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Original Article

Survival and Harvest-Related Mortality of White-Tailed Deer in Massachusetts

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ABSTRACT We monitored 142 radiocollared adult (≥1.0 yr old) white-tailed deer (*Odocoileus virginianus*) in 3 study areas of Massachusetts, USA, to estimate annual survival and mortality due to legal hunting. We then applied these rates to deer harvest information to estimate deer population trends over time, and compared these to trends derived solely from harvest data estimates. Estimated adult female survival rates were similar (0.82–0.86), and uniformly high, across 3 management zones in Massachusetts that differed in landscape composition, human density, and harvest regulations. Legal hunting accounted for 16–29% of all adult female mortality. Estimated adult male survival rates varied from 0.55 to 0.79, and legal hunting accounted for 40–75% of all mortality. Use of composite hunting mortality rates produced realistic estimates for adult deer populations in 2 zones, but not for the third, where estimation was hindered by regulatory restrictions on antlerless deer harvest. In addition, the population estimates we calculated were generally higher than those derived from population reconstruction, likely due to relatively low harvest pressure. Legal harvest may not be the dominant form of deer mortality in developed landscapes; thus, estimates of populations or trends that rely solely on harvest data will likely be underestimates.

KEY WORDS hunting, management, Massachusetts, mortality, *Odocoileus virginianus*, population, white-tailed deer.

In the Northeast United States, state fish and wildlife agencies often rely on data derived from the legal harvest to estimate trends in white-tailed deer (*Odocoileus virginianus*) populations, at both regional (e.g., wildlife management unit [WMU] or deer management zone [DMZ]) and statewide scales (Williamson 2003, Rosenberry et al. 2004). For each DMZ, agencies commonly collect information on the number and age of deer killed by sex; they may also collect physical information such as body mass, antler beam diameter (in mm) for males, and lactation status of females from a sample of the legal harvest. Age is usually estimated by tooth wear and replacement (Severinghaus 1949) or, less commonly, cementum annuli counts, and deer classified into 0.5-yr-old, 1.5-yr-old, and ≥2.5-yr-old age classes (though some jurisdictions may add older age classes before pooling ad). Hunters are usually required to report each deer killed and the DMZ in which it was taken, either in person at a checking station, via a report card, over the telephone, or through the Internet. Agencies also conduct mail or e-mail surveys of licensed hunters, either post-hunting-season or with in-season diaries, to estimate hunter effort and cross-check the reported harvest.

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Deer harvest data have been analyzed using a variety of techniques (Roseberry and Woolf 1991). Historically, many states in the Northeast did not estimate populations directly but used harvest-to-index trends (Williamson 2003). Other jurisdictions have employed some form of sex–age–kill (SAK) estimator (Creed et al. 1984, Williamson 2003, Millspaugh et al. 2009) or population reconstruction (Downing 1980, Davis et al. 2007), among other techniques (Roseberry and Woolf 1991). The buck kill index (BKI) has been a common trend estimator in the Northeast for decades (Williamson 2003) and is simply the number of adult males killed per area (e.g., square mile of habitat), often restricted to forested habitat. Use of the BKI to monitor population trends assumes that hunter effort is relatively constant (or known), hunters have access to most of the area under consideration, and hunters kill male deer as encountered. In practice, these assumptions are likely violated and result in misleading trend information.

Techniques have been developed that combine age-at-harvest data with information on hunter effort or telemetry-derived estimates of survival to refine population reconstruction estimates (Gove et al. 2002, Skalski et al. 2007), though these are not commonly used in the Northeast. To produce actual estimates of the deer population, these estimators would have to satisfy several assumptions: 1) all deer killed are reported; 2) deer are killed at random within each sex; and 3) hunter access to deer is uniform. In practice, these assumptions are never met; thus, the estimates that are produced are best considered as indices to the actual population. However, like the BKI, even as indices these estimates are flawed because the nature and severity of the assumption violations are rarely known and likely vary among years and DMZs. This is especially true in suburban and urban areas where local restrictions on hunting and firearm or arrow discharge create refugia for deer. Conversely, regulations may be structured to increase antlerless (F and young) harvests and restrict male harvests in areas of high deer density (Van Deelen et al. 2010) and hunter or landowner preferences may dictate that males are not harvested at random. Thus, population estimators that rely on age-at-harvest data are likely to be biased (Millspaugh et al. 2009), and this bias may be high or low compared to the true population.

The legal harvest of deer, however, comprises a large proportion of the total annual mortality, even in developed areas, and agencies typically have a legal mandate to collect information on the number of deer taken by hunters. Thus, it is logical to try to use this harvest information to feed the management process, despite the flaws of harvest-based estimators. An estimator that has few assumptions to satisfy or is robust to violation of any inherent assumptions would be useful to deer managers. A simple estimator can be derived using a representative sample of radiomarked deer; managers can estimate the percentage of total annual mortality that is due to legal hunting and simply divide the legal harvest by that rate to estimate the preharvest population. This technique requires adequate sample sizes of radiomarked deer and accurate information on the total legal harvest at a scale appropriate to the distribution of those deer. It does not necessarily require age-at-harvest information and the method and results are easily interpreted by managers and the public. This approach does assume that hunting mortality is constant from year to year in the geographic area to which it is applied if annual estimates are not generated.

The Massachusetts Division of Fisheries and Wildlife (MDFW) instituted mandatory registration for legally harvested deer in 1966. Since that time, each deer killed by hunters has been physically taken to a deer-check station; information on sex, age, and location of kill is recorded; and each deer is tagged with a numbered metal seal. Various techniques have been used to develop population or trend estimates with the resulting data. However, in the 1990s, as deer abundance increased in suburban eastern Massachusetts, USA, hunter numbers decreased statewide, and the distribution of hunter effort shifted from rural western DMZs to the east, confidence in the results of those models declined as assumption violations mounted. Because of these assumption violations, deer managers desired to supplement the check-station data to address issues such as poor hunter access and nonrandom harvest. Mayer et al. (2002) used an aerial mark–resight population estimation effort in southeastern Massachusetts that did not use harvest data and resulted in population estimates that were 2–3$\times \geq$ harvest-based estimates. However, given agency funding constraints and the difficulty of sighting deer in heavily forested parts of the state, this method was not viable at larger scales. The MDFW then decided to use telemetry-derived estimates of survival and mortality in a number of DMZs across the state to supplement harvest data and produce useful population estimates.

Thus, our objectives were to 1) estimate annual and seasonal survival of male and female white-tailed deer $>$1-yr old; 2) estimate the percentage of total annual mortality of these deer that was due to legal hunting; and 3) compare these estimates among areas within Massachusetts that have different deer management strategies.

STUDY AREAS

Myles Standish Study Area

The 60-km^2 Myles Standish Study Area (MSSA) included most of Myles Standish State Forest in the Plymouth County towns of Carver and Plymouth and was in the 676-km^2 DMZ 12 (Fig. 1). The topography varied from plains to hilly moraines of excessively drained sandy soils with elevations from 12 m to 65 m. The area contained multiple ponds of varying size and was surrounded by a matrix of cranberry (*Vaccinium macrocarpon*) bogs and residential areas. Mean annual precipitation was 123 cm and mean snowfall was 90 cm; however, snowfall in this region usually melted quickly.

The most abundant overstory tree species were pitch pine (*Pinus rigida*) and white pine (*P. strobus*). Scrub oak (*Quercus ilicifolia*), red pine (*P. resinosa*), other mixed oaks (*Quercus* spp.), Scots pine (*P. sylvestris*), heath, open areas, and mowed fields in and around a wildlife management area also were present (Massachusetts Department of Environmental Management 2001). The Forest was open to hunting and fishing, and had camping in the summer months. The Forest had a paved road system (0.74 km/km^2) and dirt roads, horse trails, and bike and footpaths (1.9 km/km^2); however, vehicles were prohibited from unpaved roads. Human density in Plymouth County was 276/km^2; potential predators of deer (other than humans) included coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and domestic dogs.

Eastern Study Area

The 3,700-km^2 Eastern Study Area (ESA) was centered on the town of Carlisle in Middlesex County in northeastern Massachusetts (Fig. 1) and was in DMZ 10. Topography was mostly flat but with remnant glacial moraines, meandering rivers, and scattered wetlands, with elevations ranging from 0 m to 560 m. Mean annual precipitation was 114 cm with a mean snowfall of 116 cm, but this was highly variable year to year and snow often melted quickly.

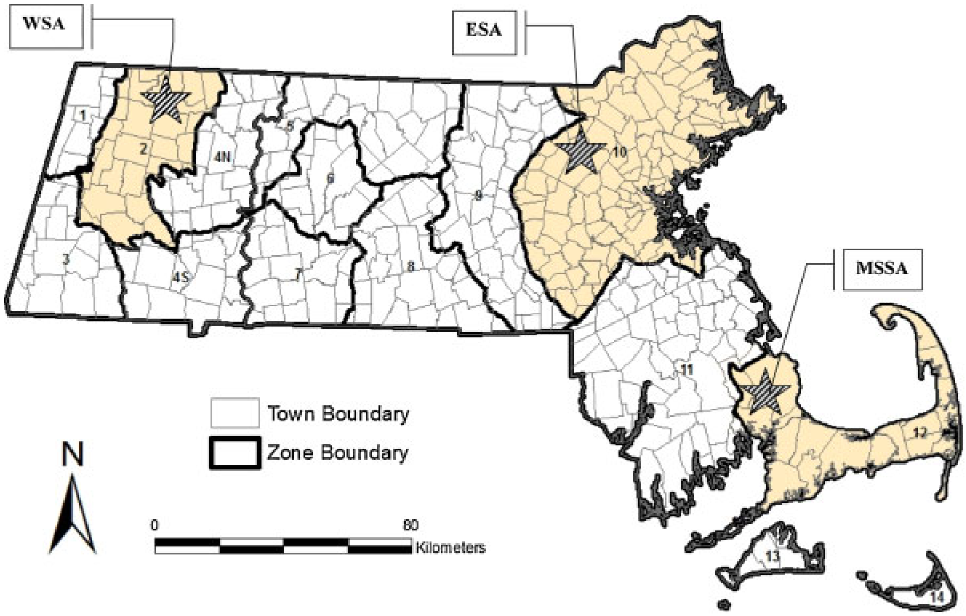

Figure 1. Deer management zones (DMZs) and study areas (WSA, Western Study Area; ESA, Eastern Study Area; MSSA, Myles Standish Study Area), Massachusetts, USA.

Forest cover in the ESA consisted primarily of the central hardwoods-hemlock (*Tsuga canadensis*)-white pine forest region, but also contained transitional hardwood and white pine forests. The central hardwoods region was predominantly composed of red oak (*Q. rubra*), black oak (*Q. velutina*), and white oak (*Q. alba*), hickories (*Carya* spp.), gray birch (*Betula populifolia*), yellow birch (*B. alleghaniensis*), black birch (*B. lenta*), and beech (*Fagus grandifolia*). Major conifers were white pine and eastern hemlock. On wetter sites red maple (*Acer rubrum*) dominated the canopy. Pitch and red pines were found on sandy glacial outwashes. Forested areas were often highly fragmented by suburban homes with landscaped yards, shopping centers, cities and towns and, to a lesser extent, public parks, farmland, orchards, and pasture. Highways consisted of multilane interstates with median barriers as well as 2-lane roads. The mean road density was generally medium (3–5 km/km^2) to very high (up to 70 km/km^2) on a gradient west to east. Human density in Middlesex County was 6,871/km^2; potential predators of deer (other than humans) included coyotes, bobcats, and domestic dogs.

Western Study Area

The 1,500-km^2 Western Study Area (WSA; DMZ 2; Fig. 1) was in northern Berkshire County and western Franklin County in western Massachusetts and was generally hilly terrain with elevations from 120 m to 750 m. Mean annual precipitation was 109 cm, with 180-cm average snowfall.

Forest cover in the WSA consisted predominantly of northern hardwoods-spruce and northern hardwoods forest regions at higher elevations, and transitional hardwoods-white pine forest region at lower elevations. Major northern hardwoods species included beech, sugar maple (*Acer saccharum*), and yellow birch. Paper birch (*B. papyrifera*), quaking aspen (*Populus tremuloides*), and big tooth aspen (*P. grandidentata*) were early successional species in this region. Major species of the transitional hardwoods were yellow birch, paper birch, beech, sugar maple, red maple, and white pine. Warmer, drier sites were dominated by oaks and hickories, cooler well-drained sites included hemlock, and poorly drained sites often contained red maple, black ash (*Fraxinus nigra*), and American elm (*Ulmus americana*). The WSA was comprised of small towns and large tracts of forested lands in both private and public ownership intermixed with some urban and suburban areas. Farmland, orchard, pasture, and valley cities and towns with shopping centers, landscaped yards, and public parks fragmented the forested areas. Major highways were all 2-lane roads without median strip barriers and the mean road density was low ($\leq$3 km/km^2). Human density in Berkshire County was 56/km^2; potential predators of deer, other than humans, included coyotes, black bears (*Ursus americanus*), bobcats, and domestic dogs.

Hunting and Deer Management

Massachusetts had 3 nonoverlapping deer-hunting seasons: archery (3–6 weeks in late Oct and Nov); shotgun (6 days in the MSSA and 12 days in the ESA and WSA beginning the Monday after Thanksgiving in all areas); and muzzleloader (3–19 days immediately following the end of the 12-day shotgun season). The yearly bag limit was either 2 antlered deer or combinations of $\leq$2 antlered deer and various numbers of antlerless deer taken by permit. Antlerless deer permits were allocated by DMZ and awarded through a lottery when the number of applicants was greater than the allocation; there was no application fee, but permits cost US$5.00 and there was no preference for state residents. Hunting was not allowed on Sundays. In some years archers and muzzleloader hunters could harvest one antlerless deer without a permit (except as noted below for the WSA); in all years and in all DMZs, shotgun hunters were restricted to antlered deer unless the hunter had an antlerless deer permit. Beginning with the 2002 hunting seasons, a permit was required to take antlerless deer in each season and DMZ.

Different management schemes were being applied to the deer populations in each study area because the population goals varied among DMZs. In the WSA, the MDFW's goal was to increase deer densities, and female harvest was, thus, restricted by limiting the number of antlerless permits allocated each year prior to and during this study (Table 1); the odds of an applicant drawing a permit in this DMZ were around 10%. Beginning in 1996, to reduce female harvest, hunters in DMZ 2 were required to have an antlerless deer permit to take antlerless deer during the muzzleloader season; prior to 1996, any hunter with a valid license could take deer of either sex in that DMZ. In the MSSA, the goal was to maintain the deer population around the starting density. Thus, the number of antlerless permits allocated for DMZ 12 was essentially stable during this study; the odds of an applicant drawing a permit in this DMZ were about 100% each year. In the ESA, the management goal was to reduce the deer population in this mostly suburban and urban area. Thus, the number of permits allocated for DMZ 10 increased each year of this study and always exceeded the initial number of applicants, the archery season was increased from 18 days to 36 days beginning with the 1999 season, and hunters were permitted to buy multiple antlerless deer permits for DMZ 10 beginning in 1998.

METHODS

Capture and Marking

We captured deer in the MSSA during January 1997 and 1998 via helicopter and net-gun (Helicopter Wildlife Management, Salt Lake City, UT) and without drugs (Mayer et al. 2002). During winter and early spring of 1998–2001 in both the ESA and WSA, we baited deer (with apples and corn) in forest openings or the edges of private yards, and darted them after sunset from tree stands (Gaughan and DeStefano 2005). Darts containing a 3-cm^3 mixture of telazol, xylazine, and sterile water were administered using cartridge-powered dart rifles (model 171; Pneu-Dart, Inc., Williamsport, PA). Standard dosages were prepared and realized doses ranged from 8 mg/kg to 15 mg/kg telazol:1 mg/kg to 6 mg/kg xylazine. Shooters sat in tree stands <20 m from the bait to ensure accuracy, and dart-guns were outfitted with lights with finger-operated pressure switches. The darts were barbed and fitted with radiotransmitters to locate the immobilized deer (Pneu-Dart, Inc.). In all areas, we captured deer without regard to sex or age.

We marked all captured deer with bronze, round-post, individually numbered ear tags (National Band and Tag Co., Newport, KY), and brown, 164–165-mHz radiocollars equipped with a 3-yr battery and an 8-hr mortality switch (Advanced Telemetry Systems, Inc., Isanti, MN; mention of trade names does not imply endorsement by federal or state governments). Transmitters were not equipped with precise event timers. In the MSSA only, we marked the top of each collar with a 5-cm × 5-cm portion of bright orange paint and yellow vinyl electrical tape to aid in identification from the air (Mayer et al. 2002). We placed collars equipped with foam padding on fawns to allow for growth. We handled no deer for >10 min and capture protocols were approved by the University of Massachusetts Institutional Animal Care and Use Committee (Protocol nos. 17-2-2 and 21-02-05).

Survival Monitoring

We located and monitored radiocollared deer for mortality biweekly, either from the ground or fixed-wing aircraft (Mech 1983) and we monitored all deer immediately prior to the beginning of the hunting seasons in each study area. We actively monitored deer between January 1997 and May 2001 in the MSSA, between March 1997 and May 2005 in the ESA, and between January 1998 and May 2006 in the WSA. We made a minimum of 3 aerial searches for each missing deer before we censored it from the study (White and Garrott 1990). When a mortality signal was heard, a ground search was conducted to locate the collar as soon as possible (<72 hr) to identify the cause of death. For this study, we report mortality as either due to legal hunting (i.e., reported at check-stations) or nonhunting. Legally harvested deer were required to be physically tagged at check-stations during all hunting seasons. The MDFW widely publicized

Table 1. Legal harvest of adult male and adult female[a] white-tailed deer and number of antlerless deer permits (ADP) sold[b] in 3 Deer Management Zones (DMZs) in Massachusetts, USA, 1997–2005.

	DMZ 2			DMZ 10			DMZ 12[c]		
Yr	Ad M	Ad F	ADP	Ad M	Ad F	ADP	Ad M	Ad F	ADP
1997	259	58	98	449	252	3,490	210	95	1,608
1998	261	40	95	446	216	3,289	202	109	1,310
1999	202	31	99	533	258	3,233	190	106	1,316
2000	259	43	104	645	380	4,021	187	123	1,764
2001	283	25	99	816	410	5,479	163	85	1,257
2002	397	21	95	797	492	5,708			
2003	256	22	98	1,003	533	6,583			
2004	249	18	95	1,097	757	8,323			
2005	261	23	142	1,076	730	7,906			

[a] Ad F harvest estimated by subtracting % fawn F in harvest as determined at physical check-stations.
[b] Antlerless deer permits sold do not equal the no. of permits available in each DMZ; in most yr, fewer permits were sold than the total no. available.
[c] DMZ 12 boundaries were changed beginning with the 2002 hunting seasons and, thus, not comparable to previous yr.

before and during hunting seasons the fact that ear-tagged and collared deer were legal to harvest. We recorded nonhunting causes of mortality if they could be determined (e.g., wounding loss, vehicle collisions, predation, poaching) but analyses here only concern hunting versus nonhunting mortality. We did not record as hunting mortalities the radiomarked deer that died after being wounded by hunters but which were not recovered, because these deer would not have been tallied as part of the legal harvest and would not be included in population estimates derived from harvest data.

Survival Analyses

Annual survival was estimated based on deer-years, 1 May–30 April. Thus, deer captured during late winter–early spring did not enter into survival analysis until 1 May. This common starting date allowed us to consider all collared animals as $\geq$1-yr old beginning each deer-year (deer are typically born from mid-May to early Jun in MA) and to address deer that may have died from capture myopathy or lost their collars during the first few weeks after capture due to poor fit. No deer were captured after 14 April in any year.

We used the Kaplan–Meier method to estimate female survival in each study area for deer-years with $\geq$10 individuals alive on 1 May and calculated 95% confidence intervals (CI) as described in Pollock et al. (1989); we truncated upper CIs at 1.0. For males, we estimated survival within a study area for years with $\geq$5 individuals entering the year. We used the Nelson–Aalen method to estimate male survival because it has better small-sample properties than the Kaplan–Meier method (Skalski et al. 2005). We estimated survival in 3 seasons; 1 May to the start of archery season in October (most yr), archery season through 15 January (i.e., hunting season), and 16 January to 30 April. We calculated hunting mortality rates by censoring all nonhunting mortality during the hunting season (Pollock et al. 1989). Finally, for both females and males, we pooled data for each season across years to estimate overall annual survival rates for the entire study period in each area.

Population Estimation

We estimated the hunting mortality for the entire study period in each area by simply dividing the number of observed mortalities due to legal hunting by the total number of observed mortalities. Because of the small number of mortalities observed in some years, we used a bootstrap approach to derive high and low estimates of hunting mortality. These rates were then multiplied by the overall mortality rates for each year to derive estimates of legal hunting mortality by sex for each area. Prehunt adult populations were then estimated by dividing the legal harvest of each sex by these estimated legal hunting mortality rates.

Because all radiocollared deer were $\geq$1.5-yr old during the hunting seasons we did not include fawns in our population estimates. Because male fawns were identifiable at check-stations by the presence of small antlers (i.e., buttons) and were tallied separately from adult males in all seasons, we report adult male legal harvest as the annual tally reported by checking stations. Female fawns were not tallied separately in all seasons; age was only recorded during the first 6 days of the shotgun season at selected checking stations. Thus, we used the percentage of female fawns recorded during the first week of the shotgun season at check-stations in each DMZ staffed by trained biologists (who aged deer as fawns according to tooth replacement). We multiplied this percentage by the total female harvest to obtain the estimated number of female fawns and then subtracted this number from the total harvest to estimate the number of adult females harvested in each year. In DMZ 2, few females were taken by hunters due to the low number of antlerless permits issued; in some years, no female fawns were reported. Thus, for DMZ 2, we multiplied the average percentage of female fawns for the period 2000–2005 (4/42 F aged = 0.095) by the total legal female harvest each year to estimate the number of fawns taken by hunters.

We compared our estimates of adult male and adult female populations to those derived by population reconstruction (Downing 1980) as typically estimated by MDFW using harvest data. These reconstruction estimates only accounted for mortality due to hunting and, thus, served as indices to the actual population. However, to attempt to account for nonhunting mortality, MDFW staff used various assumed correction factors (CFs) to get a rough measure of actual populations. These CFs were usually 1.5 or 2.0 (S. Christensen, Massachusetts Division of Fisheries and Wildlife, unpublished data), thus assuming hunting accounted for 33–50% of total annual mortality.

RESULTS

Captures

We captured and marked 36 deer in the MSSA (12M:24F), 47 deer (19M:28F) in the ESA, and 59 deer (19M:40F) in the WSA. Given our sample size criteria, we were able to estimate survival and hunting mortality rates for 4 deer-years in the MSSA for both males and females (May 1997–Apr 2001), 6 yr for females in the ESA (May 1999–Apr 2005) and WSA (May 2000–Apr 2006), 5 yr for males in the ESA (May 1999–Apr 2004), and 4 yr for males in the WSA (May 2000–Apr 2004).

Hunting

The archery hunting season was extended from 18 days to 36 days in the ESA and MSSA beginning with the 1999 season. In the WSA the archery season was increased from 18 days to 36 days beginning with the 2002 season. The muzzleloader season was lengthened from 3 days to 6 days statewide beginning with the 1998 season. The muzzleloader season was further extended to encompass the period from the Monday following the end of the shotgun season to December 31, providing for a season that ranged from 14 days to 18 days, depending on the year. The number of antlerless permits validated in DMZ 2 (WSA) during the period we monitored survival (2000–2005) ranged from 95 to 142 (Table 1) and the estimated adult female harvest ranged from 18 to 43. The number of antlerless permits validated in DMZ 10 (ESA) increased each year and ranged from 3,233 in 1999 to 8,323 in 2004 (Table 1) and the estimated adult female harvest ranged from 258 to 757. In DMZ 12

(MSSA), the number of antlerless permits ranged from 1,310 to 1,764 (Table 1) and the estimated adult female harvest ranged from 95 to 123.

Female Survival

Observed female annual survival rates ranged from 0.692 to 0.889 in the MSSA, 0.737 to 1.0 in the ESA, and 0.700 to 0.895 in the WSA (Table 2). Seasonal survival rates were typically >0.90 for all seasons and areas (Table 3). Legal hunting accounted for 27% of the total observed mortality over 4 yr in the MSSA (3 of 11 recorded mortalities), 29% over 6 yr in the ESA (4 of 14 recorded mortalities), and 16% over 6 yr in the WSA (3 of 19 recorded mortalities; Table 4). Pooled annual survival rates were 0.828 in the MSSA, 0.856 in the ESA, and 0.819 in the WSA.

In the MSSA, mortalities were observed in each of 4 yr, but hunting mortalities were only recorded in 2 yr. In the ESA, mortalities were recorded in 5 of 6 yr, but hunting mortalities in only 4 of those 5 yr. In the ESA, in 3 yr only a single marked deer died and legal hunting was the cause in each of those years. In the WSA, mortalities were recorded in each of the 6 yr, but hunting mortalities were only reported in 2 yr. During 2003–2004 (the year with the greatest number of mortalities [$n = 7$]), only 2 mortalities were due to legal hunting. Because of this variability in observing hunting mortalities in our marked samples of deer, we estimated overall survival and mortality rates for the entire length of the study in each area, multiplied the resulting mortality rates by the observed overall hunting mortality rates described above (27% in the MSSA, 29% in the ESA, and 16% in the WSA) to produce estimates of the hunting mortality rates for each area. The resulting hunting mortality rates were 0.047 for the MSSA, 0.041 for the ESA, and 0.029 for the WSA.

Males

Observed male annual survival rates ranged from 0.693 to 0.913 in the MSSA, 0.670 to 0.819 in the ESA, and 0.247 to 0.751 in the WSA (Table 5). Legal hunting accounted for 75% of the deaths in the MSSA, 40% in the ESA, and 46% in the WSA. The low survival (0.247) in the final year of observations in the WSA was because 5 of the 6 deer that began the year died; 2 of the 5 deaths were due to legal hunting (Table 6). The small numbers of males monitored in each area during each year resulted in wide CIs around the survival estimates. We observed mortalities in each year in each study area and ≥ 1 hunting mortality each year in the MSSA; we observed no hunting mortalities in 2 of 5 yr in the ESA and 1 of 4 yr in the WSA. The overall hunting mortality rates (calculated similar to those for F described above) were 0.153 for the MSSA, 0.118 for the ESA, and 0.204 for the WSA.

Population Estimates

Estimates of the adult male and female populations derived using composite hunting mortality rates and the relationship of these estimates to reconstructed adult populations varied among the DMZs (Fig. 2). In the WSA, regulations restricting female harvest artificially depressed both estimates; our estimates were quite sensitive to small changes in adult female harvest. For example, a decrease in harvest of 18 adult females between 2000 and 2001 in DMZ 2 (Table 1) resulted in a 42% decrease in the estimated adult female population. Further, both the composite and reconstructed populations for DMZ 2 estimated more males than females in the population (Fig. 2a,d), which is also unlikely, especially because the estimated survival rates for adult females were greater than for adult males. Trends in the reconstructed populations also did not mirror those in the composite estimates.

In the ESA, the composite population estimates for DMZ 10 were several times larger than the reconstructed population estimates, but the trends were similar (Fig. 2b,e). In 2004, when antlerless permit numbers were increased 26% from the previous year, the adult female harvest increased by 42%, yet the estimated annual survival rate in 2004 was 0.909 and the estimated DMZ adult female population increased 42%, from 13,000 in 2003 to 18,460. Both methods concluded that populations were increasing at a relatively high rate.

In the MSSA, reconstructed adult male populations for DMZ 12 were nearly equal to those estimated using the composite hunting mortality each year (Fig. 2f). This was in line with our estimates of total annual mortality and the percentage of mortality due to legal hunting. Adult female

Table 2. Annual survival estimates (*S*) for female white-tailed deer in 3 study areas in Massachusetts, USA, 1997–2006. MSSA, Myles Standish Study Area; ESA, Eastern Study Area; WSA, Western Study Area.

	MSSA			ESA			WSA		
Yr[a]	*n* enter[b]	*S*[c]	95%CI	*n* enter	*S*	95%CI	*n* enter	*S*	95%CI
1997–1998	17	0.882	0.729–1.000						
1998–1999	18	0.889	0.744–1.000						
1999–2000	16	0.813	0.621–1.000	17	0.824	0.642–1.000			
2000–2001	13	0.692	0.441–0.943	19	0.947	0.847–1.000	10	0.700	0.416–0.984
2001–2002				18	0.784	0.597–0.971	18	0.833	0.661–1.000
2002–2003				19	0.737	0.539–0.935	19	0.895	0.757–1.000
2003–2004				13	1.000	1.000–1.000	25	0.720	0.544–0.896
2004–2005				11	0.909	0.739–1.000	18	0.889	0.744–1.000
2005–2006							15	0.867	0.695–1.000

[a] Biological yr, 1 May–30 Apr.
[b] No. of deer being monitored at the start of the biological yr.
[c] Kaplan–Meier.

Table 3. Seasonal survival of radiomarked female white-tailed deer in 3 study areas in Massachusetts, USA, 1997–2006. WSA, Western Study Area; ESA, Eastern Study Area; MSSF, Myles Standish State Forest study area.

		WSA		ESA		MSSF	
Yr[a]	Period[b]	*S*[c]	SE	*S*	SE	*S*	SE
1997–1998	1					0.941	0.057
	2					0.938	0.061
	3					1.000	0.000
1998–1999	1					1.000	0.000
	2					0.889	0.074
	3					1.000	0.000
1999–2000	1			1.000	0.000	1.000	0.000
	2			0.941	0.057	0.875	0.083
	3			0.875	0.083	0.929	0.069
2000–2001	1	0.900	0.095	1.000	0.000	1.000	0.000
	2	0.889	0.105	0.947	0.051	0.846	0.100
	3	0.875	0.117	1.000	0.000	0.818	0.116
2001–2002	1	0.944	0.054	0.944	0.054		
	2	0.941	0.057	0.941	0.057		
	3	0.938	0.061	0.882	0.078		
2002–2003	1	0.947	0.051	0.895	0.070		
	2	1.000	0.000	0.824	0.093		
	3	0.944	0.054	1.000	0.000		
2003–2004	1	0.920	0.054	1.000	0.000		
	2	0.870	0.070	1.000	0.000		
	3	0.900	0.067	1.000	0.000		
2004–2005	1	1.000	0.000	1.000	0.000		
	2	0.944	0.054	0.909	0.087		
	3	0.941	0.057	1.000	0.000		
2005–2006	1	1.000	0.000				
	2	0.933	0.064				
	3	0.929	0.069				

[a] Biological yr, 1 May–30 Apr.
[b] Period 1 = 1 May–beginning of archery season (mid-Oct each yr, exact date varied); Period 2 = beginning of archery season–15 Jan; Period 3 = 16 Jan–30 Apr.
[c] Kaplan–Meier.

populations estimated by using the composite hunting mortality rate were higher than reconstruction estimates and the trend did not agree in each year, particularly in 2000, where reconstruction estimated a decrease in the population and the composite method an increase of 16%.

DISCUSSION

Survival Estimates

Estimated adult female survival rates were similar, and uniformly high, across 3 management zones in Massachusetts that differed in landscape composition, human density, and antlerless harvest opportunities. Our pooled annual female survival rates ranged from 0.82 to 0.86 in the 3 study areas and legal hunting accounted for <30% of total annual mortality of adult females in each study area. Although we did not accurately determine causation of many nonhunting mortalities, it appeared the majority were vehicle-related in each study area, similar to the results of Etter et al. (2002). Given the ubiquity of white-tailed deer in the Northeast of the United States, there were surprisingly few published reports of adult survival from the region,

Table 4. Sources of mortality for female white-tailed deer in 3 study areas in Massachusetts, USA, 1997–2006. WSA, Western Study Area; ESA, Eastern Study Area; MSSF, Myles Standish State Forest study area.

	WSA		ESA		MSSF	
Yr[a]	*n* deaths[b]	*n* hunting	*n* deaths	*n* hunting	*n* deaths	*n* hunting
1997–1998					2	1
1998–1999					2	0
1999–2000			3	0	3	2
2000–2001	3	0	1	1	4	0
2001–2002	3	1	4	1		
2002–2003	2	0	5	1		
2003–2004	7	2	0	0		
2004–2005	2	0	1	1		
2005–2006	2	0				
Total	19	3	14	4	11	3

[a] Biological yr, 1 May–30 Apr.
[b] Total no. of deaths, including those from legal hunting.

Table 5. Annual survival estimates (*S*) for male white-tailed deer in 3 study areas in Massachusetts, USA, 1997–2004. MSSA, Myles Standish Study Area; ESA, Eastern Study Area; WSA, Western Study Area.

	MSSA			ESA			WSA		
Yr[a]	*n* enter[b]	*S*[c]	95%CI	*n* enter	*S*	95%CI	*n* enter	*S*	95%CI
1997–1998	11	0.913	0.750–1.000						
1998–1999	11	0.761	0.526–0.996						
1999–2000	8	0.779	0.509–1.000	8	0.687	0.396–0.979			
2000–2001	6	0.693	0.339–1.000	9	0.694	0.405–0.983	6	0.607	0.263–0.950
2001–2002				5	0.670	0.299–1.000	6	0.587	0.231–0.942
2002–2003				7	0.734	0.418–1.000	8	0.751	0.454–1.000
2003–2004				5	0.819	0.498–1.000	6	0.247	0.000–0.536

[a] Biological yr, 1 May–30 Apr.
[b] No. of deer being monitored at the start of the biological yr.
[c] Nelson–Aalen.

but our estimated rates are comparable to those reported by Campbell et al. (2005) in West Virginia (0.88) and greater than most other hunted populations (Ricca et al. 2002). In Pennsylvania, annual survival rates of female white-tailed deer from a hunted population varied from 0.61 to 0.90 depending on the location and whether land was publicly or privately owned (Keenen 2010). Brinkman et al. (2004) reported annual survival of 0.77 for a hunted population in an agricultural area of southeastern Minnesota and Fuller (1990) reported annual survival rates for female white-tailed deer of 0.71 (95%CI = 0.63–0.80) in a declining population in northeastern Minnesota. Etter et al. (2002) reported annual survival of 0.82 for adult females in an unhunted population in suburban Illinois. Whitlaw et al. (1998) reported annual survival rates ranging from 0.75 to 0.92 for a population not exposed to hunting in northern New Brunswick and 0.48 to 0.81 in a hunted population in southern New Brunswick. We did not model variables that might have affected adult female survival, but it appears as though in each of our study areas deer were exposed to harvest rates similar to unhunted or lightly hunted deer populations. This was surprising, given that the opportunity to acquire $\geq$1 antlerless deer permit in 2 of the 3 areas was functionally ubiquitous, which may imply that hunter access was a constraint.

We had small samples of marked adult males and those results must be interpreted with caution. In all 3 study areas, estimated annual survival rates of adult males were typically >0.60, and often >0.70, in both suburban and rural landscapes. These are among the highest male survival rates reported for hunted populations of white-tailed deer (Ricca et al. 2002, Campbell et al. 2005) but are lower than that reported (0.83, $n = 13$) for an essentially unhunted suburban population in Illinois (Etter et al. 2002). We believe the high adult male survival rates observed in each of our study areas indicate these populations experienced little hunting pressure, even though there were no restrictions on adult male harvest and an annual bag limit of 2. Reinforcing this perception is the fate of males captured as fawns and observed as yearlings, the adult age class that typically has the lowest survival rate and highest hunting vulnerability. In the MSSA, 4 males were captured as fawns during their first winter, 2 were harvested as 2.5-yr olds, 1 as a 3.5-yr old, and 1 survived until its radiocollar failed after 5 yr. In the WSA, 5 male fawns were radiocollared and 3 died as yearlings, but only 2 of those were killed by hunters. In the ESA, 3 male fawns were radiocollared and 1 died as a yearling from unknown causes; the mortality did occur during the hunting season, but it was not evident that it was a wounding loss and was not classified as such. These yearling male harvest rates are similar to those reported in Pennsylvania (range = 24.7–43.2%) in areas with minimum antler point restrictions designed to protect a large segment of the yearling male cohort from hunting mortality (Norton 2010).

Further evidence suggesting low hunting pressure can be seen in the age-structure data gathered at check-stations; $\geq$2.5-yr olds comprised >50% of the adult male harvest in

Table 6. Sources of mortality for male white-tailed deer in 3 study areas in Massachusetts, USA, 1997–2004. WSA, Western Study Area; ESA, Eastern Study Area; MSSF, Myles Standish State Forest study area.

	WSA		ESA		MSSF	
Yr[a]	*n* deaths[b]	*n* hunting	*n* deaths	*n* hunting	*n* deaths	*n* hunting
1997–1998					1	1
1998–1999					3	2
1999–2000			3	2	2	2
2000–2001	3	2	3	1		
2001–2002	2	0	1	0		
2002–2003	3	2	2	0		
2003–2004	5	2	1	1		
Total	13	6	10	4	6	5

[a] Biological yr, 1 May–30 Apr.
[b] Total no. of deaths, including those from legal hunting.

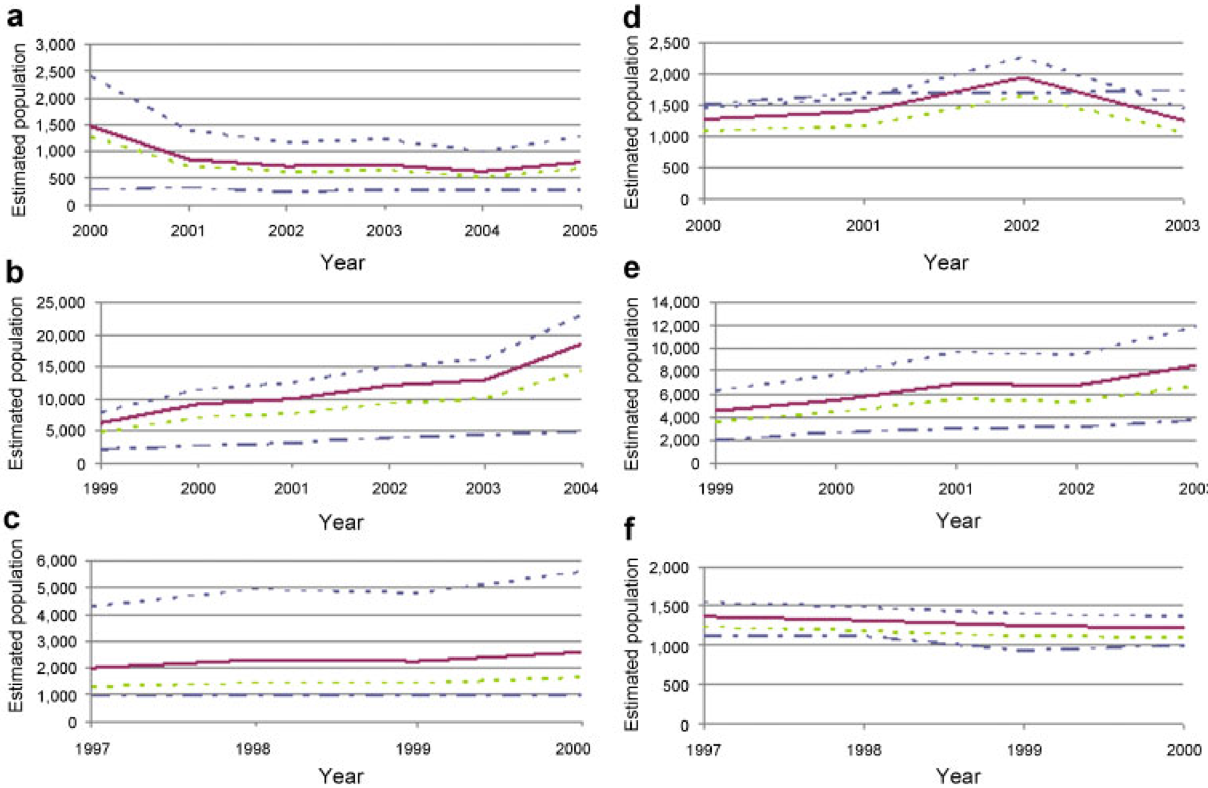

Figure 2. Female and male deer population trends estimated by population reconstruction (dash-dot lines) and using the composite hunting mortality rates (overall rate, solid line; low, dashed line; high, dotted line) in several Deer Management Zones (DMZs) in Massachusetts, USA: (a) DMZ 2 female; (b) DMZ 10 female; (c) DMZ 12 female; (d) DMZ 2 male; (e) DMZ 10 male; (f) DMZ 12 male.

each of the 3 DMZs containing our study areas each year (S. Christensen, unpublished data). Yet among our study areas, only in the suburban ESA would hunter access to deer have been considered an influence on harvest. The MSSA was largely a single block of public land open to hunting, and the WSA was mostly rural with many large blocks of public land open to hunting. Further, Massachusetts law allows hunting on private land that is not posted against trespass, though some towns have ordinances prohibiting firearm discharge or requiring written landowner permission to hunt, especially in the ESA.

Our low sample sizes of female and, particularly, male deer resulted in wide 95%CI. If we assumed 80% annual survival and desired 95%CI of ±10% (i.e., a CI that ranged from 0.72 to 0.88) using the Kaplan–Meier method to estimate survival, we would have needed to monitor 77 deer each year in each study area; if we assumed 70% survival, we would have needed to monitor 116 deer each year to obtain 95%CI of ±10%. The lower precision of our estimates was undesirable, but unavoidable given the resources available. Most telemetry studies of wildlife survival fall short of adequate samples to achieve desired precision (Murray 2006) but we recognize that does not justify our lack of precision. The estimates we obtained for female survival were consistent within each study area across all years; thus, we believe it is reasonable to use them in conjunction with harvest data to estimate realistic ranges of deer populations in each DMZ (Mayer et al. 2002).

Use of Harvest Check-Station Data

Harvest information collected at check-stations is commonly used by wildlife agencies to inform white-tailed deer management (Roseberry and Woolf 1991, Rupp et al. 2000) and check-stations provide biologists with age-at-harvest data to use in population reconstruction estimates and other modeling exercises. Wildlife agencies have increased the use of nonphysical checking (e.g., telephone and internet check-systems) for legally registering harvested animals, but many still do some form of physical checking of hunter-killed deer to obtain a sample of biological data. In Massachusetts, physical tagging of harvested deer at check-stations has been required since 1966 and, during our study, age and other biological data were obtained from an average of 32% of the total legal harvest.

Lavigne (1993) reported on the variation in check-station data with timing during a 4-week firearm deer-hunting season in Maine; estimates of many parameters (e.g., % yearling M and F) changed among weeks during the season. If check-stations are operated during a single, short window of a long hunting season, or only on certain days (e.g., Saturdays) managers should collect data when the least-expected hunter bias will occur, or distribute sampling effort in proportion to the temporal distribution of the overall harvest (Lavigne 1993) to ensure the data are as representative of the overall harvest (and hopefully, the deer population) as possible. Further, the timing of data collection should vary as little as possible from year to year. Our results also support the recommendations of Rosenberry et al. (2004) that wildlife managers should make an effort to obtain estimates of reporting rates at the appropriate management scale (e.g., DMZ), in addition to estimates of sex-specific harvest mortality rates, to effectively use harvest data for estimating deer populations.

Any system of harvest data collection is dependent on the willingness of hunters to comply with the process entailed. In a suburban area of Connecticut, estimated deer harvests were up to 2.5× lower when based on mandatory hunter report cards than from hunter surveys (Kilpatrick et al. 2005). Rosenberry et al. (2004) described many of the potential problems with check-station data and data derived from a mandatory report-card system. In Pennsylvania, report-card return rates varied between groups of hunters taking antlered and antlerless deer and among hunting seasons; predicted reporting rates ranged from 36% to 60% (Rosenberry et al. 2004). Gove et al. (2002) and Skalski et al. (2007) described techniques to compensate for those problems and used age-at-harvest data derived from check-stations to reconstruct ungulate populations.

We assumed hunters did not select or avoid killing radio-collared deer. Violation of this assumption could have led to us either overestimate (avoidance) or underestimate (selection) deer numbers using our hunting mortality-rate method. The MDFW tried to make it known that marked deer were legal to harvest, but we did not offer rewards for the return of radiocollars. It is possible that selection could have occurred (especially in females) because all marked deer were ≥1.5-yr old during the hunting season and hunters selecting the largest antlerless deer in a mixed group of adults and fawns may have selected a marked deer on the basis of body size. However, Jacques et al. (2011) reported that hunters in Wisconsin were less inclined to shoot radiocollared females than they were males and that willingness to shoot marked deer was related to length of hunting experience, with more experienced hunters than novice hunters being willing to shoot marked deer. Anecdotally, all hunters that were interviewed when checking a radiocollared deer in our study said they did not see the collar prior to shooting the animal.

Population Estimates

The composite hunting mortality rates produced realistic estimates for adult deer populations in DMZs 10 and 12; DMZ 2 estimates were negatively biased by the regulatory restrictions on antlerless deer harvest. Because few antlerless deer permits were made available in DMZ 2 (in an attempt to increase deer abundance), very few adult females were killed by hunters each year and small changes in the absolute number of deer killed resulted in relatively large percentage changes in both the reconstruction population estimates and those based on the composite hunting mortality rate. For both techniques, the resulting adult female:male estimates were <1.0 in DMZ 2, which is unrealistic given that adult male harvests were typically >250 and female harvests <30 during our study, and estimated female annual survival rates were higher than male survival rates. Thus, when regulations restrict hunter opportunities to harvest deer of specific sex or age classes, harvest-based population estimators may not be reliable.

Reconstructed population estimates were typically lower than those estimated using the composite hunting mortality rate (as expected) because reconstruction only accounts for deer mortality due to legal hunting, and the composite hunting mortality incorporated harvest-rate estimates (Downing 1980). Davis et al. (2007) suggested that reconstruction could be usefully applied to populations that have high harvest rates, low natural mortality, and do not exhibit significant changes in those rates across years. In our study, low natural mortality was evident, but harvest was estimated to be <30% of total annual mortality for females in all 3 study areas, and <50% for males in 2 of 3 study areas. We believe that population reconstruction from harvest data alone may not be adequate to develop useful population estimates under these circumstances, unless the results are combined with empirically derived harvest rates from the management area of interest (Gove et al. 2002).

Estimated deer-hunter numbers in Massachusetts declined from around 86,000 in 1995 (McDonald et al. 2002) to between 50,000 and 55,000 in 2009 (Christensen 2010), with most of the decrease occurring by 2000. Hunter effort during this period shifted from the western DMZs to eastern DMZs. In 1997, DMZs 10, 11, and 12 were estimated to contribute 25% of the total number of hunter days statewide; in 2009, those same DMZs contributed an estimated 44% of all hunter days (Christensen 2010). In our area with the highest human population density (ESA; DMZ 10) and the most liberal hunting framework, estimated hunting mortality did not seem to increase despite an increase of >100% in the number of antlerless deer permits sold over 5 yr and an increase during the study period in the adult female harvest from 380 to >700. The overall estimated harvest mortality rate in the ESA was 4.1% considering all years of data, and the resulting extremes from our bootstrap-like approach ranged from 3.3% to 5.3%. Thus, hunting likely did not stabilize the population growth rate in the ESA during our study.

MANAGEMENT IMPLICATIONS

The assumption that legal harvest comprises the bulk of annual mortality in hunted populations of white-tailed deer is convenient and allows deer managers to use information they routinely collect to estimate deer populations, or at least trends in populations. However, this assumption must be tested, especially when hunter numbers decrease or hunter access to deer is limited, as in suburban and exurban environments. Reliance on harvest-based population estimators when harvest comprises a small percentage of annual deer mortality will produce conservative estimates of deer abundance. If estimates of deer abundance are required to manage populations or develop hunting regulations, and harvest-based estimators are going to be used, managers should obtain independent estimates of deer harvest rates.

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