

# An Evaluation of Sex-Age-Kill (SAK) Model Performance

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**ABSTRACT** The sex-age-kill (SAK) model is widely used to estimate abundance of harvested large mammals, including white-tailed deer (*Odocoileus virginianus*). Despite a long history of use, few formal evaluations of SAK performance exist. We investigated how violations of the stable age distribution and stationary population assumption, changes to male or female harvest, stochastic effects (i.e., random fluctuations in recruitment and survival), and sampling efforts influenced SAK estimation. When the simulated population had a stable age distribution and  $\lambda > 1$ , the SAK model underestimated abundance. Conversely, when  $\lambda < 1$ , the SAK overestimated abundance. When changes to male harvest were introduced, SAK estimates were opposite the true population trend. In contrast, SAK estimates were robust to changes in female harvest rates. Stochastic effects caused SAK estimates to fluctuate about their equilibrium abundance, but the effect dampened as the size of the surveyed population increased. When we considered both stochastic effects and sampling error at a deer management unit scale the resultant abundance estimates were within  $\pm 121.9\%$  of the true population level 95% of the time. These combined results demonstrate extreme sensitivity to model violations and scale of analysis. Without changes to model formulation, the SAK model will be biased when  $\lambda \neq 1$ . Furthermore, any factor that alters the male harvest rate, such as changes to regulations or changes in hunter attitudes, will bias population estimates. Sex-age-kill estimates may be precise at large spatial scales, such as the state level, but less so at the individual management unit level. Alternative models, such as statistical age-at-harvest models, which require similar data types, might allow for more robust, broad-scale demographic assessments. (JOURNAL OF WILDLIFE MANAGEMENT 73(3):442–451; 2009)

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**KEY WORDS** deer, harvest, *Odocoileus virginianus*, population estimate, population reconstruction, sex-age-kill, white-tailed deer.

Population reconstruction methods have a long history of use in fisheries and wildlife management. Starting 70 years ago, wildlife managers used reconstruction techniques extensively because data (e.g., age and sex data from hunter harvest) were relatively inexpensive and easy to collect and could be used in demographic assessments for large areas (e.g., Allen 1942, Dale 1952, Petrides 1954). In addition, calculations could be performed by hand or with simple computer spreadsheets. Despite advances in statistical theory and quantitative tools for estimating animal abundance (Buckland et al. 1993, Williams et al. 2001), state agencies continue to use population reconstruction methods as a primary technique for broad-scale population assessments of game species (Skalski et al. 2005).

The sex-age-kill (SAK) model of population reconstruction is used by  $\geq 20$  state agencies to estimate white-tailed deer (*Odocoileus virginianus*) abundance (Skalski and Millspaugh 2002, Millspaugh et al. 2007). The SAK model is one variant of a large suite of reconstruction methods using hunter harvest data and was developed by the Michigan Department of Conservation in the late 1950s (Eberhardt 1960, Lang and Wood 1976, Skalski et al. 2005). Although it has been used primarily to estimate white-tailed deer abundance, variations of the SAK model have been applied

to other species, including black bears (*Ursus americanus*) and elk (*Cervus elaphus*; Bender and Spencer 1999).

Despite its widespread use, there have been few formal evaluations of the statistical properties of the SAK model (Skalski and Millspaugh 2002). Only recently have generic variance expressions been provided and precision of the technique evaluated. Skalski and Millspaugh (2002) found that precise field data were necessary to provide a useful estimate of population abundance. Even with intense data collection, however, it is unclear whether SAK-model estimates are robust to stochastic effects (i.e., fluctuations in survival and recruitment), changes in harvest strategies, or realistic violations of underlying assumptions of a stable age distribution and stationary population (hereafter stable-stationary). Effective management requires biologists to consider the utility of various analytical and sampling options with respect to population objectives.

Our objective was to examine SAK performance when stochasticity and sampling error were considered and model assumptions were violated. We evaluated the error in estimates when the stable-stationary assumption was violated (including general changes to population growth rate ( $\lambda$ ) and, more narrowly, to changes in male and female harvest rates), and under stochastic variation in model parameters. Building on the work of Skalski and Millspaugh (2002), we examined the combined effects of sampling error and parameter stochasticity on SAK estimation.

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## METHODS

### Overview of SAK Model

The following overview of the SAK model is summarized from Skalski and Millsbaugh (2002) and Skalski et al. (2005). The generic equation for the SAK model is as follows:

$$\hat{N}_T = \frac{\hat{H}}{\hat{M}_T \hat{B}} [1 + \hat{R}_{F/M} + \hat{R}_{F/M} \cdot \hat{R}_{J/F}] \quad (1)$$

where

- $\hat{N}_T$  = estimate of total abundance;
- $\hat{H}$  = estimated adult male harvest in year  $i$ ;
- $\hat{M}_T$  = total annual mortality rate of adult males;
- $\hat{B}$  = proportion of total male mortality due to harvest (male recovery rate);
- $\hat{R}_{F/M}$  = estimated ratio of adult females to adult males in the population;
- $\hat{R}_{J/F}$  = estimated ratio of juveniles to adult females in the population.

The first factor in equation 1 estimates male abundance. Multiplying male abundance by the female:male sex ratio estimates female abundance. The third term estimates juvenile abundance by the product of female abundance and the juvenile:female ratio. This generic form of the SAK model (eq 1) contains no assumptions about the structure of the population or its dynamics over time (Skalski and Millsbaugh 2002). However, to estimate some of the input parameters, the stable-stationary assumption is often invoked.

With the stable-stationary assumption,  $\hat{M}_T$  can be estimated by the proportion ( $\hat{p}_{YM}$ ) of 1.5-year-old males in the adult male segment of the population (Burgoyne 1981).

The Burgoyne (1981) estimator  $\hat{M}_T$  is based on the additional assumption that hunter harvest provides a representative sample of the age structure of the male population. Because most hunters are opportunistic in their selection of deer to harvest, this assumption of representative sampling is reasonably satisfied. Additionally,  $\hat{R}_{F/M}$  can be estimated by Severinghaus and Maguire (1955) as follows:

$$\hat{R}_{F/M} = \frac{\hat{p}_{YM}}{\hat{p}_{YF}} \cdot \hat{\theta}, \quad (2)$$

where

- $\hat{p}_{YF}$  = proportion of 1.5-year-old females in the adult female segment of the population;
- $\hat{\theta}$  = the sex ratio of fetal males:females.

Thus, the final form of the SAK model, where estimated deer abundance during the current year ( $\hat{N}_i$ ) is as follows:

$$\hat{N}_i = \frac{\hat{H}_i}{\hat{p}_{YM} \hat{B}} \left[ 1 + \frac{\hat{p}_{YM}}{\hat{p}_{YF}} \cdot \hat{\theta} + \frac{\hat{p}_{YM}}{\hat{p}_{YF}} \cdot \hat{\theta} \cdot \hat{R}_{J/F} \right]. \quad (3)$$

In addition to the stable-stationary assumption, it is assumed that sample surveys provide unbiased estimates of the input parameters (i.e.,  $H$ ,  $B$ ,  $p_{YM}$ ,  $p_{YF}$ ,  $\theta$ , and  $\hat{R}_{J/F}$ ) in year  $i$ .

### Simulation Studies

We used both deterministic calculations and stochastic simulations to investigate robustness of the SAK model (eq

3) to violations of the assumptions of a stable-stationary population. Specifically, we used a deterministic model to examine effects of direct violations of the stable-stationary assumption when  $\lambda > 1$  and when  $\lambda < 1$  and to assess how changes in harvest regulations affect SAK performance. We used a stochastic model to investigate effects of random fluctuations in recruitment or survival and to assess how the SAK model performed when both sampling error and parameter stochasticity were present.

Using a deterministic 2-sex Leslie Matrix model (Leslie 1945, Keyfitz and Murphy 1967), we simulated annual population abundance and harvest under nonstationary conditions, including when  $\lambda > 1$  and  $\lambda < 1$ . We did not include stochasticity in recruitment or survival in these calculations. The basic deterministic model used in the simulations began with a stable age distribution and a stationary population under harvest. We used natural survival rates of 0.44 for the first age classes and 0.74 for all subsequent age classes, regardless of gender. Age-specific net fecundity rates were 0.30 ( $= F_{0F} = F_{0M}$ ) for the first age class and 0.55 for all subsequent age classes (i.e.,  $F_{1F} = F_{2F} = \dots = F_{A-1M} = F_{AM}$ ). Harvest probabilities were 0.05 for the first age class and all adult female age classes. Harvest probabilities for all age (yr) class  $>1$  males were 0.20. Population levels varied depending on the objective of the analyses. We generated nonstable-nonstationary populations by varying  $\geq 1$  of the demographic parameters as described in the Results section.

We computed annual abundance and harvest numbers directly from matrix multiplication of a 2-sex model,

$$\mathbf{M} \cdot \mathbf{H} \mathbf{z}_i = \mathbf{z}_{i+1},$$

where

$\mathbf{M}$  = Leslie 2-sex model;

$\mathbf{H}$  = harvest matrix;

$\mathbf{z}_i$  = vector of abundance by sex and age in year  $i$ ;

and where

$$\begin{bmatrix} F_{0F} & F_{1F} & \dots & F_{AF} & 0 & 0 & \dots & 0 \\ S_{0F} & 0 & & & & & & \\ 0 & S_{1F} & & & & & & \\ & & S_{AF} & 0 & & & & \\ F_{0M} & F_{1M} & \dots & F_{AM} & 0 & 0 & \dots & 0 \\ & & & & S_{0M} & 0 & \dots & 0 \\ & & 0 & & 0 & S_{1M} & & \\ & & & & & & S_{AM} & 0 \end{bmatrix}.$$

$$\begin{bmatrix} h_{0F} & 0 & \dots & & & & 0 \\ 0 & h_{1F} & 0 & \dots & & & 0 \\ 0 & & \ddots & & & & \vdots \\ \vdots & & & h_{AF} & & & \\ & & & & h_{0M} & & \\ & & & & & h_{1M} & \\ & & & & & & \ddots & 0 \\ 0 & \dots & & & & & 0 & h_{AM} \end{bmatrix} \begin{bmatrix} n_{0Fi} \\ n_{1Fi} \\ \vdots \\ n_{AFi} \\ n_{0Mi} \\ n_{1Mi} \\ \vdots \\ n_{AMi} \end{bmatrix}$$

$$= \begin{bmatrix} n_{0F,i+1} \\ n_{1F,i+1} \\ n_{AF,i+1} \\ n_{0M,i+1} \\ \vdots \\ n_{AM,i+1} \end{bmatrix}, \quad (4)$$

and where

$F_{iF}$  = net number of female offspring recruited per female of age  $i$  ( $i = 0, \dots, A$ ) into the fall huntable population;

$F_{iM}$  = net number of male offspring recruited per female of age  $i$  ( $i = 0, \dots, A$ ) into the fall huntable population;

$S_{iF}$  = probability of annual survival from natural causes for a female of age  $i$  to  $i + 1$  ( $i = 0, \dots, A$ ) from fall to fall;

$S_{iM}$  = probability of annual survival from natural causes for a male of age  $i$  to  $i + 1$  ( $i = 0, \dots, A$ ) from fall to fall;

$b_{iF}$  = probability of surviving the harvest for a female of age  $i$  ( $i = 0, \dots, A$ );

$b_{iM}$  = probability of surviving the harvest for a male of age  $i$  ( $i = 0, \dots, A$ );

$n_{jFi}$  = number of females of age class  $j$  ( $j = 0, \dots, A$ ) in year  $i$  in the fall huntable population;

$n_{jMi}$  = number of males of age class  $j$  ( $j = 0, \dots, A$ ) in year  $i$  in the fall huntable population.

After multiplying through, then

$$\begin{bmatrix} n_{0F,i+1} \\ n_{1F,i+1} \\ \vdots \\ n_{AF,i+1} \\ n_{0M,i+1} \\ n_{1M,i+1} \\ \vdots \\ n_{AM,i+1} \end{bmatrix} = \begin{bmatrix} \sum_{j=0}^A n_{jFi} \cdot F_{jF} \cdot b_{jF} \\ n_{0Fi} S_{0F} b_{0F} \\ \vdots \\ n_{A-1,F,i} S_{A-1,F} b_{A-1,F} \\ \sum_{j=0}^A n_{jMi} \cdot F_{jM} \cdot b_{jM} \\ n_{0Mi} S_{0M} b_{0M} \\ \vdots \\ n_{A-1,M,i} S_{A-1,M} b_{A-1,M} \end{bmatrix}. \quad (5)$$

In the simulation runs, we modeled age (yr) classes 0.5, 1.5, ..., and 12.5. We simulated successive generations of deer by recursively using equation 5. We calculated annual harvest ( $\xi_i$ ) of deer by age and sex class as the vector

$$\xi = (\mathbf{I} - \mathbf{H})\mathbf{M}\mathbf{n}_i. \quad (6)$$

We calculated total annual harvest ( $TH_i$ ) as

$$TH_i = \mathbf{1}'(\mathbf{I} - \mathbf{H})\mathbf{M}\mathbf{n}_i = \mathbf{1}'\xi. \quad (7)$$

Deer recruitment and survival can be directly affected by annual changes in overwinter conditions and long-term habitat changes. Recruitment and survival also are affected by random chance (i.e., demographic stochasticity). These

changes in survival and recruitment affect the age and sex composition of the population in subsequent years. To evaluate effects of random fluctuations in survival or recruitment on SAK estimates, we constructed a stochastic, 2-sex Leslie matrix model (Keyfitz and Murphy 1967). The stochastic model was based on a binomial function for the natural survival and harvest processes and a Poisson recruitment function. We modeled harvest for a particular age and sex class as a binomial process, where

$$c_{ij} \sim \text{BIN}(n_{ij}, (1 - b_{ij})), \quad (8)$$

where

$c_{ij}$  = harvest for age class  $i$ , gender  $j$ ;

$n_{ij}$  = abundance for age class  $i$ , gender  $j$ ;

$b_{ij}$  = probability of surviving harvest age for class  $i$ , gender  $j$ .

We modeled next year's abundance as a binomial process conditional on  $c_{ij}$ , where

$$n_{i+1,j} \sim \text{BIN}(n_{ij} - c_{ij}, S_{ij}), \quad (9)$$

where  $S_{ij}$  = probability of surviving natural causes for age class  $i$ , gender  $j$ . Recruitment of age class 0.5 was based on the expected values in equation 5, where

$$E(n_{0j}) = \sum_{j=0}^A (n_{iF} - c_{iF})F_{ij} = \mu_{0j},$$

where

$F_{ij}$  = fecundity of age class  $i$  in producing gender  $j$  offspring,

$n_{iF}$  = number of age class  $i$  females,

$c_{iF}$  = number of age class  $i$  females harvested.

We then treated the number of recruited 0.5 age class individuals in the population as a Poisson random variable, where

$$n_{0j} \sim \text{Poisson}(\mu_{0j}). \quad (10)$$

Using this model, we examined stochastic effects in age and sex composition on the SAK abundance estimator ( $\hat{N}_i$ ). We also used simulations to determine at what abundance the stochastic effects have an insignificant effect on SAK estimates.

Because covariance among vital rates is an important contributor to population fluctuation in deer populations (Coulson et al. 2005, Boyce et al. 2006), we performed additional simulations that incorporated covariance between survival and productivity. To induce a positive covariance between survival and productivity, we used compound processes in generating the age class data. We simulated survival to the next age class as a compound binomial-uniform process

$$n_{i+1} \sim \text{BIN}(n_i - c_i, S_i(1 + \varepsilon_k)), \quad (11)$$

and production of juveniles as a compound Poisson-uniform process

$$n. \sim P \left[ \sum_{j=0}^A (n_i - c_i)F_j(1 + \varepsilon_k) \right] \quad (12)$$

where  $\varepsilon_k$  is uniformly distributed  $U(-0.20, +0.20)$  in year  $k$ . Each year, we used a new randomly generated  $\varepsilon_k$  that either increased or decreased both survival and productivity by  $\varepsilon_k \times 100\%$ . For example, if  $\varepsilon_k = 0.05$ , both the parameters  $F_i$  and  $S_i$  increased by 5% over baseline conditions that year. An  $\varepsilon_k = -0.05$  would result in  $F_i$  and  $S_i$  decreasing to 95% of their typical value. This error structure induced a positive correlation between annual survival and productivity of  $\rho > 0.90$ . Other distributions and ranges for  $\varepsilon_k$  could be used, but this is adequate for demonstration. We compared error in estimation, i.e.,

$$SE(\widehat{SAK}) = \sqrt{\widehat{\text{Var}}(\widehat{SAK})} = \sqrt{\frac{\sum_{k=1}^n (\hat{N}_{SAK,k} - N_k)^2}{n}} \quad (13)$$

where  $n = 1,000$  years of data simulated under 2 scenarios: 1) no correlation, i.e.,  $\varepsilon_k = 0 \forall k$ ; and 2) positive correlation,  $\varepsilon_k \sim U(-0.20, +0.20)$ .

In practice, values of  $p_{YM}$ ,  $p_{YF}$ , and  $R_{J/F}$  used in the SAK calculations are a function of both the stochastic effects described in the last section and the error in subsampling the population or harvest data (Appendix). To properly characterize variance in SAK calculations, both sources of uncertainty must be considered. We performed additional simulation studies to examine the behavior of SAK estimates as these successive sources of variation are considered.

We conducted additional simulations where we randomly sampled harvest and population to provide estimates of age and sex composition (i.e.,  $\hat{p}_{YM}$ ,  $\hat{p}_{YF}$ , and  $\hat{R}_{J/F}$ ). For age composition, we randomly sampled 250 males and 250 females harvested to estimate  $p_{YM}$  and  $p_{YF}$ . These sampling levels are consistent with the approximately 5% sampling rate used in Wisconsin and 10% in Pennsylvania at a deer management unit scale (Wisconsin Department of Natural Resources [WDNR] 2001, Rosenberry et al. 2004). In estimating  $R_{J/F}$ , we randomly sampled 80 females, again consistent with typical sampling rates within a management unit in Wisconsin (WDNR 2001, G.1). We assumed a stable-stationary population of  $N = 10,000$  in the analysis.

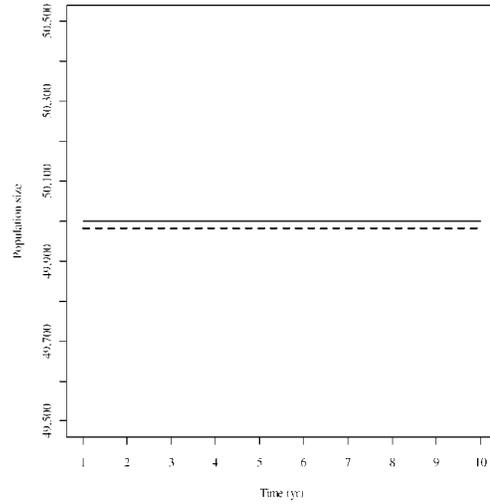
In evaluating model performance, we calculated an estimate of the mean squared error (MSE) of  $\hat{N}$  where

$$\begin{aligned} \text{MSE}(\hat{N}) &= \text{Var}(\hat{N}|N) + (E(\hat{N}) - N)^2 \\ &= \text{variance} + \text{bias}^2. \end{aligned}$$

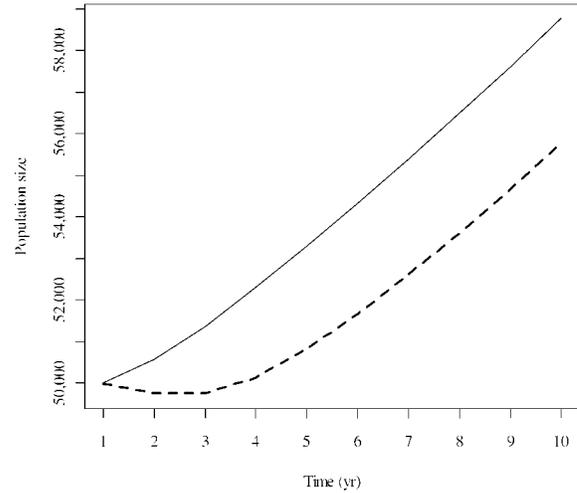
In the case of a biased estimator, MSE better characterizes the actual error in the estimate. For an unbiased estimator, the MSE is the sampling variance. Across replicate simulations ( $n$ ) and years ( $y$ ), we calculated the MSE as follows:

**Figure 1.** Population trends and corresponding sex-age-kill (SAK) model estimates of white-tailed deer abundance ( $N_t$ ) under (a) stable-stationary (stable age distribution and stationary abundance), (b) stable-nonstationary ( $\lambda > 1$ ), and (c) stable-nonstationary ( $\lambda < 1$ ) demographic conditions. Results are based on a deterministic, 2-sex Leslie matrix model. True abundance (solid line, —), SAK estimates (dashed line, - - - -) using exact demographic data (i.e., no sampling error).

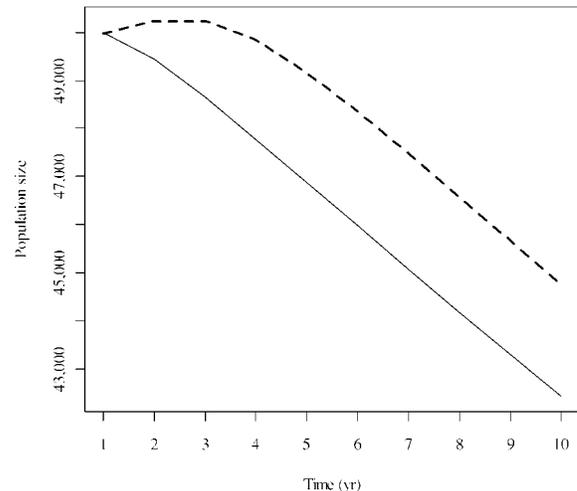
## a. Stable-stationary

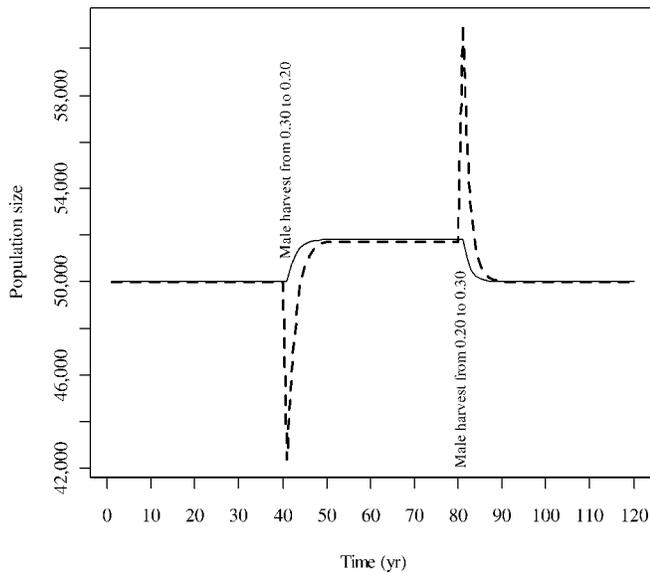


## b. Stable, $\lambda > 1$



## c. Stable, $\lambda < 1$





**Figure 2.** Population trends and corresponding sex-age-kill (SAK) model estimates of white-tailed deer abundance ( $N_i$ ), followed by a 0.10 decline in male harvest rate, followed by a 0.10 increase in male harvest rate. Results are based on a deterministic, 2-sex Leslie matrix model. Modeled abundance (solid line, —) and SAK estimates (dashed line, - - - -), based on exact demographic data (i.e., no sampling error). We generated the deer population using the Leslie 2-sex model under stable and stationary ( $\lambda = 1$ ) conditions for the first 40 years. In year 41, we changed the male harvest rate from a probability of 0.30 to 0.20 and it remained so for the next 40 years (yr 41–80). During that period, the population achieved a different set of stable and stationary conditions. Then in year 81, we reverted the male harvest back to the original rate of 0.3. Then, the population reached a new stable and stationary condition over years 81–120, the same as the original set of conditions at the beginning of the simulation.

$$\widehat{\text{MSE}} = \frac{1}{n} \sum_{i=1}^n \left[ \frac{\sum_{j=1}^y (\hat{N}_{ij} - N_{ij})^2}{(y-1)} \right]$$

We varied the number of simulations ( $n$ ) from 100 to 1,000 and set  $y = 40$ . To standardize the error in estimation relative to the actual abundance values, we computed a measurement analogous to the coefficient of variation for unbiased estimates as

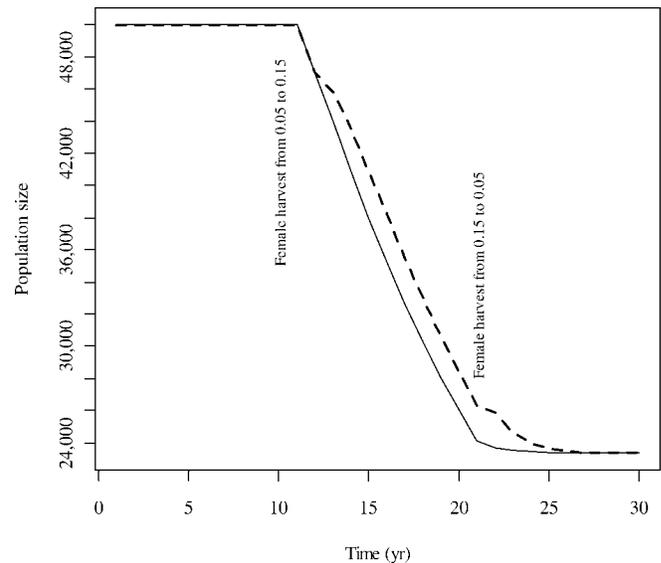
$$\text{CE} = \frac{\sqrt{\widehat{\text{MSE}}}}{\left( \frac{\sum_{i=1}^n \sum_{j=1}^y N_{ij}}{ny} \right)} \quad (14)$$

called the coefficient of error (CE). Finally, we generated estimates of male recovery rate ( $B$ ), with a CE of 10%.

## RESULTS

Under stable-stationary conditions, SAK estimates tracked the true population abundance, as expected (Fig. 1a). However, when the population had a stable age composition and  $\lambda > 1$ , the SAK model underestimated  $N_i$  (Fig. 1b). Conversely, with a stable age distribution and  $\lambda < 1$ , the SAK overestimated  $N_i$  (Fig. 1c).

Changes to male harvest rate had an immediate and



**Figure 3.** Population trends and corresponding sex-age-kill (SAK) model estimates of white-tailed deer abundance ( $N_i$ ), under a stable-stationary condition ( $\lambda = 1$ ), followed by a 0.10 increase in female harvest rate. Results are based on a deterministic, 2-sex Leslie matrix model. Simulated abundance (solid line, —), SAK estimates (dotted line, - - - -), using exact demographic data values (i.e., no sampling error).

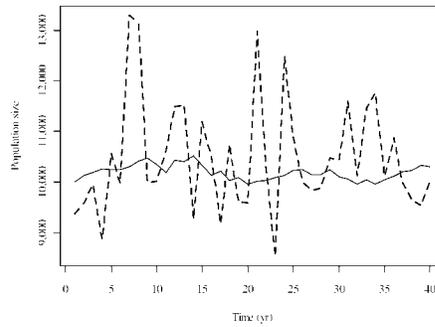
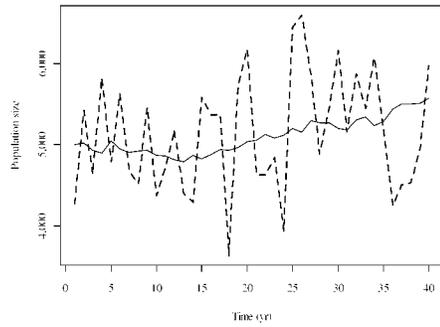
substantial impact on SAK estimates (Fig. 2). After changing male harvest rates, the SAK estimate asymptotically converged to a new stable-stationary condition. However, at the time of the shift, SAK estimates were strongly biased (Fig. 2), and this bias persisted for as long as 10 years, although diminishing with each passing year. When we increased male harvest mortality, the SAK estimator underestimated actual abundance (i.e., negative bias). When we decreased male harvest mortality, the SAK estimator overestimated actual abundance (Fig. 2).

A shift in female harvest rate from 0.05 to 0.15 did not produce the same shift in abundance estimates as male harvest changes (Fig. 3). The SAK estimates followed abundance trends with only a slight positive bias (Fig. 3).

The stochastic effects we simulated caused the annual population abundance to fluctuate about the equilibrium abundance (Fig. 4). However, random fluctuations in age composition (i.e.,  $p_{YM}$ ,  $p_{YF}$ , and  $R_{J/F}$ ) resulted in SAK abundance estimates of  $N_i$  to vary more than the population they were monitoring. Similar variability will be produced by environmental fluctuations in survival and fecundity about their equilibrium values. In a population of approximately 50,000 deer, CE was 4.6%. As expected, as population size decreased, amount of error in the SAK estimate increased. For a population of 25,000 deer, CE was 8.3%, whereas for 10,000 deer, CE was 12.4%. For a management unit with 10,000 deer, this means that abundance estimates were within  $\pm 24.3\%$  of the true value 95% of the time when there was no sampling error. Our simulations indicate that population sizes of 1–2 million are required before these stochastic effects are trivial (Fig. 5). Therefore, SAK estimates may be precise at a state level but not at smaller, management unit levels.

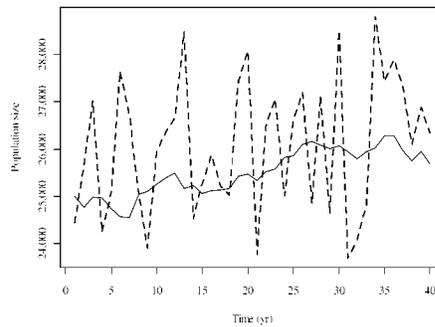
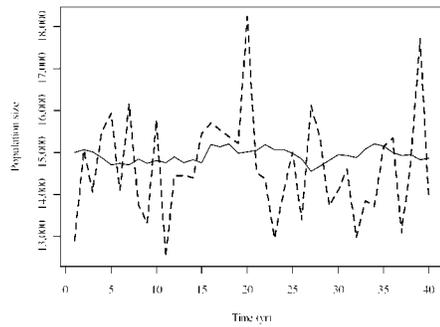
a. Population = 5,000, CV = 0.1394

b. Population = 10,000, CV = 0.1148



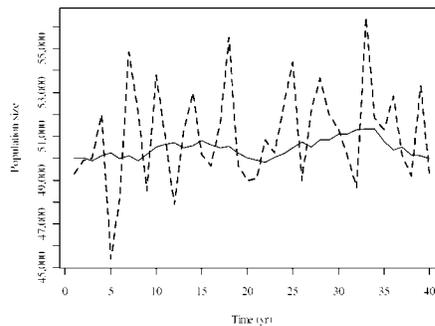
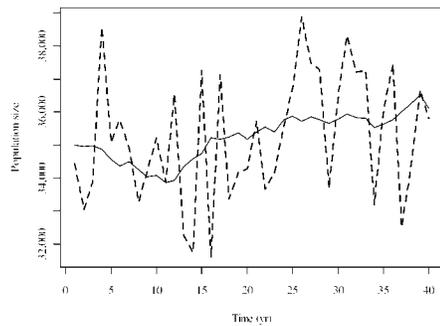
c. Population = 15,000, CV = 0.0861

d. Population = 25,000, CV = 0.0594



e. Population = 35,000, CV = 0.0521

f. Population = 50,000, CV = 0.0453

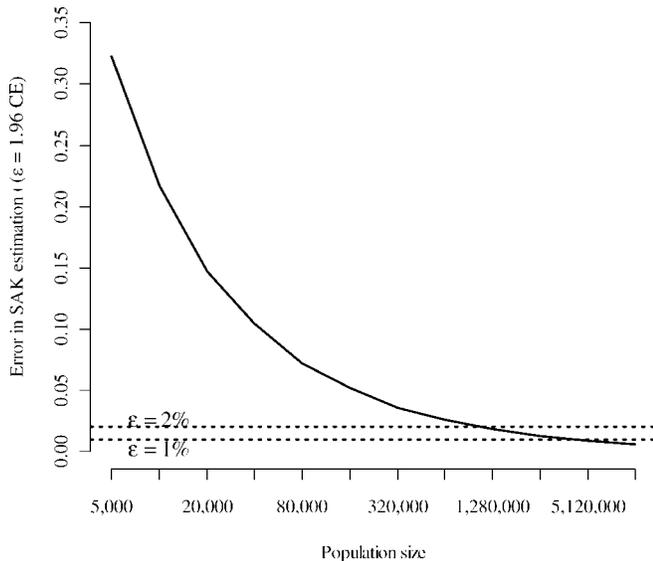


**Figure 4.** Population trends and corresponding sex-age-kill (SAK) model estimates of white-tailed deer abundance ( $N_t$ ), with random recruitment and survival for 6 population levels ranging from 10,000 to 50,000. Results are based on a stochastic, 2-sex Leslie matrix model with binomial survival and harvest, and Poisson recruitment. True abundance (solid line, —), SAK estimates (dashed line, - - - -), using exact demographic values (i.e., no sampling error). Plots are representative plots of one simulation run.

A positive correlation between survival and productivity increased variability in simulated true abundance and increased the error in abundance estimation by the SAK model. Observed standard error (eq 13) associated with correlated values of  $S_i$  and  $F_i$  ( $SE = 1818.6$ ) was greater than for uncorrelated values of  $S_i$  and  $F_i$  ( $SE = 1327.2$ ). Therefore, the SAK model will underestimate true population variability in the presence of environmental conditions that produce a positive correlation between  $S_i$  and  $F_i$ .

Without stochasticity or any sampling error, the SAK estimate would equal true abundance (Fig. 6a). When we

incorporated uncorrelated stochasticity in survival and recruitment and used exact demographic values (i.e., no sampling error) in the SAK estimator, CE was 12.1% for a population of 10,000 (Fig. 6b). In other words, even with exact demographic data, precision will be  $\pm 23.7\%$  of the true value of  $N$  95% of the time. For populations as small as 5,000, precision degrades to 33% 95% of the time. Adding sampling error to demographic values of  $p_{YM}$ ,  $p_{YF}$ , and  $R_{J/F}$  as described above, overall CE becomes 58.4% (Fig. 6c). Finally, simulating the estimated male recovery rate with a coefficient of variation of 10% raises the overall CE for the



**Figure 5.** Error in sex-age-kill (SAK) estimation ( $\epsilon = 1.96$  coefficient of error) versus population size for a simulated white-tailed deer population. This stochastic variability is based on calculating SAK values with exact demographic values (i.e., no sampling error).

SAK method to 62.2% for a population of 10,000 (Fig. 6d). Thus, with both stochastic effects and sampling error at a deer management unit level of effort, resultant abundance estimates,  $\hat{N}_i$ , were within  $\pm 121.9\%$  of the true simulated population level 95% of the time.

## DISCUSSION

The general form of the SAK model assumes a stable age distribution and a stationary population, which is unrealistic for many ungulate populations (e.g., Unsworth et al. 1999). Ungulate populations could meet these assumptions if there were strong density dependence factors keeping the population relatively constant (Eberhardt 2002, Owen-Smith 2006). However, in the northern range of white-tailed deer density independent factors may exert a greater influence on population dynamics, and when the demographic structure of a population is perturbed, the population will not possess a stable age distribution (Yearsley 2004, Koons et al. 2006). Indeed, transient dynamics are different from those of a stable age distribution (Yearsley 2004, Koons et al. 2006). Furthermore, in the presence of covariance in vital rates, there is disruption in the stable age distribution as a consequence of transient dynamics (Yearsley 2004). This covariance structure is the most important component of the demography in ungulate populations, at least in the context of determining year-to-year fluctuations in population growth (Coulson et al. 2005, Boyce et al. 2006). Thus, in reality, the stable and stationary assumptions are rarely attained. Our simulations demonstrate that violation of these assumptions results in substantial bias on population estimates.

When assumptions cannot be met, alternative estimation methods exist. For example, a modified SAK model for  $\hat{N}_i$  under stable-nonstationary conditions can be written as

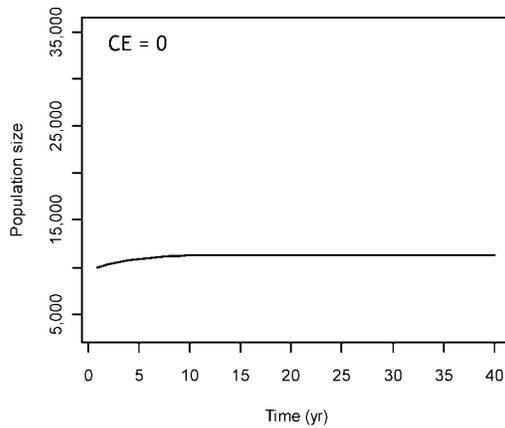
$$\hat{N}_i = \frac{H_i}{(1 - \lambda(1 - \hat{p}_{YM})) \hat{B}} \left[ 1 + \frac{(1 - \lambda(1 - \hat{p}_{YM}))}{(1 - \lambda(1 - \hat{p}_{YF}))} \theta + \frac{(1 - \lambda(1 - \hat{p}_{YM}))}{(1 - \lambda(1 - \hat{p}_{YF}))} \theta R_{J/F} \right] \quad (15)$$

and should be considered when nonstationary conditions exist. However, this solution requires additional data to estimate  $\lambda$  and may possibly require levels of precision for estimates of  $\lambda$  that are not realistically obtainable. Typically, if  $\lambda$  is near 1 (i.e., 0.95–1.05), bias will be small. Unrealistic assumptions required in the SAK model (e.g., stable-stationary assumption) might be eliminated if auxiliary data were collected to estimate age- and sex-specific harvest rates. However, collection of these auxiliary data is expensive because it requires monitoring of radiocollared deer. States that have implemented harvest regulations that result in differential harvest rates among age classes (e.g., defining legal males as having a min. no. of antler points), such as Pennsylvania, have used this approach (C. S. Rosenberry, Pennsylvania Game Commission, personal communication).

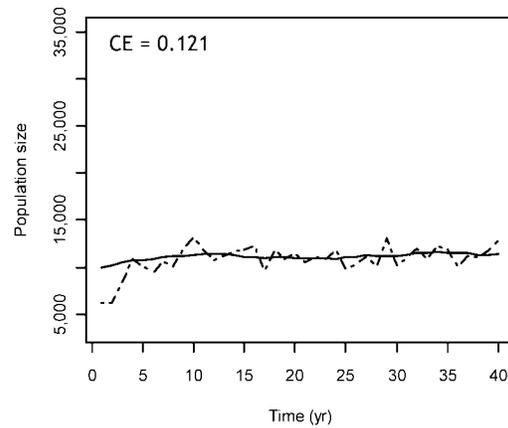
Instead, alternative estimation models that are more robust to violations of the stable-stationary assumption might be considered. For example, the statistical age-at-harvest method (Gove et al. 2002) provides a useful alternative that does not make restrictive assumptions. These second generation population reconstruction techniques hold promise for deer population estimation (Skalski et al. 2005, 2007). We encourage managers to assess the trade-off between broad-scale methods, such as SAK, and fine-scale methods, such as sightability models (Cogan and Diefenbach 1998) in light of monitoring objectives. Cost-benefit comparisons between the SAK and other population estimation techniques would be beneficial and should be performed. Furthermore, we encourage collaboration between ecologists and computer programmers to develop software that makes these techniques accessible to wildlife managers.

Our simulations suggested that sudden shifts in harvest rates can dramatically impact SAK estimates. These changes could be driven by changes in hunter regulation, hunting conditions, and hunter attitudes. Perhaps most troubling was our finding that SAK estimates were opposite the known population trend when changes in the male harvest rate were introduced. Although managers have some control over harvest rates, changes in hunter attitude and hunting styles cause additional problems with SAK estimation given its sensitivity to male harvest rate. Several states have instituted changes to deer hunting regulations that affect male harvest rates (Bishop et al. 2005). For example, in certain management units the state of Wisconsin has implemented an “earn-a-buck” program that requires that hunters harvest an antlerless deer before being authorized to harvest an antlered deer. Also, changes in hunter attitude across the country (e.g., quality deer management; Miller

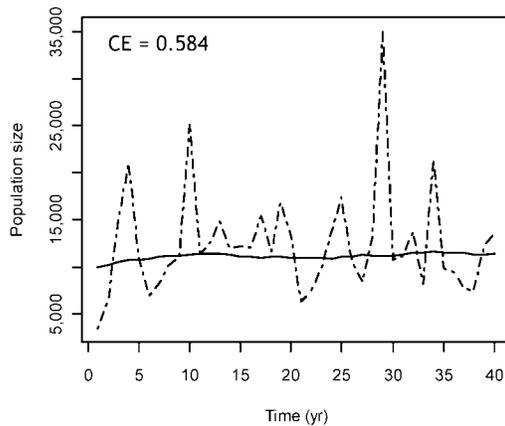
a. Deterministic model



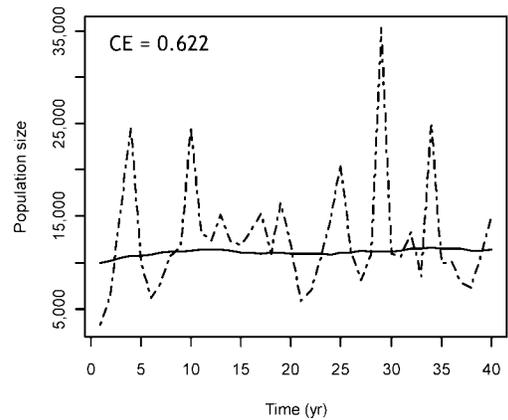
b. Stochastic harvest and survival



c. Stochastic harvest sampling



d. Stochastic buck recovery rate



**Figure 6.** Population trends and corresponding sex-age-kill (SAK) model estimates of white-tailed deer abundance ( $N_t$ ), under (a) deterministic stable-stationary (stable age distribution and stationary abundance) conditions; (b) stochastic stable-stationary conditions; (c) stochastic variation and sampling error for  $p_{YM}$  (proportion of 1.5-yr-old M in the ad M segment of the population),  $p_{YF}$  (proportion of 1.5-yr-old F in the ad F segment of the population), and  $R_{J/F}$  (estimated ratio of juv to ad F in the population); and (d) stochastic variation and sampling error for  $p_{YM}$ ,  $p_{YM}$ ,  $R_{J/F}$ , and  $B$  (proportion of total M mortality due to harvest;  $\theta = 1$ ). Abundance from projection matrix model (solid line, —) and SAK estimates (dotted line, - - - -). CE indicates coefficient of error.

and Marchinton 1995, Green and Stowe 2000, Collier and Kremetz 2006) could alter male harvest rates and changes in harvest rates among age classes. As changes to male harvest are introduced, use of SAK is questionable given its reliance on the assumption of a known constant male harvest rate. Additional factors that are often uncontrollable, such as changes in weather, induce variability in male harvest rates (Hansen et al. 1986). Thus, use of the SAK model is questionable unless independent estimates of the male recovery rate are available annually.

## MANAGEMENT IMPLICATIONS

We recommend managers consider the following: 1) The SAK model has unrealistic assumptions (stable-stationary population) that when violated bias population estimates. Under nonstationary conditions, we have offered an

alternative form of the SAK that requires an estimate of  $\lambda$  (eq 15); however, it requires additional data and the necessary level of precision for estimates of  $\lambda$  is unknown. Managers should consider whether they can meet monitoring objectives given the bias observed in our simulations. Managers should consider both stochastic effects and sampling error in their assessment of the utility of the SAK model. 2) Changes to male harvest bias SAK estimates. When changes to male harvest are introduced, SAK is expected to report population abundance in the opposite direction of the known population trend. These biases can result in faulty management prescriptions. 3) At small spatial scales, SAK estimates can be unreliable. Our simulations suggested that SAK estimates may be precise at large spatial scales, such as a state level, but less so at smaller unit levels. Precise population estimation at a management

unit level may be unattainable given sampling error and stochastic effects. Although pooling data across management units may increase sample size and improve precision of input data, pooling is only appropriate when demographic processes across pooled units are homogenous. 4) We recommend managers consider the use of likelihood-based population reconstruction methods (e.g., Gove et al. 2002; Skalski et al. 2005, 2007) in situations where assumptions are likely to be violated. The development of software would facilitate use by managers.

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## APPENDIX

The total variance associated with an estimate of the proportion of yearling males ( $\hat{p}_{YM}$ ) is a function of both sampling error and stochastic effects. Using the total variance law

$$\text{Var}(\hat{p}_{YM}) = E_2[\text{Var}_1(\hat{p}_{YM}|2)] + \text{Var}_2[E_1(\hat{p}_{YM}|2)]$$

where stage 1 refers to sampling the population and stage 2 refers to the stochastic effects. Taking the variance in stages,

$$\text{Var}(\hat{p}_{YM}) = E_2\left[\frac{P_{YM}(1 - P_{YM})}{b} \left(\frac{N_M - b}{N_M - 1}\right)\right] + \text{Var}_2[P_{YM}],$$

where  $E(\hat{p}_{YM}) = P_{YM}$ , the actual proportion of yearling males in the male segment of the population ( $N_M$ ) and  $b$  is the number of males examined for age in the harvest. Proceeding

$$\begin{aligned}
\text{Var}(\hat{p}_{YM}) &= \left[ P_{YM} - \left( \frac{P_{YM}(1 - P_{YM})}{N_M} \right) - P_{YM}^2 \right] \\
&\quad \times \left[ \frac{(N_M - b)}{(N_M - 1)b} \right] + \frac{P_{YM}(1 - P_{YM})}{N_M} \\
&= \frac{P_{YM}(1 - P_{YM})}{b} \left( \frac{N_M - b}{N_M - 1} \right) \\
&\quad + \frac{P_{YM}(1 - P_{YM})}{N_M} \left( 1 - \frac{(N_M - b)}{(N_M - 1)} \right).
\end{aligned}$$

The first term represents the variability associated with sampling the harvest, and the second term represents the variability associated with stochastic effects.

Similar two-stage variance calculations are necessary for the other variance elements in Skalski and Millspaugh (2002).

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