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Research Article

Spatio-Temporal Variation in Male White-Tailed Deer Harvest Rates in Pennsylvania: Implications for Estimating Abundance

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ABSTRACT The performance of 2 popular methods that use age-at-harvest data to estimate abundance of white-tailed deer is contingent on assumptions about variation in estimates of subadult (1.5 yr old) and adult ($\geq$2.5 yr old) male harvest rates. Auxiliary data (e.g., estimates of survival or harvest rates from radiocollared animals) can be used to relax some assumptions, but unless these population parameters exhibit limited temporal or spatial variation, these auxiliary data may not improve accuracy. Unfortunately maintaining sufficient sample sizes of radiocollared deer for parameter estimation in every wildlife management unit (WMU) is not feasible for most state agencies. We monitored the fates of 397 subadult and 225 adult male white-tailed deer across 4 WMUs from 2002 to 2008 using radio telemetry. We investigated spatial and temporal variation in harvest rates and investigated covariates related to the patterns observed. We found that most variation in harvest rates was explained spatially and that adult harvest rates (0.36–0.69) were more variable among study areas than subadult harvest rates (0.26–0.42). We found that hunter effort during the archery and firearms season best explained variation in harvest rates of adult males among WMUs, whereas hunter effort during only the firearms season best explained harvest rates for subadult males. From a population estimation perspective, it is advantageous that most variation was spatial and explained by a readily obtained covariate (hunter effort). However, harvest rates may vary if hunting regulations or hunter behavior change, requiring additional field studies to obtain accurate estimates of harvest rates.

KEY WORDS harvest rates, *Odocoileus virginianus*, Pennsylvania, spatio-temporal variation, white-tailed deer.

Managers use population modeling to monitor population trends in white-tailed deer (*Odocoileus virginianus*) and to identify management actions necessary to increase, stabilize, or decrease deer populations (Roseberry and Woolf 1991). However, failure to address model assumptions can result in inaccurate population estimates (Burgdorf and Weeks 1997, Skalski and Millspaugh 2002, Davis et al. 2007, Millspaugh et al. 2009). In particular, the 2 most commonly used methods by state agencies to estimate white-tailed deer abundance, population reconstruction and the sex–age–kill (SAK) model, are sensitive to changes and errors in estimated harvest rates of antlered ($\geq$1.5 yr old) deer (Skalski et al. 2005, Davis et al. 2007, Millspaugh et al. 2009). Similarly, likelihood-based approaches with age-at-harvest data rely on auxiliary data from radiocollared animals to estimate abundance (e.g., Gove et al. 2002). Consequently, understanding spatial and temporal patterns in harvest rates of antlered deer is critical to accurately estimate population size.

Hunting regulations are thought to influence hunter effort and effectiveness, which in turn influence harvest rates and total harvest (Hansen et al. 1986, Foster et al. 1997). However, landscape characteristics may affect harvest rates at the management unit and smaller scales. These include forest cover, land ownership, landscape ruggedness, and road density (Eberhardt 1960, Holsworth 1973, Picton and Mackie 1980, Foster et al. 1997, Broseth and Pedersen 2000, Diefenbach et al. 2005). Weather conditions during intensive harvest periods could result in temporal variability of harvest rates (Hansen et al. 1986).

Furthermore, recent shifts toward quality deer management (QDM) practices that generally protect younger antlered deer create a disparity in the harvest vulnerability

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of subadult (1.5 yr old) and adult (≥2.5 yr old) males (Miller and Marchinton 1995). Differential harvest vulnerability among antlered deer age-classes will violate assumptions of population models that assume a homogeneous rate of male harvest, such as the SAK model. Harvest regulations set by state agencies, such as restrictions on antler size, have implications similar to QDM practices.

The Pennsylvania Game Commission (PGC) uses regulations that include antler point restrictions (APRs) to protect subadult antlered deer. Under APRs a minimum number of points on at least 1 antler are required before an antlered deer is legal to harvest. In Pennsylvania, most adult male deer are legal to harvest, because most antlers exceed the APR. This results in different harvest rates between subadult and adult male deer. The SAK model uses harvest data to estimate a harvest rate for antlered deer by assuming a stable and stationary population. Alternative methods for estimating the antlered deer harvest rate must be used because this assumption is unlikely to be met in most game species populations (Millspaugh et al. 2009). One approach is to obtain harvest rate estimates by monitoring radiocollared deer. However, usually it is not logistically or financially feasible to obtain annual estimates of harvest rates across all management units unless harvest rates do not exhibit large annual variation or exhibit variation that can be predicted by other factors, such as landscape characteristics or hunter effort.

Our objective was to evaluate variability in harvest rates of antlered white-tailed deer in Pennsylvania. Because of APR regulations, we assumed different harvest rates for subadult and adult male deer and investigated spatial and annual variability for harvest rates of each age class. If we documented important spatio-temporal variability, we conducted further analyses to determine whether landscape or hunter effort variables might explain the patterns in harvest rates. We predicted harvest rates were positively correlated with hunting effort, road density, and percent of public land. Alternatively, we expected harvest rates to decrease with an increase in terrain ruggedness and percent forest cover.

STUDY AREA

During 2002–2008, we captured deer in 4 separate study areas in Pennsylvania, USA that encompassed 3 ecological regions with different physiographic characteristics (Fig. 1). We refer to each study area by the wildlife management unit (WMU) in which it was located. Forests in all 4 study areas were typically Appalachian oak forest dominated by northern red oak (*Quercus rubra*) and white oak (*Q. alba*) along with other species such as maple (*Acer* spp.), birch (*Betula* spp.), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), and hickory (*Carya* spp.). In the study area in northcentral Pennsylvania (WMU 2G), which was in a transition zone between the Appalachian oak and northern hardwoods forest, maple, beech, and black cherry were more common than in the other study areas. All study areas differed in the proportion of the landscape forested, amount and type of forest fragmentation, and topography. Deer hunting generally occurred throughout all study areas, in which antlered deer to be legal for harvest were required to have ≥3 or ≥4 antler points ≥2.5 cm on at least 1 antler depending on the WMU. These regulations protected at least 50% of the subadult males (1.5 yr old during the hunting season) from harvest, but most adult males (≥2.5 yr old during the hunting season) were legal for harvest (C. S. Rosenberry, PGC, unpublished data). Antlerless harvest was controlled via limited antlerless licenses sold on a first-come, first-served basis, except some public and private lands were enrolled in a Deer Management Assistance Program (DMAP) where landowners were allowed to issue additional antlerless permits specific to each DMAP area.

One study area (1,200 km^2) was located in Armstrong County (WMU 2D) and the Pittsburgh Low Plateau ecological region. Armstrong County was almost exclusively privately owned, and land use was primarily agricultural, with common crops including corn, soybeans, and grains. Forty-nine percent of the landscape was forested, although forests were extensively fragmented and consisted primarily

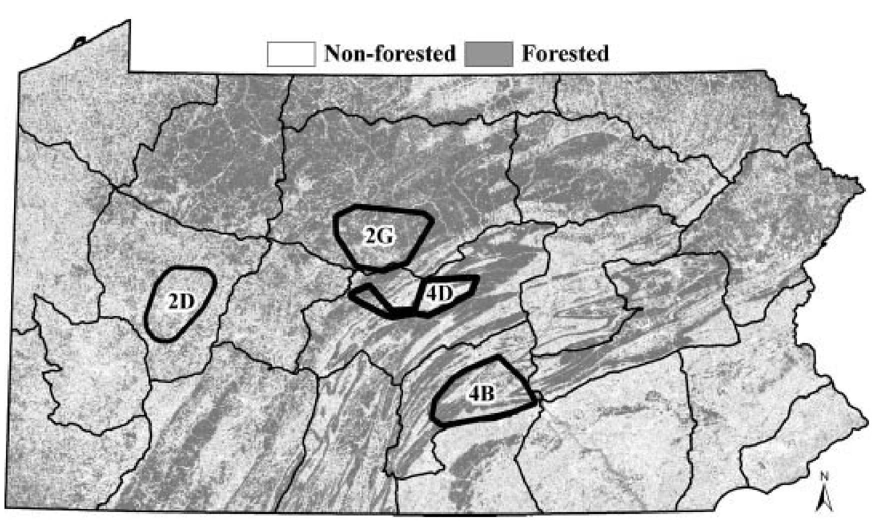

Figure 1. Map of white-tailed deer study areas in wildlife management units (WMUs) 2D, 2G, 4B, and 4D. The 22 Pennsylvania Game Commission WMUs are delineated with thin black lines, Pennsylvania, USA, 2002–2008.

of small woodlots. This study area was located in western Pennsylvania where, to be legal for harvest, antlered deer had to possess $\geq$4 antler points $\geq$2.5 cm on at least 1 antler. All other study areas were within WMUs where antlered deer had to possess at least 3 antler points $\geq$2.5 cm on at least 1 antler to have been legally harvested.

A second study area (705 km^2) was located in Centre County within WMU 4D. This study area encompassed both the Allegheny Mountains ecological region in western Centre County and the Ridge and Valley ecological region in central and eastern Centre County. This area was extensively forested (57–90%), primarily with second- and third-growth forests. At lower elevations, tree species primarily consisted of scrub oaks, including bear oak (*Q. ilicofolia*) and chinquapin oak (*Q. prinoides*), and large-toothed aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), and pitch pine (*Pinus rigida*). At higher elevations, the overstory was dominated by oak, red maple, and hickory. Eastern Centre County consisted of a series of narrowly spaced, parallel ridges and valleys, running in a northeast-southwest orientation. Land use was primarily agricultural in the valleys (row crops and dairy farms) and the long, parallel ridges were forested. Land in this area was predominately privately owned, and deer hunting occurred throughout the area.

Our third study area (1,304 km^2) was located in Clinton and Clearfield counties in WMU 2G in the Allegheny High Plateau ecological region. The landscape in WMU 2G was 90% forested and there was a tradition of deer hunting from camps (Zinn 2003). The study area included State Game Lands (SGL) 30 and 100, the southern portion of the Sproul State Forest, and privately owned land to the south and west; 29% of the study area was privately owned.

Our fourth study area (1,256 km^2) was located in Cumberland, Juniata, and Perry counties in WMU 4B in the Ridge and Valley ecological region. The western portion of the study area included a large contiguous forested area within the Tuscarora State Forest and 78% of the study area was privately owned. Similar to the WMU 4D study area, 67% of the study area was forested with valleys dominated by agricultural land use and ridges forested.

METHODS

We captured deer using Clover traps, rocket nets, and drop nets. In WMUs 2D and 4D we marked male deer during 2002–2005, we marked female deer in WMUs 2G and 4B during 2005–2006, and during 2007–2008 we marked both male and female deer in WMUs 2G and 4B. All marked deer were fitted with 2 ear tags and radio- or Global Positioning System (GPS)-transmitters that transmitted a mortality signal (110 pulses per minute) upon lack of movement for 4 hr. Ear tags and transmitters were labeled with a unique identification number and a toll-free telephone number. We collected survival and location data weekly via bi-angulated telemetry locations and program LOAS (version 2.10.1; Ecological Software Solutions, Sacramento, CA). Upon detection of a mortality signal, we attempted to determine cause of death following protocol used in previous studies (Vreeland et al. 2004, Long et al. 2008). We handled all animals in accordance with protocols approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC no. 26886).

We estimated harvest rates ($\hat{H}$) for subadults and adults as the complement of survival estimated using the known-fates (KF) procedure in Program MARK (White and Burnham 1999)

$$\hat{H} = 1 - \prod_{j=1}^{t} \left(1 - \frac{d_j}{r_j}\right)$$

where r_j is the number of animals at risk during time period j, and d_j is the number of legally harvested deer during the same time period. We used $t = 8$ bi-weekly intervals from early October through early January for harvest rate estimates for all years. Because nearly 75% of the annual deer harvest in Pennsylvania occurs during the 2-week modern firearms season (Rosenberry et al. 2004), we structured our intervals so the sixth bi-weekly interval would include the entire modern firearms season. When we modeled the probability of harvest (d_j/r_j) with covariates (see below) we used a logit link.

For each bi-weekly interval, we considered a deer available if it was known to be alive at the beginning of each interval. However, we censored deer (removed from r_j) that died from causes other than legal harvest or whose fate was unknown because of radiocollar failure for all subsequent bi-weekly intervals. Because censoring deer that die from causes other than legal harvest violates the assumption that censoring is independent of fate, we evaluated potential bias. One hundred seventeen of our 166 (70%) subadult male mortalities were legally harvested and 115 of our 140 (82%) adult male mortalities were legally harvested. According to Heisey and Patterson (2006; Fig. 2), the expected relative bias for both subadult and adult deer would be $<$1.1. Personal communication with hunters and other evidence suggested that some hunters were uncooperative and would discard and sometimes attempt to destroy radiocollars of legally harvested deer. Therefore, we assumed 2 radiocollared deer that we could not locate during the hunting seasons, and could not find after subsequent ground and aerial searches, to be legally harvested. Likewise, we assumed 44 radiocollars found with the collar cut and abandoned during a hunting season were legally harvested. Hunter selection or avoidance of radio- or GPS-collared deer is possible (Jacques et al. 2011), but we have no evidence for different harvest rates between collared and ear-tag transmittered deer or reward ear-tagged deer and radio- or GPS-collared deer (D. R. Diefenbach, U.S. Geological Survey, unpublished data).

We measured characteristics of the WMU and individual deer that we believed might explain variation in harvest rates. For each WMU, we used data collected by a single annual questionnaire mailed to a random sample of 2% of hunters (C. S. Rosenberry, unpublished data) to estimate number of days hunters pursued deer and expressed this hunting effort on an area basis (hunter-days/km^2). We defined a hunter-day as the number of days, regardless of hours per day, a license holder hunted in a WMU during a specific deer hunting

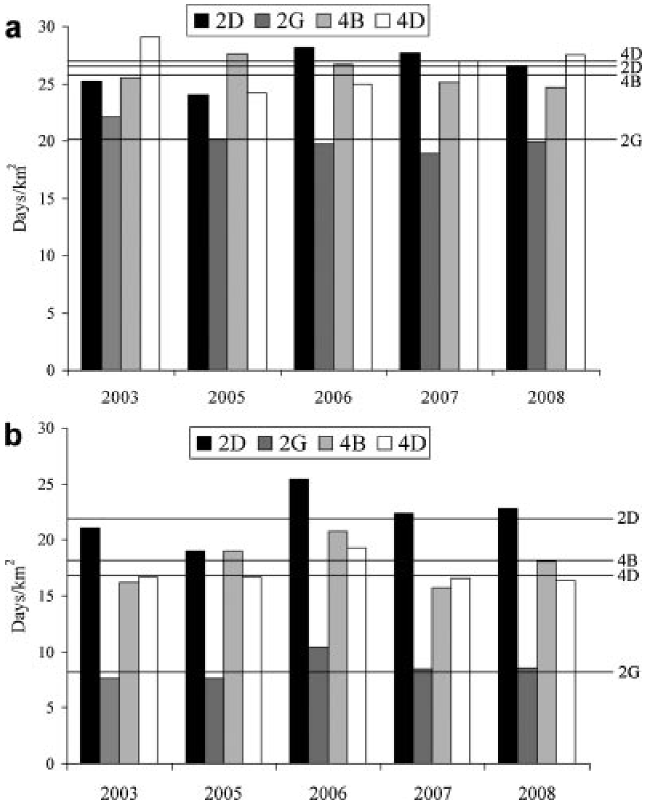

Figure 2. Hunting effort by wildlife management unit (WMU; hunter-days/km^2) from 2003 to 2008 (excluding 2004) during the 2-week firearms hunting season (a) and six 2-week periods of archery hunting (b) for white-tailed deer, Pennsylvania, USA. Horizontal lines represent mean values for respective WMUs.

season. Because no hunter effort data were available in 2002 and 2004, we averaged hunter effort across years (Fig. 2). Response rates for the survey were >50% which provided a sample of 46,566 respondents from 2003, 2005, 2006, 2007, and 2008 and harvest estimates from these surveys did not differ from those obtained using the methods described by Rosenberry et al. (2004; C. S. Rosenberry, unpublished data).

For individual deer, we estimated percent forest cover, percent public land, ruggedness (SD of elevation), and an index to road density within their estimated home range. Because we lacked detailed location information for all deer, we first estimated a mean home range size using a fixed kernel home range estimator in Hawth's Tools (Hawth's Analysis Tools for ArcGIS, www.spatialecology.com/htools, accessed 22 Jun 2009) based on location data for 44 male deer fitted with GPS collars. The average home range was 5.4 km^2 (SE $= 0.4$), which we represented with a 1,314 m buffer radius around the median location for each deer. We estimated median home range locations for November and December when most white-tailed deer were harvested ($n = 159$ deer). However, for deer with no locations during these months we used October locations ($n = 29$ deer), which is the early archery hunting season, or locations from other non-hunting months ($n = 12$ deer). We performed all spatial data analysis using ArcGIS 9.2 using data available on the Pennsylvania spatial data access (PASDA) website (Pennsylvania State University 2008). We used PAMAP Land Cover for Pennsylvania, and maps from PGC State Game Lands and Department of Conservation and Natural Resources (DCNR) State Forests to quantify percent forested land and percent public land. We calculated an index to road density as the sum of meters of all public roads within the buffer area around the median location of each deer, which was proportional to road density because all buffers around the median home range location were the same size.

We first investigated how harvest rates varied spatially and temporally for adult and subadult males. Because Pennsylvania hunting regulations were designed to reduce harvest rates of subadult males, we analyzed data separately for each age class. For the simplest (NULL) model a harvest rate was estimated for each of the 8 bi-weekly time periods. To this model structure we added dummy variables for year (YEAR) or study area (AREA) as additive effects such that the pattern in variation of bi-weekly harvest rates was the same among years or study areas, but differed by a constant amount on the logit scale. Because we collected data on the 4 study areas in different years we had to compare models for WMU 2D and 4D separately from WMUs 2G and 4B to investigate any YEAR effect. For example, in our WMU 2D and 4D study area, we used 3 dummy variables (β_1, β_2, and β_3) to represent year 2002 (1 0 0), 2003 (0 1 0), 2004 (0 0 1), and 2005 (0 0 0), respectively. The β estimate for each dummy variable represented the difference between the year each dummy variable was associated with and the reference year, which is 2005 in this example. If we failed to detect any temporal effects, we analyzed data from all 4 study areas to investigate spatial variation in harvest rates. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002), maximized log likelihoods, and Akaike weights to identify the best model and important explanatory variables. We explored temporal or spatial variability if model weights including YEAR or AREA exceeded the NULL model weight. If there was evidence for temporal or spatial variability, we employed an exploratory approach to evaluate the relative variable importance of explanatory variables using summed Akaike weights across all models that included each explanatory variable. For our explanatory variables, we considered models competitive and model averaged if models were within 2 AIC_c units and differed by >1 parameter or were within 2 AIC_c units and included mutually exclusive slope parameters (Arnold 2010).

We investigated spatial variation in harvest rates of adults by including variables such as hunter effort during the archery and firearms seasons (EFFORT), terrain ruggedness, road density, percent forested land, and percent public land as additive effects to bi-weekly harvest rates. We constructed all possible models using these variables and estimated the relative importance of each variable by summing Akaike weights (Burnham and Anderson 2002:168). We did not include 2005 data in this analysis because we lacked home range information for adult males needed to quantify individual deer covariates.

Table 1. Number of male white-tailed deer monitored by year, wildlife management unit (WMU), and age class used to estimate harvest rates on 4 study areas in Pennsylvania, 2002–2008.

Age class	WMU	2002	2003	2004	2005	2007	2008	2002–2008
Adult	2D	3	16	55	27			101
	4D	1	14	42	21			78
	4B					10	19	29
	2G					12	28	40
Subadult	2D	43	82	63				188
	4D	16	49	52				117
	4B					29	20	49
	2G					18	25	43

For subadult males we investigated only the effect of hunter effort on harvest rates, because defining characteristics of the home range (road density, percent forested, etc.) is problematic for deer during dispersal and because hunter effort best explained harvest rates for adult deer (see Results Section). However, because harvest data (C. S. Rosenberry, unpublished data) indicated that a greater proportion of the harvest of subadult males occurred during the firearms season compared to harvest of adult males, we investigated 2 additional models for subadult males in which harvest rates were a function of hunting effort during either the archery or firearms season only.

RESULTS

We captured 397 subadult and 225 adult male deer (Table 1) whose home range varied greatly according to topography, forest cover, and land ownership (Table 2). Because we monitored some adult deer for >1 yr (10.2%), total number of adult deer monitored was greater than the number captured. For example, a deer that survived 2 separate hunting seasons, roughly October through January, would have been included in both years in the analysis. Both the rate of mortality that occurred at the capture site (1.4%) and capture-related mortality rates (mortalities that occurred within 4 weeks of capture; <5.0%) were lower than similar studies with white-tailed deer (Beringer et al. 1996).

Table 2. Summary statistics from individual deer ($n = 200$) of characteristics of the home range (5.4 km^2) for covariates used to predict adult male white-tailed deer harvest rates in Pennsylvania, 2002, 2003, 2004, 2007, and 2008.

Covariate	$\bar{x}$	SD	Range
% Forest cover	0.74	0.21	0.27–1.00
% Public land	0.29	0.40	0.00–1.00
Ruggedness (SD of elevation)	43.58	25.14	9.00–134.00
Road density (meters)	24,413	35,496	0–165,122

For both adults and subadults, we found that harvest rates exhibited greater variation among study sites than years (Tables 3 and 4). We pooled data for adults from all 4 WMUs for 2002–2004 and 2007–2008 because of little evidence of temporal variability in harvest rates. For adult males, average archery and firearms season hunting effort (EFFORT; Fig. 2, Table 5) had the greatest relative variable importance (0.88) compared to landscape characteristics of the home range (terrain ruggedness = 0.35, amount of public land = 0.37, % forested land = 0.29, and road density = 0.27). During the firearms season, our model predicted harvest rates for adult males to vary from 0.25 to 0.65 across the range of hunter effort measured from mail questionnaires (Fig. 3). During the archery season, we estimated harvest rates varied between <0.05 and 0.30 depending on hunter effort (Fig. 3). Also, a model that included the variable EFFORT was more parsimonious than a model that simply estimated different harvest rates among WMUs ($\Delta AIC_c = 3.98$).

For subadult males, we pooled data from all 4 WMUs and restricted our evaluation to those models in which harvest rates were a function of hunter effort (Table 6). We found that hunter effort during the firearms season best explained the variation in harvest rates and harvest rates during the archery season exhibited little variation in relation to hunter effort (Fig. 4). Harvest rates for the eight 2-week periods for

Table 3. Model selection results for rates of harvest in adult (≥2.5 yr old) male white-tailed deer for 2 groups of study areas. All models allowed for different harvest rates among eight 2-week hunting periods (min $K = 8$). For wildlife management units (WMU) 2D and 4D, data were collected 2002–2005 and for WMUs 2G and 4B data were collected 2007–2008, Pennsylvania, USA.

Study areas	Model	K[a]	Log(ℓ)[b]	AIC_c[c]	ΔAIC_c[d]	Akaike weight
2D and 4D	AREA	9	−164.2	346.5	0.00	0.62
	NULL	8	−166.4	348.7	2.21	0.21
	YEAR + AREA	12	−162.9	349.7	3.21	0.12
	YEAR	11	−164.8	351.7	5.18	0.05
2G and 4B	AREA	9	−52.3	122.5	0.00	0.38
	NULL	8	−53.4	122.8	0.28	0.33
	YEAR + AREA	10	−52.2	124.3	1.80	0.16
	YEAR	9	−53.4	124.7	2.18	0.13

[a] No. of parameters.
[b] Log likelihood.
[c] Akaike's information criterion adjusted for sample size.
[d] Difference in AIC_c for the current model relative to the model with the lowest AIC_c.

Table 4. Selection results for models of harvest rates of subadult (1.5 yr old) male white-tailed deer for 2 groups of study areas. All models allowed for different harvest rates among eight 2-week hunting periods (min $K = 8$). For wildlife management units (WMUs) 2D and 4D, data were collected 2002–2005 and for WMUs 2G and 4B data were collected 2007–2008, Pennsylvania, USA.

Study areas	Models	K[a]	Log(ℓ)[b]	AIC$_c$[c]	ΔAIC$_c$[d]	Akaike weight
2D and 4D	NULL	8	−243.99	503.98	0.00	0.59
	AREA	9	−243.80	505.60	1.61	0.26
	YEAR	10	−243.78	507.56	3.57	0.10
	YEAR + AREA	11	−243.58	509.15	5.17	0.04
2G and 4B	AREA	8	−72.89	161.78	0.00	0.41
	NULL	7	−74.14	162.28	0.50	0.32
	YEAR + AREA	9	−72.90	163.79	2.01	0.15
	YEAR	10	−72.15	164.29	2.51	0.12

[a] No. of parameters.
[b] Log likelihood.
[c] Akaike's information criterion adjusted for sample size.
[d] Difference in AIC$_c$ for the current model relative to the model with the lowest AIC$_c$.

Table 5. Hunter effort (hunter-days/km^2), estimated harvest rates ($\hat{H}$), and associated measures of precision for radiocollared adult (>2.5 yr old) and subadult (1.5 yr old) male white-tailed deer in 4 wildlife management units (WMUs) in Pennsylvania, 2002–2005 and 2007–2008.

	Hunter effort		Adult			Subadult		
WMU	Firearm	Archery	$\hat{H}$	$\widehat{SE}(\hat{H})$	95% CI	$\hat{H}$	$\widehat{SE}(\hat{H})$	95% CI
2D	68	57	0.612	0.044	0.52–0.69	0.347	0.027	0.30–0.40
4D	69	44	0.591	0.046	0.50–0.60	0.355	0.029	0.30–0.41
2G	52	22	0.318	0.080	0.18 –0.49	0.234	0.058	0.14–0.37
4B	67	47	0.570	0.041	0.49–0.65	0.339	0.026	0.29–0.39

subadult males were lower than adult males and exhibited less variability (Table 5, Figs. 3 and 4).

DISCUSSION

Pennsylvania historically has used accounting models (Lang and Wood 1977) or change-in-ratio type models (Shope 1978, Diefenbach et al. 1997) to estimate white-tailed deer abundance, but these models assume that all antlered deer experience equivalent harvest rates. Since 2002, this assumption has been violated because of APR harvest regulations, so the PGC used a modified SAK model in which harvest rates for subadult and adult males were estimated from radio telemetry studies (Norton 2010). Based on limited data from 2 study areas, the PGC applied a constant adult male harvest rate to WMUs within both the 3- and 4-point antler restriction areas. Our results indicated even greater spatial variation in harvest rates, in which adult harvest rates were 1.4–2.1 times that of subadults, adult male harvest rates varied more than subadult male harvest rates, and substantial spatial variation occurred across WMUs (0.36–0.69 for adult males and 0.26–0.42 for subadult males; Figs. 3 and 4).

The fact that we found greater spatial than temporal variation in harvest rates is important for population monitoring. Fortunately, hunter effort is readily quantified and use of WMU-specific hunter effort to predict harvest rates should

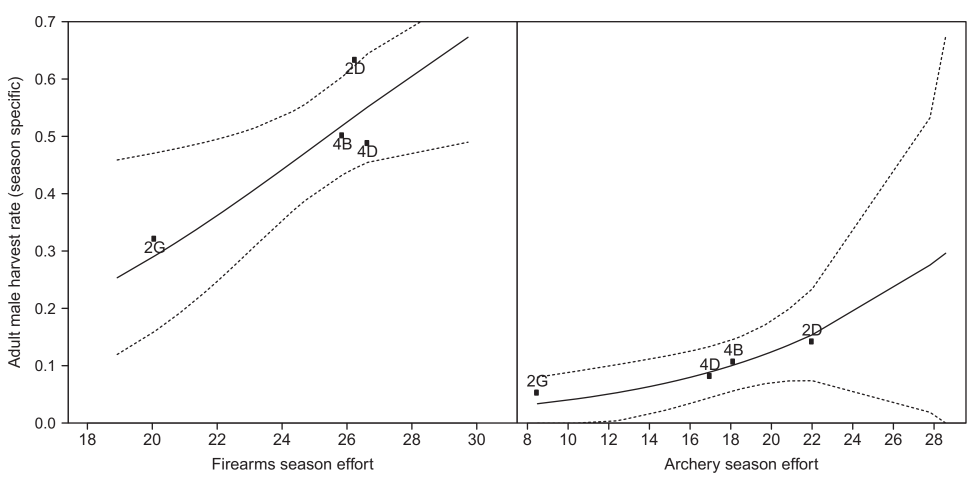

Figure 3. Predicted harvest rates of white-tailed deer by hunting season for adult (≥2.5 yr old; solid line) males with 95% confidence intervals (dashed lines) modeled as a function of hunter effort (hunter-days/km^2) in Pennsylvania, USA, 2002–2008. Point estimates for study area-specific harvest rates are included. Values on the x-axis indicate the range of hunter effort (hunter-days/km^2) among 19 wildlife management units.

Table 6. Comparison of models of harvest rates in subadult male white-tailed deer using data from 4 wildlife management units. Explanatory variables included effort during archery hunting season (ARCHERY), effort during firearms hunting season (FIREARM), effort during both archery and firearms seasons (EFFORT), and study areas (AREA), Pennsylvania, 2002–2008. All models allowed harvest rate to vary over the 8-week hunting period and the NULL model included no other explanatory variables.

Models	K[a]	Log(ℓ)[b]	AIC$_c$[c]	ΔAIC$_c$[d]	Akaike weight
FIREARM	9	−321.37	660.73	0.00	0.41
NULL	8	−322.75	661.49	0.76	0.28
EFFORT	10	−321.34	662.69	1.95	0.15
ARCHERY	9	−322.72	663.45	2.71	0.10
AREA	11	−321.35	664.70	3.97	0.06

[a] No. of parameters.
[b] Log likelihood.
[c] Akaike's information criterion adjusted for sample size.
[d] Difference in AIC$_c$ for the current model relative to the model with the lowest AIC$_c$.

improve the accuracy of the population estimates based on age-at-harvest data and models that incorporate auxiliary data from radiocollared deer (e.g., Gove et al. 2002, Norton 2010).

We found harvest rates of subadult males to be less variable than for adult males, which was not expected. Because antler growth is dependent on weather and food availability and quality (French et al. 1956), protection rates for subadult males under APRs were thought to be variable given the range in forest vegetation conditions, annual variability in hard mast production, and winter severity in Pennsylvania. Furthermore, because of the number of hunters in Pennsylvania and high harvest rates prior to antler restrictions (e.g., approx. 80% of antlered deer were harvested annually; Long et al. 2008), and because most adult males were legal for harvest, we expected harvest rates for adult males to be high and less variable than for subadult males. In retrospect, even if the proportion of subadult males protected from harvest by APR regulations varies, overall subadult male harvest rate variability is limited because each year a substantial proportion of the population is not legal to harvest. Consequently, under antler restrictions with protection levels similar to Pennsylvania's, subadult male harvest rates may vary less than adult male harvest rates.

Our results illustrate one of the challenges of obtaining accurate estimates of deer population sizes using age-at-harvest models and auxiliary data on harvest or survival rates to relax certain assumptions. Although hunter effort best explained variation in harvest rates, we have not excluded the possibility of temporal variation in the future or that the relation between hunter effort and harvest rates may change over time. Consequently, without annual collection of auxiliary data, one is forced to ignore temporal variation and make assumptions about variability in harvest rates. Moreover, harvest management decisions need to explicitly acknowledge the uncertainty in such population estimates and perhaps give greater emphasis on monitoring population trends, rather than estimating absolute population abundance.

MANAGEMENT IMPLICATIONS

Use of auxiliary data to estimate rates of harvest for antlered deer can eliminate restrictive and unrealistic assumptions required for models based on age-at-harvest data (Gove et al. 2002, Millspaugh et al. 2009). Model performance, however, is contingent on the accuracy of parameter estimates based on auxiliary data. Our results suggest that most variability in rates of harvest of adult male white-tailed deer

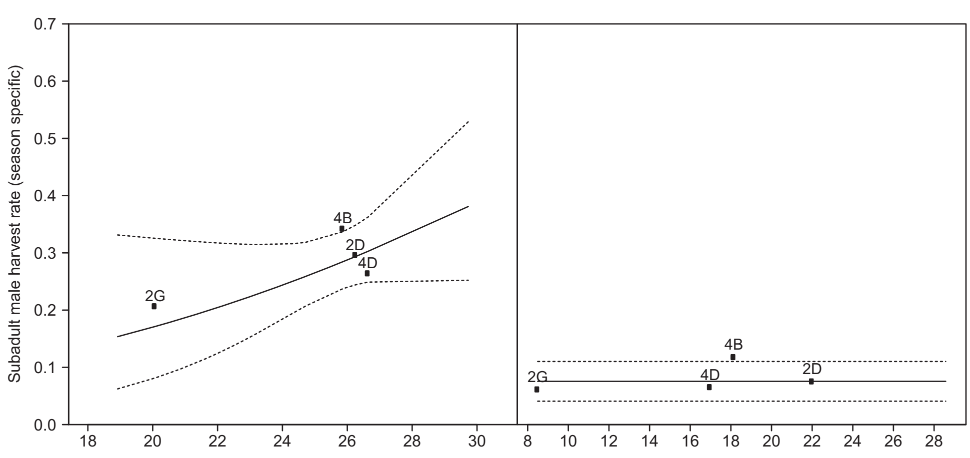

Figure 4. Predicted harvest rates of white-tailed deer by hunting season for subadult (1.5 yr old; solid line) males with 95% confidence intervals (dashed lines) modeled as a function of hunter effort (hunter-days/km^2) in Pennsylvania, USA, 2002–2008. Point estimates for study area-specific harvest rates are included. Values on the x-axis indicate the range of hunter effort (hunter-days/km^2) among 19 wildlife management units.

in Pennsylvania can be explained by spatial variation in hunting effort. Similar variability exists in subadult male harvest rates; however, it seems that APR regulations in Pennsylvania limit the extent of variability.

Caution should be used, however, when applying modeled or constant harvest rates to other management units. For example, we would not recommend using equivalent values for hunter effort to estimate harvest rates in management units with different hunting regulations (e.g., sporting arm restrictions or extended seasons), such as WMUs in Pennsylvania that encompass urban and suburban areas of Philadelphia and Pittsburgh. Although our models indicated less evidence for temporal variation in antlered harvest rates, temporal changes in hunting regulations or hunter behavior could change male harvest rates. For example, because of increasing interest by hunters in QDM practices and protection of younger-aged male deer, harvest rates of subadult male deer may change over time, as well as over space.

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