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Management and Conservation

Incorporating Harvest Rates Into the Sex-Age-Kill Model for White-Tailed Deer

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ABSTRACT Although monitoring population trends is an essential component of game species management, wildlife managers rarely have complete counts of abundance. Often, they rely on population models to monitor population trends. As imperfect representations of real-world populations, models must be rigorously evaluated to be applied appropriately. Previous research has evaluated population models for white-tailed deer (*Odocoileus virginianus*); however, the precision and reliability of these models when tested against empirical measures of variability and bias largely is untested. We were able to statistically evaluate the Pennsylvania sex-age-kill (PASAK) population model using realistic error measured using data from 1,131 radiocollared white-tailed deer in Pennsylvania from 2002 to 2008. We used these data and harvest data (number killed, age-sex structure, etc.) to estimate precision of abundance estimates, identify the most efficient harvest data collection with respect to precision of parameter estimates, and evaluate PASAK model robustness to violation of assumptions. Median coefficient of variation (CV) estimates by Wildlife Management Unit, 13.2% in the most recent year, were slightly above benchmarks recommended for managing game species populations. Doubling reporting rates by hunters or doubling the number of deer checked by personnel in the field reduced median CVs to recommended levels. The PASAK model was robust to errors in estimates for adult male harvest rates but was sensitive to errors in subadult male harvest rates, especially in populations with lower harvest rates. In particular, an error in subadult (1.5-yr-old) male harvest rates resulted in the opposite error in subadult male, adult female, and juvenile population estimates. Also, evidence of a greater harvest probability for subadult female deer when compared with adult (≥2.5-yr-old) female deer resulted in a 9.5% underestimate of the population using the PASAK model. Because obtaining appropriate sample sizes, by management unit, to estimate harvest rate parameters each year may be too expensive, assumptions of constant annual harvest rates may be necessary. However, if changes in harvest regulations or hunter behavior influence subadult male harvest rates, the PASAK model could provide an unreliable index to population changes.

KEY WORDS bootstrap, *Odocoileus virginianus*, Pennsylvania, precision, robustness, sensitivity, sex-age-kill model, white-tailed deer.

Population monitoring is considered essential to deer management (Roseberry and Woolf 1991, Focardi et al. 1996, Mourão et al. 2000, Matsuda et al. 2002). However, wildlife managers rarely have complete counts to monitor deer abundance and therefore generally rely on samples of harvest data and population models to monitor deer populations (Williams et al. 2001, Matsuda et al. 2002, Milner et al. 2006, Morellet et al. 2011). Accordingly, knowledge of the effect of violation of assumptions on accuracy and precision of population estimates is necessary when using model estimates to make management decisions.

The sex-age-kill (SAK) model (Eberhardt 1960, Creed et al. 1984, Millspaugh et al. 2009), originally developed in the 1950s, has been used widely in the United States to estimate population size for white-tailed deer because all management agencies have formal methods of collecting data on harvests on public and private lands. The simplicity of the model and the ability to use readily available age-at-harvest data is appealing. However, only recently has this model been critically evaluated (Skalski and Millspaugh 2002; Millspaugh et al. 2007, 2009).

Criticism of the SAK model includes the assumption of a stable age distribution and stationary population, which is unlikely to be met in most environments, and sensitivity to

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changes in male harvest rate (Millspaugh et al. 2009). A recent evaluation of the SAK model, as applied in Wisconsin, indicated several additional difficulties: 1) not all input parameters had measures of precision, 2) sensitivity to stochasticity in input parameters, and 3) large sample sizes required to obtain precise estimates (Millspaugh et al. 2007). Computer simulation has been used to estimate precision and evaluate the influence of stochastic variability (Focardi et al. 1996, Matsuda et al. 2002, Grund and Woolf 2004, Millspaugh et al. 2007). Although these evaluations provide a better understanding of model sensitivity to specific parameters, they have been constrained by the use of relatively arbitrary levels of parameter variation because of limited empirical data. Specifically, previous versions of the SAK model have used subjective criteria for estimating and modeling variation in the percent of antlered deer mortality associated with legal, recovered harvest (Wisconsin Department of Natural Resources 2001).

An estimate of sampling variability for all input parameters is required for a statistically rigorous method of estimating precision (Skalski and Millspaugh 2002). Additionally, empirically based estimates of parameter variance can be used to evaluate model robustness via computer simulation (Fieberg et al. 2010). Information about parameter variability also can be used to efficiently allocate resources to monitor populations (Skalski and Millspaugh 2002).

The Pennsylvania Game Commission (PGC) modified the SAK model (hereafter termed PASAK model) to eliminate the assumption of a stable and stationary population by using empirical estimates for all input parameters. In 2002, the PGC initiated antler point restriction regulations, requiring antlered deer harvests to have $\geq$1 antler with either $\geq$3 or $\geq$4 points, depending on the wildlife management unit (WMU), which protect approximately 50% of the subadult (1.5-yr-old) male population from harvest. Most 2.5-year-olds and older male deer are legal to harvest and are subject to higher harvest rates (Norton et al. 2012). Consequently, the age structure of the harvest does not represent the age structure of the population because of different harvest rates by age class. The PASAK model accounts for differential harvest rates among age classes by obtaining separate population estimates for adult ($\geq$2.5-yr-old) and subadult males based on empirical estimates of harvest rate by age class using known-fate data from radio telemetry studies. In addition, evidence for hunter selectivity in harvesting adult female versus juveniles (0.5-yr-old) required modification of other parameter estimates in the SAK model.

Although the PASAK model addressed several important criticisms regarding the assumptions of the SAK model, not all concerns with model performance were eliminated. Questions still remained concerning assumptions and deterministic and stochastic effects arising from demographic, temporal, and spatial variability in harvest rates, as well as changes in management strategies and data collection. Specifically, in Pennsylvania, parameter estimates for harvest rates from radiocollared deer have been applied to WMUs without representative samples and in years after deer were radiocollared. Additionally, collection of harvest data is costly and we were interested if agency resources could be allocated more efficiently, in particular the number of harvested deer checked by agency personnel and the method in which harvested deer were reported by hunters.

For the PASAK model, our objectives were to 1) estimate precision of abundance estimates, 2) identify the most efficient harvest data collection with respect to precision of parameter estimates, and 3) evaluate PASAK model robustness to the violation of assumptions of constant antlered deer harvest rate across space and time and constant harvest rates between subadult and adult female age-classes. To accomplish these objectives we 1) used a Monte Carlo resampling procedure to estimate precision, 2) evaluated changes in precision with different sampling intensities of harvest data, and 3) used computer simulation to assess model robustness to violation of assumptions based on empirical estimates of harvest and harvest rates.

STUDY AREA

Pennsylvania deer abundance is estimated by WMU. Twenty-two WMUs have been delineated to encompass areas with similar vegetation types and patterns, physiographic features, and human population characteristics and to provide a suitable scale to collect data to estimate harvest parameters. Besides collecting harvest data from each WMU, we estimated survival and harvest rates, from known-fate data from radiocollared deer during 2002–2008 in 4 geographic areas in Pennsylvania, USA. These 4 study areas encompassed 3 ecological regions, each with different physiographic characteristics (Fig. 1), and we refer to each study area by the WMU where it primarily 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.). 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 $\geq$3 or $\geq$4 antler points $\geq$2.5 cm on at least 1 antler depending on the WMU. These regulations protected at least 50% of the subadult males (1.5-yr-old during the hunting season) from harvest, but most adult males ($\geq$2.5-yr-old during the hunting season) were legal for harvest (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

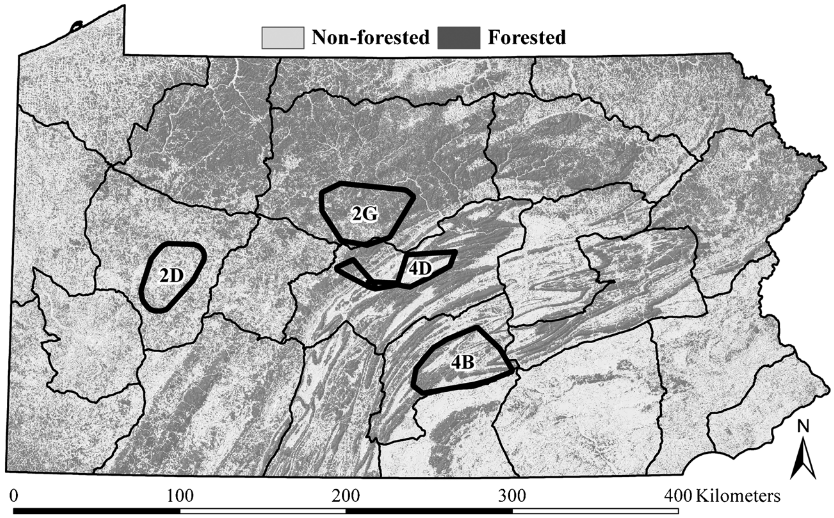

Figure 1. Map of white-tailed deer study areas in wildlife management units (WMU) 2D, 2G, 4B, and 4D. Twenty-two Pennsylvania Game Commission WMUs are delineated with thin black lines, Pennsylvania, USA, 2002–2008.

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

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. This region was in a transition zone between the Appalachian oak and northern hardwoods forest. The landscape in WMU 2G was 90% forested and had a tradition of deer hunting from camps (Zinn 2003). The study area included State Game Lands 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 forested ridges.

METHODS

Abundance Estimation

Hunter harvest data and estimation of survival and harvest rates of radiocollared deer provided the input required to estimate deer abundance using the PASAK model (Norton 2010, Norton et al. 2012). We aged deer aged to 3 age classes, juvenile (6–10 months old), subadult (18–20 months old), and adult ($\geq$30 months old), by evaluating tooth wear and replacement (Severinghaus 1949). The following explanation of the PASAK model refers to how we estimated deer abundance in a given WMU.

We estimated the adult male harvest rate (H_{AM}) from radio telemetry data using logistic regression (Norton et al. 2012). Hunter selection or avoidance of radio- or Global Positioning System (GPS)-collared deer is possible (Jacques et al. 2011), but we have failed to detect differences in male and female harvest rates among deer fitted with radiocollars, less visible ear tag transmitters (Wallingford 2012), and reward ear tags that were only detectable after a deer was harvested (D. R. Diefenbach, unpublished data) in Pennsylvania. The pre-season adult male population estimate ($\hat{N}_{AM}$) was the adult male harvest estimates ($\hat{K}_{AM}$) divided by $\hat{H}_{AM}$,

$$\hat{N}_{AM} = \frac{\hat{K}_{AM}}{\hat{H}_{AM}}$$

We estimated sex- and age-specific harvests (K) for each WMU, each year using a Lincoln–Petersen (LP) estimator corrected for small sample size (Chapman 1951),

$$\hat{K} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

where n_1 was the number of harvested deer checked in the field, n_2 was the number of harvested deer reported, and m_2 was the number of harvested deer checked and reported (Rosenberry et al. 2004). Harvested deer were reported by hunters who were required to report any legal deer harvest by mail or internet (Rosenberry et al. 2004). Trained PGC personnel collected biological information and verified harvest in the field from local deer processors during the regular Pennsylvania firearms hunting season (Rosenberry et al. 2004).

Similar to the adult male abundance estimate, we divided the subadult male (1.5-yr-old) harvest estimate ($\hat{K}_{YM}$) by the subadult male harvest rate ($\hat{H}_{YM}$), estimated from radio-collar data, to provide a subadult male pre-hunting season abundance estimate ($\hat{N}_{YM}$),

$$\hat{N}_{YM} = \frac{\hat{K}_{YM}}{\hat{H}_{YM}}$$

After we estimated the mature ($\geq$1.5-yr-old) male population (N_{Amtld}), $\hat{N}_{Antld} = \hat{N}_{AM} + \hat{N}_{YM}$, we used ratios to estimate abundance of other age and sex classes. Specifically, we used mature female to mature male ratios ($\hat{p}_{F:M}$) and juvenile to mature female ratios ($\hat{p}_{J:F}$) to estimate mature female N_F and juvenile N_J population sizes, respectively:

$$\hat{N}_F = \hat{N}_{Antld} \times \hat{p}_{F:M}$$

$$\hat{N}_J = \hat{N}_F \times \hat{p}_{J:F}$$

We estimated the $p_{F:M}$ by dividing the proportion of subadult males in the mature male population ($\hat{p}_{YM:Antld}$),

$$\hat{P}_{YM:Antld} = \frac{\hat{N}_{YM}}{\hat{N}_{AM} + \hat{N}_{YM}}$$

by the proportion of subadult (1.5-yr-old) females in the mature female population ($\hat{p}_{YF:F}$) obtained from harvest data (Severinghaus and Maguire 1955):

$$\hat{p}_{F:M} = \frac{\hat{p}_{YM:Antld}}{\hat{p}_{YF:F}}$$

Because antler point restrictions protect roughly half the subadult male population from harvest, we did not assume the antlered deer harvest age structure was representative of the antlered deer population. Thus we modified the original method (Severinghaus and Maguire 1955) by using abundance estimates calculated using the PASAK model for the $\hat{p}_{YM:Antld}$ instead of using harvest data.

We estimated juvenile to mature female ratios ($p_{J:F(t)}$) using 3 steps. First, we estimated a juvenile to mature female ratio for the previous year ($p_{J:F(t-1)}$). To do this, we back-calculated a juvenile population for the previous year from the $\hat{N}_{YM(t)}$. We assumed subadult males and females to be recruited equally, so we could multiply the $\hat{N}_{YM(t)}$ by 2 to estimate a subadult population ($\hat{N}_{yrlg(t)}$), which we then divided by subadult non-harvest survival $S_{yrlg(nonharv)}$, to provide a juvenile population for the previous year, excluding harvest. We then added the juvenile harvest, ($\hat{K}_{J(t-1)}$), to estimate the juvenile population in the previous year. We divided the pre-season juvenile population by the $\hat{N}_{F(t-1)}$ to estimate the juvenile to mature female ratio for $t - 1$ ($p_{J:F(t-1)}$),

$$\hat{p}_{J:F(t-1)} = \frac{((\hat{N}_{YM(t)} \times 2)/\hat{S}_{yrlg(nonharv)}) + \hat{K}_{J(t-1)}}{\hat{N}_{F(t-1)}}$$

Second, we divided the $p_{J:F(t-1)}$, from the previous step, by the juvenile to mature female ratio from harvest data ($\hat{p}_{J:F(harvest)(t-1)}$),

$$\frac{\hat{p}_{J:F(t-1)}}{\hat{p}_{J:F(harvest)(t-1)}}$$

which provided a correction factor ($\hat{C}_{J:F(t-1)}$) to account for hunter selectivity for mature females over juveniles. This correction factor used data from previous and future years depending on available data. For the current year t, we averaged $\hat{C}_{J:F}$ across years $t - 1$, $t - 2$, and $t - 3$. For years $t - k$, when $k \geq 1$, we updated the correction factor using harvest data from $(t - k) + 1$.

For the third and final step, we estimated the $p_{J:F}$ by multiplying the $\hat{p}_{J:F(harvest)}$ by the appropriate correction factor. The abundance of all sex-age classes combined was:

$$\hat{N} = \hat{N}_{Antld} + \hat{N}_F + \hat{N}_J$$

Precision

We quantified precision of the PASAK model using a Monte Carlo parametric bootstrapping method (Efron 1979) similar to Millspaugh et al. (2007). We conducted 1,000 Monte Carlo bootstraps of the empirical data to generate 1,000 population estimates from a random sample of the data selected with replacement. A fundamental assumption of the parametric bootstrap is that each parameter has an underlying distribution with a specific mean and variance (Millspaugh et al. 2007). Because all PASAK model parameters were constrained between 0 and 1, we conducted the bootstrap using either a binomial distribution, $B(n, p)$, or a beta distribution, $Beta(\alpha, \beta)$, based on empirical data collected by the PGC. Precision of population estimates was the standard deviation of the replicate simulation estimates of N. We estimated 90% confidence intervals from the 5th and 95th percentiles of simulation estimates of N. Also, we calculated the coefficient of variation (CV) as $(\widehat{SE}(\hat{N}))/\hat{N} \times 100\%$. We estimated population size and precision for each WMU in Pennsylvania from 2002 to 2008.

We evaluated the effect of varying sample sizes on the precision of abundance estimates to establish adequate harvest data collection efforts. The harvest data collected by PGC personnel were: 1) age and sex of deer checked in the field, and 2) proportion of deer checked that were reported by hunters via Internet or mail-in report cards. We calculated a mean CV across WMUs when hypothetical sample sizes associated with the harvest data were doubled and halved, then compared the CVs to our estimated CVs using actual sample sizes. Because PASAK model estimates are updated in year $t-1$ using data from the following year, we compared CV differences in years $\leq t-1$ separately from year t. Notably, changing the number of harvested deer checked (n_1) or reported (n_2) did not change the LP harvest estimates, because our hypothetical change in the number of harvested deer checked or deer reported was similarly reflected with a proportionate change in the number of harvested deer reported and checked (m_2). In reality, these hypothetical changes could be the result of a change in effort by the management agency to check more or less deer in the field or influence hunter reporting rates.

Robustness

We evaluated model robustness by comparing 50 years (t) of a simulated population trajectory, generated via a stage-structured deterministic population model, with associated PASAK model estimates based on perfect sampling with no stochastic errors from the simulated population (Millspaugh et al. 2007). Let

M, 2-sex Leslie matrix model;
H, harvest matrix;
$\mathbf{n}_t$, vector of age and sex specific abundance immediately preceding the hunting season;
R_a, recruitment of 6-month-old females or males in year $t+1$ from age class a (a = 0.5-yr-old, $\geq$1.5-yr-old in year t) females immediately following the harvest;
S, probability of annual survival excluding legal harvest;
H_{as}, probability of harvest for age class a (a = juvenile, subadult, adult) females (s = F) or males (s = M);
$n_{as,t}$, number of age class a (a = 0.5-yr-old, 1.5-yr-old, $\geq$2.5-yr-old) females (s = F) or males (s = M) in the population immediately preceding the harvest in year t;
N_t, number of deer in the population immediately preceding the harvest in year t, summed across all age and sex classes.

Then the deterministic simulated population is calculated as follows

$$n_{t+1} = M \times Hn_t$$

where

$$\begin{bmatrix} n_{0.5\mathrm{F},t+1} \\ n_{1.5\mathrm{F},t+1} \\ n_{\geq 2.5\mathrm{F},t+1} \\ n_{0.5\mathrm{M},t+1} \\ n_{1.5\mathrm{M},t+1} \\ n_{\geq 2.5\mathrm{M},t+1} \end{bmatrix} = \begin{bmatrix} R_{0.5} & R_{\geq 1.5} & R_{\geq 1.5} & 0 & 0 & 0 \\ S & 0 & 0 & 0 & 0 & 0 \\ 0 & S & S & 0 & 0 & 0 \\ R_{0.5} & R_{\geq 1.5} & R_{\geq 1.5} & 0 & 0 & 0 \\ 0 & 0 & 0 & S & 0 & 0 \\ 0 & 0 & 0 & 0 & S & S \end{bmatrix}$$
$$\times \begin{bmatrix} 1-H_{\mathrm{J}} & 0 & 0 & 0 & 0 & 0 \\ 0 & 1-H_{\mathrm{YF}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 1-H_{\mathrm{AF}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-H_{\mathrm{J}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 1-H_{\mathrm{YM}} & 0 \\ 0 & 0 & 0 & 0 & 0 & 1-H_{\mathrm{AM}} \end{bmatrix}$$
$$\times \begin{bmatrix} n_{0.5\mathrm{F},t} \\ n_{1.5\mathrm{F},t} \\ n_{\geq 2.5\mathrm{F},t} \\ n_{0.5\mathrm{M},t} \\ n_{1.5\mathrm{M},t} \\ n_{\geq 2.5\mathrm{M},t} \end{bmatrix}$$

and

$$\sum_{a}^{\infty} n_{a\mathrm{F},t} + \sum_{a}^{\infty} n_{a\mathrm{M},t} = N_t$$

Under this scenario, we assumed an independent study had estimated all parameters used in the PASAK model with no sampling error. Thus, population estimates from the PASAK would coincide exactly with the simulated population. We individually varied parameters used in our simulated population to evaluate effects of process variation, and possible violation of assumptions, specifically related to H_{YM}, H_{AM}, and H_{F}. The PASAK model uses constant $\hat{H}_{\mathrm{YM}}$ and $\hat{H}_{\mathrm{AM}}$ each year, and predicts spatial variation in $\hat{H}_{\mathrm{YM}}$ and $\hat{H}_{\mathrm{AM}}$ as a function of hunter effort (Norton et al. 2012). We evaluated the potential implications when using constant $\hat{H}_{\mathrm{YM}}$ and $\hat{H}_{\mathrm{AM}}$ across time for PASAK model estimates, while simulated parameters (H_{YM} or H_{AM}) varied across some interval. We also evaluated implications of biased estimates of $\hat{H}_{\mathrm{YM}}$ and $\hat{H}_{\mathrm{AM}}$ by considering simulated parameters that were consistently above or below estimated parameters. In addition, because harvest data are used to calculate $\hat{p}_{\mathrm{YF:F}}$ for the PASAK model, subadult and adult female harvest rates are assumed to be similar. We evaluated the influence of different harvest detection rates between subadult and adult female deer by varying H_{YF} and H_{AF}.

To evaluate the influence of each parameter on model performance, we fixed all other simulated population parameters (i.e., deterministic model), except for the parameter of interest. For example, simulated adult male harvest rates (H_{AM}) uniformly varied between 0.292 and 0.422, whereas all other simulated parameters did not vary. In this scenario, the PASAK model would use a constant $\hat{H}_{\mathrm{AM}}$ of 0.357. This would allow us to evaluate error of the PASAK model when it does not account for hypothetical process variance in H_{AM}. We also used higher or lower harvest rates in the simulated population to assess a hypothetical bias of harvest rate estimates in addition to process variance. For example, simulated H_{AM} uniformly varied between 0.556 and 0.686, whereas the PASAK model would use a constant, underestimated $\hat{H}_{\mathrm{AM}}$ of 0.357. This does not necessarily represent variation likely occurring in all population parameters, but allowed us to evaluate model sensitivity, with respect to empirically supported measures of precision and bias, of individual parameter inputs.

We used conservative estimates of process variance to construct interval endpoints for individual simulated harvest rates that varied. First, we estimated the standard deviation for annual estimates of the parameter of interest from a previous study in Pennsylvania (Norton 2010, Norton et al. 2012). Because this standard deviation contained both process variance and sampling variance, we overestimated the actual process variance (Lukacs et al. 2009). We used a 95% confidence interval based on a standard Normal distribution, but uniformly varied parameters within this interval rather than concentrating them about the mean value.

To evaluate the effects of biased point estimates of H_{YM} or H_{AM}, we first calculated the standard deviation from 4 Pennsylvania study area estimates (Norton et al. 2012). We then centered the known, simulated interval, 1.96 standard deviations above (or below) the harvest rate used for the PASAK model estimate. Under this scenario, in addition to considering process variance, we evaluated PASAK model sensitivity when harvest rates are consistently underestimated and overestimated by levels supported by empirical data. We evaluated PASAK model robustness to errors in H_{YM} and H_{AM} based on estimates from WMU 2G and 4B (Norton et al. 2012).

Because H_F by WMU are not directly used in the PASAK model, we evaluated differential harvest vulnerability of older age female deer, related to the assumption that H_F were constant across age classes. First, we evaluated how subadult female harvest rates (H_{YF}) and adult female harvest rates (H_{AF}), sampled from the same uniform distribution and varied independently of one another, affected abundance estimates. Next, we considered differential vulnerability of H_{AF} relative to H_{YF}. For example, when older females were more vulnerable to harvest, H_{YF} was sampled from U(0.100–0.168) and H_{AF} from U(0.164–0.232). Similar to male harvest rates, we used results from previous research to suggest levels of variation and the extent of possible bias in female harvest rates (Norton 2010).

We quantified model sensitivity to process variance and bias using 2 statistics that compared the known simulated population (N_{ti}) to the PASAK model estimates of the population ($\hat{N}_{PASAK,ti}$), indexed for each year t ($t = 1, 2, \ldots, T$; where $T = 50$) and each simulation i ($i = 1, 2, \ldots$, I; where $I = 10{,}000$). First, we averaged the difference between PASAK model population estimates and true simulated populations to calculate bias,

$$\text{bias} = \frac{\sum_{t=1}^{T}\sum_{i=1}^{I}(\hat{N}_{PASAK,ti} - N_{ti})}{T \times I}$$

then divided each error by N_{ti} to calculate percent relative bias (PRB),

$$\text{PRB} = \frac{\sum_{t=1}^{T}\sum_{i=1}^{I}((\hat{N}_{PASAK,ti} - N_{ti})/N_{ti})}{T \times I}$$

Finally, we calculated mean squared error and a pseudo-coefficient of variation (CV_{pop}) as precision estimates. Similar to bias and PRB, we averaged the squared difference between PASAK model population estimates and true simulated populations to calculate mean squared error (MSE),

$$\text{MSE} = \frac{\sum_{t=1}^{T}\sum_{i=1}^{I}(\hat{N}_{PASAK,ti} - N_{ti})^2}{T \times I}$$

then divided each squared error by N_{ti} to calculate CV_{pop},

$$CV_{pop} = \frac{\sum_{t=1}^{T}\sum_{i=1}^{I}(((\hat{N}_{PASAK,ti} - N_{ti})^2)/N_{ti})}{T \times I}$$

We used SAS (SAS Institute, Cary, NC) to simulate a population trajectory and estimate abundance.

Table 1. Summary statistics of the coefficient of variation ($CV = (SE(\hat{N}))/\hat{N} \times 100\%$) for white-tailed deer abundance estimates in 19 wildlife management units (WMU) in Pennsylvania, 2002–2008. Urban and suburban WMUs that encompass the cities of Pittsburgh (WMU 2B) and Philadelphia (WMUs 5C and 5D) are not included.

	CV			
Year	Min.	Median	90th percentile	Max.
2002	6.6	7.3	9.2	10.2
2003	6.3	7.2	9.6	12.8
2004	6.8	7.5	9.5	12.7
2005	6.6	7.5	9.4	13.2
2006	6.7	7.8	10.2	13.4
2007	6.9	7.9	9.3	16.1
2008	11.5	13.2	16.4	23.8

RESULTS

We obtained population estimates by WMU that had a median CV of ≤13.2%, and in all but 2007 and 2008, the maximum CV among all WMUs was <14% (Table 1). Median CV estimates were >10% in the most recent (i.e., current) year because subadult male population estimates from the following year were not yet available. Doubling the number of harvested deer aged improved precision of population estimates better than doubling the number of deer reported. If twice as many harvested deer were aged, we estimated mean CV across WMUs would decrease by 2.69% in year t, whereas mean CV would increase by 4.69% if half as many harvested deer were aged (Table 2). Similarly, if twice as many deer harvests were reported in the most recent year, mean CV decreased by 1.91%, whereas mean CV would increase by 3.28% if half as many deer harvests were reported

Table 2. A comparison of estimated coefficients of variation ($CV = (SE(\hat{N}))/\hat{N} \times 100\%$) for white-tailed deer abundance estimates for different sample sizes of data collection, from 2002–2008. The difference and percent change to mean CVs across 19 wildlife management units in Pennsylvania for year t (14.1%) and year $\leq t-1$ (8.0%) are reported when sample sizes are doubled and halved for number of deer checked and aged, and number of deer reported. Urban and suburban wildlife management units for Pittsburgh (WMU 2B) and Philadelphia (WMU 5C and 5D) are not included.

		Sampling effort			
		Doubled		Halved	
Year	Parameter	Mean difference	% change	Mean difference	% change
t	No. of deer checked and aged	−2.69	−19.12	4.69	33.36
t	No. of deer reported	−1.91	−13.59	3.28	23.34
$\leq t-1$	No. of deer checked and aged	−1.16	−14.98	2.02	26.42
$\leq t-1$	No. of deer reported	−1.07	−13.76	2.00	26.20

Table 3. Pennsylvania sex-age-kill (PASAK) model robustness statistics considering uniform variation (process variance) only and uniform variation with bias ($\pm 1.96 \times$ SD) to: subadult male harvest rate (H_{YM}) and adult male harvest rate (H_{AM}) using $\hat{H}_{YM}$ and $\hat{H}_{AM}$ from wildlife management units (WMUs) 2G and 4B. Mean abundance ($\overline{N}$) across 50 years and 10,000 simulations provides an indication of the simulated population size.

Parameter	WMU	Bias	PASAK used[a]	Actual interval	$\overline{N}$	ME[b]	PRB[c] (%)	MSE[d]	CV_{pop}[e] (%)
H_{YM}	2G	None	0.255	0.222–0.288	54,411	−109	0.21	17,384,974	5.82
H_{YM}	2G	0.136	0.255	0.086–0.152	55,958	−24,238	−25.51	636,932,079	43.34
H_{YM}	2G	−0.136	0.255	0.358–0.424	52,864	24,022	61.93	640,196,172	45.43
H_{YM}	4B	None	0.420	0.387–0.453	50,880	−107	−0.21	10,484,478	4.82
H_{YM}	4B	0.136	0.420	0.251–0.317	52,046	−14,745	−28.33	238,966,233	28.33
H_{YM}	4B	−0.136	0.420	0.523–0.589	49,713	14,549	29.25	239,685,239	29.25
H_{AM}	2G	None	0.357	0.292–0.422	54,411	−103	−0.19	11,340,957	4.67
H_{AM}	2G	0.264	0.357	0.028–0.158	61,014	−11,286	−18.32	148,485,757	18.33
H_{AM}	2G	−0.264	0.357	0.556–0.686	51,803	4,270	8.25	31,510,728	8.77
H_{AM}	4B	None	0.555	0.490–0.620	50,880	−96	−0.20	8,010,182	4.19
H_{AM}	4B	0.264	0.555	0.226–0.356	53,355	−3,643	−6.83	21,621,698	7.26
H_{AM}	4B	−0.264	0.555	0.754–0.884	49,627	1,687	3.40	11,337,361	5.13

[a] Parameter estimate used in PASAK model.
[b] Mean error $\left(\left(\sum_{i=1}^{n}(\hat{N}-N)\right)/n\right)$.
[c] Percent relative bias.
[d] Mean squared error $\left(\left(\sum_{i=1}^{n}(\hat{N}-N)^2\right)/n\right)$.
[e] Pseudo-coefficient of variation.

(Table 2). Changes in the number of deer aged and reported had similar, but smaller effects on precision prior to the most recent year (Table 2).

The model was most sensitive to error in $\hat{H}_{YM}$ (Table 3). When $\hat{H}_{YM}$ was under or overestimated ($\pm$13.6%), CV_{pop} and PRB were >25%. The greatest sensitivity occurred when the PASAK model underestimated H_{YM} in WMU 2G ($CV_{pop} = 45.43\%$, PRB = 61.93%) because this WMU had the lowest harvest rates of any study area. The PASAK model indicated less sensitivity to variation and error in $\hat{H}_{AM}$ than $\hat{H}_{YM}$ (Table 3). When $\hat{H}_{AM}$ was under or overestimated ($\pm$26.4%), CV_{pop} and PRB were <20%. However, overestimating the H_{AM} in WMU 2G doubled CV_{pop} and PRB when compared to other biases in $\hat{H}_{AM}$. Considering differential female age-class harvest vulnerability, the PASAK model was more sensitive when $\hat{H}_{AF} > \hat{H}_{YF}$ (PRB 14.5% and CV_{pop} 14.86%) compared to $\hat{H}_{AF} < \hat{H}_{YF}$ (PRB −9.48% and CV_{pop} 9.83%; Table 4).

DISCUSSION

The median CV across WMUs was sufficiently precise ($\leq$12.8%; Robson and Regier 1964, Skalski and Millspaugh 2002) for management studies of game species, except in the current year (e.g., 2008 in our data) where the median CV (13.2%) was slightly above the benchmark. The lesser precision in 2008 was inherent to the structure of the model. As described in the methods, population estimates for year $t - 1$ and earlier were updated with data from following years. Because updated estimates for the juvenile to adult female ratio correction factor were not available in the current year, the PASAK model used the average from prior years, which decreased precision of population estimates.

For harvest data collection, WMU CVs in the current year were most sensitive to changes in the number of deer aged and checked. The mean CV across WMUs in the current year could be improved to levels acceptable for management studies of game species ($\leq$12.8%; Robson and Regier 1964, Skalski and Millspaugh 2002) if reporting rates or the number of deer checked and aged were doubled. Because precision was nearly doubled when population estimates were updated in years $\leq t - 1$, doubling or halving sampling effort associated with deer harvest data was relatively negligible in years $\leq t - 1$. Consequently, CVs for estimates in the current year were most sensitive to changes in data collection effort. Although the PGC requires mandatory harvest reporting, the average reporting rate from 2002 to 2008

Table 4. Pennsylvania sex-age-kill (PASAK) model robustness statistics considering independent uniform variation (process variance) only and uniform variation with differential age-class harvest vulnerability ($H_{AF} \neq H_{YF}$), suggesting an assumption violation. Mean abundance ($\overline{N}$) across 50 years and 10,000 simulations provides an indication of the simulated population size.

Age-class variation	H_{YF}[a]	H_{AF}[b]	$\overline{N}$	ME[c]	PRB[d] (%)	MSE[e]	CV_{pop}[f] (%)
$H_{AF} = H_{YF}$	0.116–0.184	0.116–0.184	50,852	183	0.35	17,993,959	6.23
$H_{AF} > H_{YF}$	0.100–0.168	0.164–0.232	32,812	4,748	14.47	34,466,176	14.86
$H_{AF} < H_{YF}$	0.164–0.232	0.100–0.168	47,236	−4,478	−9.48	29,180,106	9.83

[a] Subadult female harvest rate.
[b] Adult female harvest rate.
[c] Mean error $\left(\left(\sum_{i=1}^{n}(\hat{N}-N)\right)/n\right)$.
[d] Percent relative bias.
[e] Mean squared error $\left(\left(\sum_{i=1}^{n}(\hat{N}-N)^2\right)/n\right)$.
[f] Pseudo-coefficient of variation.

was 41.4% (C. S. Rosenberry, PGC, unpublished data). The PGC has recently added point of sale licensing with online harvest reporting, which has the potential to improve reporting rates (Rupp et al. 2000). Regardless of changes in reporting rates, current levels of data collection provide precise population estimates.

The PASAK model proved to be sensitive to variability and bias in subadult male harvest rates. The primary reason the PASAK model was sensitive to changes in this parameter, but robust to changes in the adult male harvest rate was related to the calculation of the $\hat{p}_{\mathrm{F:M}}$ (Severinghaus and Maguire 1955):

$$\hat{p}_{\mathrm{F:M}} = \frac{\hat{p}_{\mathrm{YM:Antld}}}{\hat{p}_{\mathrm{YF:F}}}$$

If N_{YM} was overestimated, which occurred when H_{YM} was underestimated, an overestimate of p_{FM} would result. Because $\hat{N}_{\mathrm{F}}$ was calculated by multiplying $(\hat{N}_{\mathrm{YM}} + \hat{N}_{\mathrm{AM}})$ by $\hat{p}_{\mathrm{F:M}}$, a compounding effect occurred in the bias of N_{F}. Furthermore, an overestimate of N_{YM} would also cause N_{J} to be overestimated in a similar compounding manner. These results indicate how errors in subadult male harvest rates were magnified in subsequent cohort estimates, thus increasing the importance of accurate subadult male harvest rate estimates. In contrast, the only population cohort sensitive to bias in $\hat{H}_{\mathrm{AM}}$ was the adult male population, similar to sensitivity of the subadult male population to bias in $\hat{H}_{\mathrm{YM}}$. These results are similar to conclusions of the Wisconsin SAK model evaluation (Millspaugh et al. 2007).

In general, sensitivity will increase when H_{YM} or H_{AM} decreases as illustrated by the increase in bias and variability in WMU 2G when compared to WMU 4B. As expected, this occurred because the antlered deer harvest rates are denominators in the PASAK model. For example, if 100 adult male deer were harvested and the estimated harvest rate was 80%, a $\pm$ 1% error in the harvest rate would result in a $\pm$ 1.25% relative bias. Alternatively, if 100 adult male deer were harvested and the estimated harvest rate was 20%, a $\pm$ 1% error in the harvest rate would result in a $\pm$ 5.00% relative bias.

We found that hunter selectivity for or against adult female deer compared to subadult females affected the population estimate generated by the PASAK model. Data from Pennsylvania indicated hunters were more likely to harvest subadult females than adult females (Norton 2010). Using $\hat{H}_{\mathrm{YF}}$ and $\hat{H}_{\mathrm{AF}}$ estimated in Pennsylvania (Norton 2010), the population would be underestimated by 9.48%, assuming every other parameter was estimated accurately. This is because $\hat{p}_{\mathrm{F:M}}$ is a ratio (Severinghaus and Maguire 1955):

$$\hat{p}_{\mathrm{F:M}} = \frac{\hat{p}_{\mathrm{YM:Antld}}}{\hat{p}_{\mathrm{YF:F}}}$$

and when $p_{\mathrm{YF:F}}$ is overestimated p_{FM} is underestimated, and population size is consequently underestimated.

Our computer simulations evaluated the effect of bias in individual parameters on total population estimates, not age-sex specific population estimates. Management decisions based on age-sex specific cohort trends or estimates produced by the PASAK model could be incorrect or biased. For example, a biased adult male population estimate would have less of an effect on total population estimates because of the subsequent opposite bias to the adult female population estimate.

Our results demonstrated the challenges of using SAK population estimates to guide deer management decisions. Without annual monitoring of harvest rates in every WMU, making assumptions about the input parameters will remain the most practical alternative for monitoring and estimating deer populations using SAK based models. For WMUs that lack representative samples, harvest rates in Pennsylvania can be predicted using an empirically based relationship between harvest rates and hunter effort, however, this predictive model of harvest rate does not address other sources of variation in harvest rates that may lead to temporal variability (Norton et al. 2012). Consequently, the current structure of the PASAK model lacks a temporal component for male harvest rate estimates and temporal variability in abundance estimates is contingent only on variation in annual harvest. For example, if 1,000 male deer are harvested in both 2009 and 2010, a harvest rate $= 0.50$ would produce an estimate of 2,000 male deer for each year. However, if the model used the stationary harvest rate $= 0.50$, and the actual harvest rate decreased in a particular year, the result of hunter selection or environmental stochasticity during the hunting season (e.g., weather or timing of the rut), the PASAK would not capture the actual increase in the population. Other independent harvest indices that may suggest trends introduced via changes in harvest rate could be used in combination with the PASAK and measures of deer–habitat and deer–human interactions could provide information to monitor this variability (Hayne 1984, McCullough 1984, Morellet et al. 2007). Based on our results, the PASAK will only provide reliable population estimates in Pennsylvania and other regions that use a similar model if stable subadult male harvest rates persist (Norton et al. 2012). Moreover, if subadult female deer are harvested at a greater rate than older females, the population will be underestimated. This will be the case with any SAK model that estimates a $\geq$1.5-year-old male to female ratio using the technique suggested by Severinghaus and Maguire (1955).

Our analysis demonstrated variability and potential for biases in PASAK results. When managing a population across large areas, managers often take a conservative approach to management decisions. For example, continued use of assumptions that result in a negative bias will lead to lower deer population estimates. This may prevent managers from overharvesting a deer population, but also may fail to detect deer population increases that may adversely affect natural communities or exacerbate deer–human conflicts. Undetected deer impacts are less of a concern in Pennsylvania than in deer programs based solely on deer abundance estimates or indices, because the PGC uses independent measures of forest regeneration and deer–human conflicts.

MANAGEMENT IMPLICATIONS

The use of independent harvest rates estimated from empirical data in the PASAK model was an improvement over the SAK model. Harvest rate estimates eliminated the assumption of a stable and stationary population so that deer populations that experienced differential harvest rates by age class could be modeled more accurately. Provided subadult and adult male deer harvest rates are estimated accurately, subadult males and females are equally recruited, and the antlerless harvest age-structure is representative of the antlerless population, the PASAK model can provide reliable abundance estimates needed for deer management decisions.

Monitoring efforts that accurately estimate changes in the subadult male harvest rate due to regulation changes or changes in harvest selectivity by hunters would provide the greatest improvement to PASAK model robustness. Substantial data about subadult and adult male harvest rates are needed to generate precise and accurate population estimates. Without annual harvest rate estimates for every management unit, the PASAK model, similar to other population models, requires extrapolating harvest rates from study areas to other management units. As a result, the PASAK model and other models may be more useful for tracking population trends within management units. When management objectives are not defined by deer abundance, population trend information is adequate for deer management decisions (Hayne 1984). However, sensitivity of the PASAK model to individual parameter estimates highlights its potential to produce erroneous population trends and managers should be mindful of these shortcomings when interpreting trends. Additional independent indices could be used to support of refute trends suggested from PASAK model results.

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