-antlered males (rP_s), females:all males (rP_d), and fawns:females (rP_f). Demographic ratios based on SPO (s): spike males:branch-antlered males (sP_s), females:all males (sP_d), and fawns:females (sP_f).

Table 2. Comparing abundance of males, females, and fawns, in Mianus River Gorge Preserve, Westchester County, New York, USA, 2009.

Sex–age group	Method	Mean	95% PI
M	IBAM + RPO[a]	28.30	24.74–35.57
	IBAM + SPO[b]	31.54	27.35–35.92
	PNE + RPO[c]	19.46	12.40–29.72
	PNE + SPO[d]	26.12	20.59–32.62
F	IBAM + RPO	70.86	45.54–113.69
	IBAM + SPO	60.43	44.78–77.38
	PNE + RPO	49.50[e]	38.70–63.40
	PNE + SPO	49.50[e]	38.70–63.40
Fawns	IBAM + RPO	15.56	8.67–29.05
	IBAM + SPO	41.79	28.00–61.76
	PNE + RPO	10.80	6.77–16.58
	PNE + SPO	35.04	25.33–46.42
Total deer	IBAM + RPO	106.96	79.09–147.06
	IBAM + SPO	134.89	111.82–162.31
	PNE + RPO	80.26	71.79–92.54
	PNE + SPO	110.52	99.34–123.89

[a] IBAM + RPO—Abundance method using demographic ratios calculated from raw photographic occurrences (RPO) to extrapolate from a min. no. of individual branch-antlered M (IBAM) enumerated by Jacobson et al.'s (1997) criteria.

[b] IBAM + SPO—Abundance method using demographic ratios calculated from standardized photographic occurrences (SPO) to extrapolate from a min. no. of branch-antlered M (IBAM) enumerated by Jacobson et al.'s (1997) criteria.

[c] PNE + RPO—Abundance method using demographic ratios calculated from raw photographic occurrences (RPO) to extrapolate from the mean F estimate generated by McClintock et al.'s (2008) mark–resight Poisson log normal estimator (PNE).

[d] PNE + SPO—Abundance method using demographic ratios calculated standardized photographic occurrences (SPO) to extrapolate from the mean F estimate generated by McClintock et al.'s (2008) mark–resight Poisson log normal estimator (PNE).

[e] PNE—Mean no. of F deer calculated using McClintock et al.'s (2008) mark–resight Poisson log normal estimator (PNE).

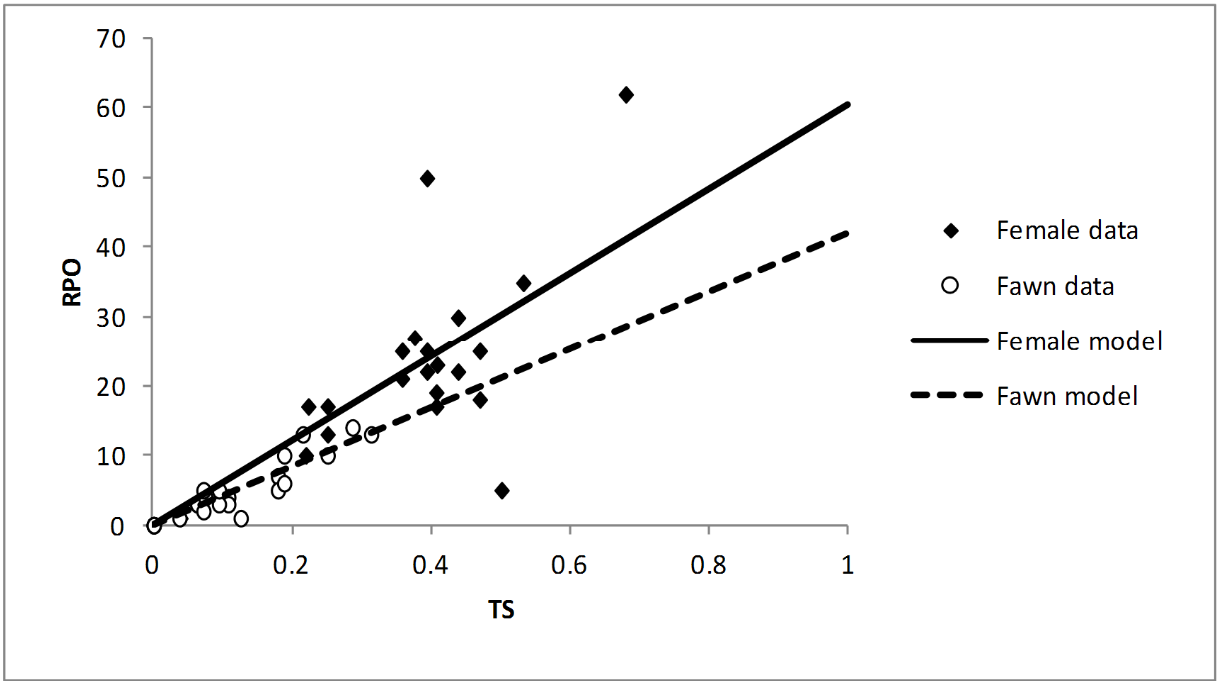
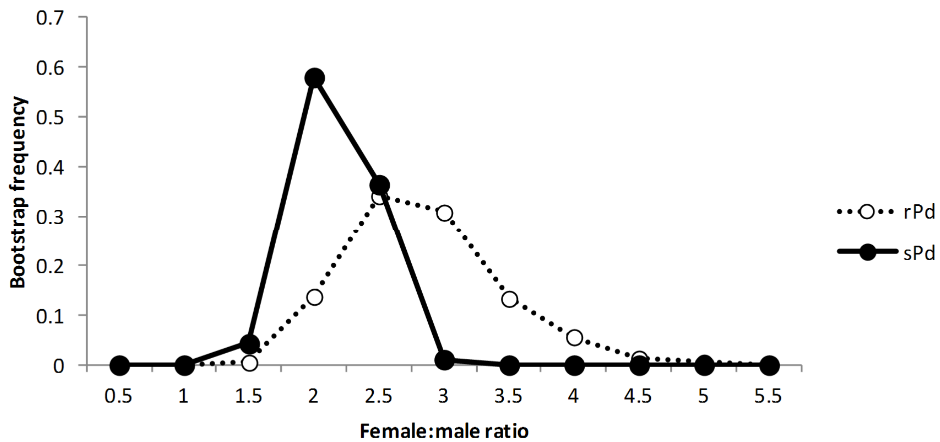
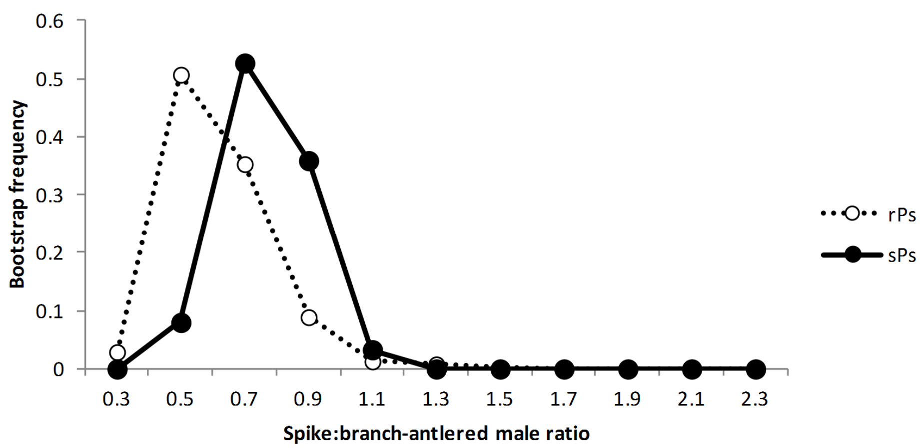


Figure 1. Linear functions relating raw photographic occurrences (RPO) to trap success (TS) for females and fawns. Mianus River Gorge Preserve, Bedford, New York, USA, 2009.





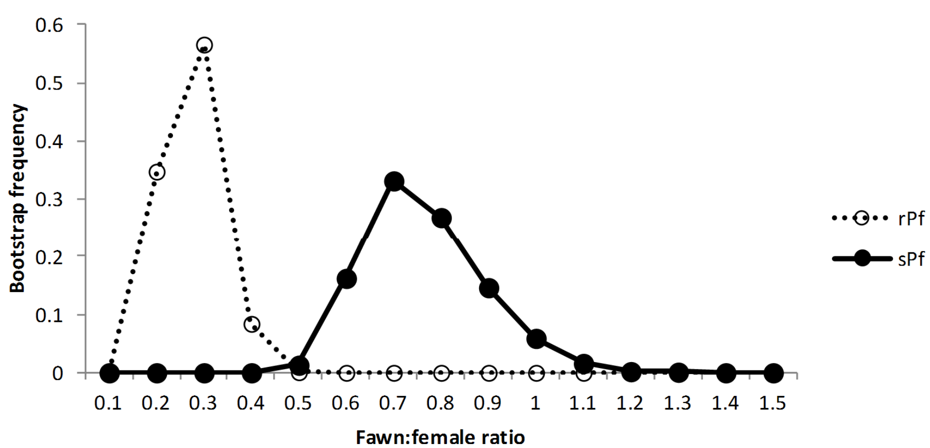


Figure 2. Frequency distribution for demographic ratios computed by nonparametric bootstrapping using both raw photographic occurrences (RPO, white circles) and standardized

photographic occurrences (SPO, black circles). Demographic ratios based on RPO (r): spike males:branch-antlered males (rP_s), females:all males (rP_d), and fawns:females (rP_f). Demographic ratios based on SPO (s): spike males:branch-antlered males (sP_s), females:all males (sP_d), and fawns:females (sP_f), Mianus River Gorge Preserve, Bedford, New York, USA, 2009.

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Chapter 4: Fine-scale genetics of an overabundant white-tailed deer population in Westchester County, NY, USA

Abstract

Female white-tailed deer *Odocoileus virginianus* are believed to exist in matrilineal social-units whose members exhibit low rates of dispersal. The idea that social units expand, and deer populations spread, by succeeding generations adopting overlapping home ranges has been called the rose-petal hypothesis. Previous studies have suggested that philopatry and low dispersal rates leave a genetic fingerprint, such that female deer separated by short distances (< 1.0 km) tend to be genetically related. Using 7 microsatellite loci and spatial autocorrelation analyses of hunter-killed and live-captured deer, I evaluated whether a high density deer herd in suburban Westchester County, NY was structured following the rose-petal hypothesis. There was no evidence of fine-scale genetic structure across samples collected at the County level. At the Mianus River Gorge Preserve, samples collected from the same geographic coordinate were genetically similar (r^2=0.21). However, this positive genetic-geographic correlation became non-significant for deer separated by $\geq$ 230m. The density of the Westchester deer herd exceeded those considered in previous genetic spatial autocorrelation analyses. High deer densities resulting in overlapping ranges of non-related social units may have weakened a broader genetic signature.

Introduction

The socio-biology of white-tailed deer *Odocoileus virginianus* has received a great amount of attention in the last two decades (McNulty et al. 1997, Comer 2005, Miller et al. 2010, Cullingham et al. 2011) following the development the rose-petal hypothesis (RPH) of deer population structure and expansion (Porter et al. 1991, Matthews and Porter 1993). The RPH suggests that female deer are organized in multi-generational, spatially-distinct social groups whose members consist of related females that exhibit high philopatry and low rates of dispersal (Porter et al. 1991, Matthews and Porter 1993). Successive generations of females adopt overlapping home ranges analogous to petal formation on a rose. The RPH was first applied to deer management in a low density herd in the Adirondacks, NY (McNulty et al. 1997). Removing most members of a social group resulted in an area (1.4 km^2) of lowered deer density lasting a minimum of 5 years (Porter et al. 1991, Oyer and Porter 2002). Owing to a high fidelity to one's natal range, deer from neighboring social units did not shift their activities towards the reduction area (Oyer and Porter 2002). These observations are contradictory to those expected from traditional source-sink models (Pulliam 1988) or ideal free distributions (Fretwell 1972). Under these frameworks, deer are expected to move towards areas of lower density where competition for resources, such as foraging and parturition sites, is presumably lowered (Porter et al. 1991).

Fine-scale deer management targeted at the removal of social units is very attractive for managers operating in suburban ecosystems where forested areas are fragmented both in the biological and political sense. Management areas are often relatively small and adjacent natural areas can be under the jurisdiction of many different entities including non-governmental organizations and state and town agencies. In addition, opposition to lethal management can vary across the landscape resulting in a patchwork of deer management effort. The RPH, in theory, would allow independent action by individual land managers despite regionally high deer populations (Porter et al. 1991).

There is strong support for deer residing in matrilineal social groups (Hawkins and Klimstra 1970, Marchinton and Hirth 1984, Nelson and Mech 1984, Matthews 1989). However, the maintenance of such groups and resulting philopatry is believed to be linked to the development of an older age-structure that would allow for the cultural transmission of foraging patterns, and thus, familial home ranges (DeGayner and Jordan 1987, Comer et al. 2005). In suburban ecosystems, where deer are overabundant and the age-structure is advanced (Williams et al. 2008), females appear to be highly philopatric and have low dispersal rates (Etter et al. 2002, Porter et al. 2004) supporting the basis for fine-scale, localized management.

Over the past decade, land managers in suburban Westchester County, NY have begun instituting largely independent, bow-only deer management programs (DMPs) to reduce overabundant deer herds. These DMPs are conducted on properties ranging in size from 1 km^2 to 25 km^2, the appropriate scale for localized management under the RPH (Oyer and Porter 2002). The objective of this study was to indirectly test the applicability of the RPH using molecular methods. Matrilineal organization coupled with high philopatry has been shown to leave a genetic fingerprint such that female deer separated by short distances (< 1.0 km; Laseter 2004, Miller 2008) tend to be genetically related (<1000m). Using 7 microsatellite loci and spatial autocorrelation analyses of hunter-killed and live-captured deer, I evaluated whether Westchester deer exhibited this putative signal. Previous fine-scale molecular studies have focused on unhunted, low density (4.9 – 6.8 km^{-2}) herds in the forested Adirondacks, NY (Matthews 1989); hunted, low density (5 km^{-2}) herds in contiguous forests of South Carolina (Comer et al. 2005);

and unhunted, high density (12 – 20 km^{-2}) herds of a forested area of West Virginia (Laseter 2004, Miller 2008). This study was the first to be conducted in a suburban setting. It also considered deer densities (22 – 44 km^{-2}, Daniels et al. 2009) exceeding other studies.

Methods

Study Area

Westchester County (1115 km^2), directly north of New York City, is characterized by a strong south-to-north urban-to-rural gradient. Human population densities ranged from 4200 km^{-2} (Yonkers) to 80.0 km^{-2} (Pound Ridge). Tissue collection was focused on northern Westchester County (Figure 1) where hunting effort was most concentrated. Samples were opportunistically collected from the lower reaches of the county and from a DMP in adjacent Fairfield, CT. Forested areas were predominately 70-100 year old late successional hardwood stands previously under agricultural or livestock production. Deer densities ranged from 22 km^{-2} (Bedford, NY) to 44 km^{-2} (Lewisboro, NY; Daniels et al. 2009). Detrimental impacts of deer over-browsing on woody regeneration have been documented across the study area (Brash et al. 2004, Weckel et al. 2006, CTWF 2008).

Tissue Collection

I collected ear and heart tissue for genetic analysis from harvested animals and ear clippings from live-captured deer. At the Mianus River Gorge Preserve (MRGP) in Bedford, NY, an effort was made to sample all deer harvested in the program from 2007 to 2010. In 2008, tissue samples were collected from other DMPs (Greenwich Audubon, Ward Pound Ridge, Town of Pound Ridge, and Rockefeller State Park), as well as from a check station operated by the New York State Department of Environmental Conservation (DEC). Hunters were instructed to provide information on the sex, age, and location of harvested animals. Regarding sample locations, every effort was made to get an exact location of the sample. Hunters from the MRGP and check station were interviewed by one of the authors (MW) to encourage detailed and accurate reporting of harvest locations. For the MRGP, hunter tree stands were recorded with a GPS and hunters were asked to confirm the location of harvests using a topographic map. At a minimum, hunters interviewed at the check station were asked to provide the name of the property they hunted and the street address closest to the harvest to be included in the study. Hunters who submitted samples directly through DMPs other than the MRGP were not interviewed. In these cases, hunters listed the property or management unit within the DMP they hunted. The centroid of the property was then used to map harvest locations. Hunters were informed, both in writing and verbally, that location data of harvested animals was confidential to ensure accurate reporting. Street addresses were converted to latitude and longitude using Batchgeo (http://batchgeo.com/).

At the MRGP, I captured live adult female deer ($\geq$1.5 years) between June and September of 2008 and 2009 using immobilizing drugs remotely delivered by cartridge powered darts (Pneu-Dart, Wiliamsburg, PA). Darts contained 1.0-1.5 ml solution of butorphanol (50mg/ml), azaperone (100mg/ml), and medetomidine (40mg/ml) in a ratio of 6:2:3 (Wildlife Pharmaceuticals, Inc., Fort Collins, CO). Deer were revived by intramuscular injections of 3-ml antisedan (5mg/ml), 1-ml naltrexone (50mg/ml), and 1-ml tolazoline (200mg/ml). Each deer received a uniquely color-coded ear tag embedded with a 14.7g M170 radio-frequency identification transponder (RF Code, Austin, TX). I removed a 2 cm^2 of ear tissue from each deer's lower ear. Immobilization and tagging were carried out under IACUC protocol 0715 approved by the City College of the City University of New York. All samples were stored at -70˚C in long-term cryostorage at the American Museum of Natural History.

Genetic Analysis

I extracted DNA using the Qiagen DNEasy isolation kit (Qiagen Inc., Valencia, California, USA). Seven microsatellite loci (Table 1), identified to be polymorphic in white-tailed deer (Anderson et al. 2002), were amplified by PCR. Reactions were locally optimized and thus deviated slightly from those of Anderson (2002). Forward primers were augmented with a CAG tail on the 5' end and associated with one of three fluorescent labels [NED (yellow), 6-Fam (blue), or VIC (green)]. PCR were carried out in 14 µl reactions containing 0.1 µl AmpliTaq Gold [Applied Biosystems, Forester City, California, USA], 1.5 µl TaqGold buffer [Applied Biosystems], 1.5 µl dNTP (25 nM), 1.0 µl CAG label (5µM), 6.9 µl H_2O, 1.0 µl Bovine Serum Albumin (250µg/ml), 0.9 µl $MgCl_2$, 0.1 µl forward primer (10µM), and 1.0 µl reverse primer (10µM). Reactions were carried out under the following conditions: denaturation at 95°C for 12 min; 35 cycles consisting of denaturation at 95°C for 15 s, annealing at 54°C (loci OarFCB193, N, BM6505, INRA011, and Cervid1) or 58°C (loci Q and D) for 30 sec, and an extension period of 72°C for 60 sec; followed by a final extension of 72°C for 45 min. PCR products were diluted by 1:10 for genotyping. Allele sizes were measured on an ABI3730XL (Applied Biosystem) using an internal size standard (GeneScan™ LIZ600 or 500; Applied Biosystems). Loci OarFCB193 (NED), BM6505 (VIC), and N (6-Fam) were multiplexed as were loci Q (6-Fam) and D (VIC). Cervid1 (6-Fam) and INRA011 (6-Fam) were analyzed singularly. Alleles were characterized by an automated binning procedure and visually inspected using GENMAPPER 3.7 (Applied Biosystems). Only female deer ≥1.5 years were included in subsequent genetic analyses.

Data Analysis

Each locus was tested for departure from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using GENEPOP (http://wbiomed.curtin.edu.au/genepop; Raymond and Rousset 1995) incorporating Bonferroni correction. A disproportionate number of samples were collected from the MRGP. Therefore, descriptive statistics were generated for the entire dataset, as well as for a subset from 2008 to determine if MRGP samples produced biased estimates of allele frequencies. For subsequent population genetic analyses, the larger dataset including all years of data were used unless otherwise specified.

The presence of null alleles can lead to erroneous estimates of allele frequencies and an underestimation of heterozygosity (Girard 2011). MicroChecker was used to screen for null alleles and other types of genotyping error, including short-allele dropout and errors in scoring stutter peaks (van Oosterhout et al. 2004). For each locus, the program compares the frequency distributions of observed homozygotic and heterozygotic genotypes to those randomly generated using observed allele frequencies. Short-allele dominance is identified by an excess of homozygotes at either extreme of genotype size classes. Systematic error in scoring stutter peaks is identified by a deficit of heterozygotes whose alleles are separated by less than one repeat. Lastly, null alleles are identified by an overall excess of homozygotes across genotype size classes. A deficiency in homozygotes across all loci is considered support for deviation from panmixia and not genotype error.

MicroChecker assumes the population is in HWE (van Oosterhout et al. 2006) in identifying null alleles. However, detecting null alleles in populations characterized by non-random mating, as is believed the case for deer with a strong matrilineal social structure, is complicated by the difficulty in discriminating between excess homozygosity resulting from genotyping errors or from actual inbreeding (Girard 2011). I used a recently developed method by Girard (2011) that makes the assumption that independent loci share a common demographic history and therefore should have comparable values for inbreeding coefficients, Fis (Beaumont and Nichols 1996). Null alleles are identified by extreme Fis values presumably inflated by the action of both inbreeding and genotyping error (Girard 2011). Using an island-migration model (Wright 1951) and the observed Fis averaged across all loci, expected Fis values are simulated across a range of heterozygosities. The number of realizations was set to 20,000 following the recommendation of Girard (2011). Loci with probable null alleles are identified as having an observed Fis values greater than expected given the locis' observed heterozygosities. Analyses were conducted using FDist2 (Beaumont and Nichols 1996).

Owing to the continuous distribution of deer across suburban Westchester and few barriers for dispersal, it is unlikely that Westchester deer exhibit substantial genetic structure due to fragmentation. Nevertheless, sub-structuring would influence how subsequent spatial autocorrelation analyses were conducted. The significance of spatial autocorrelation indices is evaluated by permuting genotypes across available geographic locations to generate null distributions of no relatedness. In the case of substantiated population sub-structure, permuting values across demes may result in conservative null distributions. Thus, I used BAPS v5.4 (Corander et al. 2008) and STRUCTURE (Pritchard et al. 2000) to confirm this hypothesis of one single population. For BAPS analyses, individual clustering analyses were performed where spatial information on sample locations was used as an informative prior and correlated allele frequencies were permitted. For these analyses, K putative populations from 1 to 10, with 10 replicate runs each, were evaluated. The posterior probability was used to identify the best estimate of K (Corander et al. 2004). Spatial priors were not included for the STRUCTURE analyses; however, genetic admixture across populations was permitted (Falush et al. 2003). As with the BAPS analysis, K putative populations from 1 to 10, with 10 replicate runs each, were evaluated. I used a burn-in of 200,000 Markov chain Monte Carlo (MCMC) steps and an additional 200,000 iterations following the burn-in period. Pritchard et al. (2000) identified the best estimate of K where the likelihood of the data given K, Pr(X | K), was maximized. This approach was supplemented with an ad-hoc statistic, ΔK, that evaluates the second order rate of change in the likelihood of the data given the hypothesis of K populations (Evanno et al. 2005).

Moran's *I* relatedness coefficient (*r*) in SPAGeDI 1.3 (Hardy and Vekemans 2002) was used to investigate fine-scale genetic structure. The Moran's *I* statistic does not make assumptions of HWE (Miller 2008), a favorable property for the current dataset (see results).This spatial autocorrelation technique compares genetic and geographic distances between all deer pairs, or dyads, and generates *r*-values for each distance class. For subsequent analyses, dyads were grouped into 11 distance categories. Distance breaks were chosen to promote equal samples sizes per group. A jackknife procedure (1000 randomizations) was used to generate standard errors for each *r*-value. The significance of *r*-values was determined by permutation analysis where individual genotypes are randomly assigned to new geographic locations generating confidence sets for the null hypothesis of no spatial autocorrelation. One-sided tests were performed to investigate whether observed *r*-values were greater than expected by chance. Spatial autocorrelation analyses were conducted on all samples and MRGP samples alone.

Results

From 2007 to 2010, I obtained 246 tissue samples from female deer ≥1.5 years old that could be successfully geocoded. I collected 122, 29, and 90 (37%) samples from the NYS DEC check station, DMPs, and the MRGP, respectively. Of the MRGP samples, 22 came from the live capture of deer. I collected 165 samples in 2008 of which only 30 (18%) came from the MRGP.

In both the entire dataset and the 2008 data set, 4 out of 7 loci exhibited significant deviation from HWE (Table 1). For the complete dataset, there was evidence of linkage disequilibrium for BM6506 and N, and for Cervid and Q ($p < 0.002$). However, there was no evidence for linkage disequilibrium for the 2008 data set. Average Fis across loci were similar between the two datasets (all samples = 0.12 and 2008 samples = 0.10). I found no evidence of short-allele dominance or error in scoring stutter peaks. Microchecker did flag 3 loci as containing potential null alleles: BM6505, D, and N. Using Fdist2, there is support for locus D containing null alleles, with 92.9% of simulated Fis values found to be lower than the observed value (0.336; Table 2).

There was overwhelming evidence for a single population using both STRUCTURE and BAPS. Regarding the later, the posterior probability for K=1 was 1.0 (SE=0.0). For the STRUCTURE analysis, Pr(X | K) was largely flat for K=1 – 5, declining at $K>5$. The standard deviation of Pr(X | K) increased steadily with K. While Evanno et al.'s (2005) ΔK statistic cannot be evaluated for K=1, ΔK was greatest at K=2 and declined as K increased (Figure 2). As loci not in HWE are known to bias STRUCTURE (Kaeuffer et al. 2007, Belanger et al. 2011), I re-ran STRUCTURE analyses on the 3 loci in HWE and found continued support for a single population using both ΔK and Pr(X | K) statistics.

There was no genetic spatial autocorrelation for any distance category in the County-level data set. For the MRGP sub-set, samples collected from the same location were genetically similar (r=0.21; SE = 0.06; p = 0.07). Genetic similarity became non-significant by the next distance class ($\bar{x}$ =230 m). To ensure that these results were not impacted by the inclusion of putative null alleles, I repeated spatial autocorrelations analysis on MRGP females using only 4 loci (Cervid1, OARFCB193, Q, INRA011). There was supporting evidence for genetic similarity (r=0.18; SE =0.13; p = 0.05) for dyads separated by 0 m.

Discussion

Across all samples collected from Westchester County, there was no evidence of distinct sub-populations or substantial genetic structure at finer scales. For MRGP data, samples collected at the same location were genetically similar; however, spatial autocorrelations became non-significant by the next distance class ($\bar{x}$ =230 m). Previous studies have identified positive genetic clustering among dyads at distance classes up to 900 m (Laseter 2004, Miller 2008, Cullingham et al. 2011). These patterns have been interpreted as evidence for limited female dispersal and a matrilineal social organization (Cullingham et al. 2011). The absence of a broader relationship (over several hundreds of meters) in this study does not refute previous findings. Rather, I suggest the rapid decay in the genetic signal may be a consequence of high deer densities, as well as a sampling strategy artifact. High deer densities would have implications for the RPH and its application to localized management.

The lack of fine-scale structuring at the County scale is not surprising. Samples collected from check stations and DMPs were georeferenced by the nearest street address or by the centroid of the management unit. Error associated with sample locations may have obfuscated any potential genetic signal. At the MRGP, all samples were plotted on topographic maps or with the aid of a GPS, so spatial error was minimal (<10m). Nevertheless, harvest locations may not be representative of space use. While deer are not likely to shift or abandon their range during bow hunts (Hygnstrom et al. 2011), a harvest location is akin to single telemetry point. It probably falls within the animal's typical range, but may not be descriptive of the central tendency of that individual. Accordingly, the distances between dyads based on harvests alone may not be representative. In comparing geographic and genetic distances, Comer et al. (2005) found correlations to be weaker when genetic samples were collected from harvested deer rather than from live captures, thus suggesting the pattern observed for MRGP female deer might be broader.

The strongest evidence of fine-scale genetic structure has been noted by authors who used more traditional methods of inquiry (e.g. telemetry) that allowed for the delineation of social units based on shared space use or measures of association (Matthews 1989, Miller 2008) followed by genetic analysis. In comparing social units, Using microsatellite analysis, Laseter (2004) and Miller (2008), reported average Fst values of 0.05, and 0.08, respectively, suggesting that matrilineal organizations explained a considerable amount of genetic variation at local scales. More ad-hoc approaches to exploring fine-scale structure, such as comparing geographic and genetic distances, generate more subtle patterns. Furthermore, these approaches are influenced by how individuals are analyzed and what geographic distance measures are used. Using Moran's I, Miller (2008) reported positive genetic structuring up to 900 m when using the centroid of each individual deer's home range for its geographic location. However, the genetic signature was considerably weaker when all deer belonging to the same social group (based on visual observations) were assigned to the same coordinate. Samples collected at 0 m were genetically similar (r=0.09); however, spatial autocorrelations became non-significant by the next distance class ($\bar{x}$ =376 m), matching the pattern observed for the MRGP. This underlines the need for very precise measure of space use to discern small-scale genetic patterns.

Lack of a broader genetic signal in the MRGP herd is probably a consequence of deer density. Studying the same high density deer herd (12-20 km^{-2}) as Miller (2008), Laseter (2004) found evidence for matrilineal social structure. However, he challenged the notion that social units are spatially exclusive, as suggested by others (Porter et al. 1991, Kilpatrick and Spohr 2000). Laseter (2004) documented shared ranging patterns by related female deer, but also tolerance for other non-related social units whose ranges overlapped. Using spatial autocorrelation analyses of Smouse and Peakall (1999), Laseter (2004) reported that genetic-geographic correlations became non-significant at approximately 300 m with the strongest correlations recorded at just 100 m, again similar to the results of this study and those of Miller (2008). It is probably that high deer densities resulting in overlapping home ranges by non-related social units is obscuring a stronger genetic signature at the MRGP. Similarly, Blanchong et al. (2007) reported that high densities caused by feeding stations eroded fine-scale genetic structuring as non-related matrilines converged on the same sampling location. In British Columbia and Saskatchewan, where deer densities (1–7 km^{-2}; C. Cullingham, University of Alberta, personal communication) are considerably lower than those of Westchester County, Cullingham et al. (2011) reported very robust positive genetic structuring at 500 m becoming non-significant at 1 km. It should be noted that Cullingham et al. (2011) uncovered this strong pattern despite their reliance on samples collected from harvested deer.

Based on evidence of positive, albeit narrow, geographic-genetic correlations at the MRGP, together with literature support for conserved space use (Kilpatrick et al. 2001) and low dispersal rates in female yearlings and fawns (Etter et al. 2002, Porter et al. 2004), there is continued support for the RPH in suburban ecosystems with some modification. Support, however, may not translate to successful localized deer management. The RPH model suggested that distinct social units were spatially exclusive (Porter et al. 1991) and in low density herds, they might be. However, under conditions of higher densities, genetically distinct social units may overlap (Laseter 2004). Aside from eroding a local genetic signature, a “compound” rose structure, will hamper efforts to remove entire social units. Miller et al. (2010) removed approximately 80% of deer from a 1.1 km^2 area. Even this drastic reduction can leave a sizable founding population when one considers the high intrinsic rate of increased of deer (λ=1.6; Porter et al. 1991). Second, support for the RPH is seen as support for low-capita dispersal rates (5-10%, Porter al. 1991). Yet at high deer densities, even low per-capita dispersal rates can result in the rapid colonization of reduction areas and the need for continued management (Chapter 4). Three years their initial herd reduction, Miller et al. (2010) removed another 36 deer from the same areas. Using genetic techniques, Miller et al. (2010) concluded these deer were unrelated to the deer originally removed. These deer were likely to be immigrants or adjacent deer shifting their range towards the reduction area. I caution that even if the RPH accurately describes deer population structure, in areas of high densities, one-time localized removal of deer may not translate into long-lasting reductions in the local deer herd.

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Table 1. Locus names, allele count, observed (Ho) and expected heterozygosity (He,) p-values for Hardy-Weinberg equilibrium, and Wright's inbreeding coefficient (Fis) for female deer (≥1.5 yrs old) sampled between 2007 and 2010, Westchester County, NY, USA.

	All females (n = 248)					2008 females (n = 165)				
Locus	Alleles	Ho	He	P-val	Fis	Alleles	Ho	He	P-val	Fis
BM606	13	0.69	0.86	0.00*	0.20	13	0.70	0.86	0.00*	0.18
Cervid1	17	0.83	0.85	0.01*	0.02	17	0.86	0.85	0.01*	-0.01
D	10	0.56	0.84	0.00*	0.34	10	0.58	0.83	0.00*	0.30
N	14	0.63	0.86	0.00*	0.26	14	0.65	0.85	0.00*	0.24
OarFCB193	11	0.87	0.86	0.28	-0.02	11	0.89	0.86	0.27	-0.05
Q	12	0.81	0.82	0.28	0.00	12	0.82	0.82	0.04	-0.01
INRA011	3	0.48	0.49	0.89	0.01	3	0.49	0.49	0.64	0.00

* Locus is not in Hardy-Weinberg equilibrium following Bonferroni adjustment.

Table 2. Results from null allele test using Microchecker[a] and Fdist2[b] on all female deer sampled (n=248), Westchester County, NY, USA.

Locus	Microchecker: Null allele	Fdist2: Prob (simulation Fis <sample Fis)
BM606	Yes	0.67
Cervid1	No	0.10
D	Yes	0.93
N	Yes	0.83
OarFCB193	No	0.10
Q	No	0.07
INRA011	No	0.08

[a] van Oosterhout et al. 2004

[b] Beaumont and Nichol 1996; Girard 2011

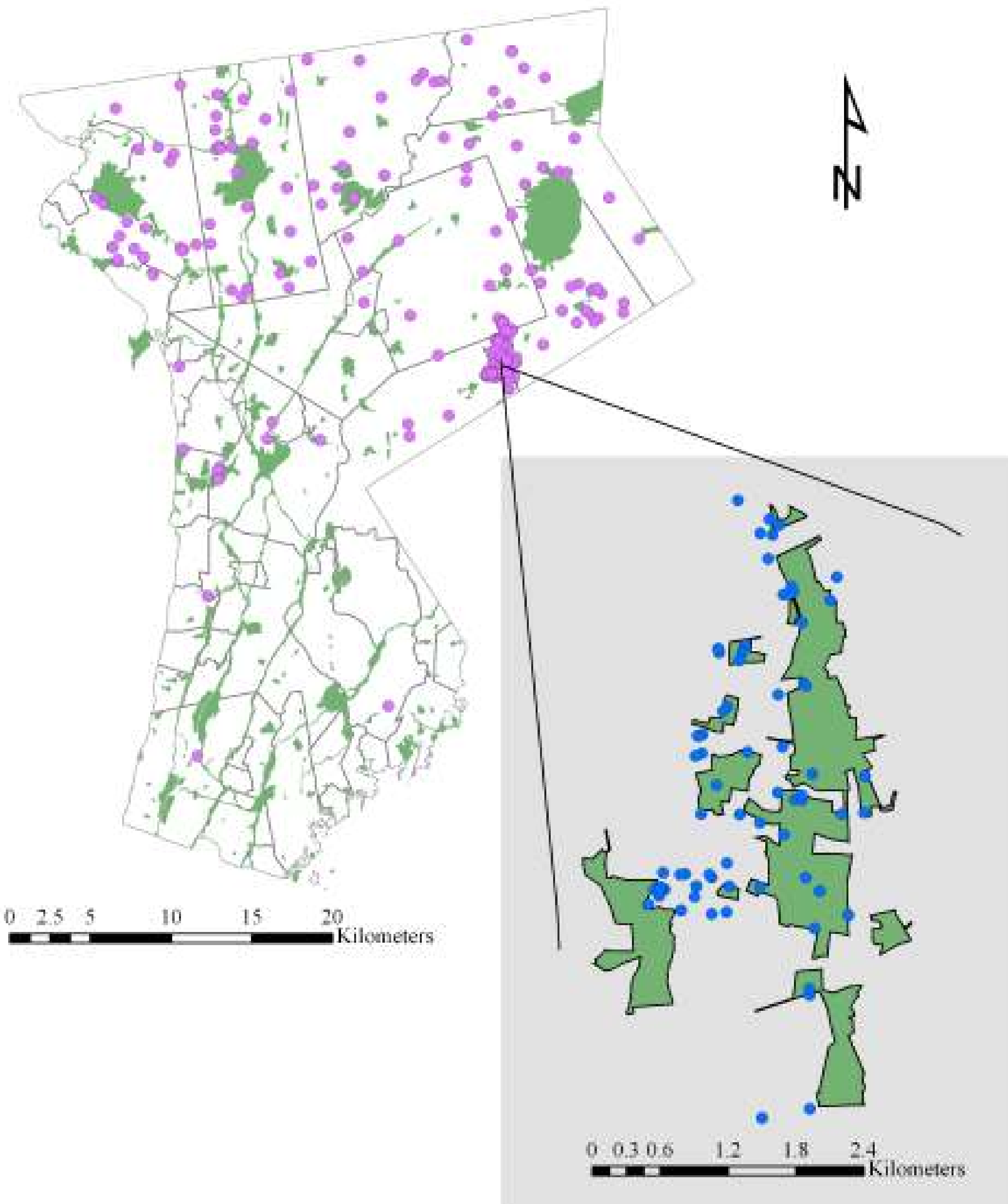

Figure 1.Distribution of genetic samples (; n=246) in County data set (purple circles), Grey inset: Subset of samples (n=90) from the Mianus River Gorge Preserve (blue circles). All samples were taken from female deer > 1.5 years of age; Westchester County, NY, U.S.A, 2007-2010.

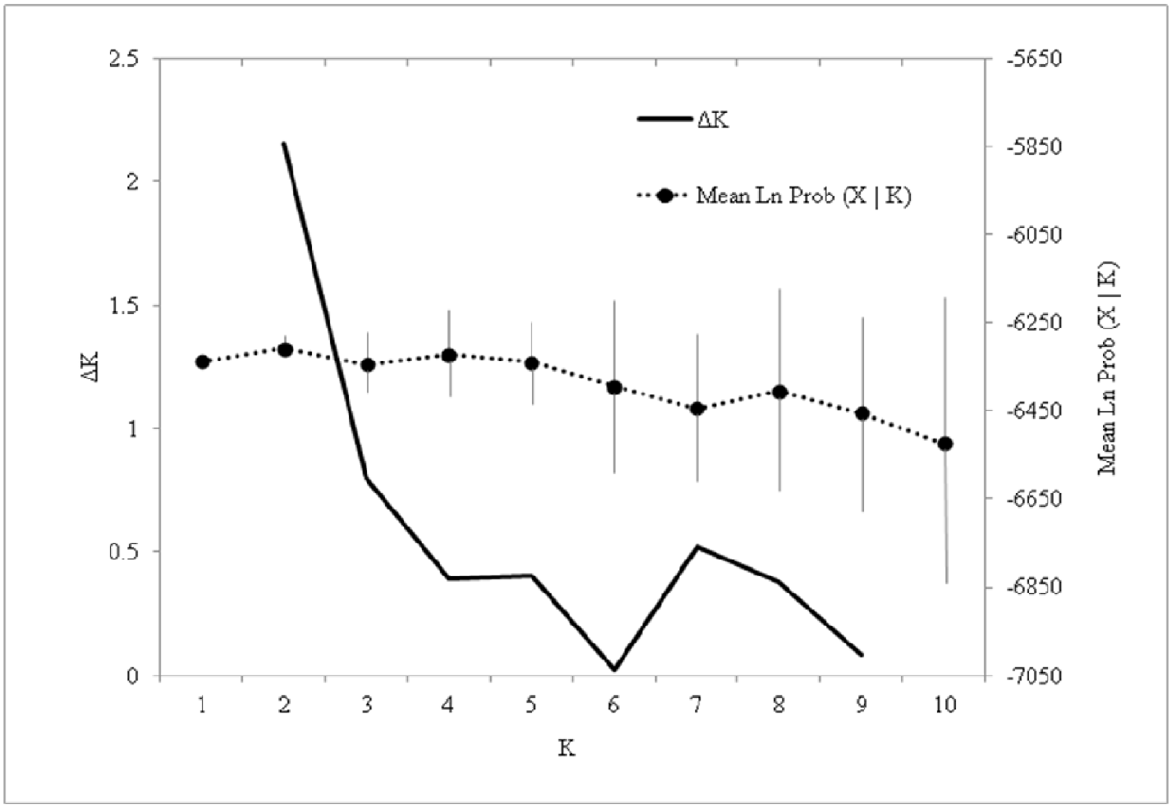

Figure 2. Graph of average Pr(X | K) with standard deviations and Evanno et al.'s ΔK as a function of K possible populations; Westchester County, NY, U.S.A, 2007-2010

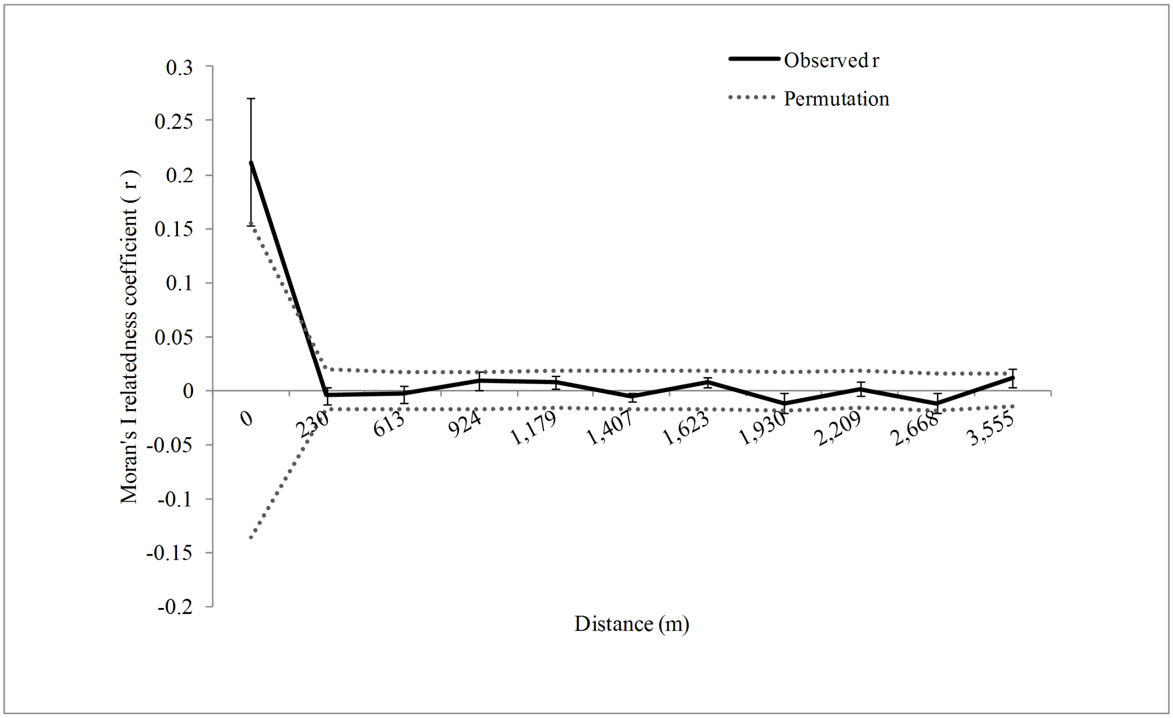

Figure 3. Mean and standard error of Moran's I correlation coefficients as a function of distance for genetic samples (n=90) collected from female deer (> 1.5 years of age) at the Mianus River Gorge Preserve; Westchester County, NY, U.S.A. Mean distances of dyads are reported on the x-axis.

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Chapter 5: Can controlled bow hunts reduce overabundant deer populations in suburban ecosystems and by how much?

Abstract

In the northern suburbs of NYC, land managers have begun implementing bow-only hunts to reduce overabundant white-tailed deer (*Odocoileus virginianus*) herds and to promote forest regeneration. However, there have been no attempts to model the impact of bow hunting on deer population growth. I used harvest statistics from the Mianus River Gorge Preserve in Westchester County, NY to model the population growth of female deer exhibiting density-dependent growth and survival across a range of carrying capacities, immigration rates, and harvest intensities. Simulated bow hunting resulted in densities believed necessary for forest regeneration (2.89 female km^{-2}) only in closed populations where carrying capacity = 13.8 female km^{-2}, representing the lower end of deer overabundance and only after 20 years of management. At harvest rates simulating those observed at the Mianus Gorge, herd reduction was more modest (~21 %). Sustaining harvests over multiple decades is the biggest challenge facing bow-only hunts. Hours per harvest increased rapidly as population declined ($C_F(t) = 0.0041N_F(t)$; R^2=0.56), requiring nearly 5x the effort as female density approached target levels. As controlled bow hunts are executed by volunteer sportsmen, realized reductions will be contingent on hunters' incapacity or unwillingness to increase effort. Consequently, bow hunting will likely result in deer densities lower than historical peak values, yet higher than is currently assumed necessary for forest regeneration.

Introduction

Deer overpopulation continues to be a major environmental problem facing urbanized ecosystems. Ideal habitat conditions have allowed for geometric growth and have brought changes to forest composition (Rooney and Waller 2003, Côté et al. 2004, McGraw and Furedi 2005), an elevated risk of Lyme's disease (Wilson et al. 1985), and increased deer-automobile collisions (Conover et al. 1995, Etter et al. 2002). In many of these urbanized areas, traditional management practices that rely on gun hunting are prohibited, opposed by the public, or infeasible owing to public safety concerns and restricted access to large tracts of huntable land (Jones and Witham 1995, Kuser 1995, Mayer et al. 1995). Bow hunting is often a more suitable approach for these human dominated landscapes because of the discreetness and safety of bow hunting (Shono 2003). In addition, bow-only deer management programs (hereafter, DMPs) that work within the normal hunting season are easier to implement than sharpshooting or immunocontraception, which can face logistical (Kevin Clarke, NYS DEC Big Game and Furbear Biologist, NYS DEC, Region 3, personal communication) and financial hurdles (Doerr et al. 2001). Accordingly, in Westchester County, NY and Fairfield County, CT – northern suburbs of New York City – some land managers have implemented bow hunting-only DMPs. Since 2004, over 10,000 acres of county, private, and state land have been opened to bow-hunting in Westchester for the primary purpose of reducing deer density in the interest of forest regeneration.

Bow hunting has been criticized for being relatively inefficient (Hansen and Beringer 1997) and producing slow, moderate, or incomplete herd reductions (Ellingwood and Spignesi 1986, Krueger et al. 2002). Documented successes often include only a few years of management activities (Kilpatrick and Walter 1999) or are achieved through a combination of bow hunting and sharpshooting (Ver Steeg et al. 1995) or shotgun hunting (Kipatrick et al. 2002, Hygnstrom et al. 2011). Despite concerns over the efficacy of bow hunting and the lack of empirical support for bow-only DMPs, there have been no studies that attempt to model the impact of bow hunting on deer population dynamics. Nor is there information on how the catch-per-unit effort of bow hunters changes as a function of time or deer density (e.g. bow hunting functional response). This information is readily available for other hunting methods such as shotgun and rifle hunting (Holsworth 1975, Harden et al. 2005). For land managers whose options are limited to bow hunting, simulating the impact of bow harvests on population growth would assist managers in understanding the scenarios under which bow hunting is more likely to be effective, in defining realistic target densities, and in designing programs that meet management goals.

In this paper, I incorporate harvest data from the Mianus River Gorge Preserve (MRGP) DMP, a small-scale, bow-only program in Westchester County, into projection models to explore the potential impact of harvests on the population growth of suburban female deer. I simulated bow-hunting at observed rates as well as under a range of hypothetical harvest intensities. I also explored the performance of bow hunting under different permutations of carrying capacities and immigration rates that reflect biologically plausible values. For each scenario, I investigated the magnitude of herd reduction, whether target densities could be met, and the time required to do so. I also explored how total deer harvest per hour and female harvest per hour changed as a function of density using population estimates from the MRGP. Finally, I discuss the functional response of bow hunters and its implications for management goals and the sustainability of bow hunting-only DMPs.

Methods

Study Area

I used harvest data from the MRGP (763 acres) for harvest simulations. The MRGP consists of an old-growth hemlock (*Tsuga canadensis*) forest and 70-100 year old hardwood forest located in northeastern Westchester County, NY. Dominant overstory hardwood species include black birch (*Betula lenta)*, yellow birch (*Betula alleghaniensis*), black oak (*Quercus nigra),* red oak (*Quercus rubra*), red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*). The MRGP lies along the Mianus Greenway and is surrounded by large estates, smaller suburban developments, and protected reservoir land.

Started in 2004, the MRGP DMP is one of the longest running controlled hunts in Westchester County. It includes both the preserve and adjacent residential properties and the amount of land accessible to hunters has grown from 2.34 to 4.11 km^2. This increase has been contiguous extending the reduction area outward from the center of the preserve. The DMP is overseen by staff biologists (including author MW) and a board of hunter representatives elected by the DMP's members. Participants in the DMP are required to pass a proficiency test of 5 out 5 arrows in a 324.3 cm^2 plate at 18.3 m. The number of hunters has varied between 5 and 14 hunters per season. ($\bar{x}$ = 3.3 hunters km^{-2}). I also present harvest data from DMPs managed by the Town of Pound Ridge (TPR; Westchester County, NY), Westchester County Parks (WC Parks; Westchester County, NY), and Greenwich Audubon (GA; Fairfield County, CT). Descriptive statistics from these programs are included for comparative purposes and were not used in subsequent modeling analyses as deer density and harvest sex ratios were not provided.

Harvest data

Mianus River Gorge Preserve hunters were required to complete daily hunter logs detailing 1) the number of hours spent in the tree stand; 2) the group size, sex, and age of deer observed; and 3) the sex and age of harvests. Hunter logs were used to calculate the mean female harvest per hour $C_F(t)$ and total deer harvest per hour $C(t)$ at time t, where t = age of the DMP (notation follows Van Etten et al. 1965).

In subsequent projection models, estimates of deer population size are expressed as densities (km^{-2}), thus, adults, yearlings, and fawns female harvests were expressed per km^{-2}. Simply dividing harvests by land area accessible to hunters may lead to over-estimates of harvest intensity (e.g. deer harvested at the periphery of the reduction area are likely to reside in some unknown area beyond the core reduction zone). To estimate the effective management area, I calculated a 100% minimum convex polygon of hunter tree stands hereafter, the hunter polygon, using ArcGIS 9.1 (ESRI, Redlands, California, USA). I used all stand locations over all seven years to estimate the hunter polygon; hence, the management area was fixed over time. Second, I buffered this polygon based on the unweighted mean radius of several published winter home ranges for female suburban deer (Table 1). I used winter home ranges as they are generally larger than summer ranges generating a larger buffer and therefore a more conservative estimate of harvest intensity.

Modeling the impact of bow hunting on deer population growth

Model parameterization. I simulated the potential impact of bow hunting on a hypothetical suburban deer herd parameterized using published vital rates. Only the female portion of the population was modeled. Population growth was modeled under six scenarios (Table 2) based on different combinations of parameter values for immigration (3-levels) and carrying capacity (2-

levels). These scenarios are believed to represent a broad range of conditions under which deer management may be employed. All projections were performed on a population with a 3-yr age structure (fawn, yearlings, adult) characterized by deterministic, density dependent fertility and survival rates. To parameterize a pre-breeding Lefkovitch-style matrix, I modeled fecundity and survival as a function of carrying capacity using linear regression models described by Porter et al. (2004). Porter et al.'s (2004) original regression models were calculated as a function of abundance specific to their study area. I used Porter et al.'s (2004) estimate of carrying capacity (K) to recalculate their original regression models as a function of K (Table 3).

The carrying capacity for the MRGP deer herd is unknown. Between 2000-2007, deer density estimates from unmanaged, forested areas adjacent to the MRGP (<7 km) averaged 23.4 deer km^{-2} (SE=0.76, n=3; Brash et al. 2004, CTWF 2008, Daniels et al. 2009) however densities as high as 44.1 deer km^{-2} (DeNicola and William 2008, Daniels et al. 2009) have been reported from other suburban areas in the NYC metropolitan region. I used this range of density estimates as a proxy for carrying capacity and explored the efficacy of bow hunting where carrying capacity was low (23.0 km^{-2}) and twice as high (46.0 km^{-2}). However, as harvest simulations were conduction only on female deer, I needed to adjust these numbers accordingly. DeNicola et al. (2008) consistently observed skewed female-to-male sex ratios in unmanaged suburban deer herds across four states. In their modeling exercises (DeNicola et al. 2008), the authors use a 3:2 female-to-male ratio which I adopt in setting female carrying capacity at low (K_{low} = 13.8 females km^{-2}) and high estimates (K_{high} = 27.6 females km^{-2}).

I ran simulations under three levels of immigration (I), zero or geographically closed I_0, low I_L, and high I_H. Where $I > 0$, two demes, one hunted and one unhunted (the control) were projected. To make bow hunting simulations more conservative, I modeled the hunted population as an ecological trap (Battin 2004). Deer from the control herd were permitted to emigrate to the hunted herd; however, deer from the hunted herd never emigrated. Thus population losses in the hunted herd resulted only from mortality. Parameterizing immigration is challenging as direct estimates of immigration are lacking in the literature; therefore, I assumed that dispersal/emigration rates were a good approximation of *I*. Zero immigration rates are unlikely yet may approximate isolated urban herds or true island populations. Suburban deer populations are believed to exhibit high rates of philopatry and low immigration rates (Porter et al. 2004, Porter et al. 1991). To parameterize I_L, I used data from suburban herds describing these characteristics. Specifically, I calculated the weighted means of dispersal rates for adults (I_{LA} = 7.7%), yearlings (I_{LY} = 8.8%), and fawns (I_{LF}= 7.0%) using data from Etter et al.'s (2002) and Porter et al.'s (2004) study on suburban white-tailed deer. Some of the highest rates for female dispersal have been reported for fawns and yearlings in agricultural areas of the Midwest, thus, I include these rates as extreme and unlikely, yet plausible, immigration rates for suburban deer. I calculated the weighted means of dispersal rates for yearlings (I_{HY}= 38.2%), and fawns (I_{HF} = 44.2%) using data from Nixon et al. (2007, 1995, 1991). Adults (>24 mo) are less likely to disperse with only 7.5% of adult female mortalities attributed to dispersing deer (see Nixon et al. 2001). Thus, for modeling purposes $I_{HA} = I_{LA}$.

All simulations began with both the hunted and control populations at carrying capacity at their expected stable age distributions and I simulated harvests over a 50 year period. I parameterized harvest rates for female adults, yearlings, and fawns deer using mean values observed for the MRGP DMP. However, I also conducted hunting simulations at lower and higher values of adult female harvests (1.0 – 5.0 km^{-2}). As they represented a small percentage of total harvests at the MRGP, yearling and fawn harvests were not manipulated to simplify analyzes.

The stated goal of the DMPs reviewed in this paper is forest regeneration (Shono 2003, MRGP 2004, CTWF 2008). Following a study by Tilghman (1989), many managers cite 5.8 deer km^{-2} as a target deer density although the actual deer density required for advanced forest regeneration depends on local factors (Tilghman 1989, Matonis et al. 2011). Other authors have argued that deer densities should be even lower to maximize wildflower and woody biodiversity (Sage et al. 2003). Using Tilghman's (1989) estimate as a benchmark, I have chosen a female density of 2.9 km^{-2} as a naive target density. The primary modeling objective was to determine under which scenarios and harvest intensities meeting the target was possible and how long the reduction would take. I pay particular attention to scenario 2 (see Table 2) parameterized to be most representative of MRGP deer with regards to carry capacity (K_{low}) and immigration (I_L). Regarding the later, in a companion study (see Chapter 4), I found evidence for genetic spatial autocorrelation among MRGP female deer indicative of the RPH (e.g. high philopatry and low dispersal rates; Miller 2008). Population models were constructed using MatLab 13 (The MathWorks, Natick, MA).

Exploring the functional response of bow hunters

To explore the relationship between deer density and harvest rates, I estimated the abundance of MRGP deer in 2009 and 2010, year 6 and 7 of the MRGP DMP. I used camera-trapping and two analytical methods for estimating abundance from photographic data: the mark-resight Poisson log-normal estimator (PNE; McClintock et al. 2008), and the individual branch-antlered male method (IBAM; Jacobson et al. 1997, Weckel et al. 2011).

Immobilizing and marking female deer. To estimate deer abundance using the PNE mark-resight estimate, I marked and monitored female deer. I captured adult female deer (≥1.5 years) between June and September of 2008 and 2009 using immobilizing drugs remotely delivered by cartridge powered darts (Pneu-Dart, Wiliamsburg, PA). Darts contained 1.0-1.5 ml solution of butorphanol (50mg/ml), azaperone (100mg/ml), and medetomidine (40mg/ml) in a ratio of 6:2:3 (Wildlife Pharmaceuticals, Inc., Fort Collins, CO). Deer were revived by intramuscular injections of 3-ml antisedan (5mg/ml), 1-ml naltrexone (50mg/ml), and 1-ml tolazoline (200mg/ml). Each deer received a uniquely color-coded ear tag embedded with a 14.7g M170 radio-frequency identification transponder (RF Code, Austin, TX). Transponders actively broadcasted over an average range of 131 m at the MRGP (M. Weckel, unpublished data) allowing authors to determine whether animals were alive and within the study area during the camera survey. Immobilization and tagging were carried out under IACUC protocol 0715 approved by the City College of the City University of New York.

Camera trap design. The 2009 camera survey was conducted from 16 August to 16 October 2009. I sampled the MRGP in two contiguous blocks of 12 and 11 cameras each. The 2010 camera survey was conducted from 26 June to 3 September 2010. I sampled the MRGP in two contiguous blocks of 10 and 9 cameras each. Camera stations were randomly chosen; however, locations were adjusted in the field so that well-used trails were sampled. To minimize departures from the mark-resight assumption that no animal had a zero probability of being photographed, camera stations were separated by no more than 500 meters. This configuration was based on the average summer home range (21.4 ha) of suburban female deer documented by Porter et al. (2004) in suburban Irondequoit, NY. Camera stations were conservatively spaced as the Porter et al. (2004) estimate was equal or smaller than many other female suburban deer home ranges (Kilpatrick and Spohr 2000, Etter et al. 2002, Grund et al. 2002, Storm et al. 2007). At each camera station, I deployed a Reconyx RC55 (Reconyx, Holmen, WI) camera affixed to a tree between 0.5 – 0.75 m off the ground and 0.5–1.0 m off the trail. These cameras use an infrared flash and are passively triggered by heat and motion. Cameras were programmed to take five successive photos when triggered and had no delay between successive trigger events allowing for near continuous photographic captures at the rate of one photograph per second. For each event I recorded the age, sex, and number of deer seen. Cameras were not baited for this study.

Abundance and density estimates. The PNE used individual capture histories of marked females and the number of photographs of unmarked females to estimate female abundance (adults and yearlings) in Program Mark (White and Burnham 1999). The IBAM method generated a minimum count of branch-antlered males based on antler configuration as determined from photographs (Jacobson et al. 1997). Using estimates of female (PNE) and adult male (IBAM) abundance as a starting point, the abundance of other demographic groups were estimated using sex and age ratios, as determined from camera data, for extrapolation. I followed Weckel et al.'s (2011) method for estimating sex ratios which accounts for not only the raw number of individuals photographed but also the detection probability (hereafter, trap success) of each demographic group. Owing to the fact that 2 cameras broke mid-survey during in 2010, skewing trap effort across camera stations, I used photographs per trap night to avoid bias. Also, since male and female fawns cannot be distinguished via photographs, I assumed the female: male ratio of fawns was 1:1 when estimating female fawn abundance.

Lastly, I calculated the density of the MRGP herd by dividing IBAM and PNE estimates by a measure of the study area. To estimate the effective camera survey areas, I first calculated a

100% minimum convex polygon (MCP) of camera stations for both 2009 and 2010 (ESRI, Redlands, California, USA). I then buffered this polygon based on the unweighted mean radius of several published summer home ranges for female suburban deer (Table 4).

Comparing harvest rates to deer density. I explored whether $C(t)$ and $C_F(t)$ changed as a function of total deer density N(t) and female density $N_F(t)$, respectively, to estimate the hunting efficiency (E) of bow hunters given the equation $C(t) = E\mathrm{N}(t)$ (Holsworth 1973). Modeling the functional response of bow hunters required population data from the first year of the MRGP DMP. For pre-hunt estimates, I set total deer and female deer density as 23.0 deer km^{-2} and 13.8 deer km^{-2}, respectively, based on population surveys conducted adjacent to the MRGP (see above). I model both $C(t)$ and $C_F(t)$ as a Type 1 response (Real 1977) which assumes that catch-per-unit effort increases linearly with density and does not show any asymptotic behavior at high densities (Type 2 and 3) or slower rates of increase at very low densities (Type 3). While Type 2 and Type 3 functional responses are believed to be more realistic approximations of hunter functional responses (VanDeelen and Etter 2003), and may better approximate the behavior of hunters, I currently do not have sufficient data to model these non-linear relationships. I modeled the relationship by forcing a structural y-intercept of zero (VanDeelen and Etter 2003) assuming that hunter success can fall to zero only when deer have been locally extirpated. It is possible to assume that that success can fall to zero at positive values of deer density; however, I do not have enough data at this time to explore this hypothesis. After fitting a type 1 model, I predicted $C(t)$ and $C_F(t)$ over a range of densities from 0 to 23 deer km^{-2} and 0 to 15 females km^{-2}, respectively. Predictions were then inverted to attain hours per deer harvest and hours per female harvest which were then plotted as function of density. These allowed me to explore the amount of hunting effort in hours required to sustain harvests at lower densities and to compare bow hunting to hunting by rifle.

Results

Harvest data

Two hundred and twenty eight deer were harvested in the MRGP DMP over a seven year period, 75% of which were female (Table 5). Using the mean radius (0.42 km) of seven published female white-tailed deer winter home ranges to buffer the 100% MCP hunter polygon (6.6 km^2), I estimated the size of the MRGP MA at 12.1 km^2. Mean harvest per km^{-2} for female adults, yearlings, and fawns was 1.79 (SE=0.20), 0.14 (SE=0.04), and 0.09 (SE=0.06), respectively. These 7 year averages were used as the observed harvest rates in subsequent harvest simulations.

Across several DMPs (Table 6), *C(t)* ranged from a high of 0.09 deer/hr (1st year of the MRPG DMP and GA DMP) to a low of 0.02 deer/hr (1st year of Westchester County DMP at Mountain Lakes Preserve). For the three DMPs with more than 3+ years of harvest records, *C(t)* decreased yearly [$C(t) = -0.0076t + 0.077$; $R^2 = 0.43$, $p=0.0045$).

Modeling the impact of bow hunting on deer population growth

Regardless of harvest intensity or years hunted, simulated bow hunting was incapable of reaching the target density in open populations irrespective of immigration rate or carrying capacity (Figure 1). For scenario 2 ($K_{low,} I_L$), at the observed MRGP female adult harvest rate (1.79 km^{-2} yr^{-1}), population density reached a new equilibrium of 11.0 females km^{-2} early in the second decade of management, a 21% herd reduction (Figure 2). Under scenario 2, substantial herd reductions (>70%) were possible when sustained adult harvests were greater than 2.4 km^{-2} yr^{-1}. This would require a 34% increase over current MRGP harvest levels. At 2.4 km^{-2} yr^{-1}, 40 years of sustained harvests were necessary before reaching a new equilibrium density of 4.0 females km^{-2}. The reduction period could be halved by increasing sustained adult female harvest to 2.6 km^{-2}.

Simulated bow hunting was only capable of reaching the target female density in closed populations (scenario 1 and 4), yet required high harvest rates and long reduction times. For scenario 4 ($K_{high,}$ I_0), the target density was reached at adult harvests $\geq$ 4.0 km^{-2} yr^{-1} and required over 40 years of sustained harvests (Figure 3). For scenario 1($K_{low,}$ I_0) the target density was reached at harvest rates observed at the MRGP, yet required over 20 years of sustained yields (Figure 2). For scenario 1, target density could be reached in as few as 10 years, yet required harvest levels at least 68% greater than the current observed MRGP rate.

Exploring the functional response of bow hunters

Camera data Fourteen female deer were marked and remained alive within the study area during the 2009 camera survey. During this period, camera stations were operated for a total of 662 trap nights. I collected 130, 66, 480, and 112 photos of branch antlered males, spike males, females (adults and yearling), and fawns, respectively. Using Jacobson et al.'s (1997) criteria, I identified 19 distinct branch-antlered males. Using camera data on trap success to standardize photographic occurrences via linear regression I predicted the mean standardized photographic rate for each sex-age class: spike males (β = 27.86, 95% PI = 19.64 – 33.98), branch antlered males (β = 42.65, 95% PI = 33.58 – 54.04), all males (β = 40.02, 95% PI = 31.28 – 48.70), for females (β = 60.57, 95% PI = 49.16 – 72.99), and fawns (β = 42.02, 95% PI = 35.85 – 47.54).

Fourteen female deer were marked and remained alive within the study area during the 2010 camera survey. During this period, camera stations were operated for a total of 309 trap nights. I collected 130, 28, 190, and 86 photographs of branch antlered males, spike males, females, and fawns, respectively. Using Jacobson et al.'s (1997) criteria, I identified 26 distinct branch-antlered males. Using camera data on trap success to standardize photographic occurrences via linear regression I predicted the mean standardized photographic rate for each sex-age class: spike males (β = 1.14, 95% CI = 1.15–1.93), branch antlered males (β = 1.91, 95% PI = 1.04 – 2.71), all males (β = 1.86, 95% PI = 1.13 – 2.65), for females (β = 1.86, 95% PI = 1.62 – 2.12), and fawns (β = 1.47, 95% PI = 1.15 – 1.93). Standardize photographic rates from 2009 and 2010 were used to estimate demographic ratios (Table 7) which were subsequently used to estimate deer abundance.

Abundance and density estimates I used two methods (IBAM and PNE) to estimate deer abundance from camera data resulting in two estimates each for male, female, fawn, and total deer abundance (Table 8). The size of the camera trap area declined in 2010 owing to fewer available cameras so direct comparison of abundance is not advised. I used the mean radius of seven published female deer summer home ranges (0.38 km) to buffer the 2009 and 2010 camera array and estimated the sample area to be 7.12 km^2 and 6.31 km^2, respectively. Averaging PNE and IBAM deer densities by year, I estimated the 2009 ($\bar{x}$ = 17.23 deer km^{-2}) and 2010 ($\bar{x}$ = 18.65 deer km^{-2}) total deer density. Assuming the female:male ratio of fawns was 1:1, I estimated total female density (adults, yearlings, fawns) in 2009 and 2010 to be 10.42 km^{-2} and 9.49 km^{-2}, respectively. These density estimates were used to explore the functional response of MRGP bow hunters.

Comparing harvest rates to deer density I fitted a linear, Type 1 model describing $C(t)$ as a function of $N(t)$ both by forcing a y-intercept: $C(t) = 0.003N(t)$; r^2=0.49. Bow hunters were more efficient when considering female harvests only: $C_F(t) = 0.0041N_F(t)$; r^2=0.56. The inverse of $C_F(t)$, hours per female deer harvest, plotted as a function of female density showed accelerating effort as densities approached the target female density (Figure 4) and target total deer density (Figure 5). At the target female density, bow hunters would have to exert over 80 hours per female harvest compared to approximately 18 hours where female density = 13.8 km^{-2}.

Discussion

Based on harvest simulations and descriptions of hunter functional response, bow hunting seems largely inadequate to meet the management objective of advanced forest regeneration based on the bench mark of 2.9 females km^{-2}. This target density was only achieved for closed populations (Scenarios 1 and 4) and only under very specific, and probably unrealistic, harvest conditions. For Scenario 4 (K_{high}), MRGP harvest rates would have to double and then sustain for 40 years. Under Scenario 1 (K_{low}), current harvests are sufficient, yet still would require a two decade commitment.

Evaluating the relative impact of bow hunting becomes more complicated for the more realistic Scenario 2, an open herd with low rates of immigration and at a lower “overabundant” carrying capacity. Under scenario 2, at current MRGP harvest rates, deer densities were reduced to 11 females km^{-2} by the second decade of management, a 21% reduction. Our empirical monitoring of the MRGP population thus far supports these predictions with female density estimated at 9.49 km^{-2} following eight years of management. Furthermore, empirical studies of 4 suburban controlled hunts suggest that bow and shotgun hunters are incapable of reducing total deer density below 17 – 18 deer km^{-2} (S. Williams, Connecticut Agricultural Experimental Station, unpublished data), the approximate density of the entire MRGP herd following several years of management. A more dramatic reduction (~ 50%) brought by controlled bow-hunting has been reported for the suburban community of Groton Long Point, CT (Kilpatrick and Walter 1999); yet, this reduction was based on the removal rate of a small number of radio-collared deer

(5 out of 10; Kilpatrick and Walter 1999) and therefore may be overestimated. Nevertheless, it should also be noted that the Kilpatrick and Walter (1999) study was conducted on a peninsula and immigration rates may approximate more closely a closed population, thus explaining the large population reduction.

Simulations did suggest a broad range of theoretical herd reductions (10% to 70%) for scenario 2 which were dependent on discrete harvest levels. However, the relative inefficiency of bow hunting makes sustaining large population reductions under any scenario improbable. With regards to all deer, the efficiency (E) of MRGP bow hunters was 0.003 deer km^{-2}. In comparison, Holsworth (1973) and Van Etten et al. (1965) found the E of rifle hunters to be 0.017 and 0.010, respectively, making rifle hunting approximately 3.3 times more efficient. In other words, to maintain total deer density at 5.8 km^{-2}, a MRGP bow hunter would have to invest over 55 hours per deer as compared to only 15 hours for the rifle hunter (Figure 6). Even for the modest herd reduction documented at the MRGP, hunters were faced with an average of 23 hours per deer to maintain the status quo as compared 11 hours per deer for the first year of the DMP (Table 5).

To sustain total harvests, hunters will have to either increase their efficiency or total hunter-hours must increase. Managers may consider more hunters; however, at some point, too many hunters may serve to educate deer to the predation risk. This could result in range shifts or nocturnal behavior that will also erode harvests (Williams et al. 2008). Conversely, requiring more effort out of individual hunters has limitations. Where controlled hunts are executed by volunteer sportsmen, there will be a cap as to how much time hunters will chose to or be able to contribute in the face of diminishing returns on their efforts (VanDeelan and Etter 2003). Suburban bow hunters have other options including hunting private land and other DMPs that may make long term retention of hunter interest challenging (Weckel et al. 2011).

This last point raises the question as to whether it is the bow or the hunter that is relatively inefficient. I have treated hunters as a uniform predator and have demonstrated that, on average, hunters across DMP in Westchester require more hours per deer as these programs progress in age. However, post-hoc, I examined the relationship between the coefficient of variation of $C_F(t)$ and time for 7 MRGP hunters having participated 4+ years in the MRGP DMP. The correlation was not significant (p=0.186), however, variation in efficiency among hunters did appear to increase slightly (R^2=0.32). This suggests that individual hunters may respond differently as DMPs progress. These differences are in part due to differences in innate ability, but they are also a consequence of individual harvest decisions. People hunt for a diversity of reasons (e.g. the relaxation that accompanies the outdoors, for food, to simply see deer, and to harvest a trophy buck, Hendee 1974). Participants in DMPs will balance their own motivations for hunting with the demands (rules and regulations) of the management program. This will result in varying hunter success. Manager should design DMP policies that maximize the productivity of hunters while also acknowledging that hunters are volunteers and that not all volunteer sportsman will want to participate in DMPs where the emphasis is on sustained high harvests.

The fragmented nature of suburbia may also drive the functional response of hunters and contribute to the observed basement on population reduction. Suburban management areas will always have properties that cannot be hunted (refugia) owing to mandated set-backs from residential dwellings (Kilpatrick et al. 2011) or to landowner opposition to deer management. A shift in deer activity towards these refugia will limit harvest rates regardless of the creative solutions adopted to increase it (S. Williams, Connecticut Agricultural Experimental Station, unpublished data). For example, in 2007, MRGP hunters and managers adopted a minimum yearly time commitment. This time commitment is set by a progressive accounting rule where hunters are required to invest 125% of the hourly antlerless deer (females and fawns) take, averaged across all years, to offset the increased difficulty in harvesting deer. This rule helped to maintain harvest rates over the short run (2008 – 2010). However, in 2011 (data not included in current analysis), a poor mast crop was believed to have resulted in deer shifting their activity away from forests to adjacent suburban residences, where hunting was not permitted, to feed off lawns and ornamental plants (M. Weckel, personal observation). A radio telemetry study of Greenwich CT deer confirmed that deer use of forested areas declined by 20% during poor mast years (Kilpatrick et al. 2011). Consequently, harvest rates skyrocketed to 65 hours per antlerless deer and the deer harvest plummeted. This observation was shared across all Westchester DMPs (D. Aitchinson, Westchester County Parks Curator of Wildlife, personal communication). While hunters were willing to invest effort, their time was spent in the wrong places.

Some will interpret its moderate reductions and relative inefficiency as a confirmation that bow hunting is ultimately insufficient to reach forestry management goals and thus, is futile. However, there is a broad spectrum of potential tangibles that can result from deer management (DeCalesta and Stout 1997) and the state of forest recovery in fragmented suburban woodlands following bow-only hunts is unclear. Our target female density of 2.9 km^{-2} serves as rough benchmark developed for rural Pennsylvania (Tilghman 1989). While it is likely that diverse hardwood stands developed under low deer densities (Sage et al. 2003), it is not a strict rule for regeneration for all species everywhere. Relatively unpalatable species such as black birch and American beech will begin to recover at higher deer densities (Long et al. 2007). At the MRGP, the abundance of American beech (*Fagus grandifolia*) saplings increased by 142% following 8 years of bow hunting (M. Weckel, unpublished data; see Weckel et al. 2006 for methodological details). Forest community structure will also depend on the adoption of other forestry practices, such as canopy/light manipulation or the removal of undesirable plant communities (Sage et al. 2003) in addition to deer management control. For most of the 20th century, natural areas in Westchester were managed as preserves and followed a “hands-off” approach to management. As such, these forests are often even-aged and have closed canopies. Furthermore, suburban forest face numerous stressors other than deer that influence the trajectory of succession, including non-native earthworms (Hale et al. 2006), altered nutrient cycling (McDonnell et al. 1997), invasive flora (Baiser et al. 2008), and changes in the soil microbial community (Karpati et al. 2011). All of these factors are drivers of suburban forests and linked with declines in native biodiversity in their own right.

In Westchester County there are currently few alternatives to bow-hunting. One option that has been suggested and implemented in other NYS management units is sharpshooting. Sharpshooting is a method by which professional marksmen remove or cull large numbers of deer from discrete areas using rifles. These professionals are often aided by the use of baiting and permission to remove deer at night (DeNicola and Williams 2008). Sharpshooting is inherently more efficient than hunting; however, it faces similar challenges with regards to long-term sustainability. Miller et al. (2010) simulated high-intensity culling by removing approximately 80% (39 female, 20 male) of deer from 1.1 km^2 in West Virginia where deer herds averaged 12 – 20 deer km^2. The study herd was characterized by high philopatry and exhibited low rates of dispersal (Campbell et al. 2004). Within three years, the local population had increased such that an additional 31 deer (26 females, 5 males) were removed from the same area. Results from genetic analyses suggested that these deer were likely immigrants or adjacent deer that had shifted their home range towards the reduction area. This rapid repopulation suggests that low per-capita dispersal rates may be moot where deer density is high: Regional overabundance can result provide many opportunities for immigration events even if the probability of any one female deer dispersing is low. To demonstrate this point, I simulated a one-time removal of female deer where 100%, 90%, and 80% of the herd was removed under conditions of scenario 2. Within 3 years, the culled population had reached 50% of K (Figure 6) across all 3 cull levels. Sharpshooting may quickly reduce overabundant deer herds to levels commensurate with advanced forest regeneration. However, sustaining these levels will require the continued effort of professional sharpshooters (Van Deelen and Etter 2003), possibly as frequently as every few years, as populations will be too low to be effectively managed by volunteer sportsman.

Going forward, deer managers and hunters must be aware of the inherent limitations of suburban bow hunting and clearly define their goals or risk losing public support. The political process by which lethal management was adopted in much of Westchester was (and continues to be) a difficult for those involved. In more urbanized southern Westchester towns, local stakeholders are still engaged in a divisive political battle as they decide whether to rescind town bans on bow hunting (Kevin Clarke, NYS DEC Big Game and Furbear Biologist, NYS DEC, Region 3, personal communication). Transparency is key to long-term support for deer management, especially amongst suburban stakeholders who can hold a diverse set of values on wildlife and how to live with it. Furthermore, setting unreasonable expectations will undermine faith in land managers to the detriment of adaptive deer management. Where bow hunting is adopted, managers, community residents, hunters, and state agencies need to be prepared for continued discussions on additional measures if goals are not met. This may include confronting contentious issues such as the mandated training of hunters to improve efficiency, the legalization of cross bow (S. Williams, Connecticut Agricultural Experimental Station, unpublished data), or more frequent sharpshooting culls. In the short-term, bow hunting is a political compromise and offers readily implementable, legal, safe tool to mitigate overabundant deer populations and to begin the process of adaptive management.

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Table 1. Winter home ranges of suburban white-tailed deer.

Study	Home range estimation method	State	Home range km^2
Storm et al. 2007	Fixed Kernel (95%)	IL	0.91
Kilpatrick and Spohr 2000	Adaptive Kernel	CT	0.85
Grund et al. 2002	Adaptive Kernel (90% use)	MN	0.85
Etter et al. 2002	Minimum convex polygon (95%)	IL	0.51
Cornicelli et al. 1996	Modified minimum area polygon	IL	0.37
Woodard 2001	Minimum convex polygon (95%)	NY	0.22
Porter et al. 2004	Minimum convex polygon (90%)	NY	0.22

Table 2. Parameter values for sex ratios, carrying capacity, immigration rates, and harvests levels used to model demographics of white-tailed deer managed by bow hunting.

	Parameter set used in model					
	Scenario	Scenario	Scenario	Scenario	Scenario	Scenario
Parameter [a]	1	2[c]	3	4	5	6
Sex ratio of unmanaged herd (female:male)[1]	3:2	3:2	3:2	3:2	3:2	3:2
Carrying capacity (female km-2) [2,3,4,5]	13.8	13.8	13.8	27.6	27.6	27.6
Immigration[6,7,8,9,10]						
Fawns (%)	0.0	7.0	44.2	0.0	7.0	44.2
Yearling (%)	0.0	8.8	38.2	0.0	8.8	38.2
Adults (%)	0.0	7.7	7.7	0.0	7.7	7.7
Harvest						
Fawns (female km-2)[b]	0.09	0.09	0.09	0.09	0.09	0.09
Yearling (female km-2)[b]	0.14	0.14	0.14	0.14	0.14	0.14
Adults (female km-2)	1.0 – 5.0	1.0 – 5.0	1.0 – 5.0	1.0 – 5.0	1.0 – 5.0	1.0 – 5.0

[a] Parameter values derived from following published sources as indicated by superscript: DeNicola and Ward (2008)[1], Daniels et al. (2009)[2], CTWF (2008)[3], Brash et al.(2004)[4], DeNicola and William (2008)[5], Etter et al. (2002)[6], Porter et al. (2004)[7], Nixon et al. (2007)[8], Nixon et al. (1995)[9], Nixon et al. (1991)[10].

[b] Harvest stats derived from MRGP DMP hunter log data.

[c] Scenario 2 contains parameter values for immigration and carrying capacity considered to be the most likely approximation of a Westchester suburban deer herd.

Table 3. Regression models for parameterizing fecundity and survival of white-tailed deer. Models were recalculated from figures and tables presented by Porter et al. (2004).

Vital	Age	Regression[a]	R^2
Fecundity	Adult	$y_F = -1.2004x + 2.7469$	0.98
Fecundity	Yearling	$y_F = -1.1978x + 2.4249$	0.76
Fecundity	Fawn	$y_F = -1.6902x + 2.1703$	0.27
Survival	Adult and Yearling	$y_S = -0.1362x + 0.9614$	0.89
Survival	Fawn	$y_S = -0.3267x + 0.5496$	0.99

[a] y_F = fecundity and y_S = survivorship as a function of x, where x = the population size as a proportion of carrying capacity.

Table 4. Summer home ranges of suburban white-tailed deer.

Study	Home range estimation method	State	Home range km^2
Storm et al. 2007	Fixed Kernel (95%)	IL	0.53
Grund et al. 2002	Adaptive Kernel (90% use)	MN	0.5
Kilpatrick and Spohr 2000	Adaptive Kernel	CT	0.5
Etter et al. 2002	Minimum convex polygon (95%)	IL	0.26
Porter et al. 2004	Minimum convex polygon (90%)	NY	0.21
Woodard 2001	Minimum convex polygon (95%)	NY	0.21
Cornicelli et al. 1996	Modified mimium area polygon	IL	0.17

Table 5. Deer harvest by sex and by age at the Mianus River Gorge Preserve, Westchester County, NY, 2004-2010.

Calendar Year	Years hunted	Hours	Harvest				$C(t)$[a]	$C_F(t)$[b]
			Female Adult	Female Yearling	Female Fawn	Male		
2004	1	464.75	32	1	1	8	0.09	0.07
2005	2	672.733	22	0	0	9	0.05	0.03
2006	3	439.2	18	3	0	12	0.08	0.05
2007	4	952.8	17	3	2	8	0.03	0.02
2008	5	919.75	13	3	0	8	0.03	0.02
2009	6	1139.25	25	1	5	3	0.03	0.03
2010	7	790.5	25	1	0	8	0.04	0.03

[a] $C(t)$ = total deer harvest per hour at time t, where t = age of DMP

[b] $C_F(t)$ = female harvest per hour at time t, where t = age of DMP

Table 6. Deer per hour C(t)[a] for bow-only deer management programs in the NYC metropolitan area, 2003-2010.

Years Hunted	GA[b]	MRGP[c]	TPR[d]	Lasdon[e]	Muscoot[f]	WPR[g]	ML[h]
1	0.09	0.09	0.07	0.02	0.03	0.05	0.02
2	0.07	0.05	0.03	0.02	0.02		
3	0.06	0.08	0.03				
4	0.05	0.03	0.03				
5	0.05	0.03					
6	0.05	0.03					
7	0.03						

[a] C*(t)* = total deer harvest per hour at time t, where t = age of DMP.

[b]GA – Greenwich Audubon (Fairfield County, CT); 2003-2009.

[c]MRGP – Mianus River Gorge Preserve (Westchester County, NY); 2004-2010.

[d]TPR – Town of Pound Ridge (Westchester County, NY); 2006-2009.

[e]Lasdon – Westchester County Parks – Lasdon Park (Westchester County, NY); 2009-2010.

[f]Muscoot – Westchester County Parks – Muscoot Farm (Westchester County, NY); 2009-2010.

[g]WPR – Westchester County Parks – Ward Pound Ridge Reservation (Westchester County, NY); 2010.

[h]ML – Westchester County Parks – Mount Lakes Park (Westchester County, NY); 2010.

Table 7. Demographic ratios for white-tailed deer computed using standardized photographic occurrences at the Mianus River Gorge Preserve, Westchester County, New York, USA, 2009 and 2010.

	2009			2010	
Sex–age ratio	Mean	95% PI		Mean	95% PI
Spike:branch-antlered male	0.66	0.43–0.90		0.65	0.39–1.18
Female:Male	1.92	1.50–2.40		1.06	0.70–1.71
Fawn:Female	0.71	0.52–0.95		0.78	0.60–1.03

Table 8. Male, female, and fawn abundance at the Mianus River Gorge Preserve, Westchester County, NY, USA, 2009 and 2010.

		2009		2010	
Sex–age group	Method	Mean	95% PI	Mean	95% PI
	IBAM + SPO[a]	31.5	27.4–35.9	43.1	36.1–57.0
Male	PNE + SPO[b]	26.1	20.6–32.6	42.7	25.2–61.4
Females	IBAM + SPO	60.4	44.8–77.4	42.6	27.9–76.3
(Adult and Yearlings)	PNE + SPO	49.5	38.7–63.4	42.8	30.3–60.4
	IBAM + SPO	41.8	28.0–61.7	35.6	19.0–64.7
Fawns	PNE + SPO	35.0	25.3–46.4	33.2	25.8–44.5
All Females	IBAM + SPO	81.3	NA	60.4	NA
(Adults, Yearlings, Fawns[c])	PNE + SPO	67.0	NA	59.4	NA
	IBAM + SPO	134.9	111.8–162.3	124.2	94.9–168.1
Total Deer	PNE + SPO	110.5	99.3–123.9	111.2	91.3–133.3

[a] IBAM + SPO—Abundance method using demographic ratios calculated from standardized photographic occurrences (SPO) to extrapolate from a min. no. of branch-antlered M (IBAM) enumerated by Jacobson et al.'s (1997) criteria.

[b]PNE + SPO—Abundance method using demographic ratios calculated standardized photographic occurrences (SPO) to extrapolate from the mean F estimate generated by McClintock et al.'s (2008) mark–resight Poisson log normal estimator (PNE).

[c]Female:male sex ratio of fawns is assumed 1:1

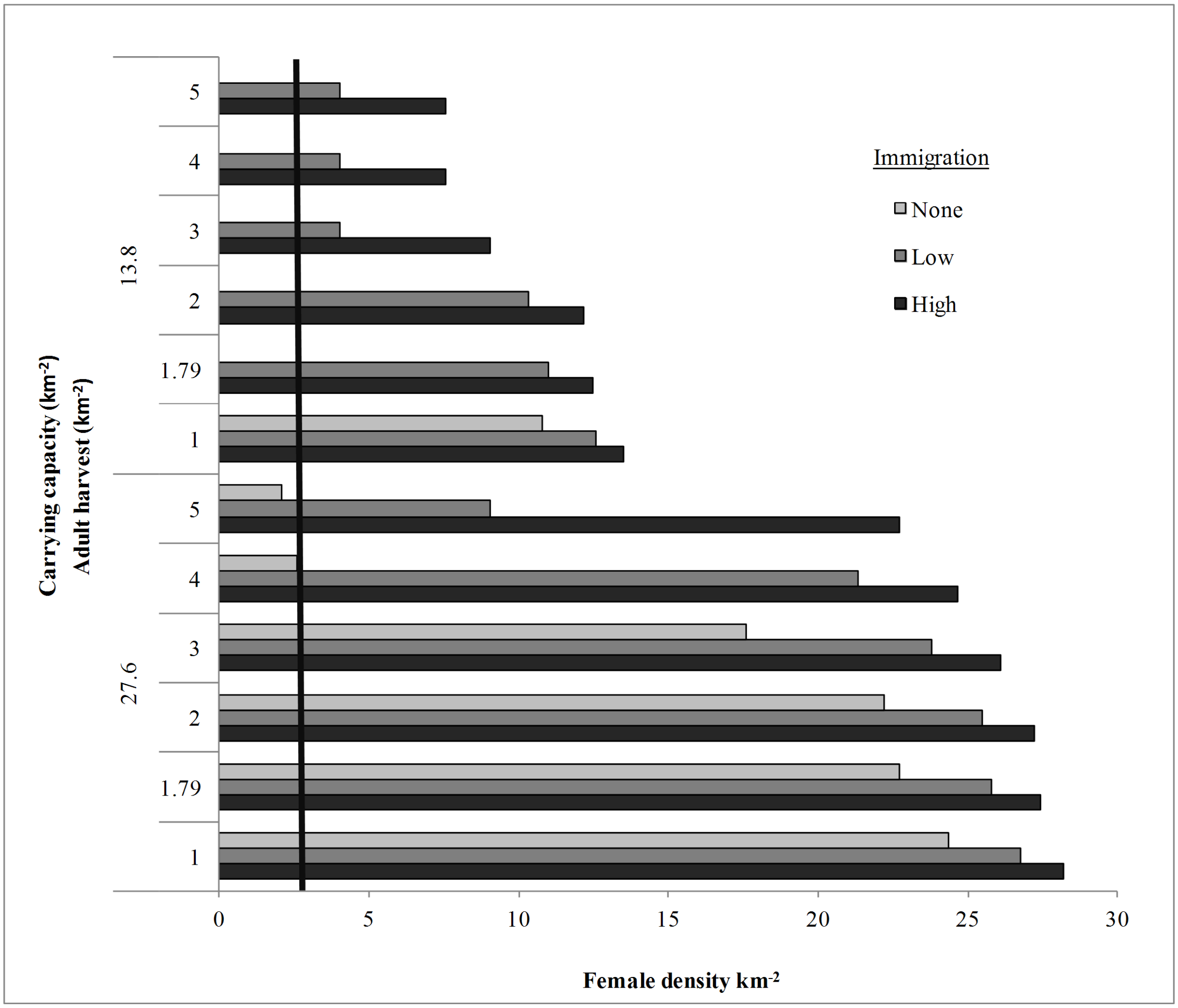
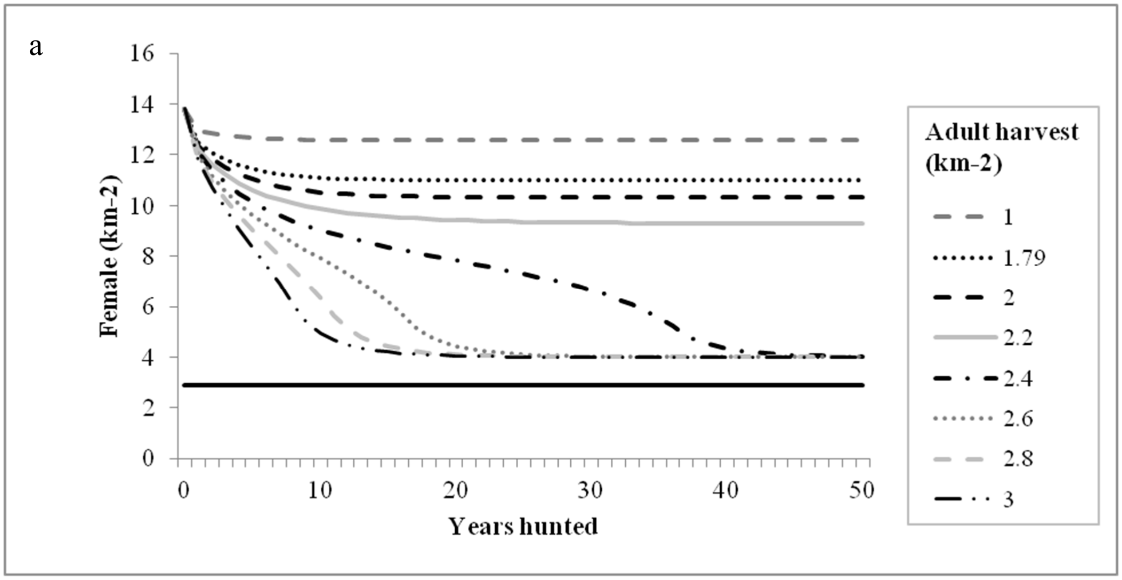


Figure 1. Female density (km^{-2}) at time t =50 years of simulated bow hunting at two levels of carrying capacity, six levels of adult harvest, and three levels of immigration (none, low, and high). Refer to Table 3 for parameter values for carrying capacity and immigration rates. Yearling and fawn harvest are fixed at 0.14 and 0.09 km^{-2}. Mean adult harvest observed at MRPG (2004-2010) = 1.79 km^{-2}. Target density of 2.89 females km^{-2} is demarcated by a vertical black line.



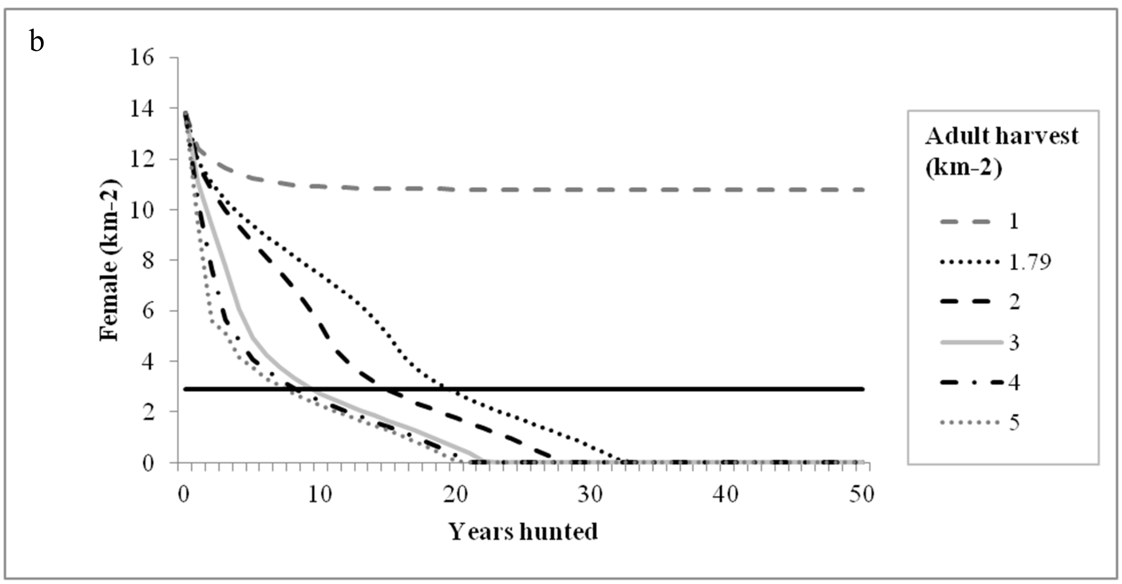


Figure 2. Female density as a function of time hunted at eight levels of adult harvest assuming female carrying capacity (K) is 13.8 km^{-2}, where immigration is low (a), and in a closed population (b). See Table 3 for parameter values for immigration rates. Mean adult harvest observed at MRPG (2004-2010) = 1.79 km^{-2}. Target female density of 2.89 km^{-2} is demarcated by a vertical solid line.

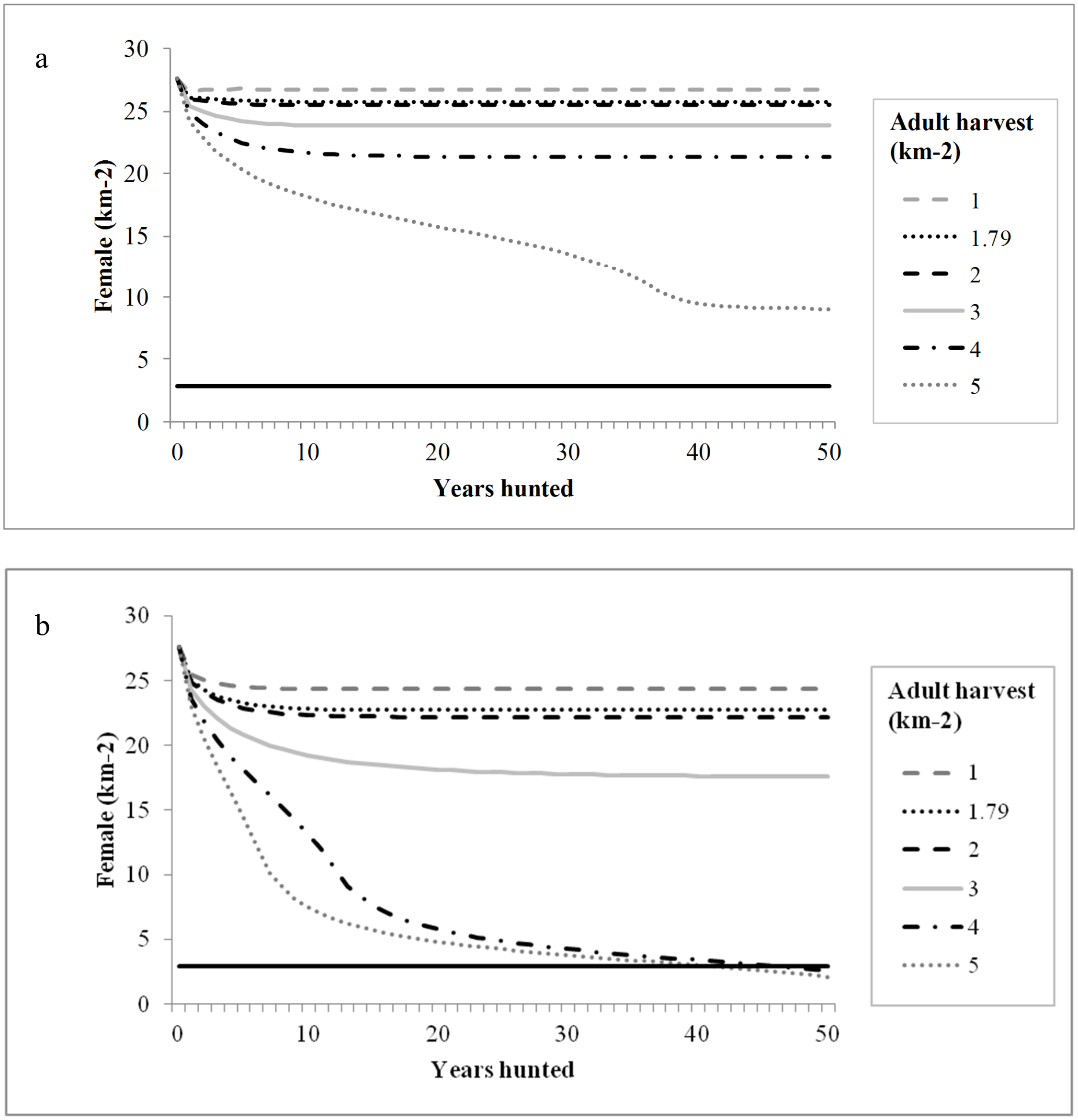


Figure 3. Female density as a function of time hunted at six levels of adult harvest where female carrying capacity (K) is 27.6 km^{-2} where immigration is low (a), and in a closed population (b). See Table 3 for parameter values for immigration rates. Mean adult harvest observed at MRPG (2004-2010) = 1.79 km^{-2}). Target density of 2.89 females km^{-2} is demarcated by a horizontal solid line.

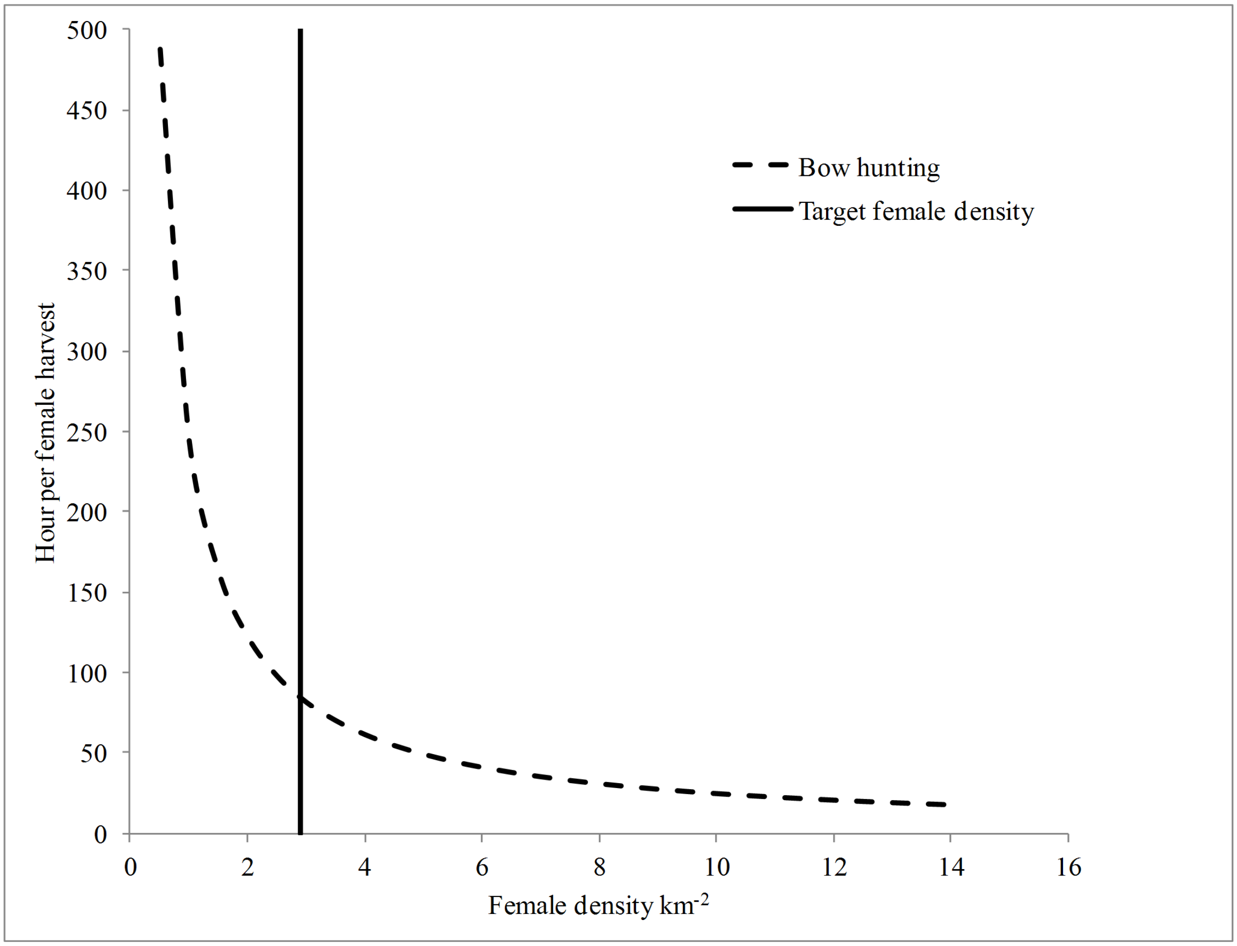


Figure 4. Hour per female harvest as a function of female density (km^{-2}). Target female density = 2.9 km^{-2}. Functional response of bow hunters is derived from female harvest data and population estimates from the Mianus River Gorge Preserve Deer Management Program, Westchester County, NY, 2004–2010.

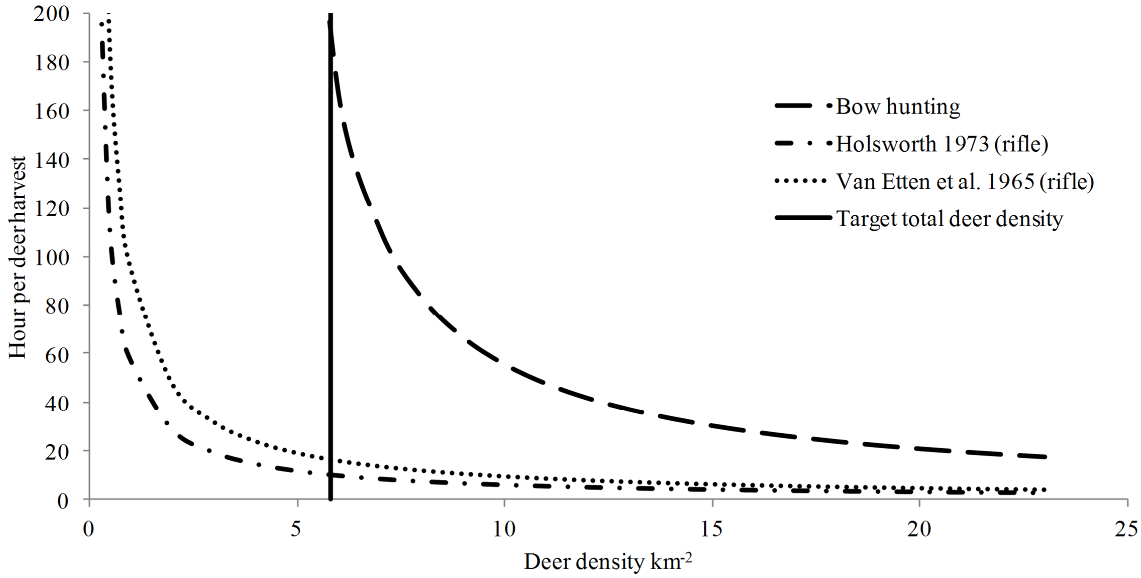


Figure 5. Hour per deer harvest as a function of total deer density (km^{-2}). Target density = 5.8 km^{-2}. Functional response of bow hunters is derived from harvest data and population estimates from the Mianus River Gorge Preserve Deer Management Program, Westchester County, NY, 2004–2010. Function response of rifle hunters is recreated from Holsworth (1973) and Van Etten et al. (1965).

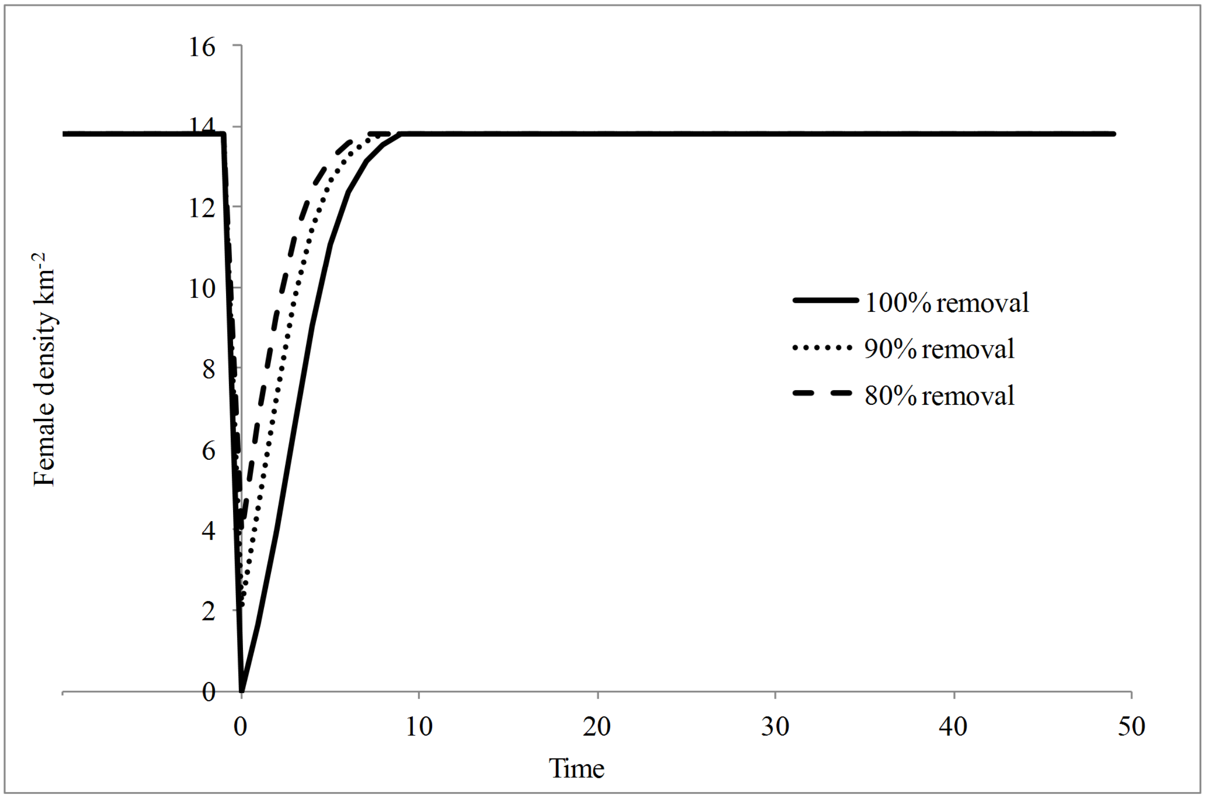


Figure 6. Female density before and after simulating a onetime cull of deer (time = 0) at three removal levels (100%, 90%, and 80% of all females removed). Population is parameterized according to scenario 2 (Table 2).

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Chapter 6: Conclusions

Overall, it appears unlikely that bow hunting can reduced deer densities to those historical levels (< 5.0 deer km^{-2}) believed necessary for advanced forest regeneration and maximum flora biodiversity (Rooney 2001). Based on our camera trap studies, bow hunting reduced the Mianus River Gorge Preserve (MRGP) deer herd from approximately 23 to 18 deer km^{-2}, a 24% reduction in line with predictions from our projection models. Other studies support these findings and suggest that bow hunting is probably incapable of reducing suburban deer herds below 17 deer km^{-2}in suburban areas.

On average, bow hunting is considerably less efficient then rifle hunting, arguably a moot point for suburban areas where rifle hunting is prohibited. The challenge facing deer managers in producing the maximum possible reduction by bow hunting is not the bow itself, but the harvest decisions made by individual hunters. Seeing wildlife is among the most important motivation for hunting. It is also the first "reward" to disappear as a herd becomes hunted. Some hunters will respond by putting in less effort, thereby contributing to declining harvests. Sustaining herd reductions, albeit moderate, requires sustaining harvests and thus incentivizing hunter effort.

It is likely that all attempts at localized suburban deer management, regardless of the harvest technique, will face serious challenges in maintaining reductions. This is not a repudiation of the rose-petal hypothesis (RPH). There is substantial literature support for philopatry and low dispersal rates in suburban female deer. Furthermore, molecular evidence from the MRGP is suggestive of the fine-scale genetic spatial patterns indicative of the RPH model. Rather, the caveat is that support for the RPH should not be grounds for fine-scale suburban deer management. Where deer densities are high, non-related social units will overlap. This will make the initial reduction more difficult and increases the possibility of leaving behind founder deer which can accelerate the repopulation of the management area. High deer densities also increase the likelihood for immigration into the reduction area even if per-capita rates of dispersal are low. Regionally high deer herds thus challenge localized reduction efforts regardless of whether bow hunting or more intensive herd reduction, like sharpshooting, is used. Sharpshooting can reduce deer densities to historic levels, but will require regular sharpshooting to keep densities in check.

Deer populations are controlled largely by three factors: harsh winters, food availability, and predation. In suburban areas, wildlife professionals are only able to manipulate one of those factors: predation by humans (aka hunting). However, in the NYC metropolitan area mild winters, ideal habitat fragmentation, and supplemental feeding will continue to support high survival rates exacerbated by the high fecundity of white-tailed deer. Introducing bow-hunting is likely to decrease suburban deer herds from historic highs, but unlikely to attain historical lows.

Appendix 1 – Online survey used to evaluate the motivation, satisfaction, and harvest decisions of participants of controlled archery hunts; Fairfield, CT; and Westchester, NY.

Deer Management Program: Archer Opinion Survey

1.

Thank you for participating in this study. The purpose of this research study is to learn about the motivations and attitudes of archers who partake in Deer Management Programs (DMP). Simply put, archers are the front line of harvest-based deer reduction programs in many suburban areas. The success and sustainability of these DMPs depend on a better understanding between managers of DMPs and hunters.

I hope the results of this research can be used to make deer management programs both more efficient and more enjoyable for hunters.

This survey is completely anonymous and participation in this study is completely voluntary. You may exit the survey at any time.

All research is reviewed by a committee that works to protect your rights and welfare. If you have questions or concerns about your rights as a research subject you may contact, anonymously if you wish, Lissy Wassaff (212.650.5397 or irb@ccny.cuny.edu) at the Institutional Review at City University of New York.

2.

*** 1. Are you currently a member of a deer management program (DMP) in Westchester, Fairfield, Suffolk, or Putnam Counties.**

(Deer Management Programs are also referred to as controlled hunts. DMPs are often organized by large private landowners, government agencies, agricultural businesses, or nature preserves with the goal of reducing the size of deer herds on their property)

- ◯ Yes
- ◯ No

3. Survey is for archers in deer management programs

This survey is ONLY for archers that participate in controlled archery hunts, aka deer management programs (DMP).

*** 2. If you do participate in a DMP and wish to continue the survey, please press "Previous Question" and proceed.**

If you DO NOT participate in a DMP and wish to exit the survey, please press "Exit Survey" on the top right hand corner of this page.

- ◯ Previous Question

4.

Deer Management Program: Archer Opinion Survey

* 3. Please provide the name of the deer management program or the name of the property on which the controlled hunt is being conducted. Please list only ONE deer management program.

(If you participate in multiple DMPs, we ask that you complete additional surveys for those programs after you complete this one. It is important that managers get feedback specific to individual programs.)

5.

4. Please provide your age.

5. Please provide the town and state where you live.

6. What is your profession?

* 7. Did you hunt growing up?

- ◯ Yes
- ◯ No

6.

8. Growing up, in what setting did you commonly hunt. Please click yes for all that apply.

	Yes	No
Urban/Suburban	◯	◯
Rural/Farmland	◯	◯
Forest	◯	◯
Private land	◯	◯
Public land	◯	◯

7.

9. At what age did you start to hunt?

Deer Management Program: Archer Opinion Survey

8.

10. Please rate the following reasons for hunting:

	Very Important	Important	No Opinion	Not Important
Recreation	◯	◯	◯	◯
Solitude	◯	◯	◯	◯
The opportunity to see wildlife	◯	◯	◯	◯
The opportunity to harvest a big, mature male deer	◯	◯	◯	◯
Food	◯	◯	◯	◯
Heritage / Tradition (e.g. the skill of hunting has been passed down through your family)	◯	◯	◯	◯
Nostalgia (e.g. the act of hunting brings back pleasant memories of a former time in your life)	◯	◯	◯	◯
The opportunity to bond with friends and family	◯	◯	◯	◯
Deer population control	◯	◯	◯	◯
A passion for bow hunting	◯	◯	◯	◯
To test one's skills	◯	◯	◯	◯

Other (please specify)

9.

* 11. Can you hunt on your own property?

◯ Yes

◯ No

10.

12. Do you hunt on your own property?

◯ Yes

◯ No

If no, please explain why you do not hunt on your property.

11.

Deer Management Program: Archer Opinion Survey

13. Deer hunters get information on basic deer biology (e.g where deer live, what they eat); and deer management (e.g. how to hunt deer, the impact of sex ratios and herd age structure) from a variety of sources.

Please rank how important each of these sources are to you when you are looking for information on deer.

	Very Important	Important	No Opinion	Not Important
Hunting blogs	○	○	○	○
Deer Management Programs	○	○	○	○
State Wildlife Departments (e.g. NYS DEC, CT DEP)	○	○	○	○
Scientific Journals	○	○	○	○
Quality Deer Management Association	○	○	○	○
Magazines	○	○	○	○
Websites	○	○	○	○

Other

14. Do you think it is ethical to harvest:

	Yes	No Opinion	No
Adult females	○	○	○
Adult males	○	○	○
Yearling females	○	○	○
Yearling males	○	○	○
Fawns	○	○	○

Please explain your answer.

15. What impact, if any, do you believe the current deer population has on :

	Positive	No Impact	Negative
Human health and safety	○	○	○
Forest health and quality	○	○	○

12.

Deer Management Program: Archer Opinion Survey

* **16. Deer Management Programs (DMP) have the goal of deer population reduction. Do you believe that archery can reduce the deer population on the land your DMP controls?**

○ Yes

○ No

13.

17. Do you believe such a reduction could be large enough to:

	Strongly Agree	Agree	No Opinion	Disagree	Strongly Disagree
lower deer-automobile accidents near the DMP property	○	○	○	○	○
lower the prevalence of Lyme's disease on the DMP property	○	○	○	○	○
increase the regeneration of trees and shrubs on the DMP property	○	○	○	○	○
decrease damage to ornamental plantings on residential properties near the DMP	○	○	○	○	○
decrease your enjoyment hunting in the DMP	○	○	○	○	○
decrease the quality of bucks	○	○	○	○	○
increase the quality of bucks	○	○	○	○	○

14.

18. Please rate the following reasons for participating in the DMP listed above.

	Very Important	Important	No Opinion	Not Important
Additional hunting spot	○	○	○	○
Only hunting spot	○	○	○	○
To reduce the deer population	○	○	○	○
Opportunity to hunt previously unhunted land	○	○	○	○
Opportunity to harvest a mature, trophy buck	○	○	○	○
Opportunity to socialize and interact with other hunters	○	○	○	○

Other (please specify)

15.

Deer Management Program: Archer Opinion Survey

19. Antler-restriction is an effort to protect younger bucks from harvest by placing a limit on the smallest antler size than can be harvested from a property.

	Strongly Agree	Agree	No Opinion	Disagree	Strongly Disagree
Do you support antler restrictions on this DMP property?	◯	◯	◯	◯	◯

20. Earn-a-buck programs require hunters to harvest a minimum number of female deer PRIOR to harvesting a male deer.

	Strongly Agree	Agree	No Opinion	Disagree	Strongly Disagree
Do you support "Earn-a-buck" incentives on this DMP property?	◯	◯	◯	◯	◯

21. Would you harvest fawns if required by your DMP?

◯ Yes

◯ No

22. Would you harvest fawns if they counted as female deer in "earn-a-buck" programs.

(Earn-a-buck programs require hunters to harvest a minimum number of female deer PRIOR to harvesting a male deer.)

◯ Yes

◯ No

23. .

	Strongly Agree	Agree	No Opinion	Disagree	Strongly Disagree
Do you believe that your opinions are considered in the design and organization of the DMP listed above (either through a representative or directly)?	◯	◯	◯	◯	◯

Please provide any examples

24. Are you satisfied with the rules and regulations of the DMP listed above?

	Very satisfied	Satisfied	No opinon	Dissatisfied	Very dissatisfied
Choose one:	◯	◯	◯	◯	◯

Deer Management Program: Archer Opinion Survey

25. Do you believe that the opportunity to participate in this deer management program will exist in:

	Yes	No
10 years?	◯	◯
15 years?	◯	◯
20 years?	◯	◯

Why?

16.

26. Regarding male deer in the Deer Management Program you named above, do you believe there are:

◯ Too many

◯ A good number

◯ Too few

27. Regarding female deer in the Deer Management Program you named above, do you believe there are:

◯ Too many

◯ A good number

◯ Too few

17.

*** 28. Is the upcoming season your first time participating in this DMP?**

◯ Yes

◯ No

18.

29. How many years have you hunted in this DMP? (Do not count the upcoming hunting season)

Deer Management Program: Archer Opinion Survey

30. Please indicate if you agree or disagree with the following statements:

	Strongly Agree	Agree	No Opinion	Disagree	Strongly Disagree
My enjoyment in the DMP has increased since I started with the DMP	○	○	○	○	○
Harvesting a male deer has become increasingly more difficult	○	○	○	○	○
Harvesting a female deer has becoming increasingly more difficult	○	○	○	○	○
The number of male deer that I have observed has increased since I started the DMP	○	○	○	○	○
The number of female deer that I have observed has increased since I started the DMP	○	○	○	○	○

31. Below are a list of potential reasons explaining the number of female deer harvested by a hunter.

Please indicate how important each of these statements are to explaining the number of female deer YOU harvest in an average year in your deer management program.

	Very Important	Important	No Opinion	Not Important
My freezer is already full of venison for the year. I have no need for more female deer.	○	○	○	○
I have (or I choose) to spend time in other deer management programs (DMP)	○	○	○	○
I have (or I choose) to spend time on non-DMP lands	○	○	○	○
I don't see many deer in my stand, so I don't hunt as much as I could	○	○	○	○
I did not have any further opportunities in the stand to harvest more female deer	○	○	○	○
I have used up all my hunting tags	○	○	○	○
I pass up shots of females during the rut	○	○	○	○
I pass up shots of females if I am buck hunting	○	○	○	○

Other reasons (please specify)

Deer Management Program: Archer Opinion Survey

32. Please rank the following criteria for deciding whether or not a hunter should be retained in the deer management program you provided above.

	Very Important	Important	No Opinion	Not Important
How well a hunter follows the rules and regulations of the DMP	◯	◯	◯	◯
How actively a hunter participates in the DMP process	◯	◯	◯	◯
How well a hunter interacts with the general public	◯	◯	◯	◯
The hours committed to the program	◯	◯	◯	◯
How respectful a hunter is to other hunters	◯	◯	◯	◯
The number of female deer harvested	◯	◯	◯	◯
The number of male deer harvested	◯	◯	◯	◯
The hunter's wounding rate	◯	◯	◯	◯

Other (please specify)

33. Please rank the following criteria for deciding how hunters should be given access to new or more hunting spots in the deer management program (DMP) you provided above.

	Very Important	Important	No Opinion	Not Important
How well a hunter follows the rules and regulations of the DMP	◯	◯	◯	◯
How actively a hunter participates in the DMP process	◯	◯	◯	◯
How well a hunter interacts with the general public	◯	◯	◯	◯
The hours committed to the program	◯	◯	◯	◯
How respectful a hunter is to other hunters	◯	◯	◯	◯
The number of female deer harvested	◯	◯	◯	◯
The number of male deer harvested	◯	◯	◯	◯
The hunter's wounding rate	◯	◯	◯	◯

Other (please specify)

19. The End

You are finished with the survey!

If wish to submit your data, please click the below button.

At this time if you wish to exit the survey without submitting your responses, press the "Exit" link at the top right hand corner of this page.

If you participated in other deer management programs and would like to provide feedback on these

Deer Management Program: Archer Opinion Survey

DMPs:
1) First, submit the results of this survey.
2) Second, re-enter the survey by following original web link.

Thank you very much for your participation in this study.

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