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Can controlled bow hunts reduce overabundant white-tailed deer populations in suburban ecosystems?

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ABSTRACT

In the northern suburbs of NYC, land managers have begun implementing bow-only hunts to reduce overabundant white-tailed deer (*Odocoileus virginianus*) herds in an effort to promote forest regeneration. However, there have been no attempts to model the impact of bow hunting on deer population growth. Using harvest statistics from the Mianus River Gorge Preserve in Westchester County, NY we simulated the impact of bow hunting on a population of female deer exhibiting density-dependent growth and explored a range of carrying capacities, immigration rates, and harvest intensities. Simulated bow hunting (adult harvest $\geq$ 1.8 females km^{-2}) was capable of achieving deer densities believed necessary for forest regeneration (2.9 females km^{-2}) in closed populations where carrying capacity = 13.8 females km^{-2}, representing the lower end of deer overabundance. At this carrying capacity and low immigration rates, the impact of bow hunting was more variable, producing population declines ranging from 20 to 70% contingent on harvest rates. Hours per harvest increased rapidly as the deer population declined requiring nearly 5 times the hourly effort as female density approached target levels. Sustaining harvests over multiple decades, particularly as effort per deer harvest increases, is one of the biggest challenges facing bow-only hunts. As controlled bow hunts are executed by volunteer sportsmen, reductions will be determined by hunters' capacity or willingness to increase effort and efficiency. Bow hunting will therefore likely result in deer densities lower than historical peak values, yet higher than is currently assumed necessary for forest regeneration.

1. Introduction

High-density herds of white-tailed deer (*Odocoileus virginianus*) continue to be a major environmental problem facing suburban ecosystems. Suburban sprawl has created a patchwork of woodlots, park land, and residential lots that supply a diversity of food sources for deer (e.g. mast, browse, ornamental plants). These ecosystems have also seen the extirpation of large natural predators and declines in human hunting (McShea et al., 1997) that, when coupled with preferred edge habitat, have resulted in ideal conditions for geometric growth of deer populations (Alverson et al., 1988). Sustained deer densities at or near carrying capacity, often referred to as deer overpopulation, have brought dramatic 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). The risk that deer pose to ecological systems and public health alike have driven continued discussion both in town halls and scholarly literature on how to best to manage suburban deer herds (Raik et al., 2005).

In North America, hunting has been the traditional management tool for regulating wildlife populations (Geist et al., 2001). However, in many suburban areas, the discharge of firearms is illegal and/or is opposed by the public due to safety concerns (Jones and Witham, 1995; Kuser, 1995; Mayer et al., 1995). In addition, as suburban natural areas are fragmented, so too is support for lethal management (DeStefano and DeGraaf, 2003). This generates a patchwork of hunting effort based on the independent decisions of home owners, land managers, and government agencies. Under these conditions, bow hunting is often a more suitable approach to deer management. Bow hunting is often the only legal type of hunting, is relatively discreet, and can be used to safely harvest deer in close proximity to residences (Shono, 2003). Accordingly, in Westchester County, NY and Fairfield County, CT – northern suburbs of New York City – some land managers have begun implementing bow hunting-only deer management programs (DMPs). From 2004 to 2010, over 4000 ha of county, private, and state land were opened to

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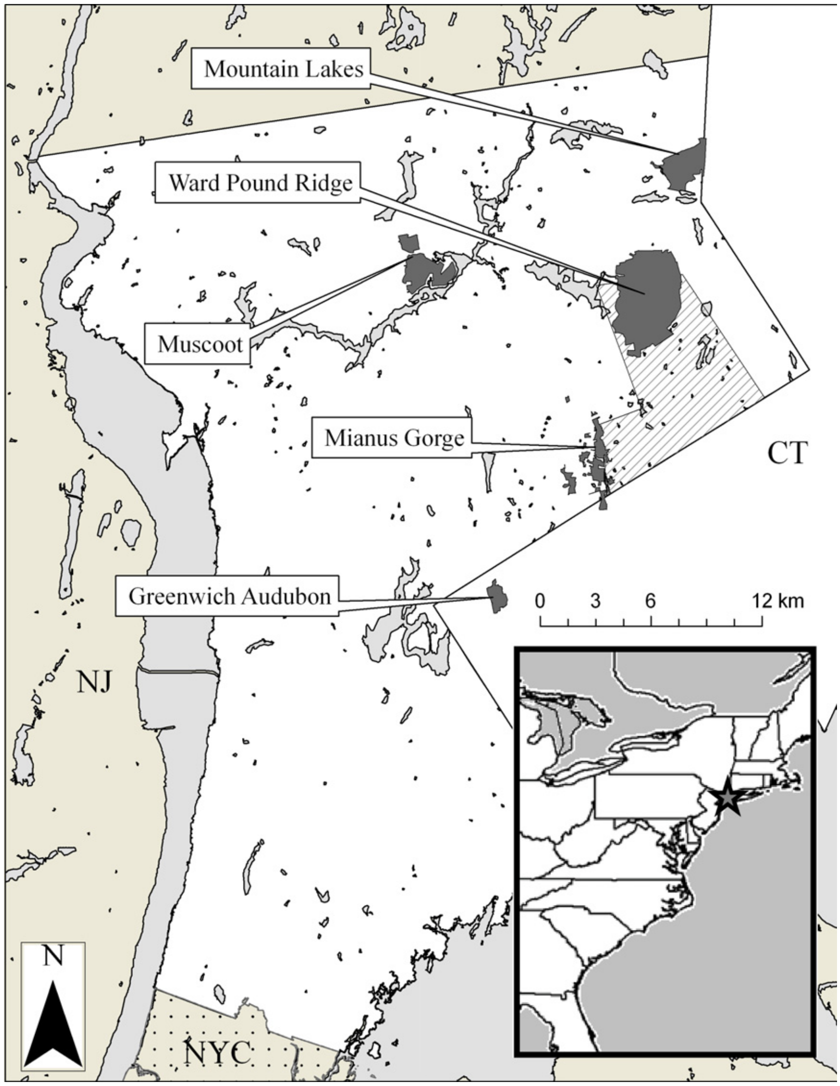

Fig. 1. Map of deer management programs used in current study, Westchester, NY and Fairfield County, CT.

bow-hunting in Westchester alone across several properties ranging in size from 20 to 2000 ha (Fig. 1).

These DMPs face two distinct challenges. First, as a consequence of their small size and relative independence, deer management areas are localized, raising the question as to whether sustained population reduction can be realized despite a contiguous population of unmanaged deer existing at or near carrying capacity at the landscape level. Localized herd reduction has been theorized for female white-tailed deer owing to their philopatric nature, and thus low dispersal rates (Porter et al., 1991; Mathews and Porter, 1993); however, evidence for successful small-scale management is conflicting (Oyer and Porter, 2004; Miller et al., 2010). Second, the management tool, 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 population monitoring immediately following a controlled bow hunt (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).

In this paper, we incorporate harvest data from the Mianus River Gorge Preserve (hereafter, Gorge Preserve) 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. To our knowledge, there have been no studies that attempt to model the impact of bow hunting on deer population dynamics. We explored the performance of bow hunting under different permutations of carrying capacities and immigration rates that reflect conditions observed in suburban deer, as well as other biologically plausible values. For each scenario, we investigated the magnitude of herd reduction, whether target densities could be met, and the time required to do so. For comparison, we use our deer model to simulate the use of sharpshooting, an alternative management technique by which professional marksmen remove or cull large numbers of deer from discrete areas using rifles (Doerr et al., 2001). We also explored how the catch-per-unit effort of bow hunters changes as a function of time or deer density (e.g. bow hunting functional response), information not available in the literature. We also present data on the catch-per-unit effort of a more traditional management option, recreational rifle hunting, to contrast its efficacy to bow hunting. Where deer management strategies are currently limited to bow hunting, simulating harvests and modeling the functional response of bow hunters can 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.

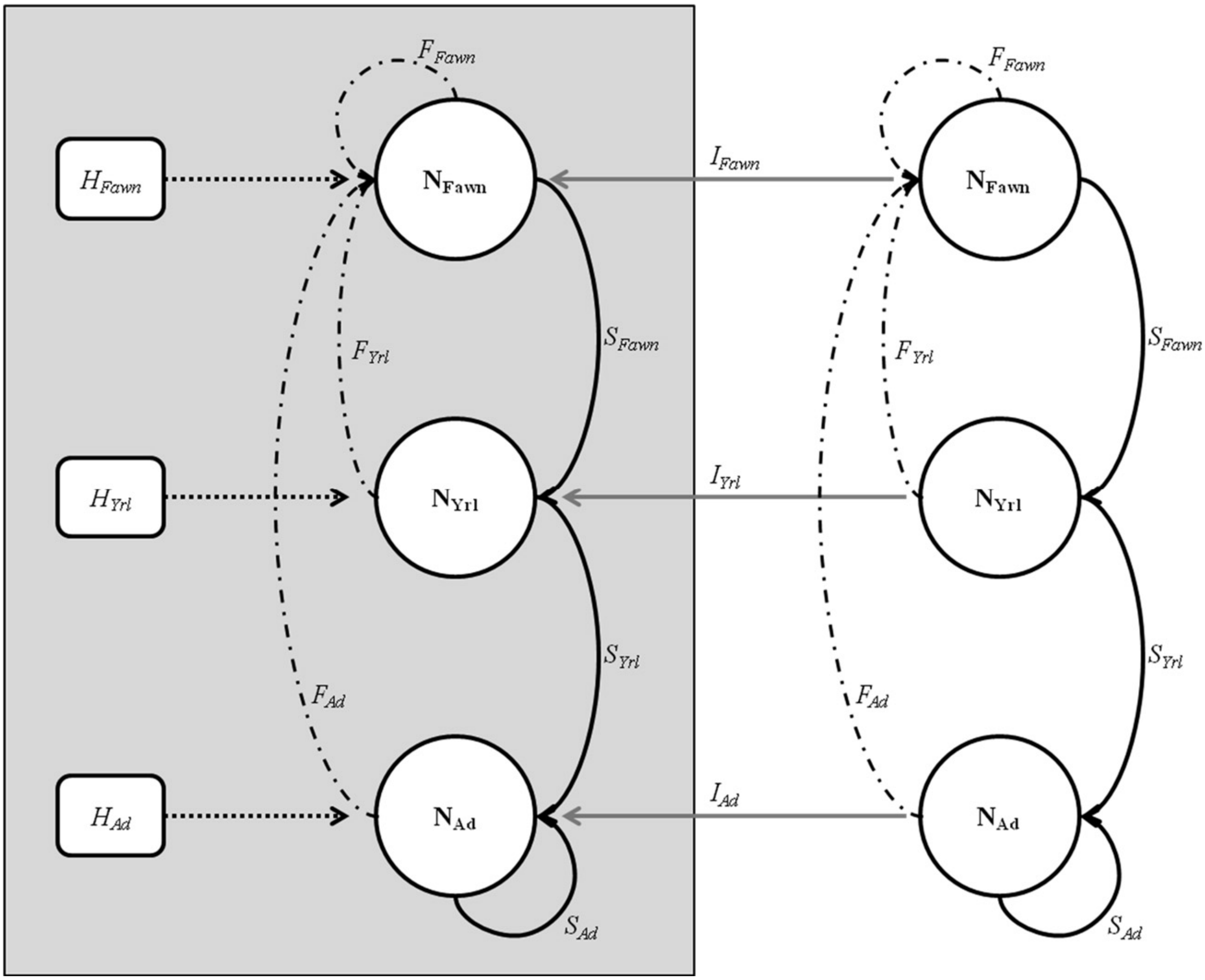

Fig. 2. Conceptual diagram describing deer model structure.

2. Site description

We used harvest data from the Gorge Preserve (308.8 ha) to parameterize simulations. The Gorge Preserve consists of an old-growth hemlock (*Tsuga canadensis*) forest and a 70–100 years old hardwood forest. The Gorge Preserve is surrounded by large estates, dense suburban development, and protected reservoir land. The pre-hunt deer density of the Gorge Preserve is unknown; however, deer density estimates from unmanaged, forested areas adjacent to the Gorge Preserve (<7 km) averaged 23.4 deer km^{-2} (SE = 0.76, n = 3; Brash et al., 2004; CTWF, 2008; Daniels et al., 2009). The Gorge Preserve DMP was started in 2004 and it includes both the preserve and adjacent residential properties. Since its inception, the amount of land accessible to hunters has grown from 2.3 to 4.1 km^2. This increase has been a contiguous extension of 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. We also present harvest data from DMPs managed by the Town of Pound Ridge (Westchester County, NY), Westchester County Parks (Westchester County, NY), and Greenwich Audubon (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.

3. Methods

3.1. Model description and simulation objectives

Our goal was to develop a model to evaluate the relative success of localized, bow-only DMPs in suburban ecosystems, with particular attention paid to natural areas reflecting the Gorge Preserve. As this is the first attempt to model the impact of bow hunting, we followed the principles of simplicity, accuracy, and management orientation as described by Xie et al. (1999). We constructed a deterministic, density dependent model to track the female portion of the population. Two populations are modeled, one hunted and one unhunted, the latter representing the overabundant regional deer herd (Fig. 2). Modeling fecundity and survival as density dependent reflects empirical data (Keyser et al., 2005); but more importantly provides for a more conservative test of bow hunting by increasing the intrinsic growth rate as the population declines. So that our model results may be interpreted beyond our system, we evaluate changes in deer density rather than abundance.

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 we acknowledge that the actual deer density required for advanced forest regeneration depends on local factors (Tilghman, 1989; Matonis et al., 2011). Using Tilghman's (1989) estimate as a benchmark and assuming a 1:1 sex ratio, we

Table 1
Parameter values for sex ratios, carrying capacity, and immigration rates levels used to model demographics of white-tailed deer managed by bow hunting.

Parameter[a]	Parameter set used in model					
	Scenario 1	Scenario 2[c]	Scenario 3	Scenario 4	Scenario 5	Scenario 6
Sex ratio of unmanaged herd (female:male)[1]	3:2	3:2	3:2	3:2	3:2	3:2
Carrying capacity (females 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 (females km^{-2})[b]	0.09	0.09	0.09	0.09	0.09	0.09
Yearling (females km^{-2})[b]	0.14	0.14	0.14	0.14	0.14	0.14

[a] Parameter values derived from following published sources as indicated by superscript: DeNicola and Williams (2008)[1], Daniels et al. (2009)[2], CTWF (2008)[3], Brash et al. (2004)[4], DeNicola and Williams (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 Gorge Preserve 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.

have chosen a female density of 2.9 km^{-2} as a the target density. The primary modeling objectives were to determine (1) under which scenarios and harvest intensities could that target be met and (2) how long the reduction would take. Where the target was not met, we explored the maximum reduction possible and time required to realize said reduction. Population models were constructed using MatLab® 13 (The MathWorks, Natick, MA).

3.2. Deer model structure

We simulated the potential impact of bow hunting on a hypothetical deer herd parameterized using published female deer vital rates. Population growth was modeled under six scenarios (Table 1) 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-year stage structure (fawn, yearlings, adult) characterized by deterministic, density dependent fertility and survival rates.

To parameterize a pre-breeding, Lefkovitch matrix, we modeled fecundity and survival as a function of carrying capacity using linear regression models described by Porter et al. (2004). Stage-specific fertilities in the projection matrix were the product of the computed stage-specific fecundities and fawn survival rate. Porter et al.'s (2004) original regression models were calculated as a function of abundance specific to their study area. We used Porter et al.'s (2004) estimate of carrying capacity to recalculate their original regression models as a function of K (Figs. 3 and 4). While previous white-tailed deer models (Lubow et al., 1996; Collier and Krementz, 2007) have relied on the survival functions of Bartmann et al. (1992) empirically derived from observations of mule deer (*Odocoileus hemionus*), Porter et al.'s (2004) models are derived from suburban white-tailed deer in upstate New York, and are thus considered more relevant to this these simulation exercises. However, we do report the survival functions of Bartmann et al. (1992) for comparison (Fig. 4).

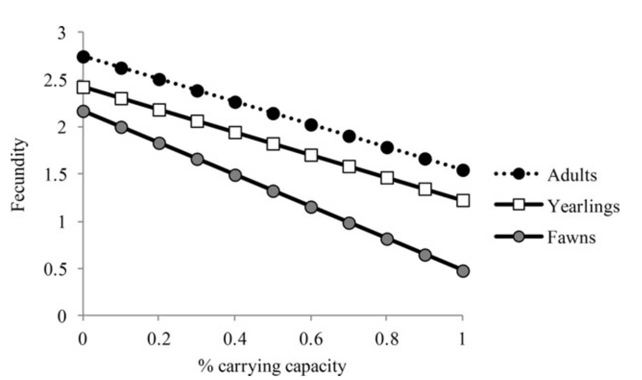

Fig. 3. Fecundity as a function of carrying capacity. Porter et al.'s (2004) regressions were used in the current analysis for modeling fawn ($y = -1.6902x + 2.1703$), yearling ($y = -1.1978x + 2.4249$), and adult ($y = -1.2004x + 2.7469$) birth rates as a function of density x.

Between 2000 and 2007, deer density estimates from unmanaged, forested areas adjacent to the Gorge Preserve (<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 Williams, 2008; Daniels et al., 2009) have been reported from other suburban areas in the NYC metropolitan area. We 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}). As harvest simulations were conducted only on female deer, we adjusted these numbers accordingly. DeNicola et al. (2008) consistently observed skewed female-to-male sex ratios in unmanaged, high density 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 we used to estimate low (K_{low} = 13.8 females km^{-2}) and high (K_{high} = 27.6 females km^{-2}) female carrying capacity.

We 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 groups, one hunted and one unhunted (the control) were projected. We parameterized the unhunted population to remain at carrying capacity so that its population did not decline through emmigration. The effect was to retain the regional, unhunted herd at carrying capacity. Furthermore, to make bow hunting simulations more conservative, 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, we used dispersal/emigration rates as an 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., 1991, 2004). To parameterize I_L, we used data from suburban herds describing these characteristics. Specifically, we 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. To parameterize I_H, we used estimates from agricultural areas of the Midwest where some of the highest rates of female fawn and yearling dispersal have been reported. We include these rates

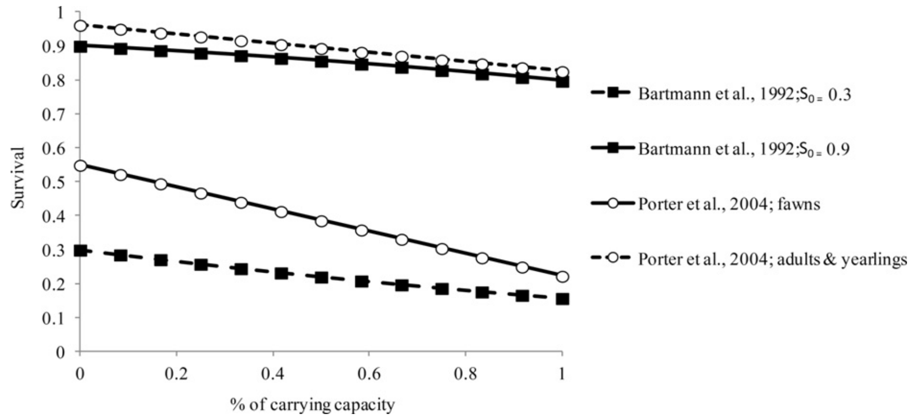

Fig. 4. Survival as a function of carrying capacity. Porter et al.'s (2004) regressions were used in the current analysis for modeling fawn ($y = -0.3267x + 0.5496$) and yearling/adult ($y = -0.1362x + 0.9614$) survival. Included for comparison are the survival curves of Bartmann et al., 1992 based on the model $S(t) = 1/(1 + e^{-(\alpha - 0.00691D(t))})$ where α = survival at 0 deer km^{-2}. For simplicity, we include two extreme values of α (0.3 and 0.9).

as extreme and unlikely, yet possible, immigration rates for suburban deer. We 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). For modeling purposes, we set $I_{HA} = I_{LA}$ assuming that that the majority of dispersal events can be attributed to fawns and yearlings (see Nixon et al., 2001).

3.3. Adding bow hunters

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 (male + female) harvest per hour $C(t)$ at time t, where t = age of the DMP (notation follows Van Etten et al., 1965).

Determining the number of deer harvested per unit area is based on how one estimates the size of the management area. Subtle changes in the size of the management area can lead to substantial changes in harvest intensity, and thus, population projections. Therefore we used three different estimates of the size of the management area to express adult, yearling, and fawn harvest per km^2. Our first estimate of the management area was a 100% minimum convex polygon of hunter tree stands (MCP). For our second, we made the assumption that deer harvested at the periphery of tree stands were likely to reside in some unknown area beyond the core reduction zone. We thus buffered the 100% MCP (MCP + buffer) based on the unweighted mean radius of several published winter home ranges for female suburban deer (Appendix A, Table 1). We used winter home ranges as they are generally larger than summer ranges. This generated a wider buffer and therefore a more conservative (e.g. lower) estimate of harvest intensity.

Lastly, we employed kernel density estimation (KDE) for a third estimate of the management area. Kernel density estimation has been widely used in wide variety of applications from animal habitat use studies (Wal and Rodgers, 2012) to mapping wildfire frequency (Kuter et al., 2011). To our knowledge, it has not been used to define management boundaries. However, KDE does offer a promising way to convert harvests (point locations) into a continuous surface, thus defining the management area by the 95% isopleth of relative intensity. Computing isopleths requires defining a reference smoothing parameter traditionally estimated by least squares cross-validation (Worton, 1989). As this approach is strongly biased (Park and Marron, 1990), and is frequently intractable (Rodgers and Kie, 2011) in the case of overlapping data points (e.g. multiple deer harvested at the same location), we used the ad hoc approach of Berger and Gese (2007). Here, the smoothing parameter is selected by first calculating the reference bandwidth $h_{ref} = n^{-1/6}\sqrt{(var_x + var_y)/2}$ (Worton, 1989), which, in the case of a univariate distribution of locations (e.g. a single cluster of harvests), would suffice as the smoothing parameter. Where data are not uniformly distributed, as in the present case, the value of the smoothing parameter is determined by iteratively reducing the value of h_{ref} and identifying the smallest value that generates a contiguous 95% isopleth.

In calculating the three management area estimates, harvest and stand locations from all years of the Gorge Preserve DMP were pooled; hence, the management area was fixed over time. We refer to the resulting harvests rates as MCP, MCP + buffer, or KDE according to the method used to estimate the management area. Analyses were conducting using ArcGIS 9.1 (ESRI, Redlands, CA, USA) and the Home Range Tools extension (Rodgers et al., 2007).

All simulations began with both the hunted and control populations at carrying capacity at their expected stable age distributions and we simulated harvests over a 50-year period. Harvests were deterministic and used the annual mean values observed for MCP, MCP + buffer, and KDE harvest rates, respectively. We investigated how the three different estimates of harvest intensity impact population projections. Lastly, we compared bow hunting to sharpshooting by simulating a one-time removal of female deer at three levels (100%, 90%, and 80% of the herd) under conditions of scenario 2, parameterized to be most representative of the Gorge Preserve deer herd with regards to carrying capacity (K_{low}) and immigration (I_L). Here we were interested in the time required for populations to recover following such dramatic reductions in the presence of low immigration pressure.

3.4. Exploring the functional response of bow hunters

To explore the relationship between deer density and harvest rates, we estimated the abundance of Gorge Preserve deer in the late summer of 2009 and 2010, immediately preceding years 6 and 7 of the DMP. We used camera-trapping and two analytical methods for estimating abundance from photographic data: the mark–resight Poisson log-normal estimator (McClintock et al., 2008), and the individual branch-antlered male method (Jacobson et al., 1997; Weckel et al., 2011). We used ear-tagged female deer for the McClintock et al. (2008) analysis, while we relied on distinctive antler patterns for the Jacobson et al.'s (1997) method. While McClintock et al.'s (2008) estimator is most robust, we used the results of both methods as future population monitoring will rely on the Jacobson et al.'s (1997) method, which is non-invasive and

Table 2
Deer harvest by sex and by age in the Mianus River Gorge Preserve bow-only deer management program, Westchester County, NY, 2004–2010.

Calendar year	Years hunted	# of hunters	Hours	Harvest				$C(t)$[a]	$C_F(t)$[b]
				Female adult	Female yearling	Female fawn	Male		
2004	1	5	464.8	32	1	1	8	0.09	0.07
2005	2	9	672.7	22	0	0	9	0.05	0.03
2006	3	10	439.2	18	3	0	12	0.08	0.05
2007	4	23	952.8	17	3	2	8	0.03	0.02
2008	5	16	919.8	13	3	0	8	0.03	0.02
2009	6	18	1139.3	25	1	5	3	0.03	0.03
2010	7	12	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

requires no marking period. We calculated the density of the Gorge Preserve herd by dividing the average of both estimators by the size of the camera array. See Appendix B for details regarding capture of deer (B.1), camera trap design (B.2), and abundance estimation (B.3).

Using estimates of post-hunt and pre-hunt deer density for the Gorge Preserve (see Section 2), we explored whether $C(t)$ and $C_F(t)$ of Gorge Preserve hunters 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 $C(t) = EN(t)$ (Holsworth, 1973). We 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 (Types 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 (Van Deelen and Etter, 2003), and may better approximate the behavior of hunters, we currently do not have sufficient data to model these non-linear relationships. Furthermore, we were most concerned with exploring catch-per-unit effort curves where prey density is low, a region of parameter space where Types 1 and 2 curves converge (Smout et al., 2010). We modeled the Type 1 relationship by forcing a structural y-intercept of zero (Van Deelen and Etter, 2003) assuming that hunter success can fall to zero only when deer have been locally extirpated. It is possible that success can fall to zero at positive values of deer density; however, we do not have enough data at this time to explore this hypothesis. After fitting a type 1 model, we predicted $C(t)$ and $C_F(t)$ over a range of densities from 0 to 23.4 deer km^{-2} (pre-hunt total deer density) and 0 to 13.8 females km^{-2} (pre-hunt female deer density), respectively. Predictions were then inverted to attain hours per deer harvest and hours per female harvest, which were then plotted as function of density.

4. Results

4.1. Harvest data

Two hundred and twenty eight deer were harvested in the Gorge Preserve DMP over a seven year period, 75% of which were female (Table 2). Mean female harvest per year for adults, yearlings, and fawns was 21.7 (SE = 2.4), 1.7 (SE = 0.5), and 1.1 (SE = 0.7), respectively. The estimated size of the management area was largest for the MCP + buffer method (12.1 km^2), followed by the KDE method (8.3 km^2), and the MCP method (6.6 km^2, see Fig. 5). Consequently, using the MCP + buffer generated the most conservative, or lowest, estimates of harvest per unit area (Table 3) and MCP the highest harvest rates.

Across several DMPs (Table 4), $C(t)$ ranged from a high of 0.09 deer/h (1st year of the MRPG DMP and GA DMP) to a low of 0.02 deer/h (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 [$C(t) = -0.0076t + 0.077$; $R^2 = 0.43$, $p = 0.005$).

4.2. The impact of bow hunting on deer population growth

At the highest estimate of female carrying capacity (K_{high}), simulated bow hunting was incapable of reaching the target density except in the case of a closed population, at MCP harvest levels, and only after 35 years of sustained harvest effort (Fig. 6b). Simulated bow hunting produced insignificant declines (Fig. 6d; K_{high}, I_L) under scenario 5 and even produced higher post-hunt densities in scenario 6 where immigration was high (Fig. 6f, K_{high}, I_H).

Where female carrying capacity was low (K_{low}), simulated bow hunting drove island populations (scenario 1) to extinction within twelve to thirty five years depending on harvest level (Fig. 6a). At the other extreme, where immigration was high (Fig. 6e), the highest harvest rates (MCP) produced a maximum population reduction of only 33%, 3 times the target level needed for forest regeneration. The efficacy of bow hunting was more ambiguous for scenario 2 (Fig. 6c), where the three estimates of harvest intensity had more variable outcomes. Here, MCP harvest rates drove the population below the target after only fifteen years of hunting, while MCP + buffer rates never produce the target density. Regarding the latter, the population reached a new equilibrium of approximately 11 females km^{-2} early in the second decade of management. The more moderate harvest rates (KDE), drove the population close to the target density, yet required twice as long as MCP rates to get there. For scenario 2, where we simulated a one-time removal of female deer where 100%, 90%, and 80% of the herd, the culled population had reached 50% of K (Fig. 7) across all 3 cull levels within four years.

4.3. The functional response of bow hunters

We used two analyses (McClintock et al., 2008; Jacobson et al., 1997) to estimate deer abundance from camera data resulting in two estimates each for male, female, fawn, and total deer abundance (Table 5; see Appendix C for a complete description of camera trap results). The size of the camera trap area declined in 2010 owing to fewer available cameras so direct comparison of abundance is not advised. We used the mean radius (0.38 km) of seven

Table 3
Estimated size of management area and deer harvest per square kilometer by sex in the Mianus River Gorge Preserve bow-only deer management program, Westchester County, NY, 2004–2010.

Method	Area (km^2)	Harvest		
		Female adult	Female yearling	Female fawn
MCP + buffer	12.1	1.8	0.1	0.1
KDE	8.3	2.6	0.2	0.1
MCP	6.6	3.3	0.3	0.2

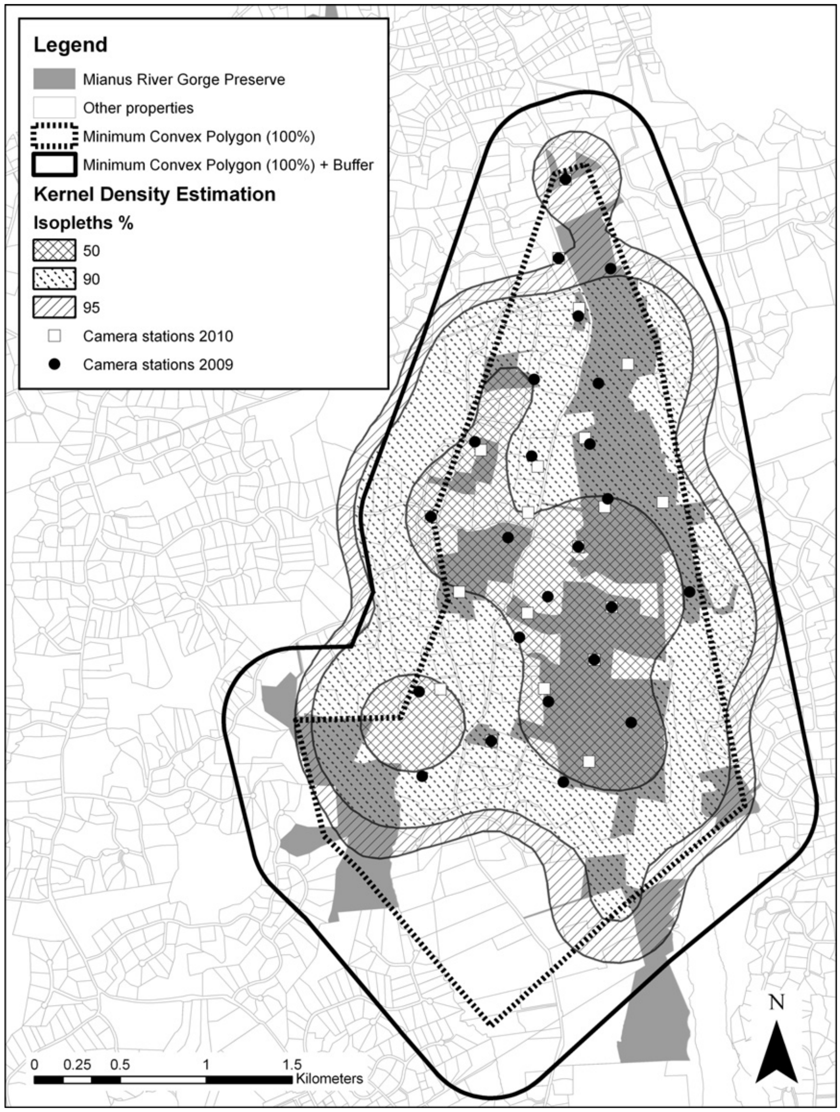

Fig. 5. Map of Mianus River Gorge Preserve, Westchester, NY describing location of cameras stations in 2009 and 2010, and three estimates of the deer management area: minimum convex polygon (MCP), minimum convex polygon + buffer (MCP + buffer), and kernel density estimation (KDE). For MCP + buffer, the buffer was calculated using the mean radius (0.42 km) of seven published female white-tailed deer winter home ranges (Appendix A, Table 2). For KDE, the smoothing parameter = 270.2($h_{ref}\times 0.9$).

published female deer summer home ranges (Appendix A, Table 2) 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 McClintock et al. (2008) and Jacobson et al. (1997) estimates by year, we calculated 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, we estimated total female density (adults, yearlings, fawns) in 2009 and 2010 to be 10.42 km^{-2} and 9.49 km^{-2},

Table 4
Deer per hour $C(t)$[a] and size of management area (km^2)[b] for bow-only deer management programs in the NYC metropolitan area, 2003–2010.

	Greenwich Audubon		Gorge preserve		Town of pound ridge		Lasdon[c]		Muscoot[c]		Ward pound ridge[c]		Mountain lake[c]	
Years	2003–2009		2004–2010		2006–2009		2009–2010		2009–2010		2010		2010	
Program age	$C(t)$	km^2	$C(t)$	km^2	$C(t)$	km^2	$C(t)$	km^2	$C(t)$	km^2	$C(t)$	km^2	$C(t)$	km^2
1	0.09	1.2	0.09	2.3	0.07	1.0	0.02	0.95	0.03	2.5	0.05	13.3	0.02	2.3
2	0.07	1.7	0.05	2.7	0.03	1.4	0.02	0.95	0.02	2.5				
3	0.06	1.7	0.08	2.9	0.03	4.9								
4	0.05	2.2	0.03	3.4	0.03	6.2								
5	0.05	2.2	0.03	4.0										
6	0.05	2.4	0.03	4.1										
7	0.03	2.4	0.04	4.1										

[a] $C(t)$ = total deer harvest per hour at time t, where t = age of DMP.
[b] Management area – the size of the Gorge management area was computed from the polygon of hunters tree stands (see Section 3). All other areas were computed from the total acreage of properties included in the respective DMPs.
[c] Managed by the Westchester County Parks Department.

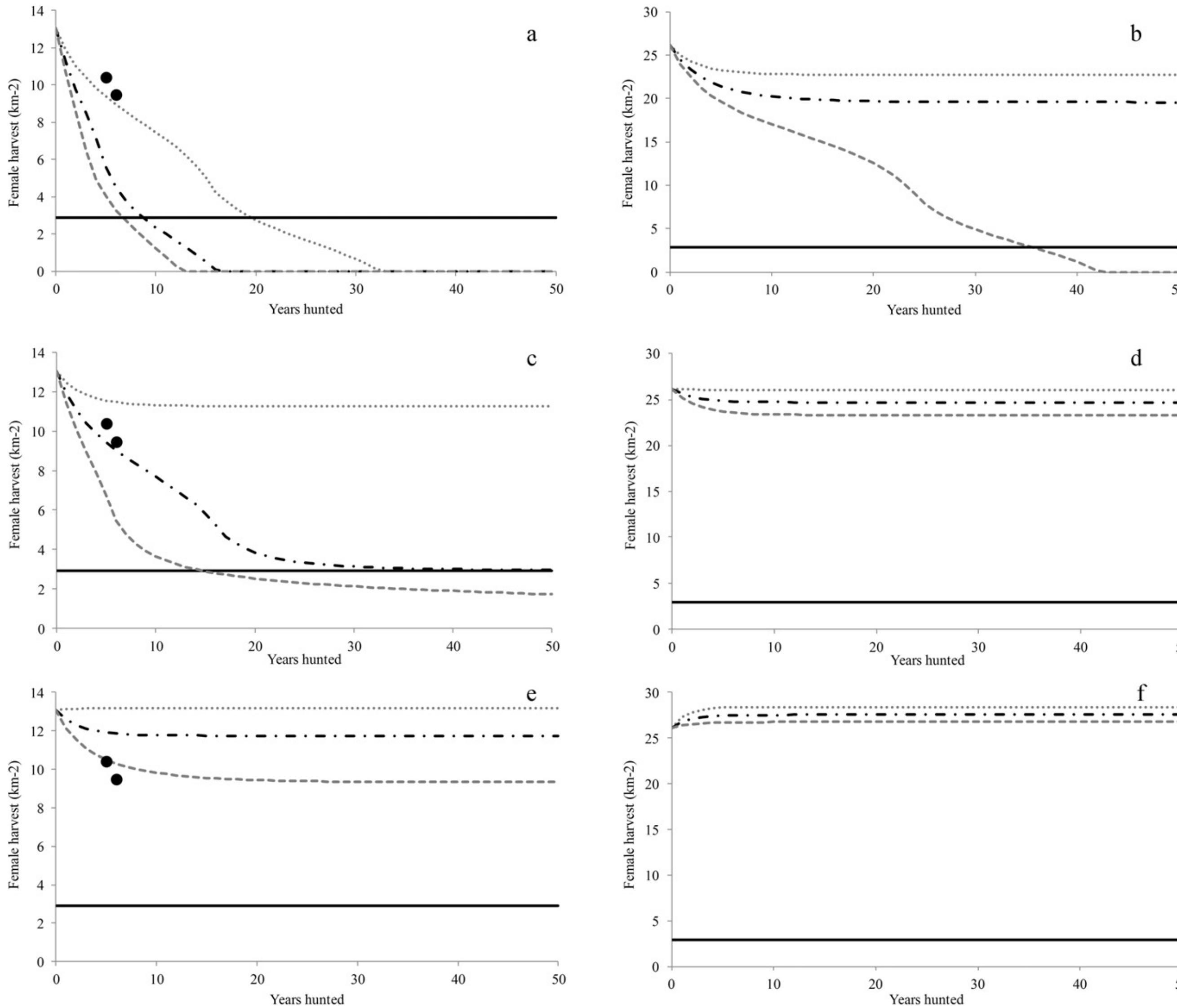

Fig. 6. Female density as a function of time hunted assuming female carrying capacity (K) is 13.8 km^{-2} for a closed population (a), where immigration is low (c), and high (e) and assuming female carrying capacity (K) is 27.6 km^{-2} for a closed population (b), where immigration is low (d), and high (f). For each scenario, three estimates of harvest rate are simulated: minimum convex polygon + buffer (MCP + buffer ●), kernel density estimation (KDE -●-), and minimum convex polygon (MCP –). Target female density of 2.89 km^{-2} is demarcated by a vertical solid line. Empirical estimates of Gorge Preserve deer herd are presented by black circles.

Table 5
Male, female, and fawn abundance at the Mianus River Gorge Preserve, Westchester County, New York, USA, 2009 and 2010.

Sex–age group	Method	2009		2010	
		Mean	95% PI	Mean	95% PI
Male	Jacobson et al. (1997)[a]	32	27–36	43	36–57
	McClintock et al. (2008)[b]	26	21–33	43	25–61
Females (adult and yearlings)	Jacobson et al. (1997)[a]	60	45–77	43	28–76
	McClintock et al. (2008)[b]	50	39–63	43	30–60
Fawns	Jacobson et al. (1997)[a]	42	28–62	36	19–65
	McClintock et al. (2008)[b]	35	25–46	33	26–44
All females (adults, yearlings, fawns[c])	Jacobson et al. (1997)[a]	81	NA	60	NA
	McClintock et al. (2008)[b]	67	NA	59	NA
Total deer	Jacobson et al. (1997)[a]	135	111–162	124	95–168
	McClintock et al. (2008)[b]	111	99–124	111	91–133

[a] Abundance method using demographic ratios calculated from standardized photographic occurrences to extrapolate from a min. no. of branch-antlered males enumerated by Jacobson et al.'s (1997) criteria.
[b] Abundance method using demographic ratios calculated standardized photographic occurrences to extrapolate from the mean female estimate generated by McClintock et al.'s (2008) mark–resight Poisson log normal estimator.
[c] Female:male sex ratio of fawns is assumed 1:1.

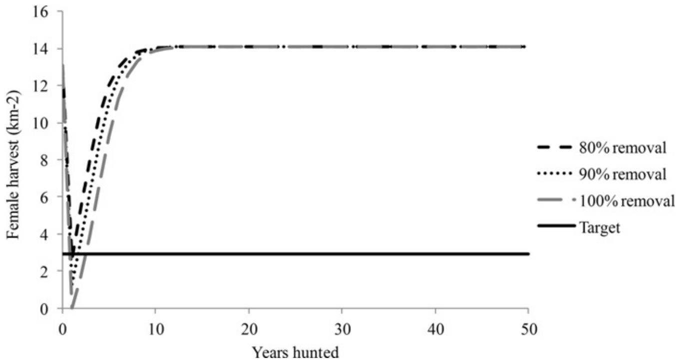

Fig. 7. Female density before and after simulating a onetime cull of deer (time = 0) at three removal levels (100%, 90%, and 80% of all females removed). Population is parameterized according to scenario 2 (see Table 1).

respectively. These density estimates were used to explore the functional response of Gorge Preserve bow hunters.

Using an estimate of pre-hunt total deer density (see Section 2) and two estimates of post-hunt density (2009 and 2010), we 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 harvested, plotted as a function of female density showed accelerating effort as densities approached the target female density (Fig. 8) and target total deer density (Fig. 9). At the target female density, bow hunters would have to exert over 80 h per female harvest compared to approximately 18 h where female density = 13.8 km^{-2}.

5. 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 benchmark 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, MCP harvest rates sustained over 35 years were necessary. Under scenario 1, MCP + buffer rates are sufficient, yet still would require a two decade commitment. Simulated bow hunting was completely unsuccessful in reaching the target density at high rates of immigration regardless of carrying capacity.

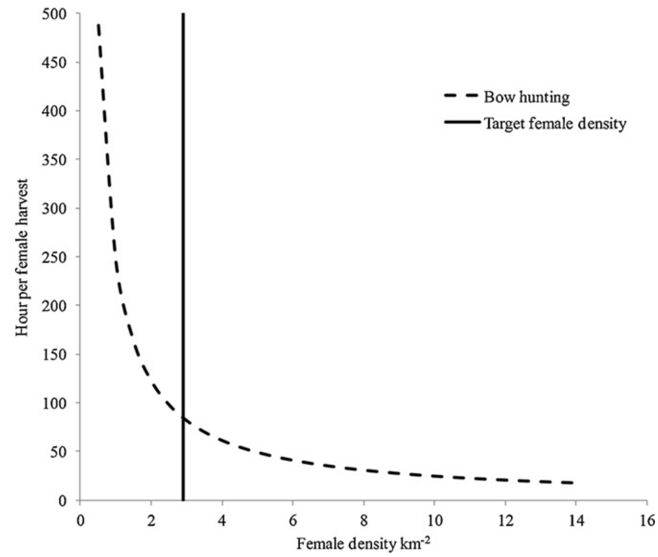

Fig. 9. Hour per deer harvest as a function of total deer density (km^{-2}). Target density = 5.8 km^{-2}. Functional response of bow hunters is derived from harvest data and population estimates from the Mianus River Gorge Preserve Deer Management Program, Westchester County, NY, 2004–2010. Function response of rifle hunters is recreated from Holsworth (1973) and Van Etten et al. (1965).

Evaluating the relative impact of bow hunting becomes further complicated for the more probable scenario 2, an open herd with low rates of immigration and at a lower "overabundant" carrying capacity. Under scenario 2, simulations suggested a broad range of theoretical herd reductions (20–70%) contingent on how harvest levels were parameterized. For the most conservative harvest rates (MCP + buffer), deer densities were reduced to 11 females km^{-2} by the second decade of management, only a 21% reduction, whereas MCP rates reached the target density within ten years.

A recent study of 4 suburban controlled hunts suggests 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 Gorge Preserve herd following several years of management. However, the trajectories of scenario 2 simulations, driven by different harvest intensities, do not widely diverge until the second decade of bow hunting. This makes our population monitoring, currently at year 7, inconclusive in understanding the ultimate trajectory of the Gorge herd and in evaluating whether a floor on population reduction has been reached. Ultimately, evaluating bow-only DMPs may require 10+ years of population data

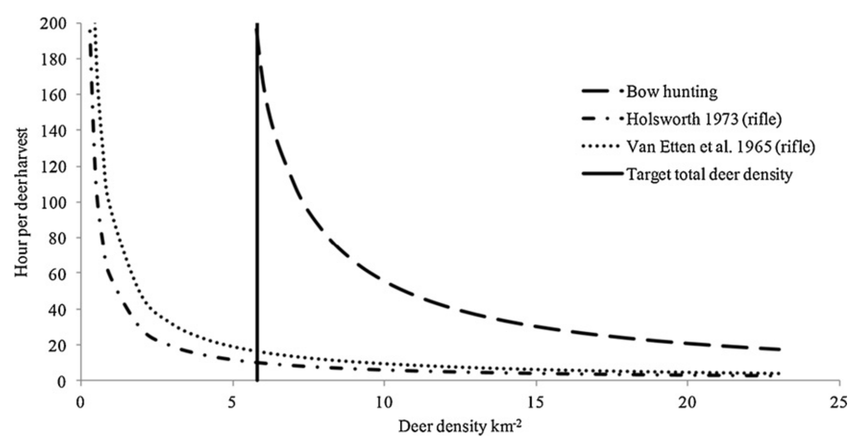

Fig. 8. Hour per female harvest as a function of female density (km^{-2}). Target female density = 2.9 km^{-2}. Functional response of bow hunters is derived from female harvest data and population estimates from the Mianus River Gorge Preserve Deer Management Program, Westchester County, NY, 2004–2010.

before trends can become clear – both in the case of success and failure. Bow hunting did produce a more dramatic (∼50%) and a more (≤3 years) rapid decline in the suburban community of Groton Long Point, CT (Kilpatrick and Walter, 1999). Quantifying 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. But it should also be noted that the Kilpatrick and Walter (1999) study was conducted on a peninsula and immigration rates may more closely approximate a closed population where our simulations suggest that rapid population reductions are possible using bow hunting.

Nevertheless, the relative inefficiency of bow hunting makes sustaining large population reductions under any scenario improbable. With regards to all deer, the efficiency (E) of Gorge Preserve 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 Gorge Preserve bow hunter would have to invest over 180 h per deer as compared to only 15 h for the rifle hunter (Fig. 8). Even for the modest herd reduction documented at the Gorge Preserve, hunters were faced with an average of 23 h per deer to maintain the status quo as compared 11 h per deer for the first year of the DMP (Table 4).

As our empirical data on Gorge Preserve bow hunters is drawn from a deer population believed to characterized by a lower carrying capacity, we explored bow hunter catch-per-unit effort where deer density ranged from 0 to 23.4 km^{-2} using a Type 1 function. However, where deer density is even greater (e.g., K_{high}), it is unlikely that bow hunters can continue to increase harvests linearly; rather, harvests rates may asymptote as predicted by a Type 2 response. The result would be to further limit the usefulness of bow hunting at the highest observed deer densities. As more empirical data is collected, future efforts need to consider the reality of a Type 2 functional response.

To sustain total harvests, hunters will have to either increase hunter efficiency or total hunter-hours must increase. Regarding the latter, managers may consider adding more hunters or requiring more effort from individual hunters, each solution having its own limitations. At some point, too many hunters may serve to educate deer to predation risk (Williams et al., 2008) or may result in greater interference among hunters (Schmidt et al., 2005) both of which may unintentionally erode harvests. On the other hand, asking more effort of volunteer sportsman is limited by how much time hunters will choose to or be able to contribute in the face of diminishing returns on their efforts (Van Deelen and Etter, 2003).

Currently, bow hunter efficiency, as measured by harvests per hour, is declining across all DMPs. However, reversing or dampening this trend may be possible through changes in DMP rules. The DMPs included in this study have been experimenting with a variety of rules that aim to maintain and increase annual harvest. These include antler restrictions, earn-a-buck incentives, minimum female harvests, and minimum time commitments. Differences in DMP rules may explain differences in the productivity of different DMPs and further research is required to determine which rules are advantageous. However, the success of individual hunters is influenced by a range of variables including the hunter attributes (e.g. motivations), as well as features of the landscape they hunt (Harden et al., 2005; Schmidt et al., 2005). In this study, the fragmented nature of suburbia itself may be a driver of the observed functional response of hunters and may contribute to the observed floor on population reduction. Suburban management areas will always include properties that cannot be hunted (refugia) due to mandated set-backs from residential dwellings (Kilpatrick et al., 2011) or due to landowner opposition to deer management. A shift in deer activity toward these refugia will limit hunter success regardless of the creative solutions adopted to increase harvests (S. Williams, Connecticut Agricultural Experimental Station, unpublished data). Similar patterns can also occur in years with poor acorn mast as deer increase the time spent foraging on residential lawns and shift their activity away from forested areas where hunters are often concentrated (*pers. obs.*).

Some will interpret bow hunting's 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 a 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), there is no uniform rule for tree regeneration applicable to all species. Relatively unpalatable species such as black birch and American beech will begin to recover at higher deer densities (Long et al., 2007). At the Gorge Preserve, the abundance of American beech (*Fagus grandifolia*) saplings increased by 142% following 7 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.

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 inherently more efficient than hunting as professional marksmen are often aided by the use of baiting and permission to remove deer at night (DeNicola and Williams, 2008). Yet our modeling suggested that under the realistic scenario 2, sharpshooting can face problems similar to bow hunting with regard to sustainability. Within 4 years, the culled population had reached 50% of K (Fig. 7) across all three removal levels. Confirming our simple modeling exercise, Miller et al. (2010) executed 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. Their study herd was characterized by high philopatry and exhibited low rates of dispersal (Miller, 2008), and thus, was an ideal candidate for localized management (Campbell et al., 2004). Within three years, the local population had increased such that an additional 31 deer (52% of the original cull) were removed from the same area. Results from genetic analyses suggested that these deer were likely immigrants or adjacent deer that shifted their home range toward the reduction area. This rapid repopulation suggests that low per-capita dispersal is insufficient justification for localized management where deer density is high: regional overabundance can provide many opportunities for immigration events even if the probability of any one female deer dispersing is low. While sharpshooting is very successful in producing rapid population reductions, sustaining said reductions will require repeated management efforts possibly as frequently as every few years. Furthermore, keeping deer densities at target levels will require continue reliance on professional sharpshooters (Van Deelen and Etter, 2003), as we have shown bow hunters to be inefficient at low deer densities.

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) 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). 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 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, but may not be able to reduce deer population abundance to desired or historical levels.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.10.018.

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