The Pennsylvania State University

The Graduate School

School of Forest Resources

AN EVALUATION OF THE PENNSYLVANIA SEX-AGE-KILL

MODEL FOR WHITE-TAILED DEER

A Thesis in

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by

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ABSTRACT

Accurately monitoring population trends is an essential component of game species management. This is especially true for white-tailed deer (*Odocoileus virginianus*) in Pennsylvania where the Pennsylvania Sex-Age-Kill (PASAK) model is used to estimate annual abundance. Historically, the PASAK model only provided point estimates of abundance. However, statistically valid estimates of precision are needed to quantify uncertainty. Additionally, assumption violations can incorporate bias into estimates, the extent of which is unknown. I estimated survival and harvest rates based on data from 1,131 radio- or GPS-collared white-tailed deer and obtained harvest data (number killed, age-sex structure, etc.) to (1) evaluate assumptions of the PASAK model, (2) develop a method to estimate precision, and (3) evaluate model sensitivity and robustness.

The PASAK model input parameters for the mature ($\geq$ 2.5 years old) male harvest rate, yearling (1.5 years old) male harvest rate, and percent yearling females in the adult ($\geq$ 1.5 years old) female population did not meet required assumptions. Mature male harvest rates differed by as much as 32.8% among wildlife management units (WMUs) studied. However, this spatial variability could be reliably modeled using a hunting effort index as a covariate. I found difficulties in the current method used to estimate yearling male harvest rates. However, direct yearling male harvest rate estimates from radiocollar data, which differed by $\leq$ 16.5% among WMUs studied, provided a suitable alternative estimate. In addition, variation in hunting effort was related to spatial variability in yearling male harvest rates. Yearling female deer were nearly 50% more

likely to be harvested than mature female deer, which caused the PASAK model to underestimate population size.

Mean coefficient of variation (CV) estimates by WMU, 14.1% in year t, were slightly above benchmarks recommended for managing game species populations ($\leq 12.8\%$). Doubling reporting rates by hunters or doubling the number of deer checked by personnel in the field would improve mean CVs in year t to recommended levels. The PASAK model was robust to variability and bias in estimates for mature male harvest rate, female harvest rate, and non-harvest mortality. However, model estimates were sensitive to variability and bias in yearling male harvest rates. Consequently, yearling male harvest rate estimates had the greatest influence on the accuracy of population estimates.

Very few studies have monitored spatial and temporal variability in male white-tailed deer harvest rates. My results support the hypothesis that the majority of variability in mature male white-tailed deer harvest rates can be explained by variation in hunting effort. Similar variability exists in yearling male harvest rates, however, antler point restrictions (APRs) in Pennsylvania limit the extent of variability. Although minimized by APRs, yearling male harvest rate variability has profound influences on PASAK model estimates. Because harvest rates in the PASAK model are assumed constant across years, potential influences of regulation changes or shifts in hunting practices that alter male harvest rates will have profound influences on model performance. Yearling male harvest estimates are similarly important, and research to evaluate their accuracy will improve reliability of PASAK model estimates. Increasing harvest reporting rates by hunters may be the most efficient approach to improve

precision of harvest estimates, whereas similar improvements by increasing the number of deer checked and aged may be more difficult or expensive to achieve. Independent estimates for the percent of yearling males in the adult male population will reduce the importance of yearling male harvest rate and harvest estimates.

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Chapter 1

Study Background

Introduction

Since the discovery of America in the 1400s, the abundance of white-tailed deer (*Odocoileus virginianus*) has varied substantially, primarily because of European colonization (McShea et al. 1997). Initial population declines from the 1500s to the early nineteenth century were the product of increased harvest exploitation by American Indians, and trading opportunities with early European settlers (McCabe and McCabe 1984). By the beginning of the nineteenth century, as American Indian influence diminished and European settlement continued to increase, harvest exploitation shifted to recreational and market hunting (Kosack 1995). More stringent harvest regulations and reduced hunting pressure during the Civil War slightly decreased the rate of decline through the 1800s (Kosack 1995), but the trajectory towards extirpation of Pennsylvania's deer herd was seemingly inevitable.

By the end of the nineteenth century, exploitation of deer had reduced the range and abundance of Pennsylvania's deer herd to the brink of extinction (Diefenbach and Palmer 1997). However, through harvest management, habitat fragmentation, and predator elimination, deer abundance rebounded and continued to increase throughout the twentieth century (Diefenbach et al. 1997, Waller and Alverson 1997). These anthropogenic alterations led to range expansion of deer in Pennsylvania, an overall increase in deer numbers, and high deer densities in some areas before the mid-20th century (Leopold et al. 1947). Throughout much of the latter part of the twentieth

century, sportsmen enjoyed increasing deer harvests. Hunting opportunities, at least the opportunity to see many deer while hunting, during this period led deer hunters to expect abundant numbers of deer, and have resulted in conflict and scrutiny of management recommendations and actions to reduce deer densities.

To address management concerns, the Pennsylvania Game Commission's (PGC) deer management program has identified a set of goals. These goals encompass management of the deer population at a level that produces a sustained yield, while balancing the population with respect to sociological and ecological carrying capacities (Pennsylvania Game Commission 2006). For these goals to be met, an accurate assessment of population trends must be known. These assessments of the deer population can be used to monitor how the deer density is related to deer reproductive rates, forest regenerative conditions, and deer-human conflicts.

Anecdotal and second-hand recounts have historically been used to provide indices of a deer population (McShea et al. 1997). Not until the twentieth century have population modeling and simulation methods been used, and population modeling is now considered essential to modern deer management (Roseberry and Woolf 1991). Additionally, precision and bias measurements can provide managers an understanding of how much confidence to place in their population estimates.

The first of these methods used in Pennsylvania to estimate white-tailed deer populations was the Lang and Wood method (Lang and Wood 1976). Shortly thereafter, the Lang and Wood method was replaced with a modified change-in-ratio (CIR) procedure (Shope 1978). With the onset of antler point restrictions (APR) in 2001, the CIR method needed to be replaced, because it was no longer possible to meet a

fundamental assumption of the method that all male age classes had the same harvest rate. Populations from 2002 to 2004 were monitored with an accounting model, which proved to be inadequate (C. S. Rosenberry, PGC, personal communication). Since then, a modified Sex-Age-Kill (SAK) model has been used, hereafter referred to as the Pennsylvania SAK (PASAK) model.

Research Justification

Rarely have deer population models been evaluated from a statistical standpoint. Typically, insufficient local data compels deer biologists to use generalizations of scientific results or popular opinion when selecting appropriate models, which could bias estimates. Furthermore, using this heuristic approach, there is no way to evaluate model performance; consequently these models provide no measure of statistical confidence to place in the estimates or indices (Skalski et al. 2005). Although the PASAK model has fewer assumptions than other SAK models, the remaining assumptions should be evaluated (Skalski et al. 2005). However, whether assumptions are violated is unimportant if resulting population estimates have no measure of bias or precision.

In light of increased public scrutiny of deer management, population models need to be subjected to thorough methods of evaluation (White and Lubow 2002). This scrutiny is arguably more intense in Pennsylvania than anywhere else in North America (Frye 2006). Although estimates of deer populations in Pennsylvania have improved over the past 30 years, conflicting opinions still remain about these estimates (Diefenbach et al. 1997).

My thesis research evaluated the PASAK model. First, I developed a bootstrap resampling procedure to estimate precision of abundance estimates. Then I tested model

assumptions regarding spatio-temporal variability in harvest and survival rates of male and female deer. Finally, I evaluated how robust the model is to violation of assumptions by simulating populations and incorporating sampling error and bias.

Study Areas

I used deer captured from two study periods, the 2D/4D study from 2002 to 2005 and 2G/4B study from 2005 to 2008. The 2D/4D study was designed to monitor adult male survival and yearling dispersal ecology (Long 2005), whereas the 2G/4B study was intended to evaluate female survival and resource selection. Both studies used deer located across two study areas, totaling four geographically exclusive study areas from 2002 to 2008 (Figure 1.1). These four study areas provided a representative sample of different physiographic regions in Pennsylvania.
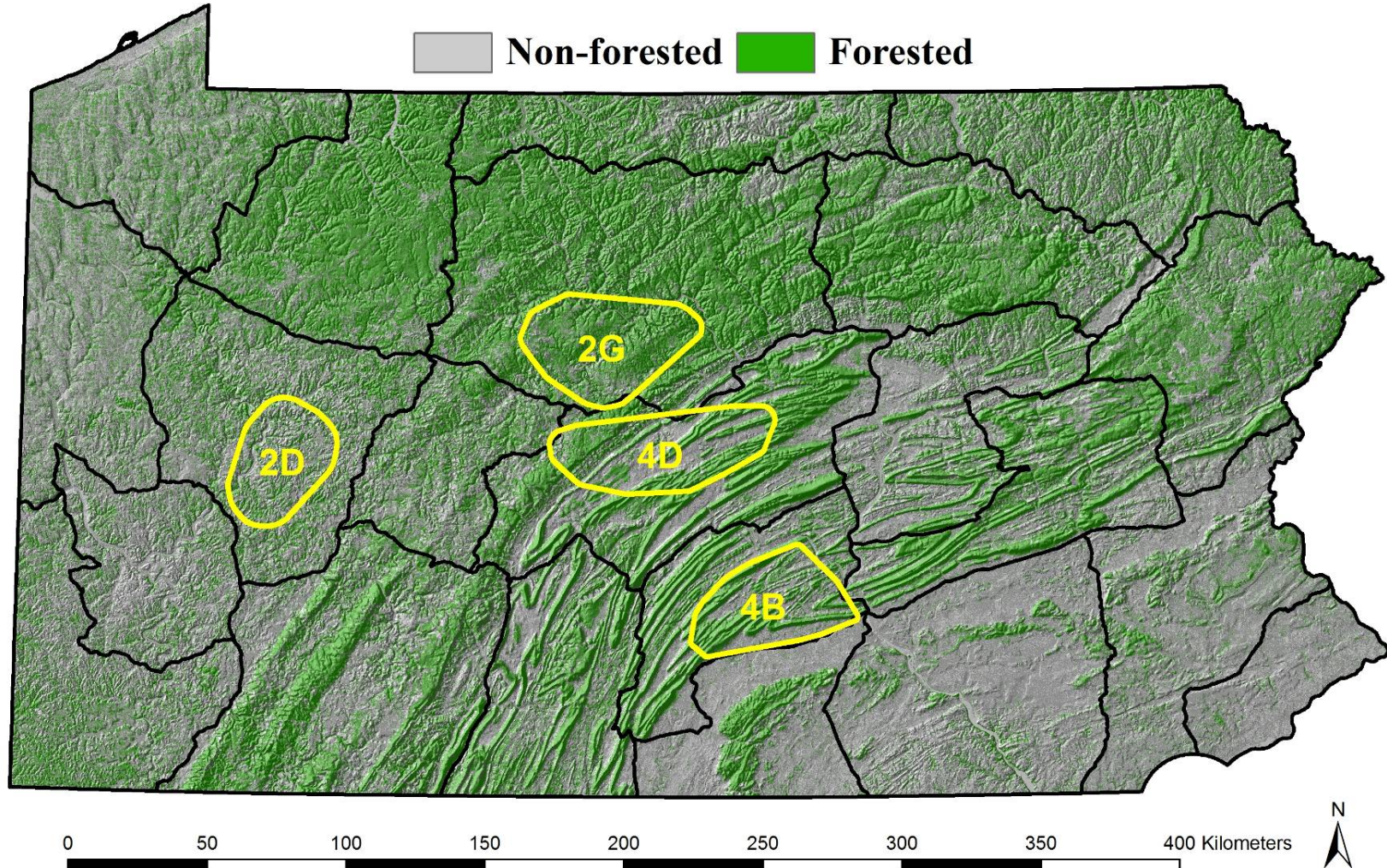
Figure 1.1: Map of two study areas, 2D and 4D, from the 2D/4D study, and two study areas, 2G and 4B, from the 2G/4B study. The twenty-two Pennsylvania Game Commission wildlife management units are delineated with black lines.

Wildlife Management Unit 2D and 4D

Both my 2D and 4D study areas used deer captured during the 2D/4D study. My western study area was located in Armstrong County, within wildlife management unit (WMU) 2D. Indicative of areas with nutrient rich soil, this WMU primarily consists of privately owned agricultural land used to grow corn, soybeans, and grains. In addition, above average yearling male antler growth in this WMU is assumed to be an indication of soil nutrient value (C. S. Rosenberry, PGC, personal communication). Small, fragmented oak (*Quercus spp.*) forests provide the majority of permanent cover for deer in the area. The abundance of edge habitat and nutrient rich soil provides ideal habitat for deer in this WMU. An extensive road network makes much of the landscape accessible for hunting.

My other study area from the 2D/4D study, WMU 4D, consists of a combination of Allegheny Plateau and Ridge and Valley physiographic regions. The majority of the Allegheny Plateau physiographic region is characterized by contiguous forest consisting of steep mountain slopes with flat plateaus at the highest elevations. The Ridge and Valley physiographic region is typically characterized by privately owned agricultural valleys and publicly owned forested ridges. Generally, the Ridge and Valley region has a much more extensive road network than the Allegheny Plateau.

Wildlife Management Unit 2G and 4B

The two study areas I used from the 2G/4B study had components similar to WMU 4D during the 2D/4D study. WMU 2G, directly north of WMU 4D is primarily made up of the Allegheny Plateau physiographic region. Cooler winters and contiguous second growth forests in this WMU have resulted in below average yearling male antler growth

(C. S. Rosenberry, PGC, personal communication). Although half of land in WMU 2G is open to public hunting, a combination of the rugged terrain and a limited road network make many areas inaccessible to a relatively low density of hunters.

Directly south of WMU 4D, WMU 4B is located in the Ridge and Valley physiographic region. The study area is similarly rugged to WMU 2G, however, a far more diverse road network provides greater landscape accessibility to a high density of hunters. Relatively mild winters, a diversity of agricultural and forested habitat, and above average yearling male antler growth suggest above average nutrition in this WMU (C. S. Rosenberry, PGC, personal communication).

Capture and Monitoring

From the 2D/4D study, I used deer captured between 2001 and 2004, whereas deer captured from 2005 to 2008 comprised my 2G/4B study sample. All the deer I used were fitted with VHF radio-ear tags, VHF radiocollars, or GPS satellite-collars that transmit a mortality signal (110 pulses per minute) upon lack of movement for 4 hours. Most deer were captured between January and April and fitted with two ear tags. The tags and collars were labeled with reporting instructions including a toll-free phone number.

I captured deer using Clover traps (Clover 1956), rocket nets, (Beringer et al. 1996) and drop nets (Ramsey 1968), with corn as bait. I also remotely darted one deer during late summer. Upon capture in Clover traps, deer were physically restrained and processed with no chemical immobilization drugs used. Deer captured in rocket nets and drop nets were sedated with 3 mg/kg of body mass xylazine hydrochloride and processed (Kreeger et al. 2002). Prior to release, I administered an antagonist to the xylazine consisting of 2 mg/kg of body mass tolazoline hydrochloride (Kreeger et al. 2002). All

animals were handled in accordance with protocols approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC No. 26886).

Immediately following capture, I monitored survival weekly, until early April. Then, I collected weekly bi-angulated deer locations, which I estimated with the program LOAS (Biotas™ 2003). I investigated mortality upon the transmission of a mortality signal from the radiocollars, and assigned a cause of death following criteria used in previous studies (Vreeland 2002, Long 2005). If no cause of death was determined, I sent deer to the Pennsylvania State University Animal Diagnostics Laboratory for necropsy.

Capture Results and Discussion

From the 2D/4D study, I used 324 and 219 male radio-marked white-tailed deer in WMU 2D and WMU 4D, respectively (Figure 1.2 and 1.3). More than 80% of the male deer captured in both study areas were juveniles (Long 2005). The trap site mortality rate averaged 1.4%, while subsequent trap-related mortalities from 730 handled known-fates deer, including recaptures, increased the estimated mortalities occurring from trapping to 3.0 percent (Long 2005).

During the 2G/4B study, I radiocollared 81 male (52 juvenile and 29 adult) and 207 female (76 juvenile and 131 adult) white-tailed deer from WMU 2G (Figure 1.4). Additionally, I radiocollared 93 male (64 juvenile and 29 adult) and 207 female (108 juvenile and 99 adult) white-tailed deer from WMU 4B (Figure 1.5). Across the two study areas, I captured 40% of the white-tailed deer in Clover traps, 34% with drop nets, 26% with rocket nets, and <1% using dart guns (Table 1.1).

Identical to the 2D/4D study, the trap site mortality rate was 1.4%, 15 of 1,061 handled deer (Table 1.1). Most trap site mortalities were due to spinal injuries self-sustained in Clover traps, or spinal injuries from other deer, typical with rocket and drop nets. Juveniles were twice as vulnerable (2.0%) to trap site mortality than adults (0.8%), but I found little difference between sexes. Because not all deer captured were fitted with radio or GPS collars, I was only able to monitor the subsequent capture-related mortality for 727 white-tailed deer (including recaptures). Of those 727, I estimated 30 (4.1%) capture-related mortalities, all within four weeks of capture. Both capture site and estimated capture-related mortality rates were lower than similar studies using white-tailed deer (Beringer et al. 1996).
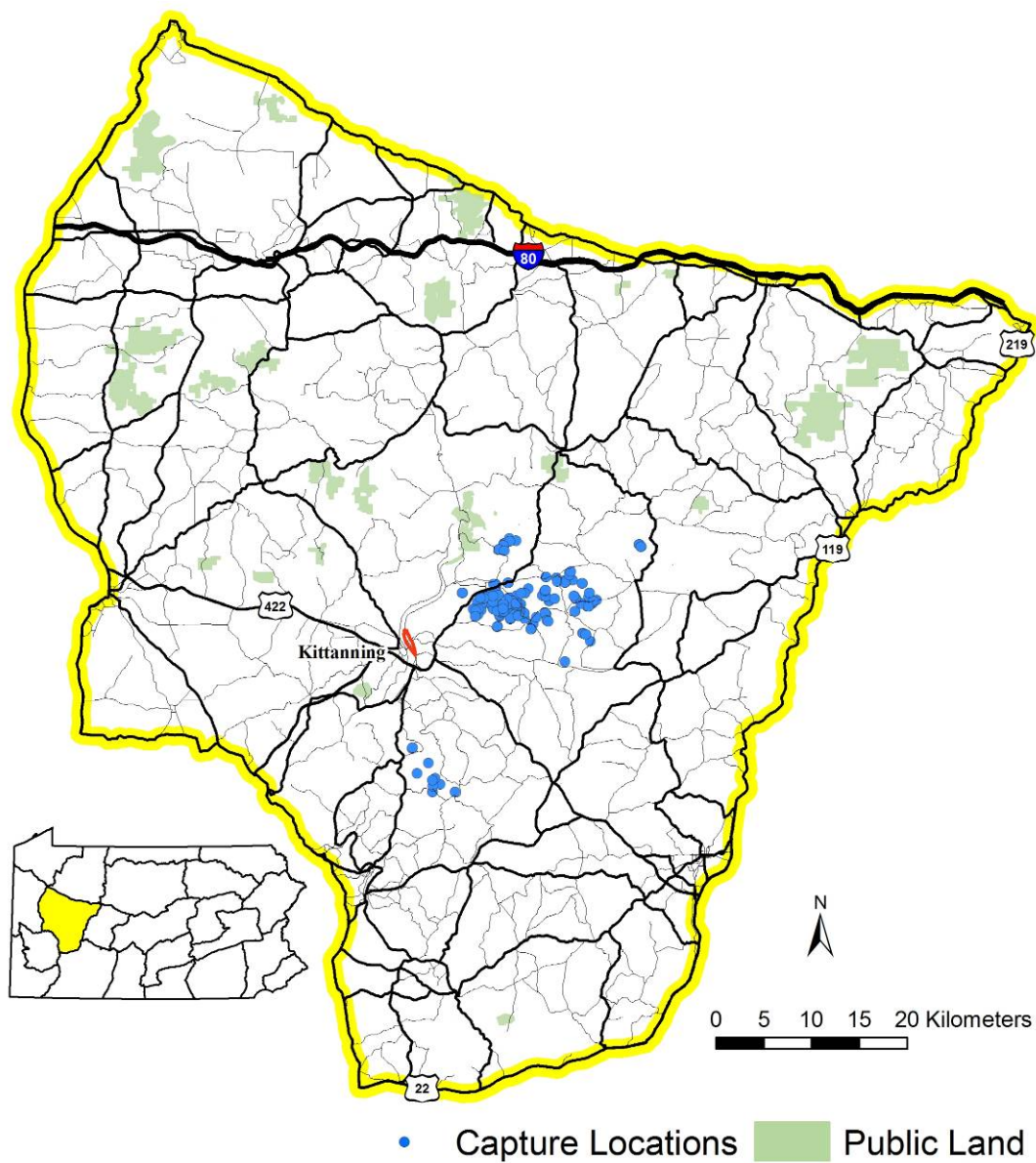
Figure 1.2: Capture locations for 324 radio-marked male white-tailed deer in WMU 2D, Pennsylvania, 2001-2004. The city of Kittanning is outlined in red for reference.
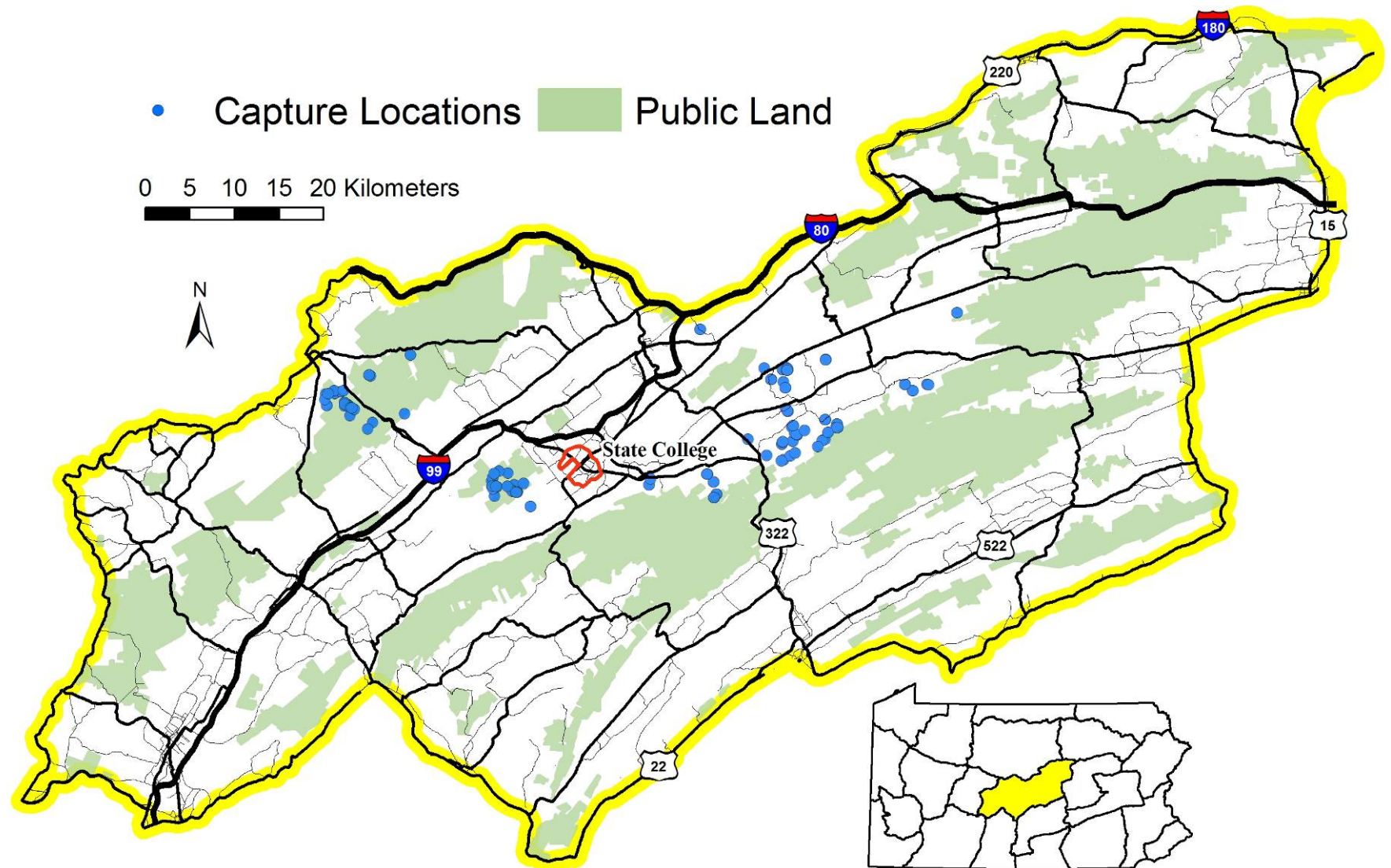
Figure 1.3: Capture locations for 219 radio-marked male white-tailed deer in WMU 4D, Pennsylvania, 2001-2004. The city of State College is outlined in red for reference.
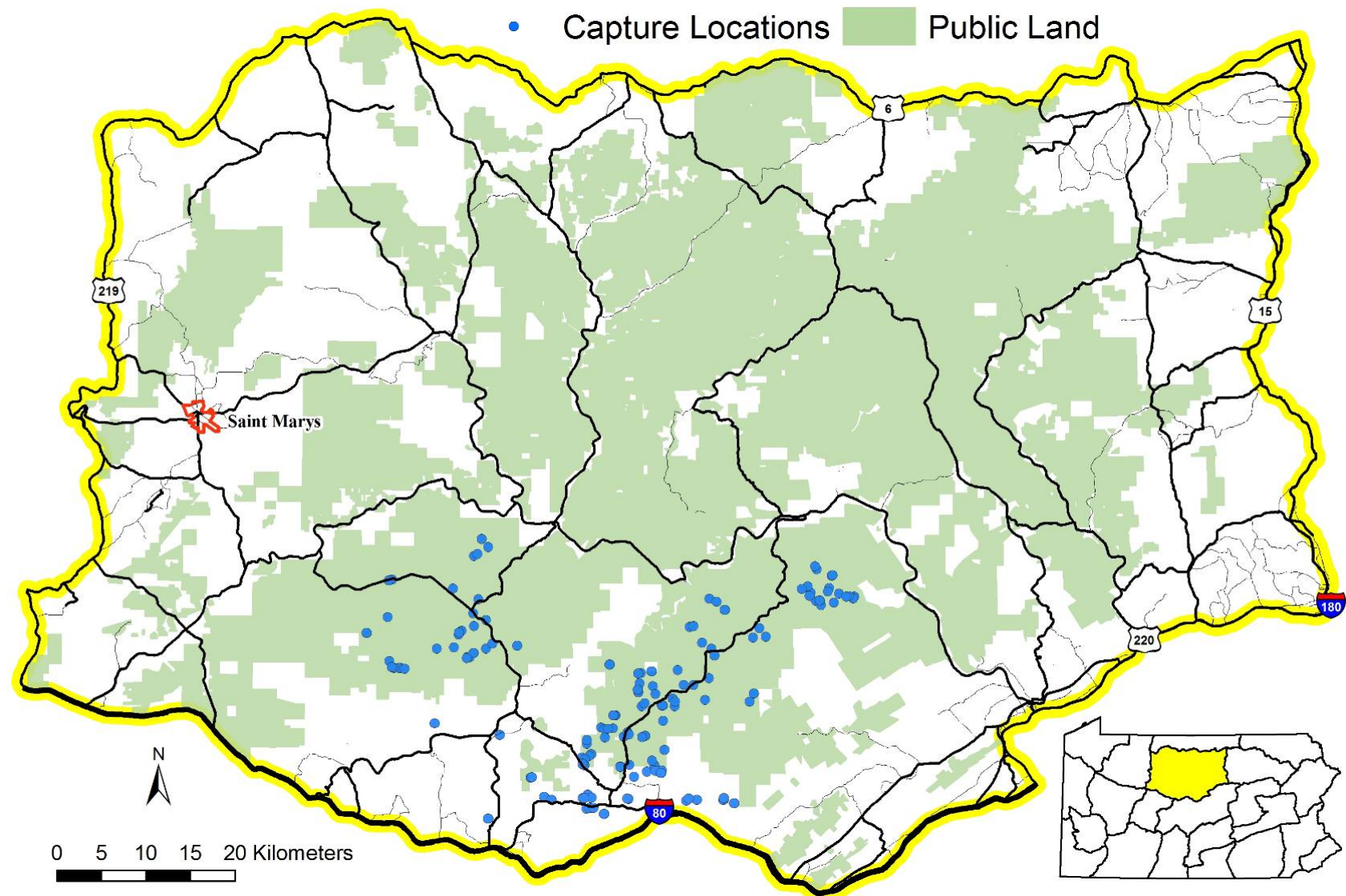
Figure 1.4: Capture locations for 81 male and 207 female radio-marked white-tailed deer in WMU 2G, Pennsylvania, 2005-2008. The city of Saint Marys is outlined in red for reference.
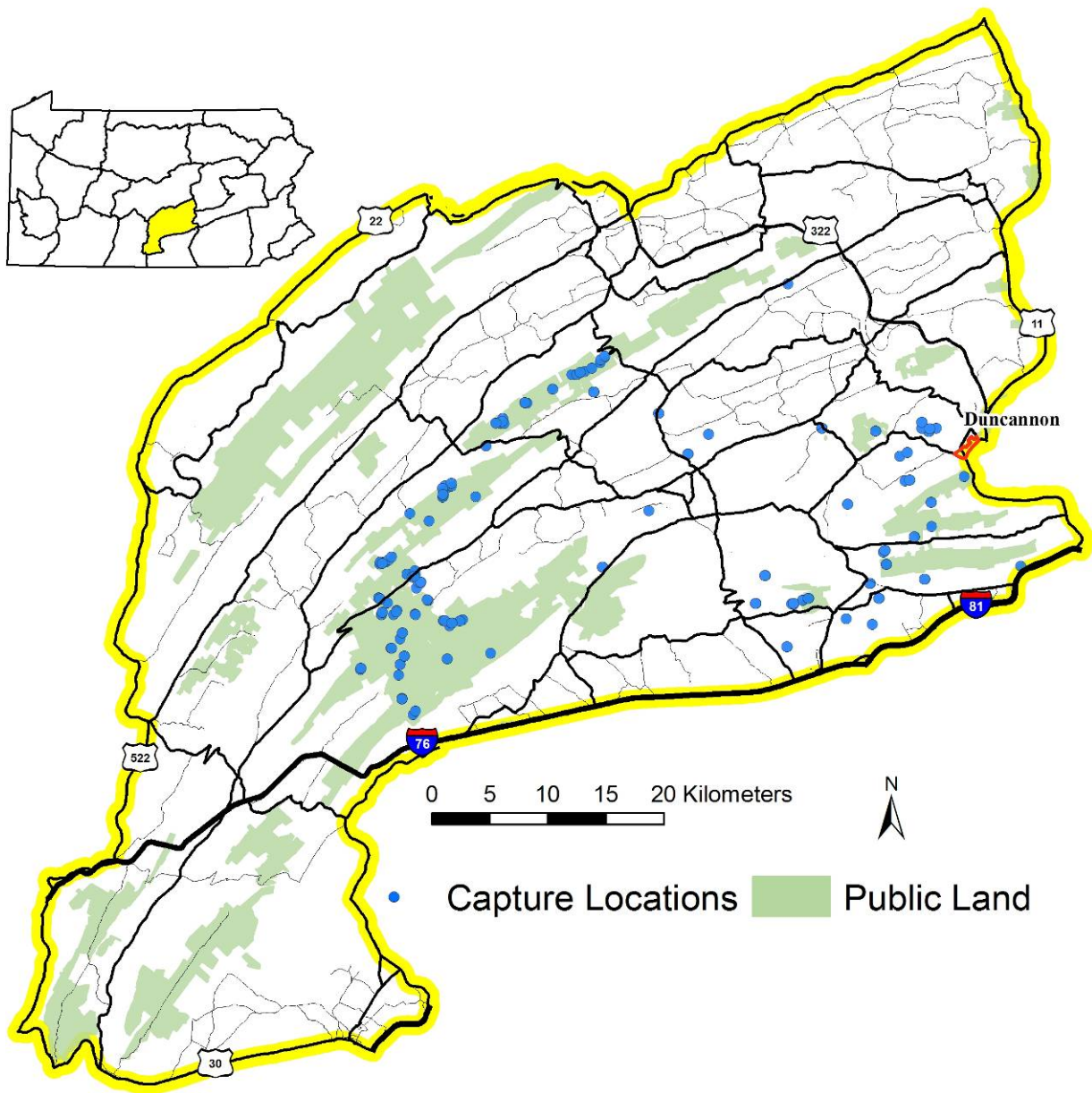
Figure 1.5: Capture locations for 93 male and 207 female radio-marked white-tailed deer in WMU 4B, Pennsylvania, 2005-2008. The city of Duncannon is outlined in red for reference.

Table 1.1: Age and sex specific capture statistics of 1,076 white-tailed deer during the 2G/4B study across WMU 2G and 4B, Pennsylvania, 2005-2008. Numbers outside the parentheses (N) indicate initial capture and marking of released deer, while numbers inside the parentheses indicate recaptured and released deer (r) and capture site mortalities (m).

Study Area	Method	Juveniles		Adults		
		Males	Females	Males	Females	Total
		N (r,m)	N (r,m)	N (r,m)	N (r,m)	N (r,m)
2G	Clover Trap	50 (26,5)	47 (19,2)	29 (10,0)	96 (17,1)	222 (72,8)
2G	Drop Net	32 (2,0)	30 (3,1)	19 (3,0)	50 (5,1)	131 (13,2)
2G	Rocket Net	29 (1,0)	18 (0,1)	11 (4,0)	43 (6,0)	101 (11,1)
2G	Dart Gun	0 (0,0)	0 (0,0)	0 (0,0)	0 (0,0)	0 (0,0)
2G	All methods	111 (29,5)	95 (22,4)	59 (17,0)	189 (28,2)	454 (96,11)
4B	Clover Trap	39 (22,0)	41 (12,0)	20 (2,0)	40 (12,1)	140 (48,1)
4B	Drop Net	39 (7,0)	54 (4,1)	22 (1,1)	58 (4,0)	173 (16,2)
4B	Rocket Net	37 (5,1)	46 (0,0)	15 (0,0)	28 (2,0)	126 (7,1)
4B	Dart Gun	0 (0,0)	0 (0,0)	0 (0,0)	1 (0,0)	1 (0,0)
4B	All methods	115 (34,1)	141 (16,1)	57 (3,1)	127 (18,1)	440 (71,4)
All study areas and methods		226 (63,6)	236 (38,5)	116 (20,1)	316 (46,3)	894 (167,15)

Chapter 2

Evaluation of assumptions associated with the Pennsylvania Sex-Age-Kill model

Introduction

Population estimation procedures are often subject to scrutiny because of their unrealistic and restrictive assumptions (Millspaugh et al. 2009). Failure to address these assumptions can incorporate bias into population estimates (Burgdorf and Weeks 1997, Skalski and Millspaugh 2002, Davis et al. 2007, Millspaugh et al. 2009). Although the PASAK model was developed to eliminate or relax some assumptions, model assumptions still must be evaluated. Independent estimates of survival and harvest rates provide a means to evaluate many important assumptions associated with the PASAK model (Gove et al. 2002).

Assumption 1: Constant mature male harvest rate across space and time

Currently, an important parameter in the PASAK model is the mature (≥ 2.5 years old) male harvest rate (H_{MM}), used to estimate mature male abundance. The H_{MM} is estimated directly from radiocollared deer. Applying this estimate, derived from four WMUs, across all twenty-two WMUs requires the assumption that H_{MM} is constant across space and time.

Assumption 2: Constant yearling male non-harvest survival or harvest rate across space and time

Another assumption is associated with the most sensitive parameter in the PASAK model, the yearling (1.5 years old) male abundance estimate, calculated in year t by

dividing the yearling male harvest by the estimated yearling male harvest rate ($\hat{H}_{YM}$).

Currently, PGC biologists use an iterative procedure based on previous years' data to

estimate H_{YM}, which assumes yearling male non-harvest survival ($\hat{S}_{(nonharv)YM}$) is

constant across space and time. This procedure involves a series of steps. First, a pre-

hunting season 2.5 year old male population ($N_{2.5M(t)}$) estimate for year t is divided by

non-harvest survival ($\hat{S}_{(nonharv)YM}$; unpublished data, PGC). All pre-hunt 1.5 year old to

pre-hunt 2.5 year old male mortalities, excluding legal harvests, are used to estimate

$\hat{S}_{(nonharv)YM}$. The subsequent quotient of $\hat{N}_{2.5M(t)}$ divided by $\hat{S}_{(nonharv)YM}$ is added to

yearling male harvest from the previous year ($\hat{K}_{YM(t-1)}$) providing a pre-season yearling

male abundance estimate. The quotient of the $\hat{K}_{YM(t-1)}$ divided by the pre-season

abundance estimate is the yearling male harvest rate for the previous year ($\hat{H}_{YM(t-1)}$).

$$\hat{H}_{YM(t-1)} = \frac{\hat{K}_{YM(t-1)}}{(\hat{N}_{2.5M(t)}/\hat{S}_{(nonharv)YM}) + \hat{K}_{YM(t-1)}}$$

The $\hat{H}_{YM(t-1)}$ is averaged with similarly calculated harvest rates for the two years

preceding ($\hat{H}_{YM(t-2)}$ and $\hat{H}_{YM(t-3)}$), which is used as the harvest rate in the current year.

Yearling male abundance for previous years can be estimated similarly; however, no

moving average is used, only harvest data from year t is used to calculate the population

for year t-1,

$$\hat{N}_{YM(t)} = (\hat{N}_{2.5M(t+1)}/\hat{S}_{nonharv(YM)}) + \hat{K}_{YM(t)}.$$

I refer to abundance estimates that do not use a moving average as updated estimates. This procedure is explained in further detail in the methods section of chapter 3. Because yearling male abundance estimates are derivatives of mature male abundance estimates, the most important estimate from radiocollar data is the $\hat{H}_{MM}$.

An alternative to the iterative and updating procedure for yearling male abundance estimates is to use harvest rates estimated directly from data collected about monitored radiocollared yearling males. Consequently, this will remove the relationship between yearling male and mature male abundance, minimizing the importance of $\hat{H}_{MM}$. However, this approach has not been used because biologists were concerned that $\hat{H}_{YM}$ may be more variable than $\hat{H}_{MM}$ as a consequence of variability in protection rates from antler point restriction regulations (APRs). Yearling male protection rates are dependent on antler development, likely related to nutritional quality and availability, which could vary across time and space (French et al. 1956). Empirical data can provide insight into both $\hat{H}_{YM}$ and $\hat{S}_{(nonharv)YM}$ variability.

Assumption 3 and 4: Constant female harvest rate across age and constant yearling survival outside the hunting season across sex, space, and time

The last two assumptions that can be tested using data from radiocollared deer are related to the adult female to male ratio ($p_{F:M}$) and the juvenile to female ratio ($p_{J:AF}$). Specifically, mature and yearling female deer are assumed to be harvested at the same rate, and deer captured as juveniles (8 months old) are assumed to be recruited into the

yearling pre-hunting season, October 1, age-class at the same rate across space, time, and sex, hereafter referred to as yearling survival outside the hunting season ($S_{(outhunt)Yrlg}$).

If evidence suggests any of these assumptions are not met, further investigations can be conducted to attempt to explain variability. Specifically, landscape and temporal covariates hypothesized to affect harvest rates or survival parameters can be quantified, and used as explanatory variables. If variation in these parameters can be explained using covariates, predictive models can be constructed. Similarly, if assumption violations involve sex or age-class variability, the PASAK model can be adjusted to account for these differences.

Variation in the harvest rate is oftentimes related to differences in hunter effort (Hansen et al. 1986, Foster et al. 1997, Broseth and Pederson 2000). However, other temporal and spatial factors may have an effect on the $\hat{H}_{MM}$ or $\hat{H}_{YM}$. Environmental factors believed to influence hunter efficiency, indirectly influencing harvest rates, could include forest cover, land ownership, landscape ruggedness, and road density (Eberhardt 1960, Holsworth 1973, Picton and Mackie 1980, Foster et al. 1997, Broseth and Pederson 2000). Weather conditions, such as rain and snow depth could explain temporal variability. I predicted harvest rates were positively correlated with hunting pressure, road density, percent of public land, and snow depth. Alternatively, I expect harvest rates to decrease with an increase in terrain ruggedness, percent forest cover, and rainfall.

In addition to the previously mentioned parameters, which are assumed to vary across all age classes similarly, the following two factors are assumed to affect only $\hat{H}_{YM}$. Because antler growth is thought to be affected in part by body condition during antler development (February to September), winter severity and mast production prior to the

hunting season, could alter the yearling male harvest vulnerability under the APRs in Pennsylvania (French et al. 1956). I predicted hard mast production would have a positive correlation with $\hat{H}_{YM}$, whereas winter severity would have a negative correlation with $\hat{H}_{YM}$.

Spatial and temporal variability in $\hat{S}_{(nonharv)YM}$ and $\hat{S}_{(outhunt)Yrlg}$ may be affected by road density, winter severity, and mast production. I predicted that both survival parameters were negatively correlated with road density and winter severity, and positively correlated with mast production. Whereas $\hat{S}_{(nonharv)YM}$ also may be negatively related to hunter effort because of additional mortality related to hunting, such as wounding loss, mistake kills, and poaching.

My objectives were to (1) evaluate variability in white-tailed deer harvest and survival rates across space, time, age, and sex as they relate to assumptions of the PASAK model, and (2) adjust parameter estimates to satisfy or relax assumptions. I used an information-theoretic approach to evaluate variability in vital rates from radiocollared deer. If estimates from radiocollar data indicated variability, I investigated covariates that could be used to relax model assumptions.

Methods

I estimated annual survival ($\hat{S}_t$) and harvest rates (1- $\hat{S}_t$) using the staggered entry design of the Kaplan-Meier (K-M) estimator,

$$\hat{S}_t = \prod(1 - \frac{d_j}{r_j})$$

$$j \mid a_j \langle t.$$

Where r_j is the number of animals at risk during a time period (a_j), and d_j is the

number of deaths during the same time period (Kaplan and Meier 1958, Pollock et al.

1989). I used 9 bi-weekly intervals from early October through early January for all

harvest rate estimates. When estimating survival, I used 12 monthly time periods starting

in October when the deer were 1.5 years old, and 8 monthly time periods starting in

February when deer were 8 months old for $S_{(nonharv)YM}$ and $S_{(outhunt)Yrlg}$, respectively.

I tested assumptions and explored spatial and temporal variability by comparing

logistic regression models from K-M estimates using Akaike's Information Criterion

values, corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2002). I then

evaluated effect size by comparing K-M point estimates and odds ratio ($\widehat{OR}$)

calculations. I used the known-fates (KF) procedure in program MARK to model

survival and harvest rates (White and Burnham 1999).

For H_{MM}, H_{YM} and $S_{(nonharv)YM}$ assumptions, I compared intercept-only or null

models to models containing study area (AREA) and year (YEAR) as covariates, for both

the 2D/4D and 2G/4B studies separately. Intercept-only models contained only

parameter estimates for individual, bi-weekly or monthly, K-M time periods. If I found

evidence (lower AIC$_c$) for temporal or spatial variation, and the variability appeared

biologically important based on point estimates and odds ratios, exploratory analysis of

variability was conducted. Because of the exploratory nature of these models and *a*

priori selection of biologically supported explanatory variables hypothesized to be

independent, I considered all possible subsets when ranking $\hat{H}_{MM}$ models. For spatial

variability, initially I used only covariates included in the most parsimonious $\hat{H}_{MM}$

model when exploring similar variability in subsequent $\hat{H}_{YM}$ and $\hat{H}_F$ models, because I

expected harvest rates to vary similarly across age-sex classes.

My suite of spatial covariates included WMU specific measures of hunter effort

(hunter days/mi^2), and individual deer home range covariates of percent forest cover,

percent public land, ruggedness (SD of elevation), and road density. I estimated hunter

effort for each WMU using PGC Game Take Survey data collected via annual mailing

surveys (PGC unpublished data). A hunter day is defined as the number of hunting days,

regardless of hours per day, a license holder reports spending in a WMU during a specific

season. I divided the estimate of hunter days by the size of the WMU to estimate a

measure of hunter effort. Because no Game Take Survey data were available in 2002 and

2004, I averaged hunter pressure across years (Figure 2.1 and Figure 2.2). All models

with hunter effort (PRESS) include two additional parameters for the archery and firearm
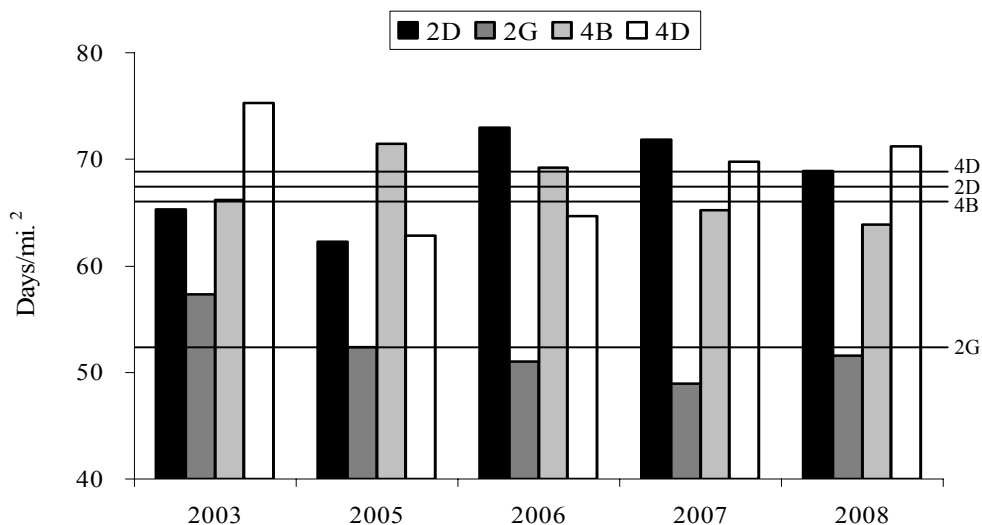
hunting seasons.

Figure 2.1: Hunting effort by WMU from 2003-2008 (excluding 2004) during the Pennsylvania white-tailed deer firearm hunting season. Horizontal lines represent mean values for respective WMUs.
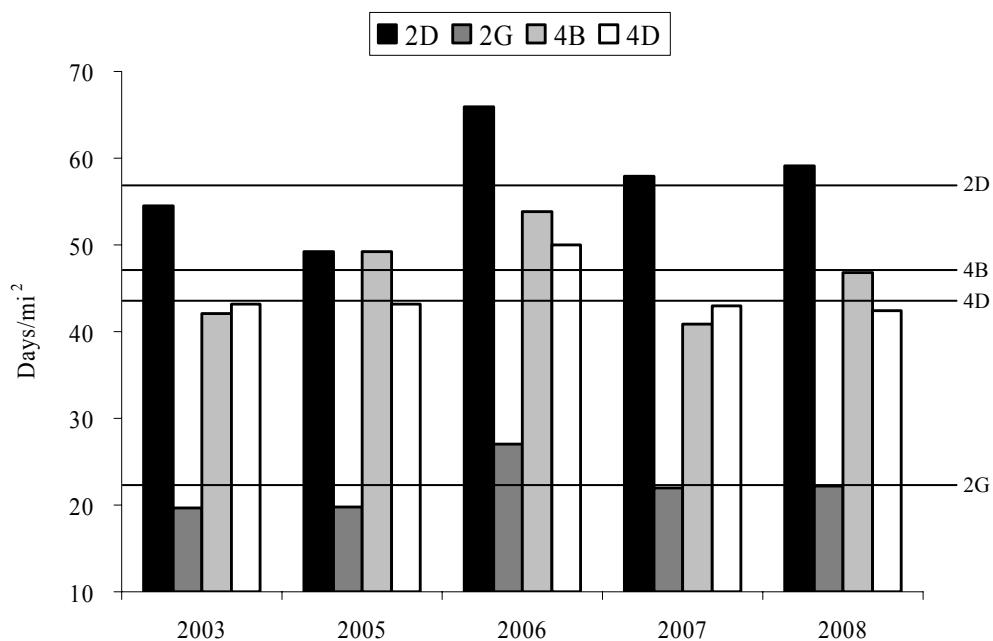
Figure 2.2: Hunting effort by WMU from 2003-2008 (excluding 2004) during the Pennsylvania white-tailed deer archery hunting seasons. Horizontal lines represent mean values for respective WMUs.

I performed all spatial data analysis using ArcGIS (Environmental Systems Research Institute v. 9.2 2006). I quantified forested land, public land, ruggedness, and road density covariates using data available on the Pennsylvania Spatial Data Access (PASDA) website (see Appendix A). I used PAMAP Land Cover for Pennsylvania, and PGC State Game Lands and Department of Conservation and Natural Resources (DCNR) State Forests to quantify percent forested land and percent public land, respectively. I estimated terrain ruggedness using the standard deviation of elevation. My road density covariate summed state and local road lengths across home ranges of individual deer.

I used the radius of a circle with an area equal to the mean area from 90% Kernel Density Home Range estimates from GPS collared deer in Pennsylvania to create buffer sizes of 1,314.10 m and 1,004.34 m for antlered (n = 38) and antlerless (n = 25) white-tailed deer, respectively (Beyer 2004, Seamann 1998). I used these buffer sizes around the median location of each deer during peak white-tailed deer hunting months in Pennsylvania, November and December, to obtain covariate information associated with analysis of harvest rates. I used the same sized buffer around the median location from all months to obtain covariate information for non-harvest survival. If no locations were estimated during November or December for harvest rate home ranges, I used October locations (early archery hunting season), then locations from other non-hunting months. If deer locations indicated two discrete home ranges, typical with yearling dispersal (Long 2005), I buffered two locations around median natal and adult home ranges separately.

I used annual PGC State Wildlife Food Surveys of red and white oak mast production which categorized hard mast availability prior to the hunting season as low, average, or

high (PGC Wildlife Management Report No. 23000, http://www.pgc.state.pa.us/). My

other temporal covariates, average rain and snow depth over the firearms season and

winter severity prior to the hunting season, were obtained from the nearest cooperative

observer sites to each study area (Pennsylvania State University 2009).

I evaluated the female harvest rate (H_F) assumption of constant harvest rates

between yearlings and adults by comparing NULL and AGE models. To evaluate the

assumption that $S_{(outhunt)Yrlg}$ is constant across space, time, and sex, I used similar methods

associated with male harvest rate assumption testing. If the NULL model was not

selected, and biologically important temporal or spatial variability was suggested, I

investigated potential covariates to explain variability.

Results

Sample Population

Of the 1,142 white-tailed deer I radiocollared, 908 were used to estimate K-M harvest

rate and survival parameters. Because deer that survive the first year can be used again in

subsequent years for mature male and female harvest rate and survival estimates, I was

able to analyze encounter histories for more than the total number of unique deer that

were captured (Table 2.1).

Table 2.1: Number of deer used (n) for the Kaplan-Meier estimator and associated mortalities by WMU, age, and sex for mature male harvest rate (H_{MM}), yearling male harvest rate (H_{YM}), yearling male non-harvest survival ($S_{(nonharv)YM}$), female harvest rate (H_F), and yearling survival outside the hunting season ($S_{(outhunt)Yrlg}$). The 2D/4D study includes data from WMUs 2D and 4D, whereas the 2G/4B study includes data from WMUs 2G and 4B, Pennsylvania, 2002-2008.

Parameter	Study Area	n 2002	2003	2004	2005	2006	2007	2008	2D/4D study n	Mortalities	2G/4B study n	Mortalities
H_{MM}	2D	3	16	55	27							
H_{MM}	4D	1	14	42	21							
H_{MM}	4B						10	19				
H_{MM}	2G						12	28				
H_{MM}	All	4	30	97	48		22	47	179	90	69	26
H_{YM}	2D	43	82	63								
H_{YM}	4D	16	49	52								
H_{YM}	4B						29	20				
H_{YM}	2G						18	25				
H_{YM}	All	59	131	115			47	45	305	89	92	28
$S_{(nonharv)YM}$	2D	51	89	64								
$S_{(nonharv)YM}$	4D	19	53	56								
$S_{(nonharv)YM}$	4B						31	22				
$S_{(nonharv)YM}$	2G						18	25				
$S_{(nonharv)YM}$	All	70	142	120			49	47	332	56	96	12
H_F	4B Mat.				17	45	66	65				
H_F	4B Yrlng.				20	21	34	16				
H_F	2G Mat.				41	74	82	62				
H_F	2G Yrlng.				13	14	18	10				
H_F	All				91	154	200	153			598	85

Table 2.1 Continued

Parameter	Study Area	*n*							2D/4D study		2G/4B study	
		2002	2003	2004	2005	2006	2007	2008	*n*	Mortalities	*n*	Mortalities
$S_{(outhunt)Yrlg}$	4B Male						34	23				
$S_{(outhunt)Yrlg}$	4B Fem.						37	18				
$S_{(outhunt)Yrlg}$	2G Male						18	28				
$S_{(outhunt)Yrlg}$	2G Fem.						21	13				
$S_{(outhunt)Yrlg}$	All						110	82			192	9

Mature Male Harvest Rate

The 2D/4D and 2G/4B study both indicated the model including only spatial variability (AREA) was the most parsimonious (Table 2.2). Using 2D/4D study data, I estimated H_{MM} = 68.5% for WMU 2D, and H_{MM} = 53.0% for WMU 4D (Table 2.3). For the 2G/4B study, H_{MM} = 55.5% for WMU 4B, and H_{MM} = 35.7% for WMU 2G (Table 2.3). These point estimates suggest there may be biologically important spatial variability in H_{MM} as it relates to the PASAK model.

Because my models indicated relatively little temporal variability, I pooled data from the 2D/4D and 2G/4B studies to evaluate $\hat{H}_{MM}$ variability. However, I was unable to use data from 2005, because no location data were collected. I used all possible combinations of the five spatial covariates when exploring $\hat{H}_{MM}$ variability. The top-ranked model included only the average hunting pressure covariate (PRESS), suggesting average hunting pressure is a better explanatory variable than WMU (AREA) across the four study areas (Table 2.4).

Table 2.2: Spatio-temporal variability in mature male harvest rates across 4 WMUs and two studies. The 2D/4D study includes data from WMU 2D and 4D (2002-2005), whereas the 2G/4B study includes data from WMU 2G and 4B (2007-2008). Models are listed with the number of parameters (K), and measures of model fit indicated by AIC_c, and delta AIC_c (Δ_i), along with the respective weights (w_i) , Pennsylvania, 2002-2008.

Study	Models	K	AIC_c	Δ_i	w_i (%)
2D/4D	AREA	5	338.48	0.00	62.20
2D/4D	NULL	4	340.69	2.21	20.64
2D/4D	YEAR+AREA	8	341.69	3.21	12.48
2D/4D	YEAR	7	343.66	5.18	4.68
2G/4B	AREA	4	114.53	0.00	38.29
2G/4B	NULL	3	114.81	0.28	33.22
2G/4B	AREA+YEAR	5	116.32	1.80	15.59
2G/4B	YEAR	4	116.70	2.18	12.90

Table 2.3: Mature male harvest rate estimates ($\hat{H}_{MM}$) and odds ratios ($\widehat{OR}_{MM}$) with associated 95% confidence intervals by area, year, and area and year. The 2D/4D study includes data from WMU 2D and 4D, whereas the 2G/4B study includes data from WMU 2G and 4B, Pennsylvania, 2002-2008.

Study	Year	WMU	$\hat{H}_{MM}$ (%)	95% CI (%)	$\widehat{OR}_{MM}$	95% CI
2D/4D		2D	68.5	57.6 - 77.7		
2D/4D		4D	53.0	41.7 - 64.0	0.55	0.31 - 0.98
2D/4D	2002		89.5	45.5 - 98.9	3.47	0.60 - 20.03
2D/4D	2003		62.5	45.3 - 77.1	0.92	0.40 - 2.08
2D/4D	2004		57.0	45.9 - 67.6	0.75	0.38 - 1.45
2D/4D	2005		64.7	51.0 - 77.2		
2D/4D	2002	2D	92.1	50.3 - 99.3		
2D/4D	2002	4D	84.1	38.0 - 97.9		
2D/4D	2003	2D	70.0	51.0 - 83.9		
2D/4D	2003	4D	55.0	36.9 - 72.2		
2D/4D	2004	2D	64.8	50.9 - 76.4		
2D/4D	2004	4D	49.4	36.6 - 62.6		
2D/4D	2005	2D	71.5	56.1 - 83.6		
2D/4D	2005	4D	56.8	41.0 - 72.3		
2G/4B		4B	55.5	35.9 - 73.6		
2G/4B		2G	35.7	21.6 - 52.9	0.47	0.18 - 1.25
2G/4B	2007		40.5	21.9 - 62.3		
2G/4B	2008		45.6	30.6 - 61.5	1.22	0.44 - 3.36
2G/4B	2007	4B	51.2	26.7 - 75.1		
2G/4B	2007	2G	31.5	14.1 - 56.3		
2G/4B	2008	4B	58.3	35.8 - 77.8		
2G/4B	2008	2G	37.7	21.8 - 56.8		

Table 2.4: Models using all combinations of 5 covariates, rifle and archery season hunting pressure (PRESS), road density (RD), percent public land (PUB), percent forested land (FOR), and ruggedness (RUG), compared to null (NULL), spatial (AREA), and temporal (YEAR) models for mature male harvest rates using pooled data from two studies in Pennsylvania across 4 WMUs and 7 years (2002-2008). Models are listed with the number of parameters (K), and measures of model fit indicated by AIC_c, and delta AIC_c (Δ_i), along with the respective weights (w_i), Pennsylvania, 2002-2008.

Models	K	AIC_c	Δ_i	w_i (%)
PRESS	6	360.35	0.00	18.26
PRESS+RUG	7	361.28	0.93	11.47
PRESS+PUB	7	361.58	1.24	9.84
PRESS+FOR	7	362.12	1.77	7.54
PRESS+RD	7	362.34	1.99	6.75
PRESS+PUB+RUG	8	362.91	2.56	5.08
PRESS+RUG+RD	8	363.29	2.94	4.19
PRESS+RUG+FOR	8	363.30	2.95	4.18
PRESS+RD+PUB	8	363.61	3.26	3.58
PRESS+FOR+PUB	8	363.61	3.26	3.58
PUB	5	364.13	3.78	2.76
PRESS+FOR+RD	8	364.13	3.78	2.76
AREA[a]	7	364.33	3.98	2.49
PRESS+RUG+FOR+PUB	9	364.64	4.29	2.14
PRESS+RUG+RD+PUB	9	364.87	4.52	1.91
PRESS+RUG+FOR+RD	9	365.32	4.97	1.52
FOR	5	365.59	5.24	1.33
PRESS+FOR+RD+PUB	9	365.63	5.29	1.30
RD+PUB	6	365.87	5.52	1.16
FOR+PUB	6	365.93	5.58	1.12
RUG+PUB	6	366.07	5.72	1.04
PRESS+RUG+FOR+RD+PUB	10	366.67	6.32	0.77
NULL[a]	4	366.89	6.54	0.70
RD	5	367.15	6.81	0.61
RD+FOR	6	367.55	7.20	0.50
RUG+FOR	6	367.59	7.24	0.49
AREA+YEAR[a]	10	367.67	7.32	0.47
FOR+RD+PUB	7	367.85	7.50	0.43
RUG+RD+PUB	7	367.86	7.51	0.43
RUG+FOR+PUB	7	367.95	7.60	0.41

Table 2.4 Continued

Models	K	AIC_c	Δ_i	w_i (%)
RUG	5	368.48	8.13	0.31
YEAR[a]	8	368.53	8.18	0.31
RUG+RD	6	369.05	8.70	0.24
RUG+FOR+RD	7	369.56	9.21	0.18
RUG+FOR+RD+PUB	8	369.86	9.51	0.16

[a] Spatio-temporal models used for comparison to models including covariates

Yearling Male Harvest Rate

Temporally varying $\hat{S}_{(nonharv)YM}$ models in both the 2D/4D and 2G/4B studies were the top-ranked models (Table 2.5), and point estimates indicated yearly differences might be biologically important. When grouped by year, $\hat{S}_{(nonharv)YM}$ ranged from 70.3% to 83.5% during the 2D/4D study, and 72.1% to 91.0% during the 2G/4B study (Table 2.6).

My direct estimates of the H_{YM}, from radiocollared data, were less variable over space and time than the $\hat{S}_{(nonharv)YM}$. The top-ranked model of the 2D/4D study data was the null, whereas the null model in the 2G/4B study was ranked second compared to the top-ranked spatially varying (AREA) model (Table 2.7). Furthermore, I found differences in $\hat{H}_{YM}$ between WMUs were smaller than differences in $\hat{S}_{(nonharv)YM}$ across years. The range in $\hat{H}_{YM}$ was 31.2% to 34.9% during the 2D/4D study, and 25.5% to 42.0% during the 2G/4B study (Table 2.8).

Because directly estimating H_{YM} from empirical data is simpler than back-calculating the $\hat{H}_{YM}$ using $\hat{S}_{(nonharv)YM}$, and direct estimates proved to be less variable, I chose to only explore the variability in the direct H_{YM} estimates. The null model was the top-ranked model, however, the hunting pressure (PRESS) model ranked better than both spatial and temporal models (Table 2.9).

Table 2.5: Spatio-temporal variability in yearling male non-harvest survival across 4 WMUs and two studies. The 2D/4D study includes data between WMU 2D and 4D (2002-2004), while the 2G/4B study includes data between WMU 2G and 4B (2007-2008). Models are listed with the number of parameters (K), and measures of model fit indicated by AIC_c, and delta AIC_c (Δ_i), along with the respective weights (w_i) , Pennsylvania, 2002-2008.

Study	Models	K	AIC_c	Δ_i	w_i (%)
2D/4D	YEAR	10	473.63	0.00	37.46
2D/4D	NULL	8	474.21	0.59	27.93
2D/4D	YEAR+AREA	11	475.01	1.38	18.76
2D/4D	AREA	9	475.35	1.72	15.85
2G/4B	YEAR	8	120.04	0.00	45.47
2G/4B	YEAR+AREA	9	120.90	0.86	29.60
2G/4B	NULL	7	122.03	1.99	16.77
2G/4B	AREA	8	123.48	3.44	8.16

Table 2.6: Yearling male non-harvest survival ($\hat{S}_{(nonharv)YM}$) and odds ratios ($\widehat{OR}_{YM}$) estimates with associated 95% confidence intervals by area, year, and area and year. The 2D/4D study includes data from WMU 2D and 4D, whereas the 2G/4B study includes data from WMU 2G and 4B, Pennsylvania, 2002-2008.

Study	Year	WMU	$\hat{S}_{(nonharv)YM}$ (%)	95% CI (%)	$\widehat{OR}_{YM}$	95% CI
2D/4D		2D	73.9	65.4 - 80.9		
2D/4D		4D	79.2	69.7 - 86.3	1.31	0.74 - 2.29
2D/4D	2002		75.5	60.6 - 86.0		
2D/4D	2003		70.3	60.5 - 78.6	0.79	0.39 - 1.61
2D/4D	2004		83.5	73.9 - 90.1	1.58	0.70 - 3.54
2D/4D	2002	2D	73.9	57.8 - 85.4		
2D/4D	2002	4D	78.5	61.9 - 89.1		
2D/4D	2003	2D	68.2	56.4 - 78.0		
2D/4D	2003	4D	73.5	60.6 - 83.4		
2D/4D	2004	2D	81.9	70.4 - 89.6		
2D/4D	2004	4D	85.3	74.7 - 91.9		
2G/4B		4B	77.8	58.6 - 89.6		
2G/4B		2G	85.3	69.0 - 93.8	1.6	0.49 - 5.18
2G/4B	2007		91.0	75.2 - 97.1		
2G/4B	2008		72.1	53.3 - 85.4	0.3	0.08 - 1.07
2G/4B	2007	4B	88.4	67.4 - 96.5		
2G/4B	2007	2G	93.8	78.1 - 98.5		
2G/4B	2008	4B	62.5	34.8 - 83.9		
2G/4B	2008	2G	78.1	55.6 - 91.1		

Table 2.7: Spatio-temporal variability in yearling male harvest rates across 4 WMUs and two studies. The 2D/4D study includes data from WMU 2D and 4D (2002-2004), whereas the 2G/4B study includes data from WMU 2G and 4B (2007-2008). Models are listed with the number of parameters (K), and measures of model fit indicated by AIC_c, and delta AIC_c (Δ_i), along with the respective weights (w_i), Pennsylvania, 2002-2008.

Study	Models	K	AIC_c	Δ_i	w_i (%)
2D/4D	NULL	6	499.98	0.00	59.20
2D/4D	AREA	7	501.60	1.61	26.42
2D/4D	YEAR	8	503.56	3.57	9.92
2D/4D	YEAR+AREA	9	505.15	5.17	4.47
2G/4B	AREA	5	155.78	0.00	41.17
2G/4B	NULL	4	156.28	0.50	32.06
2G/4B	YEAR+AREA	6	157.79	2.01	15.06
2G/4B	YEAR	5	158.29	2.51	11.71

Table 2.8: Yearling male harvest rate estimates ($\hat{H}_{YM}$) and odds ratios ($\widehat{OR}_{YM}$) with associated 95% confidence intervals by area, year, and area and year. The 2D/4D study includes data from WMU 2D and 4D, whereas the 2G/4B study includes data from WMU 2G and 4B, Pennsylvania, 2002-2008.

Study	Year	WMU	$\hat{H}_{YM}$ (%)	95% CI (%)	$\widehat{OR}_{YM}$	95% CI
2D/4D		2D	34.9	27.9 - 42.6		
2D/4D		4D	31.2	23.3 - 40.5	0.86	0.53 - 1.39
2D/4D	2002		36.2	23.9 - 50.5		
2D/4D	2003		31.3	23.5 - 40.3	0.81	0.42 - 1.57
2D/4D	2004		34.5	26.0 - 44.0	0.93	0.48 - 1.80
2D/4D	2002	2D	37.4	24.5 - 52.5		
2D/4D	2002	4D	33.5	20.2 - 50.0		
2D/4D	2003	2D	32.7	23.9 - 42.9		
2D/4D	2003	4D	29.0	19.7 - 40.6		
2D/4D	2004	2D	36.3	26.3 - 47.8		
2D/4D	2004	4D	32.5	22.8 - 43.9		
2G/4B		4B	42.0	28.3 - 57.1		
2G/4B		2G	25.5	14.4 - 41.3	0.5	0.21 - 0.64
2G/4B	2007		34.7	22.2 - 49.9		
2G/4B	2008		33.4	20.5 - 49.4	0.9	0.41 - 2.19
2G/4B	2007	4B	41.3	25.7 - 58.9		
2G/4B	2007	2G	24.7	11.9 - 44.4		
2G/4B	2008	4B	43.2	24.6 - 63.9		
2G/4B	2008	2G	26.2	13.6 - 44.4		

Table 2.9: Archery and rifle season hunting pressure model (PRESS) compared to null (NULL), spatial (AREA), and temporal (YEAR) models for yearling male harvest rates using pooled data from two studies across 4 WMUs and 6 years (2002-2008). Models are listed with the number of parameters (K), and measures of model fit indicated by AIC_c, and delta AIC_c (Δ_i), along with the respective weights (w_i), Pennsylvania, 2002-2008.

Models	K	AIC_c	Δ_i	w_i (%)
NULL	7	659.48	0.00	55.92
PRESS	9	660.67	1.19	30.85
AREA	10	662.69	3.20	11.27
YEAR	11	667.06	7.58	1.27
YEAR+AREA	13	668.24	8.76	0.70

Female Harvest Rate

The top-ranked model of $\hat{H}_F$ indicated variation between yearlings and adults, and among study areas (Table 2.10). When I modeled hunting pressure and age-class together, I was able to explain WMU and year specific variability (Table 2.10). Yearling females were harvested at a greater rate, 19.8%, than mature females, 13.4%, and females in WMU 2G were harvested at a lower rate, 12.3%, than females in WMU 4B, 18.0%, suggesting possible biologically important age-class and spatial variability (Table 2.11).

Yearling Survival Outside the Hunting Season

To compare $\hat{S}_{(outhunt)Yrlg}$ from the same time and study areas, I only used data from 2007 and 2008 in WMUs 2G and 4B. I found no model improvement when using area, year, or sex as covariates. The model including variability for sex ranked second ($\Delta AIC_c = 0.57$; Table 2.12). My estimate from the null model was 95.1%, whereas separate estimates were 96.9% for males and 93.1% for females (Table 2.13).

Table 2.10: Archery and rifle season hunting pressure (PRESS) used to explain spatio-temporal (AREA and YEAR) harvest rate variability between yearling and adult (AGE) female deer from WMUs 2G and 4B. Models are listed with the number of parameters (K), and measures of model fit indicated by AIC_c, and delta AIC_c (Δ_i), along with the respective weights (w_i) , Pennsylvania, 2005-2008.

Models	K	AIC_c	Δ_i	w_i (%)
AGE+PRESS	10	699.76	0.00	0.23
AGE+AREA	9	699.81	0.05	0.23
AREA	8	700.02	0.26	0.20
AGE	8	700.35	0.59	0.17
NULL	7	701.56	1.80	0.09
AGE+AREA+YEAR	12	704.30	4.54	0.02
AGE+YEAR	11	704.45	4.69	0.02
AREA+YEAR	11	704.97	5.21	0.02
YEAR	10	706.18	6.42	0.01

Table 2.11: Yearling and adult female harvest rate ($\hat{H}_{YF}$ and $\hat{H}_{AF}$) and odds ratio estimates ($\widehat{OR}_F$) with associated 95% confidence intervals by age, area, and age and area. Estimates include data from WMU 2G and 4B from 2005-2008, Pennsylvania, 2005-2008.

Age	WMU	$\hat{H}_F$	95% CI	$\widehat{OR}_F$	95% CI
Yearling		19.8	14.0 - 27.1		
Adult		13.4	10.5 - 17.0	0.64	0.40 - 1.03
	4B	18.0	13.8 - 23.1		
	2G	12.3	9.1 - 16.6	0.65	0.42 - 1.02
Yearling	4B	22.0	15.3 - 30.5		
Yearling	2G	16.1	10.2 - 24.4		
Adult	4B	16.0	11.6 - 21.6		
Adult	2G	11.5	8.3 - 15.7		

Table 2.12: Spatial (AREA), temporal (YEAR), and sexual (SEX) variability between yearling outside the hunting season survival from WMUs 2G and 4B. Models are listed with the number of parameters (K), and measures of model fit indicated by AIC_c, and delta AIC_c (Δ_i), along with the respective weights (w_i), Pennsylvania, 2007-2008.

Models	K	AIC_c	Δ_i	w_i (%)
NULL	5	109.45	0.00	25.87
SEX	6	110.02	0.57	19.44
YEAR	6	110.76	1.31	13.44
YEAR+SEX	7	110.98	1.54	12.00
AREA	6	111.21	1.77	10.70
AREA+SEX	7	111.86	2.42	7.73
AREA+YEAR	7	112.41	2.96	5.88
AREA+YEAR+SEX	8	112.76	3.31	4.94

Table 2.13: Yearling outside the hunting season survival estimates ($\hat{S}_{(outhunt)Yrlg}$) with associated 95% confidence intervals for: males and females. Estimates include data from WMU 2G and 4B, Pennsylvania, 2007-2008.

Sex:	Year	WMU	$\hat{S}_{(outhunt)Yrlg}$ (%)	95% CI (%)
Both			95.1	90.9 – 97.5
Male	2007	4B	97.6	90.0 - 99.5
Male	2007	2G	98.3	91.4 - 99.7
Male	2008	4B	95.2	83.0 - 98.8
Male	2008	2G	96.6	86.3 - 99.2
Female	2007	4B	94.3	83.9 - 98.1
Female	2007	2G	95.9	84.1 - 99.1
Female	2008	4B	88.6	70.1 - 96.3
Female	2008	2G	91.8	72.6 - 97.9

Discussion

Mature Male Harvest Rate

Although I found little evidence for temporal variability, my data did not support the
assumption of constant mature male harvest rate across space. Excluding 2002, when
only four deer were radiocollared to estimate harvest rates, yearly estimates for H_{MM}
ranged 7.7% for the 2D/4D study, and 5.1% for 2G/4B study. Little evidence for
variability among years justified my pooling of data from both studies to increase the
sample sizes for possible predictive models accounting for spatial variability. I found a
positive effect that both archery and firearm season hunting effort best explained spatial
variability in $\hat{H}_{MM}$. This model included a readily quantified covariate for agency
biologists to predict harvest rates across WMUs. If agency biologists continue to use the
iterative and updating procedure to estimate yearling male abundance, managers should
allocate more resources to accurately estimate mature male harvest rates.

Yearling Male Harvest Rate

To avoid the assumption of constant spatio-temporal yearling male harvest rate, the
current design of the PASAK model uses $\hat{S}_{(nonharv)YM}$ to back-calculate $\hat{H}_{YM}$ through a
multi-year iterative procedure. This procedure still involves an assumption of constant
spatio-temporal $\hat{S}_{(nonharv)YM}$, and current-year estimates are not possible.

I found direct estimates of $\hat{H}_{YM}$ to be less variable than $\hat{S}_{(nonharv)YM}$ over space and
time. In fact, I found $\hat{H}_{YM}$ to be less variable than $\hat{H}_{MM}$, which is currently directly

estimated in the PASAK model. Initial reasoning behind not using $\hat{H}_{YM}$ was that

$\hat{H}_{YM}$ variability could be greater than $\hat{H}_{MM}$ variability. Because antler growth is

dependent on weather and food availability and quality (French et al. 1956), protection

rates for yearling males under APRs are thought to be variable given the diversity of soil

types, and annual variability in hard mast production and winter severity in Pennsylvania.

However, although these protection rates may vary, the overall yearling male harvest rate

variability is diminished because there will always be a large proportion of the population

unavailable for harvest. For example, if there are 1,000 yearling male deer, and harvest

rates of available male deer spatially vary between 40% and 80%, with a 50% yearling

male protection rate, the overall yearling male harvest rate only varies between 20% and

40%. This limits the amount of possible variability, as evidenced by the range of spatial

variability I found in $\hat{H}_{MM}$, 38.5% to 68.5%, compared to $\hat{H}_{YM}$, 25.5% to 42.0%.

Given these findings, and the evidence supporting the use of hunting pressure for

predicting $\hat{H}_{MM}$, I investigated the predictive ability of using hunting pressure as a

covariate to estimate H_{YM}. Similar to $\hat{H}_{MM}$, my data indicated relatively minor

temporal variation, so data from the two studies could be pooled to better evaluate spatial

variability. Again, I found the model using hunter effort covariates during the archery

and firearm hunting seasons ranked better than the spatial model, but the null model

proved to be the most parsimonious. I found little spatial variability in the grouped

model because my sample size during the 2D/4D study, which indicated some spatial

variability, was more than three times my sample size during the more substantially

varying 2G/4B study. Even though there is no evidence for spatial or temporal variation

in the grouped model, I believe the $\hat{H}_{YM}$ spatial variability could be important. When analyzing spatial patterns in harvest rates, it is apparent harvest rates across all age and sex classes are always lower in WMU 2G than the other three WMUs. Continued monitoring of spatial and temporal trends in yearling male harvest rates could provide important insight into variability of this parameter.

Female Harvest Rate

Variability between yearling and adult $\hat{H}_F$ violates an assumption of the PASAK model. Fortunately, the model can be calibrated using estimates of yearling and mature $\hat{H}_F$. However, these results are contrary to hypotheses that hunters will select the larger, mature females that tend to be the leader of maternal groups (C. S. Rosenberry, PGC, personal communication). Alternatively, inexperience of yearling females may increase their harvest vulnerability counteracting bias from hunter selectivity. A positive or negative bias will affect the adult male to female ratio estimate, which is multiplied by the adult male population to provide an adult female abundance estimate. If the bias favors the harvest of yearling females, as my data indicate, adult female populations will be underestimated.

Because I found evidence of spatial $\hat{H}_F$ variability, these age-specific estimates could be calibrated for each WMU using the predictive model including hunting pressure. However, modeling spatial variability would have relatively minor implications for abundance estimates if yearling and mature female harvest rates vary similarly, which my results supported.

Management decisions based on female harvest rate estimates using radiocollared deer should be cautiously interpreted. Compared to adult male harvest rate estimates using radiocollared deer, female radiocollar estimates can be more susceptible to sampling bias. Because hunters have indicated they would avoid harvesting radiocollared deer (C. S. Rosenberry, PGC, personal communication), and antlerless deer are not considered trophy animals, radiocollar estimates for female deer may be biased low. However, no variability was suggested when reward tagged female harvest rates were compared to radiocollared estimates in Pennsylvania for the 2009 hunting season (Diefenbach 2010, unpublished data). Another concern is juvenile/adult aging techniques for female deer are more error prone than techniques for antlered deer, because juvenile male deer typically have visible antler buttons.

Yearling Survival Outside the Hunting Season

Although I found no indication of spatial, temporal, or sexual variability in $\hat{S}_{(outhunt)Yrlg}$, all models were competitive with an AIC$_c$ difference of only 3.31 units between the top and lowest-ranked models. I sampled a large number of deer (192), but only nine mortalities were recorded between capture and the end of September. Mortality of a single additional deer could lead to different conclusions based on model selection criteria. Consequently, evidence supporting the assumption of constant $S_{(outhunt)Yrlg}$ across space, year, and sex is relatively weak as indicated via the lack of precision in point estimates.

Finally, fawn survival from pre-hunting season to the end of the year must be included within $\hat{S}_{(outhunt)Yrlg}$. I could only estimate survival from January to October,

while the model estimates the pre-hunting season fawn population from the following

October yearling population. Data from a previous fawn study in Pennsylvania provides

insight into this rate (Vreeland 2002). Using these data, I calculated a fawn non-harvest

survival rate during the hunting season of 87.1% (95% CI = 79.0 – 92.3).

Chapter 3

Precision and Robustness of the Pennsylvania Sex-Age-Kill Model

Introduction

Developed in the 1950s, the Sex-Age-Kill (SAK) model has been widely used by state agencies to estimate population size for white-tailed deer (Eberhardt 1960, Millspaugh et al. 2009). The ability to use readily available white-tailed deer age-at-harvest data makes this type of model appealing. However, thorough evaluation of model performance must be considered, and only recently has this model been critically evaluated (Skalski and Millspaugh 2002, Millspaugh et al. 2009).

Criticisms of the SAK model include the required assumption of a stable age distribution and stationary population, which is unlikely to be met in applied situations. A recent evaluation of the SAK model as applied in Wisconsin (WISAK) indicated several additional difficulties: (1) sensitivity to changes in male harvest rate, (2) not all input parameters are estimated, (3) sensitivity to stochasticity in input parameters, and (4) large sample sizes required to obtain precise estimates (Millspaugh et al. 2007).

In light of these criticisms, the Pennsylvania Game Commission (PGC) has further modified the SAK model (PASAK), primarily by using empirical estimates for all input parameters (C. S. Rosenberry, PGC, personal communication). This provides an ability to estimate precision of resulting population estimates. Additional modifications were necessary to account for regulation changes and hunter selectivity. In 2001, the Pennsylvania Game Commission (PGC) initiated Antler Point Restrictions (APRs), requiring legal antlered deer harvests to have ≥ 1 antler with either ≥ 3 or ≥ 4 points,

depending on the WMU, protecting roughly 50% of the yearling male population. Consequently, the adult male abundance estimate is now separated into two estimates, the mature (≥ 2.5 years old) male population and the yearling (1.5 years old) male population, both of which require associated harvest rate estimates. The mature male harvest rate is estimated using radio-telemetry data, whereas the yearling male harvest rate is estimated using a running average from previous years' data. To account for hunter selectivity, the PASAK model modified parameter estimates required for female and juvenile abundance estimates, which both have traditionally used ratios estimated with harvest data.

Although modifications of the PASAK model account for several criticisms, not all concerns with model performance are eliminated. Questions still remain concerning deterministic and stochastic effects arising from demographic, temporal, and spatial variability, as well as changes in management strategies and data collection. My objectives were to (1) develop a method for estimating the precision of the PASAK model abundance estimates, (2) identify the most efficient harvest data collection strategies related to overall precision, and (3) evaluate PASAK model robustness to parameter variability and bias suggested via radiocollar data. To accomplish these objectives I (1) used a bootstrap resampling procedure to estimate precision, (2) monitored changes in precision when harvest data samples were doubled and halved, and (3) compared simulated estimates from a known population and PASAK model estimates.

Methods

Abundance Estimation

Pennsylvania deer abundance is estimated by wildlife management units (WMU). Twenty-two WMUs have been delineated across the state to best represent landscape variability while providing a suitable scale to collect sufficient amounts of data for harvest parameter estimates. The following explanation of the PASAK model refers to how deer abundance is estimated in a given WMU.

The mature (≥ 2.5 years old) male harvest rate (H_{MM}) is estimated (unpublished data, PGC) using the staggered-entry design of the Kaplan-Meier estimator using radio-telemetry data (Pollock et al. 1989). The pre-season mature male population estimate ($\hat{N}_{MM}$) is the mature male harvest estimates ($\hat{K}_{MM}$) divided by $\hat{H}_{MM}$,

$$\hat{N}_{MM} = \frac{\hat{K}_{MM}}{\hat{H}_{MM}}.$$

Rosenberry et al. (2004) found that reporting of harvest by hunters has changed over time and varies by age and sex of deer and by WMU. Consequently, sex- and age-specific harvest (K) for each WMU, each year is estimated using a Lincoln-Petersen estimator corrected for small sample size (Chapman 1951),

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

where n_1 is the number of harvested deer checked by Pennsylvania Game Commission (PGC) personnel in the field, n_2 is the number of harvested deer reported via report cards

by hunters, and m_2 is the number of harvested deer checked and reported (C. S.

Rosenberry, PGC, personal communication).

To estimate yearling male abundance, yearling male harvest rates are not estimated

from data collected about monitored radiocollared yearling males, because of the concern

that yearling harvest rates may be more variable than adult male harvest rates as a

consequence of APRs. Because antler growth is dependent on weather and food

availability and quality (French et al. 1956), the percent of protected yearling males may

vary among WMU and year. Instead of using radiocollared yearling males to estimate

yearling male abundance, an iterative procedure based on previous years' data is used for

abundance estimates in the current year.

First, a pre-hunting season 2.5 year old male population estimate ($\hat{N}_{2.5M(t)}$) is

calculated for the current year (t)

$$\hat{N}_{2.5M(t)} = \hat{p}_{2.5} \times \hat{N}_{MM(t)}.$$

This estimate is calculated by multiplying the proportion of 2.5 year olds in the ≥ 2.5

male population ($\hat{p}_{2.5}$) by the ≥ 2.5 male population estimate ($\hat{N}_{MM(t)}$). The $p_{2.5}$ is

estimated via Leslie matrix simulations of the adult male population, assuming constant

recruitment of yearling males and constant survival of mature males across space and

time (C. S. Rosenberry, PGC, personal communication). Within four iterations, a stable

age distribution is reached, and $p_{2.5}$ can be estimated. Estimates of $p_{2.5}$ from the age

distribution of teeth from harvested adult male deer determined by counting cementum

annuli, were found to be similar to $\hat{p}_{2.5}$ estimated via the PASAK model (C. S.

Rosenberry, PGC, unpublished data).

The estimate of $N_{2.5M(t)}$ is then divided by non-harvest survival ($\hat{S}_{(nonharv)YM}$, unpublished data, PGC), estimated using the staggered-entry design of the Kaplan-Meier estimator from radiocollared deer data (Pollock et al. 1989). All pre-hunt-1.5-year-old to pre-hunt-2.5-year-old male mortalities, excluding legal harvests, are used to estimate $S_{(nonharv)YM}$. The estimate of $N_{2.5M(t)}$ divided by $\hat{S}_{(nonharv)YM}$ provides a pre-season estimate of abundance, excluding harvested deer, for yearling males in the previous year (*t*-1). This estimate is then used to calculate a pre-season estimate by adding the yearling male harvest from the previous year ($\hat{K}_{YM(t-1)}$). The quotient of the $\hat{K}_{YM(t-1)}$ divided by the pre-season estimate is the yearling male harvest rate for the previous year ($\hat{H}_{YM(t-1)}$),

$$\hat{H}_{YM(t-1)} = \frac{\hat{K}_{YM(t-1)}}{(\hat{N}_{2.5M(t)}/\hat{S}_{nonharv(YM)}) + \hat{K}_{YM(t-1)}}.$$

The $\hat{H}_{YM(t-1)}$ is averaged with similarly calculated harvest rates for the two years preceding ($\hat{H}_{YM(t-2)}$ and $\hat{H}_{YM(t-3)}$), which is used as the harvest rate in the current year.

Yearling male abundance for previous years can be estimated similarly; however, no moving average is used, because harvest data from the following year can be used to estimate the population,

$$\hat{N}_{YM(t)} = (\hat{N}_{2.5M(t+1)}/\hat{S}_{nonharv(YM)}) + \hat{K}_{YM(t)}.$$

I refer to abundance estimates not based on a moving average as updated estimates because they replace estimates using data from following years.

The adult (≥ 1.5 years old) male, or antlered population (N_{AM}), is estimated as

$\hat{N}_{AM} = \hat{N}_{MM} + \hat{N}_{YM}$. After N_{AM} is estimated, ratios are used to estimate abundance of

other age and sex classes. Specifically, adult female to adult male ratios ($\hat{p}_{F:M}$) and

juvenile to adult female ratios ($\hat{p}_{J:AF}$) are used to estimate adult female (N_{AF}) and

juvenile (N_J) population sizes, respectively:

$$\hat{N}_{AF} = \hat{N}_{AM} \times \hat{p}_{F:M}$$

$$\hat{N}_{J} = \hat{N}_{AF} \times \hat{p}_{J:AF}.$$

The $p_{F:M}$ is estimated by dividing the proportion of yearling males in the adult male

population ($\hat{p}_{YM:AM}$),

$$\hat{p}_{YM:AM} = \frac{\hat{N}_{YM}}{\hat{N}_{MM} + \hat{N}_{YM}},$$

by the proportion of yearling females in the adult female population ($\hat{p}_{YF:AF}$) obtained

from harvest data (Severinghaus and Maguire 1955):

$$\hat{p}_{F:M} = \frac{\hat{p}_{YM:AM}}{\hat{p}_{YF:AF}}.$$

Juvenile to adult female ratios ($p_{J:AF(t)}$) are estimated through a series of steps. First,

a juvenile to adult female ratio is estimated for the previous year ($p_{J:AF(t-1)}$). A juvenile

population for the previous year is back-calculated from the $\hat{N}_{YM(t)}$, similar to the

yearling male pre-season estimate for the preceding year. Because yearling males and

females are assumed to be equally recruited, the $\hat{N}_{YM(t)}$ can be multiplied by 2 to estimate

a yearling population ($\hat{N}_{yrlg(t)}$). The $\hat{N}_{yrlg(t)}$ is then divided by yearling non-harvest

survival $\hat{S}_{yrlg(nonharv)}$ to obtain a pre-season juvenile population estimate for the previous

year, excluding harvest. The $\hat{S}_{yr\lg(nonharv)}$ is estimated by multiplying juvenile non-harvest

survival during the hunting season, October to January, by yearling survival from January

to October, both of which are estimated using data from radiocollared deer. To obtain a

pre-season juvenile population estimate for the previous year, the juvenile harvest from

the previous year ($\hat{K}_{J(t-1)}$) is added to the pre-season non-harvest juvenile population

estimate. The pre-season juvenile population is then divided by the $\hat{N}_{AF(t-1)}$ to estimate

the juvenile to adult female ratio for t-1 ($p_{J:AF(t-1)}$),

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

Second, because of hunter selectivity for adult females, a correction factor ($\hat{C}_{J:AF(t-1)}$)

is estimated to adjust the juvenile to adult female ratio by dividing the $p_{J:AF(t-1)}$, from the

previous step, by the juvenile to adult female ratio from harvest data ($\hat{p}_{J:AF(harvest)(t-1)}$),

$$\hat{C}_{J:AF(t-1)} = \frac{\hat{p}_{J:AF(t-1)}}{\hat{p}_{J:AF(harvest)(t-1)}} .$$

Similar to the $\hat{H}_{YM}$, this correction factor uses data from previous and future years

depending on available data. For year t, $\hat{C}_{J:AF}$ is averaged across years t-2 and t-3. For

year t-1, $\hat{C}_{J:AF}$ is averaged across years t-2, t-3, and t-4. For year t-k, when $k \geq 2$, this

correction factor is updated using yearling male harvest rates from $(t$-$k)$+1.

The iterative and updating nature of these calculations is important to understanding

increasing trends in precision of population estimates as parameters are updated. The

$p_{J:AF}$ is estimated by multiplying the $\hat{p}_{J:AF(harvest)}$ by the appropriate correction factor.

The abundance of all sex-age classes combined is simply

$$\hat{N} = \hat{N}_{AM} + \hat{N}_{AF} + \hat{N}_{J} \,.$$

Based on my results from chapter 2, I made one modification to the PASAK model when estimating precision and evaluating model robustness. Rather than using the previously described iterative procedure to calculate yearling male harvest rates, I used direct radiocollar yearling male harvest rate estimates. This modification is important when considering the updating nature of the $p_{J:AF}$. Rather than waiting until year $t+2$ to get updated estimates, $p_{J:AF}$ can be updated in year $t+1$.

Precision

I quantified precision of the PASAK model using a Monte Carlo parametric bootstrapping method (Efron 1979) similar to the evaluation of the WISAK model (Millspaugh et al. 2007). I conducted 1,000 Monte Carlo bootstraps of the empirical data to generate 1,000 population estimates from a random selection of the data taken with replacement. A fundamental assumption behind the parametric bootstrap is that each parameter is assumed to have some underlying distribution with a specific mean and variance (Millspaugh et al. 2007). Because all PASAK model parameters are constrained between 0 and 1, I conducted the bootstrap using either a binomial distribution, $b(n,p)$, or a beta distribution, $beta(\mu, \delta^2)$, based on empirical data collected by the PGC. Precision of population estimates was the standard deviation of the replicate simulation estimates of N and 90% confidence intervals were estimated from the 5th and 95th percentiles of

simulation estimates of *N*. Also, I calculated the coefficient of variation (CV) as

$\hat{SE}(\hat{N})/\hat{N} \times 100\%$. I used SAS (SAS Institute, Cary, North Carolina, USA) to estimate

population size and precision for each WMU in Pennsylvania from 2002-2008 (see

Appendix B).

To most efficiently allocate annual harvest data collection from hunters, I evaluated

the effect of varying sample sizes on the precision of abundance estimates. The different

types of harvest data collected by PGC personnel are: (1) number of deer checked and

aged in the field, and (2) number of deer reported via report cards by hunters. I

calculated a mean CV across WMUs when samples sizes associated with the harvest data

were doubled and halved, then compared the CVs to my estimated CVs using actual

sample sizes. Because PASAK model estimates are updated in *t*-1, I compared CV

differences in years $\leq$ *t*-1 separately from year *t*.

Robustness

I evaluated model robustness by comparing 50 years of a simulated population

trajectory, generated via a two-sex Leslie matrix, with associated PASAK model

estimates based on perfect sampling, no stochastic errors, from the simulated population

(see Appendix C). Under this scenario, I assumed an independent study had perfectly

estimated harvest rate and survival parameters (*i.e.*, with no sampling variability) for use

in the PASAK model. I then assessed effects of random variation and biases in important

model and population parameters, specifically yearling male harvest rates (H_{YM}), mature

male harvest rates (H_{MM}), adult female harvest rates (H_{AF}), and non-harvest mortality

($1 - S_{nonharv}$).

To understand the specific influence each parameter had on model performance, I fixed all other simulated population parameters at a constant rate (*i.e.*, no process variance), except for the parameter of interest. For example, simulated mature male harvest rates uniformly varied between 0.50 and 0.66, while all other simulated parameters did not vary and the PASAK used 0.58 for the mature male harvest rate. This does not necessarily represent natural variation in parameters that occur in the population, but allowed me to evaluate model sensitivity, with respect to precision and bias, of individual parameter inputs.

Because all fixed harvest rate and survival parameters were estimated perfectly for the PASAK model, confidence interval coverage cannot be interpreted literally, and should be considered as a relative measure of confidence interval performance. A random, representative sample used to estimate a parameter will rarely estimate the true parameter exactly. Typical simulation analysis would account for this by incorporating a measure of variance (stochastic errors) for each parameter estimate, and a 90% confidence interval would be expected to encompass the simulated population 90% of the time. Alternatively, my PASAK model confidence intervals will perform better than expected when compared to the simulated population, because all fixed simulated parameters are assumed to be estimated perfectly.

When varying individual simulated harvest or survival rates, I used conservative estimates of process variance. First, I estimated the standard deviation for yearly estimates of the parameter of interest from my radiocollar data. Because this standard deviation contains both process variance and sampling variance, I overestimated the actual process variance (Lukacs et al. 2009). Furthermore, I used a normal 95%

confidence interval based on a standard normal distribution. Finally, I uniformly varied

parameters within the interval, rather than having them concentrated about the mean

value. Because I directly estimated H_{YM}, assuming constant rates across space and time,

I used two separate measures of variation. The first measure of variation included only

annual variability, while the second considered both spatial and annual variability. To

evaluate the effects of possible biasedness of parameter inputs, I generally considered the

same variation, but centered my interval 1.96 standard deviations above or below the

actual harvest or survival rate.

I quantified model sensitivity to parameter variation and bias using three statistics

which compared the known simulated population to the PASAK model estimates. First, I

calculated the proportion of PASAK model confidence intervals that encompassed the

known population sizes, which indicated whether estimated confidence intervals were

accurate. Next, I quantified bias with associated % relative bias (PRB). I averaged the

difference between PASAK model population estimates and true simulated populations to

calculate bias,

$$bias = \frac{\sum_{i=1}^{n}(\hat{N}_{PASAK_i} - N_i)}{n},$$

then divided each error by the true population to calculate PRB,

$$PRB = \frac{\sum_{i=1}^{n}\frac{\hat{N}_{PASAK_i} - N_i}{N_i}}{n}.$$

Finally, I measured mean squared error and a pseudo-coefficient of variation (CV_{pop}) to

provide precision estimates. Similar to bias and PRB, I averaged the squared difference

between PASAK model population estimates and true simulated populations to calculate

mean squared error,

$$MSE = \frac{\sum_{i=1}^{n}(\hat{N}_{(PASAK)_i} - N_i)^2}{n},$$

then divided each squared error by the true population size to calculate CV_{pop},

$$CV_{pop} = \frac{\sum_{i=1}^{n}\frac{(\hat{N}_{(PASAK)_i} - N_i)^2}{N_i}}{n}.$$

All three statistics were averaged across 500 iterations of the 50 year population

simulation.   I used SAS (SAS Institute, Cary, North Carolina, USA) to simulate a

population trajectory and estimate abundance.

Results

Population Estimates and Precision Analysis

I found that population estimates by WMU had an average CV of $\leq$ 15% (Table

3.1). This analysis did not include WMU 2B, 5C, and 5D, which are managed separately

because of the unique urban/suburban interface created by the cities of Pittsburgh and

Philadelphia. Measures of precision, by WMU, are presented in Appendix D.

My results indicated doubling or halving the number of deer checked and aged

would have the biggest effect on the estimate of the population CV in year t. If twice as

many deer were checked and aged, mean CV across WMUs would decrease by 2.69% in

year t, whereas mean CV would increase by 4.69% if half as many deer were checked

and aged. Alternatively, if reporting rates were doubled in year t, mean CV would

decrease by 1.91%, whereas mean CV would increase by 3.28% if reporting rates were

halved (Table 3.2). Similar trends with smaller effect sizes were indicated in years $\leq t\text{-}1$

(Table 3.2).

Table 3.1: 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 in Pennsylvania, 2002-2008. Urban and suburban wildlife management units for Pittsburgh (WMU 2B) and Philadelphia (WMU 5C and 5D) are not included.

Year	Min. CV (%)	Mean CV (%)	Median CV (%)	90th Percentile CV (%)	Max. CV (%)
2002	6.6	7.6	7.3	9.2	10.2
2003	6.3	7.8	7.2	9.6	12.8
2004	6.8	7.9	7.5	9.5	12.7
2005	6.6	8.1	7.5	9.4	13.2
2006	6.7	8.2	7.8	10.2	13.4
2007	6.9	8.5	7.9	9.3	16.1
2008	11.5	14.1	13.2	16.4	23.8

Table 3.2: A comparison of estimated coefficients of variation ($CV = SE(\hat{N})/\hat{N} \times 100\%$) for white-tailed deer abundance estimates under varying levels of data collection from 2002-2008. The difference and % change to mean CVs across 19 wildlife management units in Pennsylvania for t (14.1%) and $\leq t$-1 (8.0%) are reported when sample sizes are doubled and halved for # deer checked and aged, and # deer reported. Urban and suburban wildlife management units for Pittsburgh (WMU 2B) and Philadelphia (WMU 5C and 5D) are not included.

Year	Parameter	Double Sampling Mean Difference	% Change	Halve Sampling Mean Difference	% Change
t	# Deer Checked and Aged	-2.69	-19.12	4.69	33.36
t	# Deer Reported	-1.91	-13.59	3.28	23.34
$\leq t$-1	# Deer Checked and Aged	-1.16	-14.98	2.02	26.42
$\leq t$-1	# Deer Reported	-1.07	-13.76	2.00	26.20

Robustness

A model in which all parameters were estimated correctly with no variability performed very well (Table 3.3). I found the model was most sensitive to variability and bias of $\hat{H}_{YM}$. Annual variation (± 4%) about the true estimate (34%), resulted in the model exhibiting minor sensitivity (Table 3.3). When spatial variation, which the PASAK model does not currently address, also was considered (± 24%), CI coverage declined by 38.4% and CV_{pop} increased by 7.11%, while PRB remained < 1% (Table 3.2). Model sensitivity increased when input parameters were biased. When H_{YM} was positively biased 1.96 standard deviations (+ 4%) with only annual variation (± 4%), CI coverage and CV_{pop} estimates were similar to unbiased simulations with spatial and annual variation, but PRB increased by 10.34% (Table 3.3). Modeling both spatial and annual variation (± 24%), 1.96 standard deviations (-24%) below the true H_{YM}, CV_{pop} and PRB nearly tripled, and true CI coverage was < 10% (Table 3.3).

The PASAK model indicated far less sensitivity to H_{MM} than H_{YM} (Table 3.3). In fact, model robustness considering only process variance (± 8%) with no bias in H_{MM} performed similar to the model in which all parameters were correctly estimated with no variability. When considering process variance (± 8%) and a positive bias (8%) in H_{MM}, CI coverage decreased only 0.1%, PRB increased 1.4%, and CV_{pop} increased 0.39% (Table 3.3). Because spatial variability can be accounted for by modeling H_{MM} (see chapter 2), I did not evaluate the effects of spatial variation.

Lastly, I separately evaluated the effects of variance and bias in H_{AF} and non-harvest mortality. These parameters are not directly used in the PASAK model, but do

have a profound influence on population dynamics. I found little sensitivity to variability

and biases in these parameters with CI coverage always > 99%, PRB < 2%, and CV_{pop}

< 3% (Table 3.3).

Table 3.3: PASAK model robustness statistics considering uniform variation only and uniform variation with bias to: no parameters, H_{YM} (34%), H_{MM} (58%), H_{AF} (18%), and 1-$S_{nonharv}$ (20%). Mean abundance ($\bar{N}$) across fifty years and five hundred simulations provides an indication of the simulated population size.

Parameters	Variability	Interval	$\bar{N}$	90% CI Coverage	Bias	PRB[a]	MSE	CV_{pop}[b]
None			31,499	100.0%	-1	0.00%	273,670	1.32%
H_{YM}	Year	0.30 - 0.38	31,499	98.1%	13	0.04%	2,209,632	3.87%
H_{YM}	Year and WMU	0.22 - 0.46	31,503	59.7%	-44	-0.14%	17,507,220	10.98%
H_{YM}	Bias Year	0.34 - 0.42	31,291	59.0%	3,279	10.48%	12,998,341	10.50%
H_{YM}	Bias Year and WMU	0.10 - 0.34	32,122	9.7%	-9,779	-30.44%	113,354,862	30.49%
H_{MM}	Year	0.50 - 0.66	31,498	100.0%	4	0.01%	341,960	1.48%
H_{MM}	Bias Year	0.58 - 0.74	31,197	99.9%	440	1.41%	527,762	1.87%
H_{AF}	Year	0.14 - 0.22	31,491	99.9%	4	0.01%	326,321	1.37%
H_{AF}	Bias Year	0.18 - 0.26	18,783	99.8%	7	0.06%	140,884	1.70%
1-$S_{nonharv}$	Year and WMU	0.16 - 0.24	31,413	99.9%	1	0.00%	372,190	1.56%
1-$S_{nonharv}$	Bias Year	0.20 - 0.28	12,587	99.1%	-208	-1.56%	190,789	2.97%

[a] Percent Relative Bias
[b] Pseudo-Coefficient of Variation

Discussion

Precision

The average coefficient of variation (CV) across WMUs was found to be sufficiently precise ($\leq 12.8\%$; Robson and Regier 1964, Skalski and Millspaugh 2002) for managing populations of game species, except in year t (2008) where the mean CV (14.1%) was slightly above the benchmark recommendation. The lesser precision in 2008 is inherent to the structure of the model. As described in the methods, population estimates for year t-1 are updated with data from following years. Because updated estimates for the juvenile to adult female ratio correction factor are not available in the current year, the PASAK model uses a moving average, which decreases the precision of population estimates.

For harvest data collection, WMU CVs in year t are most sensitive to increases and decreases in the number of deer aged and checked. The mean CV across WMUs in the current year can be improved to levels acceptable for managing game species ($\leq 12.8\%$; Robson and Regier 1964, Skalski and Millspaugh 2002) if reporting rates or the number of deer checked and aged are doubled. Because precision is nearly doubled when population estimates are updated in years $\leq t$-1, doubling or halving sampling effort associated with deer harvest data is relatively negligible in years $\leq t$-1. Consequently, CVs for estimates in the current year will be most sensitive to changes in data collection.

Accuracy of the estimated CVs requires all assumptions to be fully met. Assumption violations will cause CV estimates to be biased low. Continued monitoring of adult male harvest rates will improve precision estimates for year t, and provide further insight into whether model assumptions are being met. Additionally, precision will improve by improving harvest data

collection. Increasing harvest reporting rates by hunters can most efficiently improve precision

estimates. Although the PGC requires mandatory harvest reporting, the average reporting rate

from 2002 to 2008 was 41.4%. The PGC has recently added point of sale licensing with online

harvest reporting, which may improve reporting rates. Furthermore, the automated licensing

system easily allows for incentive based reporting, because individual license holders can be

tracked across years. For example, a hunter that reports their harvest (or non-harvest) could be

issued a preference point for the following year's limited antlerless license application.

Robustness

Because of modifications I made accounting for the failure to meet the assumption of

constant spatio-temporal yearling male non-harvest survival, the PASAK model proved to be

very sensitive to variability and bias in yearling male harvest rates. The primary reason the

PASAK model is sensitive to changes in this parameter, but robust to changes to the mature male

harvest rate is evident in the calculation of the $\hat{p}_{F:M}$ (Severinghaus and Maguire 1955):

$$\hat{p}_{F:M} = \frac{\hat{p}_{YM:AM}}{\hat{p}_{YF:AF}}.$$

If N_{YM} is overestimated, which occurs when H_{YM} is underestimated, there will be an

overestimate of the $p_{F:M}$. Because $\hat{N}_{AF}$ is calculated by multiplying $(\hat{N}_{YM}+\hat{N}_{MM})$ by $\hat{p}_{F:M}$, a

compounding effect occurs in the bias of N_{AF}. Furthermore, an overestimate of N_{YM} will also

cause the N_J to be overestimated in a similar compounding manner. These results emphasize

the importance of understanding the spatial variability of yearling male harvest rates.

Alternatively, if N_{MM} is overestimated, when H_{MM} is underestimated, an underestimated $p_{F:M}$ effect to the $\hat{N}_{AF}$ will be cancelled out by the overestimated N_{AM}. Because the $\hat{N}_{MM}$ is not used to estimate the $\hat{p}_{J:AF}$, there is no effect on $\hat{N}_J$. Therefore, the only population cohort sensitive to biased $\hat{H}_{MM}$ is the mature male population, similar to sensitivity of the yearling male population to bias in $\hat{H}_{YM}$. These specific cohort sensitivities are similar to results from the WISAK model evaluation (Millspaugh et al. 2007, 2009).

I found the PASAK model to be robust to changes and bias in H_{AF} and non-harvest mortality. This was expected because the H_{AF} and non-harvest mortality play relatively minor, indirect roles in calculating population estimates using the PASAK model even though H_{AF} and non-harvest survival are important to the population dynamics of deer.

It is important to note that my robustness evaluation monitored the affect of individual parameter variation 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 mature male population estimate will be cancelled out by the subsequent opposite bias to the adult female population estimate. Consequently, the total population estimate will be unbiased.

Chapter 4

Management Implications

Changes in deer harvest regulations can result in violation of the important assumption of a stable and stationary population required for application of the SAK Model. However, by incorporating independent estimates of antlered deer harvest rates into the SAK Model, the restrictive assumption of a stable and stationary population is no longer required. Model performance, however, is contingent on the accuracy of these estimates.

If accurate estimates of antlered harvest rates are obtained, other data are readily available through standard harvest data collection. Specifically, estimates of the antlered harvest, adult male to adult female ratio, and adult female to juvenile ratio require age-sex specific harvest data. Furthermore, three important assumptions to consider when using these data are: 1) equal harvest vulnerability of yearling and mature (> 1.5 years old) female deer, 2) equal recruitment of males and females into the pre-hunt yearling population, and 3) equal harvest vulnerability of juveniles and adult females. If yearling females are more vulnerable to harvest than mature females, the adult female population will be underestimated. Similarly, if adult females are more vulnerable to harvest than juveniles, the juvenile population will be underestimated. A correction factor can account for both of these biases; however, the correction factors require either age-specific harvest rate estimates or adult female and yearling non-harvest survival estimates.

Inherent to the structure of the SAK model, the PASAK model is robust to bias and lack of precision associated with parameters used to estimate adult female and juvenile population

cohorts. Because the most important estimate is of the adult male population, which is used for all other cohort estimates, subsequent adult female and juvenile population estimates are dependent on this parameter. Similar to a top-down trophic cascade, the accuracy of all other cohort estimates are dependent on the accuracy of the estimates of adult male population size. However, because of PASAK model modifications, this cascading affect is only associated with the yearling male population estimate.

A major improvement of the PASAK model is the use of independent harvest rate estimates. Not only do these estimates eliminate the assumption of a stable and stationary population, but they allow estimation of measures of precision. My results illustrated appropriate methods for calculating yearling and mature male harvest rates for all twenty-two WMUs, but data from only four WMUs were available. Caution should be used when applying modeled or constant harvest rates to other WMUs. For example, WMU 5C has shotgun only regulations during the firearm season, and hunter effort indices for the archery season are nearly double all measures from the four study area WMUs. Until adult male harvest rate estimates from urban and suburban WMUs, 2B, 5C, and 5D, are improved, PASAK model estimates can only suggest population trends rather than point estimates with measures of precision for these WMUs.

I found that estimating separate yearling male and mature (≥ 2.5 years old) male populations has profound implications on model sensitivity. While this structure makes the PASAK model robust to bias and lack of precision when estimating the mature male population, abundance estimates are sensitive to bias and variability in yearling male harvest rates. Fortunately, by protecting about half the yearling male population, antler point restrictions (APRs) limit the potential for variability in harvest rates. Even so, relatively small fluctuations in yearling male

harvest rates will have compounding effects on overall population estimates, which can influence management decisions. Therefore, the most sensitive parameter in the PASAK model is the yearling male harvest rate.

If evidence of spatial variability in yearling male harvest rate is found, hunter effort could be used to model the variability similar to mature male harvest rates. Monitoring efforts should focus on accurately estimating the yearling male harvest rate, especially in light of regulation changes or shifts in hunter selectivity. Because of increasing interest by hunters in quality deer management practices, which emphasize the protection of yearling male deer, harvest rates of yearling male deer may change over time. Also, changes to antler point restrictions, or switching to main beam length or antler spread restrictions can have profound effects on the levels of yearling male protection.

Equally important are accurate estimates of yearling male harvests, which are the dividends associated with the yearling male harvest rate divisors. Improving harvest reporting rates by hunters is the most efficient method for improving harvest estimates. Reporting rates have a similar effect on the precision of population estimates when compared with the number of deer checked and aged. Finally, to reduce the sensitivity to yearling male abundance estimates, investigations into alternative, independent estimates for the proportion of yearling males in the adult male population would improve model performance.

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Appendix A

Metadata

Metadata sources from the Pennsylvania Spatial Data Access (PASDA) website (http://www.pasda.psu.edu) used to quantify landscape covariates for mature male harvest rate estimates from 2002-2004 and 2007-2008.

1. Forest Cover
   - PAMAP Land Cover for Pennsylvania, 2005
     http://www.pasda.psu.edu/uci/FullMetadataDisplay.aspx?file=palanduse05utm18nad83.xml

2. Public Land
   - Pennsylvania Game Commission State Game Lands, 2006
     http://www.pasda.psu.edu/uci/FullMetadataDisplay.aspx?file=PGC_StateGamland200907.xml

   - Pennsylvania Department of Conservation and Natural Resources State Forest Lands, 2006
     http://www.pasda.psu.edu/uci/FullMetadataDisplay.aspx?file=dcnr_stateforestlands_2006.xml

3. Digital Elevation Models
   - National Elevation Dataset, 1999
     http://www.pasda.psu.edu/uci/FullMetadataDisplay.aspx?file=paned.xml

4. Road Density
   - Pennsylvania State Roads, 2008
     http://www.pasda.psu.edu/uci/FullMetadataDisplay.aspx?file=PaStateRoads2008_01.xml

   - Pennsylvania Local Roads, 2008
     http://www.pasda.psu.edu/uci/FullMetadataDisplay.aspx?file=PaLocalRoads2008_01.xml

Appendix B

Computer program (SAS) used to estimate abundance and precision of white-tailed deer using

the PASAK model

```
*******************************************************************************
*******************************************************************************
*
* Program to estimate PA deer population with precision by WMU using PASAK
*
*  Program as is uses direct (radiocollar) estimate for yearling male
*  harvest rate, no birth ratio correction factor, and fawn and juvenile
*  survival to reconstruct fawn crop
*
*  If user wants to use iterative yearling male harvest rate, set %let iterym=1
*  If user wants to use birth ratio correction factor, set %let bratio=1
*
*  Set first year and current year
*
*  Set all check, rep, age, and seinf to 1 for default or actual variance
*
*  INPUT VARIABLES:
*
*   firstyear = first year of data
*   currentyear = final year of data
*   yr = year data collected
*   wmu = wildlife management unit
*   area = size of WMU in square miles
*
*   Aged Deer:
*
*   Mature (=> 2.5) Male:
*   lpant = no. antlered deer aged
*   lpantrep = no. antlered deer reported
*   lpantrc = no. antlered deer aged and reported
*   cmatant = no. mature males aged
*   bhr = mature buck harvest rate (radiocollar data)
*   bse = standard error for mature buck harvest rate
*   bvar = variance for mature buck harvest rate
*   bhrbeta = beta parameter for beta distribution
*   bhralpha = alpha parameter for beta distribution
*
*   Yearling (1.5) Male:
*   cyrlant = no. yearling males aged
*   ptwoyrbuck = percent 2.5 yr old in mature deer aged
*   nptwoyrbuck = sample size used to calculate ptwoyrbuck
*   surv = yearling male non-harv. surv. from pre-hunt 1.5 to pre-hunt 2.5
*          used for iterative yrl. male harv rate calc
*   survse = standard error for yearling male survival
*   survvar = variance for yearling male survival
*   survbeta = beta parameter for beta distribution
*   survalpha = alpha parameter for beta distribution
*   ymhr = yearling male harvest rate
*   ymse = standard error for yearling male harvest rate
*   ymvar = variance for yearling male harvest rate
*   ymbeta = beta parameter for beta distribution
*   ymalpha = alpha parameter for beta distribution
*
```

```
*    Adult (=> 1.5) Female:
*    lpantless = no. antlerless deer aged
*    lpantlessrep = no. antlerless deer reported
*    lpantlessrc = no. antlerless deer aged and reported
*    birthratio = M:F fetal ratio
*    nbirthratio = sample size used to calculate birth ratio
*    cyrldoe = no. yearling does aged
*    cmatdoe = no. mature (=>2.5) does aged
*
*    Juvenile (0.5):
*    cjuvbuck = no. juvenile bucks aged
*    cjuvdoe = no. juvenile does aged
*    survj = survival from post-hunt 0.5 to pre-hunt 1.5
*    survjse = standard error for survj
*    survjvar = variance for survj
*    survjbeta = beta parameter for beta distribution
*    survjalpha = alpha parameter for beta distribution
*    survf = fawn non-harv survival during the hunting season
*    survfse = standard error for survf
*    survfvar = variance for survf
*    survfbeta = beta parameter for beta distribution
*    survfalpha = alpha parameter for beta distribution
*
*   CALCULATED VARIABLES:
*
*    Mature (=> 2.5) Male:
*    cant = no. yearling and mature male deer aged
*    canthar = no. antlered deer harvested
*    cmatanthar = no. mature antlered deer harvest
*    pmatant = mature (=>2.5) bucks:antlered harvest
*    matantpop = preseason mature male abundance
*    matantpopnxt = preseason mature male abundance in the following yr
*
*    Yearling (1.5) Male:
*    cyrlanthar = no. yearling antlered deer harvested
*    pyrlant = yearling bucks:antlered harvest
*    yrlhrave = yearling buck harvest rate (prev 3-yr running ave)
*    yrlhrcal = calibrated yearling buck harvest rate (begins in t-1)
*    yrlantpop = preseason yearling male abundance
*    yrlantpop1 = preseason yearling male abundance in the following yr
*
*    Adult (=> 1.5) Male:
*    antpop = preseason adult male abundance
*
*    Adult (=> 1.5) Female:
*    cantless = no. adult female and juveniles aged
*    cdoe = no. adult females aged
*    cdoehar = no. adult females harvested
*    cantlesshar = no. antlerless harvested
*    adsxratio = M:F adult ratio
*    pyrldoe = yearling female:adult female harvest
*    pdoeantless = adult doe:antlerless harvest
*    doepop = preseason adult female abundance
*
*    Juvenile (0.5):
*    cjuv = no. juveniles aged
*    cjuvhar = no. juveniles harvested
*    pjuv = juvenile:adult doe harvest
*    pjuvantless = juvenile:antlerless harvest
*    jfsurv = juvenile survival  * fawn survival
*    juvaddoecorrtwo = juvenile:adult doe harvest correction factor
*           for year t (t-2 and t-3 ave) – not used if direct ymhr used
*    juvaddoecorrthree = juvenile:adult doe harvest correction factor
```

```
*            for year t-1 (prev 3-yr ave) – for yr t if direct ymhr used
*    juvaddoecorrcal = calibrated juvenile:adult doe harvest correction
*            factor (begins in t-2) – begins t-1 if direct ymhr used
*    juvaddoecorr = juvenile:adult doe harvest correction factor used
*            for estimate
*    fdratio = fawn:adult doe ratio
*    juvpop = preseason juvenile abundance
*
*    Total Pop:
*    prehuntpop = preseason total deer abundance
*    prehuntdens = preseason total deer density
*    posthuntpop = postseason total deer abundance
*    posthuntdens = postseason total deer density
*
*    Sim = suffix for all simulated variables
*
*Written by Andrew S. Norton, May 2010
*
********************************************************************************
********************************************************************************


***********Import data*********************************************************
********************************************************************************
**Input file must have year, WMU, WMU area, aged and checked deer by sex and
** age class, bhr w/se, ymhr w/se, juvenile and fawn survival w/se
**If using iterative yrlg. male harv. rate calc, ptwoyrbuck w/sample size and
** yrlg male surv. w/se required
**If using birth ratio correction, birth ratio with sample size required;

**Insert correct file path for input file and 4 output files
**Also create a "\results" folder for output files;

Proc Import out=agedeer
      DATAFILE =' File path \InputFile.xls '
            DBMS = EXCEL2000 REPLACE;
    GETNAMES = YES;
proc sort; by wmu yr;
RUN;

**if using iterative ymhr make iterym=1;
%let iterym=0;
**if using birth ratio correction make bratio=1;
%let bratio=0;
**designate first and current year;
%let firstyear=2002;
%let currentyear=2008;
**double (2) or halve (0.5) sample sizes or std. error associated with number of deer
**checked, aged, reported, mature male harvest rate, yearling male harvest
**rate, yearling male, juvenile, or fawn survival;
%let check=1; %let rep=1; %let age=1;
%let bseinf=1; %let ymseinf=1; %let survseinf=1; %let jseinf=1; %let fseinf=1;
********************************************************************************
********************************************************************************


***********Calculate pre-hunting season population point estimates******************
********************************************************************************;


data pre; set agedeer;

**changes number of deer checked;
lpant=int(lpant*(&check)); lpantrc=int(lpantrc*(&check));
```

```
lpantless=int(lpantless*(&check)); lpantlessrc=int(lpantlessrc*(&check));
**changes reporting rate;
lpantrc=int(lpantrc*(&rep)); lpantrep=int(lpantrep*(&rep));
lpantlessrc=int(lpantlessrc*(&rep)); lpantlessrep=int(lpantlessrep*(&rep));
**changes number aged;
cyrlant=int(cyrlant*(&age)); cmatant=int(cmatant*(&age));
cyrldoe=int(cyrldoe*(&age)); cmatdoe=int(cmatdoe*(&age));
cjuvbuck=int(cjuvbuck*(&age)); cjuvdoe=int(cjuvdoe*(&age));

****Antlered harvest estimates (Lincoln-Petersen Estimator);
 cant=int(cmatant+cyrlant);
 cdoe=int(cmatdoe+cyrldoe);
 cjuv=int(cjuvbuck+cjuvdoe);
 cantless=cdoe+cjuv;
 canthar=round((lpant+1)*(lpantrep+1)/(lpantrc+1)-1);
 pmatant=cmatant/cant;
 pyrlant=cyrlant/cant;
 cmatanthar=round(canthar*pmatant);
 cyrlanthar=round(canthar*pyrlant);

****Antlerless harvest estimates (Lincoln-Petersen Estimator);
 cantlesshar=round((lpantless+1)*(lpantlessrep+1)/(lpantlessrc+1)-1);
 pdoeantless=cdoe/cantless;
 pjuvantless=cjuv/cantless;
 cdoehar=round(cantlesshar*pdoeantless);
 cjuvhar=round(cantlesshar*pjuvantless);

****Mature antlered population;
 matantpop=round(cmatanthar/bhr);

****Add Mature antlered population (t+1) to end;
**This allows updated YMHR and Juv:Doe to use data from the following year;
data matpop; set pre;
 mantpopnxt=matantpop;
 yr=yr-1;
 if yr<&firstyear then delete;
 keep wmu yr mantpopnxt;
data pre1; merge pre matpop; by wmu yr;

****Yearling antlered population;
**Est for year (t) use rolling ave from prev 3 yrs. if iterym=1
**Est for yr (t-1, t-2, etc) use updated yrlhr from matantpop the following yr;
if &iterym=1 then do;**Using iterative YMHR;
yrlhrave=(lag1(cyrlanthar)/(matantpop*ptwoyrbuck/surv+lag1(cyrlanthar))+
     lag2(cyrlanthar)/(lag1(matantpop)*lag1(ptwoyrbuck)/surv+lag2(cyrlanthar))+
     lag3(cyrlanthar)/(lag2(matantpop)*lag2(ptwoyrbuck)/surv+lag3(cyrlanthar)))/3;
 yrlhrcal=cyrlanthar/(mantpopnxt*ptwoyrbuck/surv+cyrlanthar);
 if yr=&currentyear then ymhr=yrlhrave;
 else ymhr=yrlhrcal;
end;

 yrlantpop=round(cyrlanthar/ymhr);

****Add Yearling antlered population (t+1) to end;
**This allows updated Juv:Doe to use data from the following year;
data yrlpop; set pre1;
 yrlantpop1=yrlantpop;
 yr=yr-1;
 if yr<&firstyear then delete;
 keep wmu yr yrlantpop1;
data one; merge pre1 yrlpop; by wmu yr;

****Antlered population;
```

```sas
  antpop=round(matantpop+yrlantpop);

****Adult female population;
 pyrldoe=cyrldoe/cdoe;

**Adult Sex ratio;
 if &bratio=1 then do;**Using birth ratio correction factor;
 adsxratio=yrlantpop/antpop/pyrldoe/birthratio;
 end;
 else do;**Not using birth ratio correction factor;
 adsxratio=yrlantpop/antpop/pyrldoe;
 end;

doepop=round(antpop*adsxratio);

****Juvenile population;
**Est for year (t) uses 2 yr rolling ave from (t-2) and (t-3), can't use (t-1),
**because of non-updated YM est in (t), only when using iterative YMHR
**Est for year (t) uses 3 yr rolling ave from (t-1), (t-2), and (t-3)
**only when using direct YMHR, if using iterative YMHR have to wait until (t-1)
**Est for year (t-1, t-2, etc) uses updated "actual" ratio
**only when using direct YMHR, if using iterative YMHR have to wait until (t-2);
 pjuv=cjuv/cdoe;

 juvaddoecorrtwo=((lag1(yrlantpop)*2/(survj*survf)+lag2(cjuvhar))/
     lag2(doepop)/lag2(pjuv)+
     (lag2(yrlantpop)*2/(survj*survf)+lag3(cjuvhar))/lag3(doepop)/lag3(pjuv))/2;
 juvaddoecorrthree=((yrlantpop*2/(survj*survf)+lag1(cjuvhar))/lag1(doepop)/lag1(pjuv)
     +(lag1(yrlantpop)*2/(survj*survf)+lag2(cjuvhar))/lag2(doepop)/lag2(pjuv)
     +(lag2(yrlantpop)*2/(survj*survf)+lag3(cjuvhar))/lag3(doepop)/lag3(pjuv))/3;
 juvaddoecorrcal=(yrlantpop1*2/(survj*survf)+cjuvhar)/doepop/pjuv;

 if &iterym=1 then do;**Using iterative YMHR;
 if yr=&currentyear then juvaddoecorr=juvaddoecorrtwo;
  else if yr=&currentyear-1 then juvaddoecorr=juvaddoecorrthree;
  else juvaddoecorr=juvaddoecorrcal;
 end;
 else do;**Using direct (radiocollar) YMHR;
 if yr=&currentyear then juvaddoecorr=juvaddoecorrthree;
  else juvaddoecorr=juvaddoecorrcal;
 end;

 fdratio=pjuv*juvaddoecorr;
 juvpop=round(doepop*fdratio);

****Final population estimates;
 prehuntpop=matantpop+yrlantpop+doepop+juvpop;
 prehuntdens=prehuntpop/area;
 posthuntpop=prehuntpop-cmatanthar-cyrlanthar-cdoehar-cjuvhar;
 posthuntdens=posthuntpop/area;

proc sort; by wmu yr;

data oneprint; set one;
  keep yr wmu canthar cantlesshar bhr ymhr matantpop yrlantpop adsxratio doepop
       fdratio juvpop prehuntpop prehuntdens posthuntpop posthuntdens;
  file ' File path \results\agesexpop';
  put yr wmu canthar cantlesshar bhr ymhr matantpop yrlantpop adsxratio doepop
       fdratio juvpop prehuntpop prehuntdens posthuntpop posthuntdens;

proc export outfile=' File path \results\agesexpop'
    dbms=dbf replace;
```

```
proc print label noobs;
 label yr='Yr' wmu='WMU' canthar='Antld harv' cantlesshar='Antless harv'
       bhr='Mat male harv rate' ymhr='Yrl male harv rate'
          matantpop='Mature male pop' yrlantpop='Yearling male pop'
          adsxratio='Ad female:ad male' doepop='Ad female pop'
       fdratio='fawn:ad doe' juvpop='Juv pop'
          prehuntpop='Preseason pop'
          prehuntdens='Preseason pop density'
       posthuntpop='Postseason pop size'
          posthuntdens='Postseason pop density';
   format canthar cantlesshar matantpop yrlantpop doepop juvpop
          prehuntpop posthuntpop comma6.0
                 bhr ymhr prehuntdens posthuntdens 6.2
          adsxratio fdratio 6.3;
   var yr wmu canthar cantlesshar bhr ymhr matantpop yrlantpop adsxratio doepop
        fdratio juvpop prehuntpop prehuntdens posthuntpop posthuntdens;
********************************************************************************
********************************************************************************


***************Monte Carlo estimation of CI************************************
********************************************************************************

**rep = # bootstrap replicates;
%let rep=999;
%let one=999; %let two=1998; %let three=2997;

proc sort data=one; by wmu yr;
data presim; set one;
****Random Seeds for CALL statements;
seed1=int(ranuni(0)*10**7); seed2=int(ranuni(0)*10**7);
seed3=int(ranuni(0)*10**7); seed4=int(ranuni(0)*10**7);
seed5=int(ranuni(0)*10**7); seed6=int(ranuni(0)*10**7);

****Calc. alpha and beta for the beta dist. for K-M rate estimates with SE;
bvar=(bse*(&bseinf))**2;
bhrbeta=(bhr-(1-bhr)*(bhr/(1-bhr)+1)**2*bvar)/((1-bhr)*(bhr/(1-bhr)+1)**3*bvar);
bhralpha=bhr*bhrbeta/(1-bhr);
ymvar=(ymse*(&ymseinf))**2;
ymbeta=(ymhr-(1-ymhr)*(ymhr/(1-ymhr)+1)**2*ymvar)/((1-ymhr)*
     (ymhr/(1-ymhr)+1)**3*ymvar);
ymalpha=ymhr*ymbeta/(1-ymhr);
survfvar=(survfse*(&fseinf))**2;
survfbeta=(survf-(1-survf)*(survf/(1-survf)+1)**2*survfvar)/((1-survf)*
        (survf/(1-survf)+1)**3*survfvar);
survfalpha=survf*survfbeta/(1-survf);
survjvar=(survjse*(&jseinf))**2;
survjbeta=(survj-(1-survj)*(survj/(1-survj)+1)**2*survjvar)/((1-survj)*
        (survj/(1-survj)+1)**3*survjvar);
survjalpha=survj*survjbeta/(1-survj);
survvar=(survse*(&survseinf))**2;
survbeta=(surv-(1-surv)*(surv/(1-surv)+1)**2*survvar)/((1-surv)*
        (surv/(1-surv)+1)**3*survvar);
survalpha=surv*survbeta/(1-surv);

do i=1 to &rep;
****Antlered harvest estimate simulations;
 call ranbin(seed1,lpant,lpantrc/lpant,xbin1);
 lpantrcsim=xbin1;
 cantharsim=round((lpant+1)*(lpantrep+1)/(lpantrcsim+1)-1);
 call ranbin(seed2,cant,pmatant,xbin2);
 cmatantsim=xbin2;
 pmatantsim=cmatantsim/cant;
```

```
 cmatantharsim=round(cantharsim*pmatantsim);
 cyrlantharsim=round(cantharsim*(1-pmatantsim));

****Antlerless harvest estimate simulations;
 call ranbin(seed3,lpantless,lpantlessrc/lpantless,xbin3);
 lpantlessrcsim=xbin3;
 cantlessharsim=round((lpantless+1)*(lpantlessrep+1)/(lpantlessrcsim+1)-1);
 call ranbin(seed4,cantless,pdoeantless,xbin4);
 cdoesim=xbin4;
 pdoeantlesssim=cdoesim/cantless;
 cdoeharsim=round(cantlessharsim*pdoeantlesssim);
 cjuvharsim=round(cantlessharsim*(1-pdoeantlesssim));

****Mature antlered population simulations;
 call rangam(seed5,bhralpha,xgam5);
 call rangam(seed6,bhrbeta,xgam6);
 bhrsim=xgam5/(xgam5+xgam6);
 matantpopsim=round(cmatantharsim/bhrsim);
 output;
 end;

****Add Mature antlered population (t+1) to end;
**This allows updated YMHR and Juv:Doe to use data from the following year;
data matpopsim; set presim;
 mantpopnxtsim=matantpopsim;
 yr=yr-1;
 i=i-1;
 if yr<&firstyear then delete;
 if i=0 then delete;
 keep i wmu yr mantpopnxtsim;
data pre1sim; merge presim matpopsim; by wmu yr i;

****Random Seeds for CALL statements;
seed7=int(ranuni(0)*10**7); seed8=int(ranuni(0)*10**7);
seed9=int(ranuni(0)*10**7);

****Yearling antlered population simulations;
if &iterym=1 then do;**Using iterative YMHR;
call ranbin(seed7,nptwoyrbuck,ptwoyrbuck,xbin7);
 ctwoyrbucksim=xbin7;
 ptwoyrbucksim=ctwoyrbucksim/nptwoyrbuck;
 call rangam(seed8,survalpha,xgam8);
 call rangam(seed9,survbeta,xgam9);
 survsim=xgam8/(xgam8+xgam9);
 yrlhravesim=(lag&one(cyrlantharsim)/(matantpopsim*ptwoyrbucksim/
        survsim+lag&one(cyrlantharsim))+
     lag&two(cyrlantharsim)/(lag&one(matantpopsim)*lag&one(ptwoyrbucksim)/
     survsim+lag&two(cyrlantharsim))+
     lag&three(cyrlantharsim)/(lag&two(matantpopsim)*lag&two(ptwoyrbucksim)/
     survsim+lag&three(cyrlantharsim)))/3;
 yrlhrcalsim=cyrlantharsim/(mantpopnxtsim*ptwoyrbucksim/survsim+cyrlantharsim);
 if yr=&currentyear then ymhrsim=yrlhravesim;
 else ymhrsim=yrlhrcalsim;
 end;
 else do;**Using direct (radiocollar) YMHR;
 ****Random Seeds for CALL statements;
 call rangam(seed7,ymalpha,xgam7);
 call rangam(seed8,ymbeta,xgam8);
 ymhrsim=xgam7/(xgam7+xgam8);
 end;

 yrlantpopsim=round(cyrlantharsim/ymhrsim);
```

```sas
****Add Yearling antlered population (t+1) to end;
data yrlpopsim; set pre1sim;
 yrlpopnxtsim=yrlantpopsim;
 yr=yr-1;
 i=i-1;
 if yr<&firstyear then delete;
 if i=0 then delete;
 keep i wmu yr yrlpopnxtsim;
data five; merge pre1sim yrlpopsim; by wmu yr i;

****Random Seeds for CALL statements;
 seed9=int(ranuni(0)*10**7);  seed10=int(ranuni(0)*10**7);
 seed11=int(ranuni(0)*10**7); seed12=int(ranuni(0)*10**7);
 seed13=int(ranuni(0)*10**7); seed14=int(ranuni(0)*10**7);
 seed15=int(ranuni(0)*10**7);

****Antlered population simulations;
 antpopsim=round(matantpopsim+yrlantpopsim);

****Adult female population simulations;
 call ranbin(seed9,cdoe,pyrldoe,xbin9);
 cyrldoesim=xbin9;
 pyrldoesim=cyrldoesim/cdoe;

****Adult Sex ratio simiulations;
 if &bratio=1 then do;**Using birth ratio correction factor;
 call ranbin(seed10,nbirthratio,birthratio/(1+birthratio),xbin10);
 malessim=xbin10;
 birthratiosim=malessim/(nbirthratio-malessim);
 adsxratiosim=yrlantpopsim/antpopsim/pyrldoesim/birthratiosim;
 doepopsim=round(antpopsim*adsxratiosim);
 end;
 else do;**Not using birth ratio correction factor;
 adsxratiosim=yrlantpopsim/antpopsim/pyrldoesim;
 end;

 doepopsim=round(antpopsim*adsxratiosim);

****Juvenile population simulations;
 call rangam(seed11,survjalpha,xgam11);
 call rangam(seed12,survjbeta,xgam12);
 survjsim=xgam11/(xgam11+xgam12);
 call rangam(seed13,survfalpha,xgam13);
 call rangam(seed14,survfbeta,xgam14);
 survfsim=xgam13/(xgam13+xgam14);
 jfsurvsim=survjsim*survfsim;
 call ranbin(seed15,cantless,pjuvantless,xbin15);
 cjuvsim=xbin15;
 cdoesim=cantless-cjuvsim;
 pjuvsim=cjuvsim/cdoesim;
 juvaddoecorrtwosim=((lag&one(yrlantpopsim)*2/jfsurvsim+lag&two(cjuvharsim))/
        lag&two(doepopsim)/lag&two(pjuvsim)+
        (lag&two(yrlantpopsim)*2/jfsurvsim+lag&three(cjuvharsim))/
        lag&three(doepopsim)/lag&three(pjuvsim))/2;
 juvaddoecorrthreesim=((yrlantpopsim*2/jfsurvsim+lag&one(cjuvharsim))/
        lag&one(doepopsim)/lag&one(pjuvsim)+
        (lag&one(yrlantpopsim)*2/jfsurvsim+lag&two(cjuvharsim))/
     lag&two(doepopsim)/lag&two(pjuvsim)+
        (lag&two(yrlantpopsim)*2/jfsurvsim+lag&three(cjuvharsim))/
        lag&three(doepopsim)/lag&three(pjuvsim))/3;
 juvaddoecorrcalsim=(yrlpopnxtsim*2/jfsurvsim+cjuvharsim)/doepopsim/pjuvsim;

 if &iterym=1 then do;**if using iterative YMHR;
```

```
   if yr=&currentyear then juvaddoecorrsim=juvaddoecorrtwosim;
   else if yr=&currentyear-1 then juvaddoecorrsim=juvaddoecorrthreesim;
   else juvaddoecorrsim=juvaddoecorrcalsim;
   end;
   else do;**if using direct YMHR;
   if yr=&currentyear then juvaddoecorrsim=juvaddoecorrthreesim;
   else juvaddoecorrsim=juvaddoecorrcalsim;
   end;

   fdratiosim=pjuvsim*juvaddoecorrsim;
   juvpopsim=(doepopsim*fdratiosim);

****Final pre-hunting season population estimates;
 prehuntpopsim=matantpopsim+yrlantpopsim+doepopsim+juvpopsim;
 prehuntdenssim=prehuntpopsim/area;
 posthuntpopsim=prehuntpopsim-cmatantharsim-cyrlantharsim-cdoeharsim-cjuvharsim;
 posthuntdenssim=posthuntpopsim/area;

****90% CI on WMU point estimates;
**Uses 5th and 95th percentiles from MC simulations for 90% CI;
**Includes 2.5th and 97.5th percentiles from MC sims for 95% CI;
proc univariate noprint;
 by wmu yr;
 var prehuntpopsim prehuntdenssim;
 output out=stats1 cv=popcv pctlpre=P_ pctlpts=2.5,5,50,95,97.5;
 output out=stats2 p5=x D_5 median=x D_50 p95=x D_95;
 data last; merge stats1 stats2; by wmu yr;
 data last1; merge one last; by wmu yr;
  keep yr wmu popcv P_2_5 P_5 prehuntpop P_95 P_97_5
       D_5 prehuntdens D_95 posthuntpop posthuntdens;
  file ' File path \results\totpop';
  put yr wmu popcv p_5 prehuntpop P_95 D_5 prehuntdens D_95;

proc export outfile=' File path \results\totpop'
   dbms=dbf replace;

proc print label noobs;
  label yr='Yr' wmu='WMU' popcv='CV' prehuntpop='Preseason pop'
        prehuntdens='Preseason pop density'
              posthuntpop='Postseason pop'
              posthuntdens='Postseason pop density'
           P_5='90% LCL' P_95='90% UCL' D_5='90% LCL' D_95='90% UCL';
  format D_5 prehuntdens posthuntdens D_95 popcv 5.1
         P_5 prehuntpop posthuntpop P_95 comma8.0;
  var yr wmu popcv P_5 prehuntpop P_95 D_5 prehuntdens D_95;

****Mean WMU Coefficient of Variation by year;
proc sort data=last1; by yr wmu;
proc means;
      by yr;
      var popcv;
      output out=coefvar MEAN(popcv)=Meanpopcv;
 proc print;run;
 *******************************************************************************
 *******************************************************************************
```

Appendix C

Robustness Simulations

Known Population

Two-Sex Leslie Matrix or Accounting Model

My known population simulation started with initial pre-hunt populations of:

1) Juvenile (0.5 years old) female

2) Yearling (1.5 years old) female

3) ≥ 2.5 years old female

4) Juvenile male

5) Yearling male

6) 2.5 years old male

7) ≥ 3.5 years old male

To best represent a typical WMU age-sex structure and population size, I used initial population estimates from WMU 4B in 2008.

Next, I set fixed age and sex specific harvest, non-harvest survival, and fecundity rates, creating a deterministic model. Harvest and non-harvest mortality rates were used to subtract annual mortalities from the population. The remaining females were multiplied by age specific fecundity rates to simulate instantaneous pre-hunting season recruitment of juveniles for the following year. Finally, all remaining individuals were aged into the next age class for the following year. This process was repeated to simulate a population through 50 years.

Stochastic variability of a specific harvest or non-harvest mortality rate was based on uniform variation of a parameter between a realistic interval, suggested via radiocollar data. This stochastic variability was considered a conservative estimate of the process variance. I will refer to models including stochastic variability to a single parameter as partially stochastic models.

Estimated Population

PASAK Model using sampling from Known Population

For all harvest rate and survival parameters used in the PASAK model, I used the exact value of the fixed known parameter from the deterministic model. When I varied the known parameter (partially stochastic model), I continued to use only the fixed parameter for the PASAK model. For example, if the simulated yearling male harvest rate was uniformly varied between 0.40 and 0.50, I used the original fixed parameter of 0.34 for all PASAK model estimates. The original fixed parameters are based on radiocollar estimates that are currently used for the PASAK model.

All other parameters required for the PASAK model were sampled from known, simulated harvest data. The Lincoln-Peterson estimator (see chapter 3), used to estimate the antlered (adult male) harvest, required three parameters, 1) number of deer checked, 2) number of deer reported, and 3) number of deer checked and reported. For the number of deer checked, I used the mean sample size from WMU 4B between 2002-2008, which remained constant throughout the 50 years. Next, I estimated the number of antlered deer reported by multiplying the number of antlered deer harvested, from the known population, by a reporting rate sampled from a binomial distribution $b(n,p)$ with p = mean

reporting rate (0.37), and n = total harvest from the known population. The total number of deer reported and checked was estimated similarly by multiplying the number of deer checked by the reporting rate sampled from the binomial distribution. I then estimated the age-specific antlered harvest. The mature antlered harvest was estimated using $b(n,p)$ with p = % of ≥ 2.5 year olds in the ≥ 1.5 years old male harvest, and n = antlered harvest, both from the known population. The yearling antlered harvest estimate was the difference between the antlered harvest and the mature antlered harvest estimate.

The remaining harvest parameters sampled from the known population for the PASAK model were used to estimate the % 2.5 year olds in the ≥ 2.5 years old male harvest, % yearlings in the ≥ 1.5 years old female population, and the % juveniles in the antlerless population. I used the mean rate across the 50 years of simulated data for the % 2.5 year olds in the ≥ 2.5 years old male harvest. The % yearlings in the ≥ 1.5 years old female population was estimated using $b(n,p)$ with p = % of 1.5 year olds in the ≥ 1.5 years old female harvest, and n = ≥ 1.5 years old female harvest, both from the known population. Similarly, the % juveniles in the antlerless population was estimated using $b(n,p)$ with p = % juveniles in the antlerless harvest, and n = antlerless harvest.

Appendix D

Coefficients of Variation

Estimated coefficients of variation (CV $= SE(\hat{N})/\hat{N} \times 100\%$) for white-tailed deer abundance estimates by WMU from 2002-2008 using the PASAK model. Urban and suburban wildlife management units for Pittsburgh (WMU 2B) and Philadelphia (WMU 5C and 5D) are not included.

	Coefficient of Variation (%)						
WMU	2002	2003	2004	2005	2006	2007	2008
1A	6.9	6.9	6.9	7.3	8.3	7.9	13.1
1B	6.6	6.3	6.8	7.0	7.2	7.3	11.5
2A	8.1	8.0	7.7	8.2	8.2	8.1	14.9
2C	6.7	6.7	6.8	6.7	6.7	7.3	11.8
2D	7.3	7.1	6.9	6.6	6.7	6.9	12.3
2E	9.2	9.1	9.4	9.5	9.9	9.0	16.3
2F	6.9	7.2	7.1	6.9	7.3	7.6	11.7
2G	7.9	9.6	10.0	9.4	11.6	8.7	15.4
3A	7.3	7.5	8.0	8.2	7.5	7.9	12.7
3B	7.0	6.5	7.3	7.5	7.0	8.2	11.9
3C	7.9	7.6	8.0	7.4	7.9	7.3	12.6
3D	7.6	7.4	7.8	8.4	8.2	8.7	15.0
4A	9.2	9.8	8.9	8.6	9.0	10.6	14.6
4B	7.5	7.1	7.4	7.7	8.0	8.4	16.7
4C	7.1	7.1	7.6	7.4	7.8	7.3	13.3
4D	7.2	6.8	7.0	7.5	7.2	7.6	13.2
4E	6.9	7.3	7.5	8.5	7.7	8.4	14.5
5A	10.2	12.8	12.7	13.2	13.4	16.1	23.8
5B	6.8	6.8	7.1	7.3	7.1	7.4	12.9
Mean	7.6	7.8	7.9	8.1	8.2	8.5	14.1