A SYNTHESIS OF BEAR POPULATION DYNAMICS IN MICHIGAN

By

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ABSTRACT

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The Michigan Department of Natural Resources (DNR) manages the black bear (*Ursus americanus*) population of Michigan primarily through manipulating the harvest by adjusting the quota of hunting licenses. Estimates of the bear population play a key role in determining the appropriate license quota to achieve the DNR's bear population objectives. Past population estimates were unreliable or infrequent, so we developed a statistical catch-at-age analysis (SCAA) of the Upper Peninsula (UP) and northern Lower Peninsula (NLP) bear populations of Michigan from 1992-2015 to inform the bear management program and to allow the DNR to more closely monitor changes in the bear population over time.

To support the models, we estimated the aging and sexing error rates of harvested Michigan black bears. We estimated aging error by comparing the true age of known-age bears to the age determined through cementum annuli aging techniques. Aging error rates were low (2%) at the lowest age categories and increased as bear age increased. We also estimated the sexing error rates by comparing the genetic sex of harvested bears to the sex hunters reported at the time of harvest. Sexing error was higher for females than males and differed by region. The error rates we estimated, however, were unlikely to have major effects on analyses based on sex and age data unless those data were heavily skewed toward one sex and the sexes exhibited large differences in age distribution.

We also described the reproductive patterns of Michigan black bears and looked for reproductive trends over age, time and geographic region. Results showed differences between the UP and NLP. Adult females in the UP began breeding at an older age than those in the NLP and had smaller litters. By 4 years old, however, the proportion of females that bred each year was approximately 50% in each region, with only occasional major fluctuations, likely due to catastrophic mast failures. Overall, the Michigan black bear populations are as or more productive than other black bear populations in eastern North America.

We developed the SCAA models for both the UP and NLP regions of Michigan to monitor the black bear population and to support the DNR's need to assess effects of past management and support decisions on future management actions. Within each region, the final selected models showed a stable to slightly increasing bear population in the UP and an increasing population in the NLP from 1992 to 2015. Model evaluation raised no major concerns of model behavior. Sensitivity analysis showed the models to be insensitive to simplifying assumptions and available data, except for the availability of mark-recapture population estimates. We recommend the DNR continue to estimate the bear populations through independent mark-recapture surveys or other means every 5 years. The SCAA models provide evidence of a stable bear population in the UP and an increasing population in the NLP. The bear populations' high annual mortality rates are offset by high fecundity.

To my children, Claire and Andrew.
You bring me such joy!

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My committee, including Juan Pedro Steibel and Bill Porter, provided support, technical advice, and understanding of my non-traditional status. Thank you to my advisor, fisheries researcher Jim Bence, for agreeing to take on a wildlife student with a wildlife project and for teaching me more than anyone else how to approach this project. Jim also figured out how to turn my objective function into a negative log likelihood that I could use for model selection and came up with the title. And special thanks to Scott Winterstein who has never stopped encouraging me and supporting me since he first took me on as a MS student all those years ago.

Several people provided data and technical support. The bear hunters of Michigan provided the data that supports this dissertation by registering their harvested bears and responding to questionnaires. The staff of the Wildlife Division and dozens of cooperators recorded those data and collected teeth from those bears. Kim Scribner and Hope Draheim provided the bear genetic sex data and the description of the genetics methodology. DNR Wildlife Disease Lab staff including Melinda Cosgrove, Michelle Clayson, Julie Melotti, and Caitlin Ott-Conn provided bear ages and bear reproduction data. Brian Frawley provided the data for the hunter effort. Matt Catalano provided R code to help with calculating the aging errors. Dan O'Brien provided a listening ear and helpful questions and suggestions when I needed to talk through a sticky stats situation. This dissertation would have taken me much longer to complete without Chris Van Horn and Caitlin Boon who provided assistance with many tasks, especially data management.

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CHAPTER 1: INTRODUCTION

Several years ago, the Michigan Department of Natural Resources (DNR) Wildlife Division found themselves sitting on a trove of data from the black bear (*Ursus americanus*) population and harvest, but they had gleaned little information from the data. The DNR had data on bear reproduction and ages of harvested bears that received only cursory review each year. The DNR attempted to manipulate the population through harvest, but their only means to monitor the population were occasional capture-mark-recapture (CMR) surveys that provided estimates of the population at best 1 year, and usually 3 years, after the survey was completed, indices such as bears harvested per hunter day, and a simple demographic model that was sensitive to the initial population size. These coarse, infrequent, and highly variable means of monitoring the bear population provided the DNR with little information on the effects of their management actions on the population.

Fisheries agencies have long collected data similar to the data the DNR maintained on the bear population, and they developed sophisticated catch-at-age analysis techniques to extract information from such data (Fournier and Archibald 1982). These techniques differed from those used in wildlife research by incorporating multiple data sources into a single model and estimating multiple demographic parameters simultaneously from those data. Gove et al. (2002) were the first to publish an application of these catch-at-age (or age-at-harvest) analysis techniques to wildlife data, and Skalski et al. (2011) were the first to use the techniques with data collected by the Michigan DNR. The analysis techniques, known by the terms statistical catch-at-age-analysis, statistical population reconstruction, and stock assessment, and others, allow the modeler to estimate demographic parameters such as recruitment, survival, harvest mortality, and population size over long temporal scales using data such as the DNR has collected for decades.

I took advantage of the long-underused data available to the DNR to develop a statistical catch-at-age analysis (SCAA) of the 2 largest Michigan bear populations and build demographic models to inform the bear management program and to allow the DNR to more closely monitor changes in the bear population over time. The SCAA models are reliant on the age and sex data provided through the process of registering harvested bears. In Chapter 2, I analyze the sex and age data and estimate error rates. In Chapter 3, I analyze the data that the DNR had available on bear reproduction from multiple sources. I used some of the information from Chapter 3 in the SCAA models and I used some as an independent check against the results of the SCAA models. Finally, Chapter 4 is the heart of the matter where I describe the SCAA models that I developed, evaluate their results, and test their sensitivity. This dissertation is intended primarily as a report to the DNR so they can assess the strengths and weaknesses of the SCAA models and determine their appropriate role in the bear management program. I have tried to include sufficient detail, however, that a person unfamiliar with Michigan's bear populations and management can put the methodology and interpretation in appropriate context.

STUDY AREA

This dissertation focuses on the black bear population in the Upper Peninsula (UP) region, excluding Drummond Island, and the northern Lower Peninsula (NLP) region of

Michigan (Figure 1.1). I use “population” to mean all black bears inhabiting each region. Despite the size of each region, there are no physical barriers to prevent bears interacting and interbreeding throughout each region and there is little movement in and out of each region.

There are many more bears in the UP than in the NLP (Bump 2009). The UP is surrounded by Lakes Superior, Michigan, and Huron, although it shares a 393 km border with Wisconsin along its western end. It is primarily forested with northern hardwoods and conifers with patches of pasture and agriculture (Albert 1995). The eastern UP is flat with poorly drained soils that support large wetland complexes while the western UP has more topographic relief, less agriculture, less wetland area, and more logging (Albert 1995). The NLP is home to the rest of Michigan’s harvestable bears. The NLP is bounded by Lakes Michigan and Huron along all but its southern border. The NLP is also largely forested with northern hardwoods and conifers, but it is a more fragmented landscape than the UP with a higher human population density and patches of row crops, pasture, orchards, and vineyards (Albert 1995). The southern border marks a transition to the more developed and agricultural landscape of southern Michigan (Albert 1995) where there are only occasional bear sightings.

Between 1990 and 2015, the DNR managed bear harvest through limited license quotas, allocated among multiple management units that divided the UP and NLP. A bear license allowed a hunter to harvest a single adult (1 year old or older) bear in the assigned management unit. Other than changing unit boundaries and quotas, the harvest regulations (including season dates, bag limits, and allowable method and manner of take) remained fairly stable during this time period. Modifications were made to exclude bait hunters (NLP only) and dog hunters (UP and NLP) for brief periods of the harvest season. The bear season was open

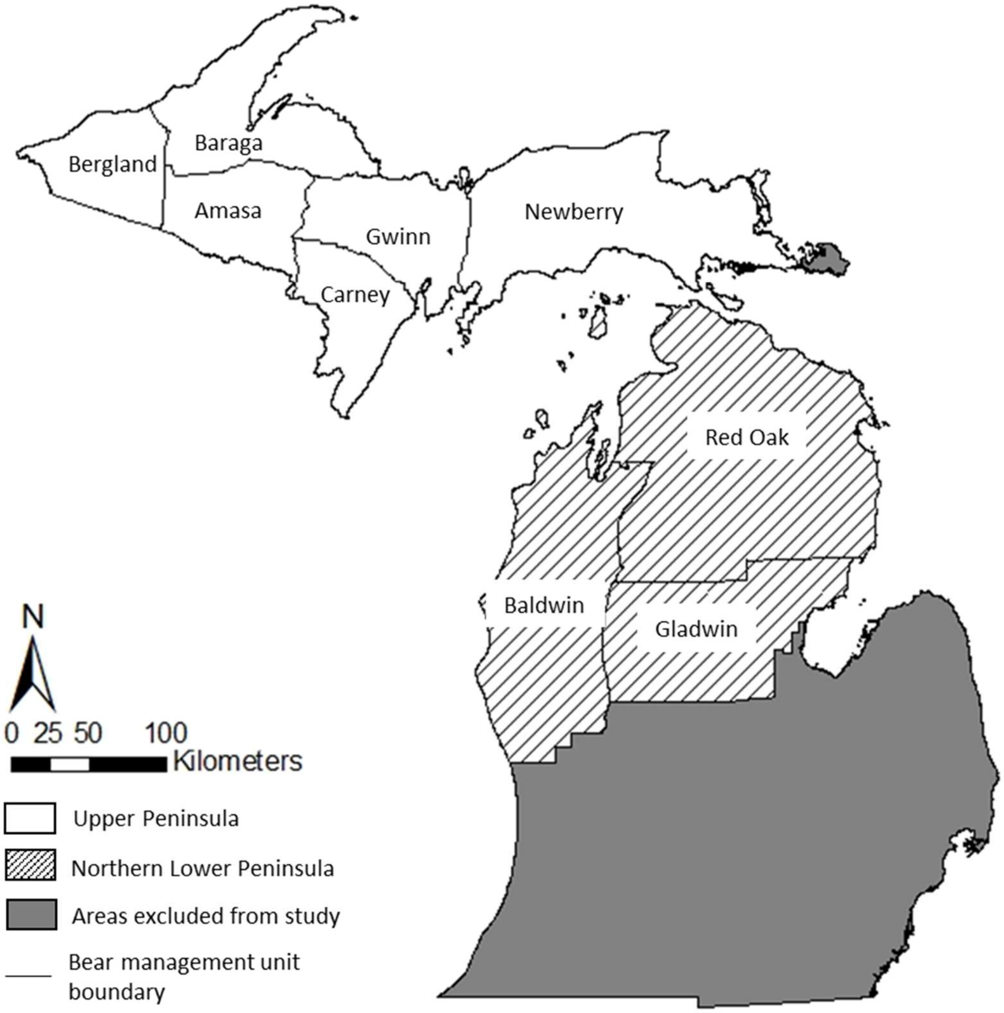

FIGURE 1.1. Black bear management unit boundaries in Michigan, USA, 2015.

for approximately 6.5 weeks in the UP and 1 to 2 weeks in the NLP during September and October. Hunters could use either firearms or archery equipment and could choose to hunt over bait, pursue bears with dogs, stand hunt, or stalk hunt. Hunting regulations protected females accompanied by cubs from harvest, but in practice that protection was not complete (Belant et al. 2011a). Every successful hunter was required to register the harvested bear with the DNR. More specific details of the harvest and registration process are included in the individual chapters, as needed.

CHAPTER 2: ERRORS IN IDENTIFYING SEX AND AGE OF HUNTER HARVESTED BLACK BEARS IN MICHIGAN

INTRODUCTION

Black bears (*Ursus americanus*) are hunted throughout eastern North American where the majority of hunting jurisdictions collect data from hunters and their harvest to support their management programs (Dobey 2015). Michigan's hunter harvested bears provide the largest source of biological information on the black bear population due to the requirement that all hunters register their take with the Michigan Department of Natural Resources (DNR). The registration record includes the sex and age of the bear, which provides vital biological information on approximately 10-25% of the bear population every year (Garshelis and Visser 1997, Dreher et al. 2007). The sex and age data are used for a variety of analyses to address management questions. The data are a valuable asset for mark-recapture surveys, population models, and characterization of the population (Bump 2009).

Although the source of the information is different, both the sex and age of harvested bears are subject to error. In most cases, hunters report the sex (field sex) of the bear at the time of registration based on their observations of the carcass prior to field processing. Error in such hunter-reported field sex can be large (Williams et al. 2011), however, and could lead to biased results when the data are used in population models or other applications (Schliebe et al. 1999). On the other hand, laboratory staff determine ages (lab age) from an extracted tooth using the methods of Willey (1974) and Coy and Garshelis (1992). These methods are also subject to error (Harshyne et al. 1998), which could introduce a second source of bias in analyses based on the registration data.

Our objectives were to quantify the error rates of the reported sex and age of bears harvested in Michigan and to assess whether they differed over important variables. To quantify sexing error, we compared the field sex of bears to the sex assigned using molecular genetic techniques, which we assumed to be the true sex. To quantify aging error, we compared the lab age of marked bears to their known age. We then calculated error rates which could be used to adjust the reported harvest data for sexing and aging errors.

METHODS

The DNR required all successful bear hunters to register their own bear at an authorized registration station. During registration, the hunter reported the date and location of harvest, the field sex of the bear, noted any tags, collars, or tattoos on the bear, and submitted a pre-molar tooth from the bear. From 1990 through 2014, annual harvest ranged from 543 to 2062 in the UP and 118 to 514 in the NLP, a slight majority of which was male in most years (Figure 2.1).

Sexing Error

Teeth extracted from harvested bears yielded tissue that was analyzed using molecular genetic techniques to determine the genetic sex. We selected a random sample of harvested bears from 2002 (NLP), 2009 (UP), and 2010 (NLP, UP) for genetic sexing. We selected years based on the availability of tissues collected for other research and to cover as long a time span as possible. We also included in this study samples from NLP bears harvested in 2006 that had already been analyzed for a separate study.

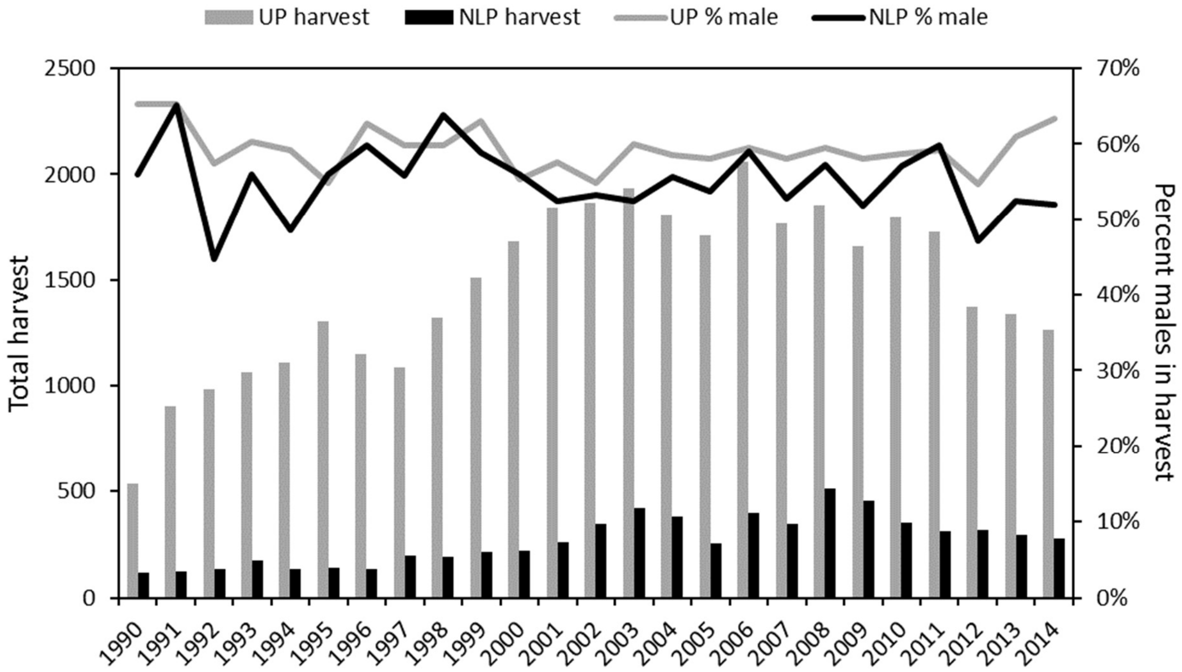

FIGURE 2.1. Annual number of black bears harvested (vertical bars) in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, and the percent of the harvest (horizontal lines) reported as male, 1990-2014.

Laboratory staff extracted DNA using Qiagen DNEasy Tissue Kits following manufacturer protocols (Qiagen Inc., Valencia, CA). DNA was quantified using a Nanodrop spectrophotometer (Thermo Scientific, Waltham, MA) and diluted to a 20 ng/µl working concentration. We amplified a region of the amelogenin gene using primers SE47 and SE48 (Ennis and Gallagher 1994). PCR reactions were performed in 15 µl volumes including 40 ng of DNA in 10 mM Tris-HCl, 50 mM KCl, 1.5 mM MgCl2, 0.25 mM of each dNTP, 1.5 pmol of each primer, and 0.5 units of Taq polymerase. We ran the amplified product with a 100 bp ladder to provide known size standards on a 1.5% agarose gel stained with ethidium bromide. Two bands, one originating from the X-chromosome (254 bp) and one from the Y-chromosome (190 bp) amplified from males; a single band (245 bp) was amplified from females. We visualized the DNA fragments using an ultraviolet light box. Two experienced lab personnel independently scored all bands.

We assumed the genetic sex was the true sex of the animal and used the genetic sex to identify whether an individual's field sex was correct. To determine the factors that were most important in predicting sexing error, we used Akaike's information criterion (AIC) to select the best fit of several models (Burnham and Anderson 2002). The models included categorical variables for genetic sex, region (UP or NLP), age (yearling or adult), and year of harvest. We included genetic sex in all models because we assumed there would be some relationship between field sex and genetic sex. We assumed there would be no discernable difference in the hunters' ability to determine sex across years and included year of harvest only in the most parameterized model as a means of evaluating that assumption. The other models reflected all possible combinations of region and age and included a model with genetic sex alone. We calculated a separate error rate for each category of bears identified in the top ranked model.

Aging Error

Since 1986, Michigan has marked bears using ear tags, radio collars, and tattoos as part of several research and management projects. We reviewed all bear registrations from 1989 through 2014 to find records that reported such markings on harvested bears. We compared the markings reported in the registration record to markings reported in research and management records to identify the bear and the date the bear was initially encountered. Although older bears cannot be reliably aged through visual inspection in the field, cubs and yearlings in the den are easily identified by their size and the presence of the mother. We assumed that any bears that were initially marked as a cub or a yearling in the den had a known year of birth and thus a known age at harvest. We compared the known age at harvest to the estimated age at harvest as determined through the examination of the cementum annuli using the techniques of Willey (1974) and Coy and Garshelis (1992). Laboratory staff conducting the annuli analysis were not aware of any previous encounter history with the bear, thus tooth ages were determined independent of any previously recorded age information.

We compared the known age to the lab age to identify whether the lab age was accurate or not and to estimate the magnitude of aging error. A bear aged incorrectly could have been assigned to any one of several age classes. Our approach was to estimate for each true age the probability a bear would be assigned each possible age (incorrect ages and the correct age), based on a statistical model for the mean and variance in assigned ages, using methods adapted from Catalano and Bence (2012). The parameters for the statistical model were estimated by maximum likelihood by comparing the observed distributions of assigned ages for each true age with the distribution predicted from the true ages given these probabilities using a multinomial distribution. Our model for the probabilities of age assignment assumed the expected value of lab age given true age as a linear function of true age assuming no bias for bears from age 1 year old to 12 years old. Aging errors could have been caused by a variety of situations (e.g. damaged tooth, crowded annuli, irregular cementum growth) so we assumed that both under- and over- estimation were equally likely. We calculated probabilities for lab age given true age based on 2 alternative underlying continuous probability distributions, the normal and gamma. The normal and gamma distributions are continuous, but bears are assigned integer ages. We calculated the estimated probability an aged bear would be assigned a particular integer age by integrating the normal or gamma cumulative distribution function from (lab age-0.5) to (lab age+0.5). These probabilities were then used in calculating the multinomial likelihood given the assumed distribution and variance form parameters. The variances for the normal and gamma distributions were determined as a function of true age (with estimated parameters) assuming 4 alternative relationships (constant standard deviation, linear standard deviation, constant CV, linear CV). Thus, we evaluated 8 alternative models (2 distributions by 4 variance forms). We used AIC to select for the best-fit model among 8 that described the error distribution of the lab age given true age.

We compiled the aging error matrix by calculating the probability that a bear of true age *a* was recorded as age *b* using the best fit model, rounded to the nearest hundredth. If rounding resulted in a row whose probabilities summed to <1.0, we increased the highest probability by the necessary amount. As bears aged, data became sparse and error rates increased, so we pooled ages ≥10 years old. For bears true age <10 years old, we summed the probabilities that a bear would be assigned to any lab age class ≥10 years old into a single 10+-years-old lab age category. For bears true age ≥10 years old, we created a single 10+-years-old true age category and averaged the probabilities of each lab age over all true ages (10 years old through 12 years old).

Corrected Harvest Composition

We used estimated sexing and aging error rates to adjust the reported composition of Michigan's combined legal state and tribal bear harvest in the UP and NLP from years with both high and low harvest and high and low proportion of males to examine the effect of sexing and aging error on a range of conditions. Within each region (R), we allocated bears of unknown sex and age to sex and age classes proportionate to the reported sex and age classes within the harvest year (H_y) to create a complete reported harvest composition matrix represented by,

$$\mathbf{H}_{\mathbf{y}}^{\mathbf{R}} = \left[h_{y,1} = \begin{bmatrix} m_{y,1} \\ f_{y,1} \end{bmatrix} \quad \cdots \quad h_{y,10+} = \begin{bmatrix} m_{y,10} \\ f_{y,10} \end{bmatrix} \right]$$

where $h_{y,a}$ = the number of bears reported in year y and age class a broken down by males ($m_{y,a}$) and females ($f_{y,a}$). We first corrected for sexing error by post-multiplying each $h_{y,a}$ by the inverse of the sexing error matrix (E_s),

$$\mathbf{E}_{\mathbf{S}} = \begin{bmatrix} 1 - e_m & e_m \\ e_f & 1 - e_f \end{bmatrix}$$

where e_m is the proportion of genetic males reported as females and e_f is the proportion of genetic females reported as males. We adjusted any results of negative bears by setting the negative $m_{y,a}$ or $f_{y,a}$ to 0 and reducing the number of the opposite sex by the same amount. This resulted in a harvest composition matrix, $\mathbf{H}_{\mathbf{y}}^{\mathbf{S}}$, corrected for sexing error for each region.

We then corrected for aging error by post-multiplying $\mathbf{H}_{\mathbf{y}}^{\mathbf{S}}$ by the inverse of the aging error matrix (E_A),

$$\mathbf{E_A} = \begin{bmatrix} e_{1,1} & \cdots & e_{1,10+} \\ \vdots & \ddots & \vdots \\ e_{10\ \ ,1} & \cdots & e_{10+,10+} \end{bmatrix}$$

where $e_{a,b}$ is the proportion of bears of true age class a that are reported as age class b. We adjusted any results of negative bears by setting the negative $m_{y,a}$ or $f_{y,a}$ to 0 and reducing the surrounding age classes proportionate to their contribution to the negative age class. We compared the recorded and corrected composition as broken down into males that were 1, 2, or 3+ years old and females that were 1, 2, 3, 4, or 5+ years old. These are age and sex categories which we would expect to have the most significant differences in demographic rates and thus be of the most interest to managers.

Effects of Aging and Sexing Error

To examine the potential effects of uncorrected sexing and aging error on analysis of harvest data, we used a catch-curve analysis similar to that presented for black bears in Skalski et al. (page 197, 2005) and an estimate of fecundity (page 93, Skalski et al. 2005). We used data based on the observed sex and age composition of the 2002 UP harvest but we treated the data as representing known, true sex and age of 1 year old through 10+ years old (Table 2.1). We applied the Robson and Chapman (1961) method to estimate male and female annual survival for such a dataset with a pooled maximum age class. We calculated fecundity as the ratio of juvenile (1-year-old and 2-year-old) females to adult (3+-year-old) females. We used these data as an example only and make no claims as to whether the data meet all assumptions for the

TABLE 2.1. Sex and age-at-harvest data used in scenarios to examine the effect of sexing and aging error on age-at-harvest data analyses. We based these data on frequencies observed for black bears harvested in 2002 in the Upper Peninsula of Michigan, USA.

	Frequency	
Age (years)	Male	Female
1	308	140
2	305	188
3	168	118
4	73	78
5	42	60
6	20	39
7	25	32
8	11	24
9	7	20
10+	21	105

analyses. We repeated the calculations for scenarios representing data with a skewed sex distribution, skewed sex and age distribution, and pulsed age distribution. Within each scenario, we looked for effects of no, low, moderate, and high aging and sexing error by adjusting each scenario's data by sexing and aging error and applying the catch-curve and fecundity calculations to the adjusted data (Table 2.2). To calculate the adjusted data, we modified the methods of the *Corrected Harvest Composition* section by post-multiplying the true data matrices by the E_S and E_A matrices.

RESULTS

Sexing Error

We compared the genetic sex and the field sex of 598 UP bears and 650 NLP bears and found 36 and 61 were sexed incorrectly, respectively (Table 2.3). The best fit model to predict sexing error (Model 4) included genetic sex and region as predictor variables and accounted for 55.1% of the AIC weight (Table 2.4). As we anticipated, year did not appear to be an important predictor of sexing error as the fully parameterized model had the lowest AIC weight (Table 2.4). Hunters had higher error in sexing females than males and sexed NLP bears incorrectly more than they did UP bears (Table 2.5). The second ranked model, Model 2, accounted for 31.8% of the AIC weight and included an age effect, so we examined the difference between error rates for Model 4 and the error rates averaged over Models 4 and 2, weighted by AIC weights. The model averaged error rates for each region differed from the Model 4 error rates by <0.01 when averaged over the yearling and adult age classes.

TABLE 2.2. Descriptions of scenarios used in analysis of effects of sexing and aging error on catch-curve and fecundity analysis of age-at-harvest data of black bears in Michigan, USA. Data scenarios represent conditions in the population or harvest that led to different compositions of the harvest from the base scenario. For each data scenario, we applied each of 4 error scenarios, assuming there was either no error (data represented a true, known harvest composition) or adjusting the data to represent the effects of different levels of aging and sexing error.

Scenario	Description
Data Scenarios	
Base	Sex and age-at-harvest frequencies as reported in Table 2.1
Skewed Sex	Male age-at-harvest frequencies same as Base; female age-at-harvest frequencies were Base*0.5
Skewed Sex and Age	Male age-at-harvest frequencies same as Base; total females were Base*0.5, and proportion of females in age classes were distributed as {0.1, 0.09, 0.08, 0.07, 0.065, 0.06, 0.055, 0.05, 0.045, 0.385}
Pulsed Age	Male and female age-at-harvest frequencies in Base multiplied by {1,1,3,1,1,1,1,1,3,1}
Error Scenarios	
No Error	The data used in the analyses were not adjusted for aging and sexing error
Low Error	The data used in the analyses were adjusted as if they had been reported with the aging and sexing error rates reported in this chapter for the UP
Moderate Error	The data used in the analyses were adjusted as if they had been reported with moderate aging and sexing error. To generate moderate sexing error, we multiplied rates as reported in this chapter for the UP by 2.0. To generate moderate aging error, we calculated the error rates as reported in this chapter but with standard deviation of the fitted model forced to 1.5 times that of the best model fit.
High Error	The data used in the analyses were adjusted as if they had been reported with high aging and sexing error. To generate high sexing error, we multiplied rates as reported in this chapter for the UP by 4.0. To generate moderate aging error, we calculated the error rates as reported in this chapter but with standard deviation of the fitted model forced to 2.0 times that of the best model fit.

TABLE 2.3. Number of samples used to estimate the error in hunter-reported sex of harvested bears from the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA. (Number of bears sexed incorrectly in parentheses.)

	Genetic	2002		2006		2009		2010	
Region	Sex	Yearling	Adult	Yearling	Adult	Yearling	Adult	Yearling	Adult
UP	Male					53 (3)	82 (0)	50 (3)	93 (2)
	Female					35 (3)	129 (14)	34 (2)	122 (9)
NLP	Male	23 (1)	40 (0)	62 (4)	143 (8)			22 (2)	41 (0)
	Female	18 (4)	68 (8)	24 (2)	124 (19)			23 (3)	62 (10)

TABLE 2.4. Logistic regression models used to predict the error in hunter-reported sex of black bears harvested in Michigan, USA in 2002, 2006, 2009, and 2010.

Model Number	Variables	AIC	Δ AIC	W_i
4	genetic sex, region	653.8	0	0.551
2	genetic sex, region, age	654.9	1.1	0.318
5	genetic sex	658.0	4.2	0.068
3	genetic sex, age	659.2	5.4	0.037
1	genetic sex, region, age, year	659.9	6.1	0.026

TABLE 2.5. Estimated proportion of black bears harvested in Michigan, USA, from 1990 to 2014 with error in the hunter-reported sex.

Region	Genetic sex	Error (SE)
UP	M	0.028 (0.007)
	F	0.089 (0.015)
NLP	M	0.046 (0.010)
	F	0.143 (0.019)

Aging Error

We identified 78 marked bears that had been marked in the den as cubs or yearlings whose identifying marks matched those reported for harvested bears (Table 2.6). Nine (11.5%) bears were aged incorrectly using cementum annuli techniques. All except one aging error were within 1 year of the true age. The best-fit model to describe the distribution of the estimated age given true age was a gamma distribution with a mean of the true age and standard deviation that was a linear function of true age, which accounted for 55.1% of the AIC weight (Table 2.7). The resulting error matrix showed increasing error as true age increases, but the majority of errors were within 1 year of the true age (Table 2.8). The second ranked model, Model 3, accounted for 37.0% of the AIC weight and included a normal rather than gamma error distribution, so we examined the difference between error rates for Model 8 and the error rates averaged over Models 8 and 3, weighted by AIC weights. The model averaged error rates differed from the Model 8 error rates by <0.01 for all age classes.

Corrected Harvest Composition

Correcting the reported harvest for both sexing and aging errors had little effect on the composition of the harvest (Figure 2.2). The most noticeable differences were when the total magnitude of the harvest was small and the proportion of males was low (Figure 2.2b).

Effects of Aging and Sexing Error

Uncorrected errors in sexing and aging in harvest data had varying effects on analyses (Table 2.9). Most data scenarios showed <10% change in survival estimates between the No

TABLE 2.6. Number of black bears harvested in Michigan, USA, from 1990 to 2014 of known age whose lab ages were later determined independently through cementum annuli aging techniques.

True Age (years)	Lab Age (years)											
	1	2	3	4	5	6	7	8	9	10	11	12
1	28	1										
2	1	22	1									
3		1	9									
4				5	1							
5				1	3							
6						2						
7												
8							1					
9												
10												
11												1
12										1		

TABLE 2.7. Models predicting lab age (determined from cementum annuli aging techniques) from true age of black bears harvested in Michigan, USA, from 1990 to 2014. Models assume the mean of the predicted lab age is equivalent to the true age (there is no bias). Variance forms describe how variance for the normal or gamma distribution changed as a function of true age: linear sigma modeled the standard deviation as a linear function, linear CV modeled the coefficient of variation as a linear function, whereas constant sigma and constant CV assumed the standard deviation or coefficient of variation, respectively, did not change with age.

Model Number	Error Distribution	Variance Form	AIC	ΔAIC	W_i
7	gamma	linear sigma	64.6	0	0.552
3	normal	linear sigma	65.4	0.8	0.370
6	gamma	constant CV	70.2	5.6	0.034
5	gamma	linear CV	70.6	6.0	0.028
1	normal	linear CV	72.9	8.3	0.009
2	normal	constant CV	73.2	8.6	0.007
4	normal	constant sigma	88.8	24.2	<0.001
8	gamma	constant sigma	88.8	24.2	<0.01

TABLE 2.8. Estimated probability that a black bear of true age was assigned to lab age based on cementum annuli aging techniques in Michigan, USA, from 1990 to 2014. Values recorded as 0.00 are estimated as <0.005.

True age	Lab age (years)									
(years)	1	2	3	4	5	6	7	8	9	10+
1	0.98	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.03	0.92	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.08	0.83	0.09	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.12	0.75	0.13	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.16	0.68	0.16	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.19	0.62	0.18	0.01	0.00	0.00
7	0.00	0.00	0.00	0.00	0.01	0.22	0.56	0.20	0.01	0.00
8	0.00	0.00	0.00	0.00	0.00	0.01	0.24	0.51	0.22	0.02
9	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.25	0.48	0.25
10+	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.10	0.89

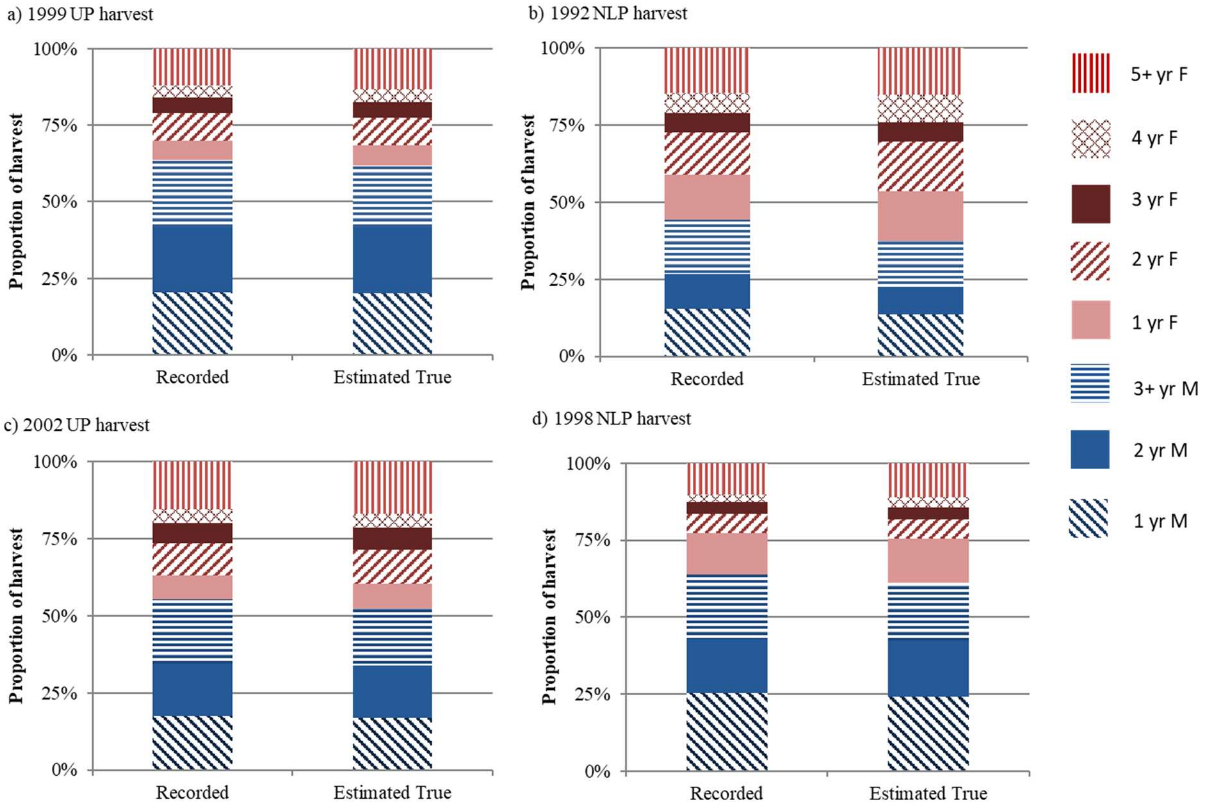

FIGURE 2.2. Composition of black bear harvest in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA as originally recorded and estimated as true when adjusted for aging and sexing errors under a variety of scenarios: a) large harvest, high proportion recorded male, b) small harvest, low proportion recorded male, c) large harvest, low proportion recorded male, d) small harvest, high proportion recorded male.

TABLE 2.9. Estimates ($\hat{S}$) and associated standard error (SE) of survival for male (m) and female (f) black bears from a catch-curve analysis and estimates of fecundity (F) calculated from age-at-harvest data presented in Table 2.1 and adjusted as described for each scenario in Table 2.2.

Data Scenario	Error Scenario			
	No error	Low error	Moderate error	High error
Base	$\hat{S}_m = 0.625$ (SE = 0.0095) $\hat{S}_f = 0.785$ (SE = 0.0071) F = 0.689	$\hat{S}_m = 0.643$ (SE = 0.0090) $\hat{S}_f = 0.780$ (SE = 0.0075) F = 0.712	$\hat{S}_m = 0.657$ (SE = 0.0086) $\hat{S}_f = 0.774$ (SE = 0.0078) F = 0.725	$\hat{S}_m = 0.679$ (SE = 0.0079) $\hat{S}_f = 0.762$ (SE = 0.0087) F = 0.797
Skewed Sex	$\hat{S}_m = 0.625$ (SE = 0.0095) $\hat{S}_f = 0.785$ (SE = 0.0101) F = 0.689	$\hat{S}_m = 0.635$ (SE = 0.0093) $\hat{S}_f = 0.776$ (SE = 0.0105) F = 0.733	$\hat{S}_m = 0.644$ (SE = 0.0091) $\hat{S}_f = 0.766$ (SE = 0.0109) F = 0.767	$\hat{S}_m = 0.659$ (SE = 0.0088) $\hat{S}_f = 0.747$ (SE = 0.0118) F = 0.884
Skewed Sex and Age	$\hat{S}_m = 0.625$ (SE = 0.0095) $\hat{S}_f = 0.900$ (SE = 0.0061) F = 0.235	$\hat{S}_m = 0.648$ (SE = 0.0091) $\hat{S}_f = 0.886$ (SE = 0.0066) F = 0.285	$\hat{S}_m = 0.668$ (SE = 0.0087) $\hat{S}_f = 0.873$ (SE = 0.0072) F = 0.339	$\hat{S}_m = 0.699$ (SE = 0.0081) $\hat{S}_f = 0.847$ (SE = 0.0083) F = 0.474
Pulsed Age	$\hat{S}_m = 0.646$ (SE = 0.0079) $\hat{S}_f = 0.775$ (SE = 0.0064) F = 0.436	$\hat{S}_m = 0.660$ (SE = 0.0075) $\hat{S}_f = 0.772$ (SE = 0.0066) F = 0.485	$\hat{S}_m = 0.671$ (SE = 0.0072) $\hat{S}_f = 0.767$ (SE = 0.0069) F = 0.544	$\hat{S}_m = 0.687$ (SE = 0.0067) $\hat{S}_f = 0.756$ (SE = 0.0076) F = 0.634

Error scenario and the High Error scenario except for males in the Skewed Sex and Age scenario (Table 2.9). Most fecundity estimates, however, changed >10% between the No Error scenario and all scenarios that incorporated aging and sexing error (Table 2.9). Standard error (SE) on the female survival estimates tended to increase with increasing error while SE on the male survival estimated tended to decrease with increasing error (Table 2.9).

DISCUSSION

Error in hunter reported sex of harvested bears in Michigan was comparable to that reported for Minnesota (Fieberg et al. 2010), but lower than error in reported field sex for bobcats (*Lynx rufus*; Williams et al. 2011) and American marten (*Martes americana*; Belant et al. 2011b) in Michigan. Although in most cases the true sex of a bear should have been obvious from observation of the external genitalia, there were at least 3 potential reasons why a hunter may have reported the wrong sex: 1) the hunters did not know the sex of their bears (either because they did not recognize the genitalia or because a guide or other companion field-dressed the bear) and guessed the sex rather than admit to not knowing the sex; 2) the hunters concluded the sex based on physical characteristics other than the genitalia; or 3) the hunters were unwilling to report the true sex. Some cases of sexing error may also have been due to recording error.

As in Minnesota (Fieberg et al. 2010), reported field sex of male bears in Michigan tended to be more accurate than field sex for females. Hunters may have drawn conclusions regarding the sex of the animal based on the size of the animal rather than the genitalia. Black bears exhibit sexual dimorphism in both length and mass, but the sexes overlap in size, especially in the younger age classes (McRoberts et al. 1998; Bartareau et al. 2012). Hunters that harvested what they perceived to be a large bear could have concluded from the body size the bear was a male. Hunters may also have tried to conceal the harvest of female bears. In Michigan, females with cubs were protected from harvest, although protection by law did not necessarily equate to protection in practice (Belant et al. 2011a). If a hunter harvested a female with cubs, the hunter may have been unwilling to report the true sex of the animal to avoid the perceived risk of legal investigation, however unlikely actual investigation would have been.

Errors in lab age of black bears in Michigan was slightly higher than that reported from Pennsylvania (Harshyne et al. 1998) and lower than that reported from New Mexico (Costello et al. 2004), both of which compared known ages to cementum annuli ages. As in both of those states, error increased with age (Harshyne et al. 1998, Costello et al. 2004), but most errors we observed were within 1 year of the true age. The patterns in the raw data are reflected in the estimated aging error matrix where accuracy decreases with increasing age, but still the majority of errors were within 1 year of the true value (Table 2.8).

Reported age and sex data from harvested animals have potential application to address a variety of management questions, but failure to account for aging and sexing errors could bias conclusions (Conn and Diefenbach 2007, Hiller et al. 2014). Michigan's reported harvest composition, however, is only slightly different from the estimated true harvest in both age and sex composition (Figure 2.2). Aging differs little because the majority of the reported ages are bears ≤3 years old (Appendix 2A) for which aging error rates are low (Table 2.8). The harvest also shows little evidence of large fluctuations in recruitment (Appendix 2A) which would bias reported harvest age composition in age classes with high error. Although the sexing error for female bears harvested in Michigan was higher than for males, the harvest was almost always >50% males (Figure 2.1), which led to a similar breakdown of males and females in the reported harvest as in the estimated true harvest (Figure 2.2).

Aging and sexing errors like those of Michigan black bears are unlikely to have major effects on analyses based on sex and age data unless those data are heavily skewed toward one sex and the sexes exhibit large differences in age distribution (Low Error scenarios in Table 2.9). The limited effect of the errors is likely due to the assumption that aging errors are unbiased, thus simultaneously moving bears into older and younger age classes. Biased aging errors would tend to raise or lower the apparent median age, which may have a greater effect on age-based assessments than we found. Harshyne et al. (1998) did not find any bias in aging error of black bears using cementum annuli techniques, supporting our assumption. Our results suggest that correcting for aging and sexing errors may not be necessary to draw reasonable conclusions from age-at-harvest data. The magnitude of the effect of aging and sexing error varied with analysis, though. Calculations of fecundity with data that was subject to errors were affected more than calculations of survival (Table 2.9).

When estimates of sexing and aging error rates are available, we recommend that managers adjust their data for aging and sexing errors to avoid the potential for such errors to bias their analyses. When aging and sexing error rates are not available, however, a sensitivity analysis using realistic estimates of the error rates may help identify the potential value of investing in their estimation.

APPENDIX

APPENDIX 2A. Reported age and sex data matrices

TABLE A2.1. Lab age based on cementum annuli aging techniques of reported male black bears harvested in the Upper Peninsula of Michigan, USA, 1990-2014.

	Lab age (years)										
Year	1	2	3	4	5	6	7	8	9	10	Unknown
1990	82	108	45	29	10	13	10	4	4	8	35
1991	135	155	127	39	21	18	13	12	5	17	46
1992	99	162	86	66	34	21	13	11	9	16	44
1993	205	131	106	44	43	20	15	8	5	22	38
1994	129	213	64	73	32	19	17	12	6	9	76
1995	218	146	152	43	43	21	14	13	9	15	39
1996	150	242	86	78	27	29	13	10	5	15	65
1997	193	153	149	33	30	10	15	6	10	15	32
1998	204	221	113	90	28	30	10	17	7	17	49
1999	286	300	142	69	42	9	21	5	4	18	53
2000	321	256	122	62	56	19	11	10	5	17	45
2001	350	305	147	77	42	29	17	12	8	11	53
2002	308	305	168	73	42	20	25	11	7	21	36
2003	344	388	152	91	45	29	10	12	12	22	42
2004	325	309	172	54	37	26	18	17	9	29	51
2005	321	285	157	80	27	22	14	9	5	26	42
2006	407	371	156	73	65	24	16	14	12	26	50
2007	354	263	138	53	33	14	12	6	5	22	118
2008	329	362	136	74	45	22	11	6	9	20	78
2009	329	261	165	54	35	22	11	14	5	21	43
2010	339	315	165	72	35	24	18	19	6	8	43
2011	313	283	161	63	61	28	18	11	9	17	52
2012	232	236	115	44	30	25	18	10	4	11	23
2013	244	242	145	50	32	19	15	13	4	24	17
2014	207	279	149	64	31	17	10	7	5	10	20

TABLE A2.2. Lab age based on cementum annuli aging techniques of reported female black bears harvested in the Upper Peninsula of Michigan, USA, 1990-2014.

	Lab age (years)										
Year	1	2	3	4	5	6	7	8	9	10	Unknown
1990	28	26	23	24	13	14	3	9	6	21	17
1991	40	63	64	38	19	15	9	10	2	28	25
1992	34	80	56	68	42	17	12	18	10	45	31
1993	65	54	79	39	50	17	17	9	18	37	34
1994	40	110	52	48	26	34	21	15	6	45	52
1995	95	78	96	36	38	39	38	25	25	65	44
1996	65	99	33	60	35	19	22	18	5	42	29
1997	73	78	69	43	28	16	18	8	18	47	26
1998	88	111	52	71	33	26	25	16	15	45	39
1999	90	122	69	57	49	24	20	15	6	51	41
2000	130	146	114	75	56	44	18	13	18	61	51
2001	149	185	108	59	49	43	35	24	9	65	38
2002	140	188	118	78	60	39	32	24	20	105	22
2003	154	181	98	60	60	42	31	18	20	59	31
2004	144	149	109	65	55	33	25	17	21	65	35
2005	155	157	86	68	30	38	27	19	10	65	36
2006	163	176	98	74	53	38	33	21	25	75	36
2007	149	131	94	43	47	35	24	19	17	74	86
2008	136	178	95	58	41	30	24	20	10	65	60
2009	127	151	95	60	47	24	28	14	13	72	36
2010	151	154	114	60	41	32	27	16	15	56	17
2011	144	137	100	49	54	17	24	27	24	47	40
2012	120	114	80	52	35	36	18	24	12	62	21
2013	75	119	89	51	24	32	25	15	11	48	14
2014	88	116	76	31	29	14	18	14	11	41	13

TABLE A2.3**.** Lab age based on cementum annuli aging techniques of unknown sex black bears harvested in the Upper Peninsula of Michigan, USA, 1990-2014.

	Lab age (years)										
Year	1	2	3	4	5	6	7	8	9	10	Unknown
1990	0	0	0	0	0	0	0	0	0	0	1
1991	1	0	0	0	0	0	0	0	0	0	0
1992	0	3	0	0	0	0	0	0	0	0	0
1993	0	0	0	0	1	0	0	0	0	0	0
1994	0	0	0	1	0	0	0	0	0	0	1
1995	2	2	1	1	0	0	0	0	1	0	0
1996	0	1	0	0	0	0	0	0	0	0	0
1997	2	2	0	3	1	1	0	0	0	1	1
1998	2	3	2	1	0	0	0	0	0	0	0
1999	3	4	0	0	1	0	1	1	0	0	0
2000	2	8	3	1	2	2	0	0	0	2	0
2001	5	5	1	1	1	0	1	0	0	0	1
2002	4	5	1	1	0	0	0	0	0	1	1
2003	8	4	2	0	0	0	1	1	0	0	0
2004	8	7	5	2	2	2	1	1	1	0	1
2005	7	6	4	3	0	1	1	0	0	0	0
2006	8	16	6	2	2	1	0	2	0	0	1
2007	4	8	0	2	0	0	0	1	0	0	4
2008	9	5	6	3	2	0	1	0	0	1	0
2009	7	4	5	1	0	0	0	2	0	1	6
2010	16	14	10	4	1	1	2	0	0	0	4
2011	11	6	2	3	2	1	2	1	1	4	6
2012	11	16	9	5	1	0	2	0	0	2	1
2013	5	5	3	0	0	0	1	1	0	2	0
2014	0	3	2	0	2	1	0	0	2	0	1

TABLE A2.4. Lab age based on cementum annuli aging techniques of male black bears harvested in the northern Lower Peninsula of Michigan, USA, 1990-2014.

	Lab age (years)										
Year	1	2	3	4	5	6	7	8	9	10	Unknown
1990	29	19	9	3	1	0	0	0	2	1	1
1991	23	26	11	5	6	2	2	1	1	3	1
1992	19	14	13	2	3	2	0	0	0	2	3
1993	40	20	14	5	3	3	2	3	1	4	3
1994	16	15	14	7	3	1	4	3	0	1	2
1995	32	20	14	4	2	1	1	0	2	2	1
1996	18	19	7	9	4	2	6	2	1	5	6
1997	27	26	24	2	6	2	2	1	3	7	9
1998	47	33	15	11	1	5	1	1	1	4	3
1999	48	24	17	10	4	0	2	3	0	3	15
2000	53	30	14	9	3	1	1	0	1	1	7
2001	58	37	13	11	4	4	2	1	1	2	4
2002	64	46	23	19	13	8	4	2	1	3	1
2003	95	53	30	14	8	4	3	5	1	5	1
2004	78	65	26	14	8	5	2	4	2	4	4
2005	45	34	15	16	7	4	5	2	3	3	2
2006	62	84	33	20	12	7	5	0	5	6	0
2007	77	46	30	15	3	2	1	2	2	3	3
2008	100	91	46	19	9	10	4	0	3	4	3
2009	96	44	33	21	12	5	6	4	1	11	2
2010	62	63	31	18	8	3	4	4	2	2	1
2011	55	65	27	12	10	5	5	3	0	3	0
2012	67	43	14	4	7	4	2	0	2	1	5
2013	39	42	28	13	7	8	2	3	1	4	5
2014	43	39	19	18	8	5	1	1	0	3	4

TABLE A2.5. Lab age based on cementum annuli aging techniques of female black bears harvested in the northern Lower Peninsula of Michigan, USA, 1990-2014.

	Lab age (years)										
Year	1	2	3	4	5	6	7	8	9	10	Unknown
1990	14	12	5	5	3	2	1	3	0	3	3
1991	10	7	9	5	0	1	0	1	2	5	4
1992	18	17	8	8	4	5	0	3	1	5	4
1993	20	19	9	5	8	2	4	1	3	5	2
1994	18	17	6	6	2	2	3	1	1	7	3
1995	14	11	11	8	2	5	1	1	0	4	5
1996	13	12	3	6	1	0	3	1	0	4	8
1997	23	23	11	5	2	4	0	2	1	6	9
1998	25	12	7	5	3	5	3	3	1	4	1
1999	16	25	16	4	3	5	1	1	1	6	7
2000	26	22	10	8	3	4	2	2	2	6	8
2001	26	44	10	8	4	4	5	1	0	10	6
2002	33	43	19	20	12	7	7	8	4	3	2
2003	44	60	24	15	18	3	6	3	7	16	3
2004	33	51	20	19	7	5	5	1	2	14	1
2005	25	37	14	8	2	3	7	3	4	10	0
2006	27	52	27	14	14	3	4	3	3	6	1
2007	51	42	22	11	9	7	6	1	0	9	1
2008	44	64	19	17	12	19	2	8	6	20	3
2009	50	52	26	20	16	16	10	7	2	14	1
2010	41	42	14	11	8	8	5	2	4	12	1
2011	24	33	18	7	7	7	7	2	2	14	1
2012	36	46	15	21	10	5	5	5	4	14	1
2013	23	36	16	12	5	7	7	6	5	10	3
2014	21	44	22	10	5	8	4	5	5	8	0

TABLE A2.6. Lab age based on cementum annuli aging techniques of unknown sex black bears harvested in the northern Lower Peninsula of Michigan, USA, 1990-2014.

	Lab age (years)										
Year	1	2	3	4	5	6	7	8	9	10	Unknown
1990	0	0	0	0	0	0	0	0	0	0	0
1991	0	0	0	0	0	0	0	0	0	0	0
1992	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0	0	0	0	0	0	0	0	0
1994	0	3	0	0	0	0	0	0	0	0	0
1995	0	0	0	0	0	0	0	0	0	0	0
1996	1	0	0	0	0	0	0	0	0	0	0
1997	0	0	0	0	0	0	0	0	0	0	0
1998	0	0	0	0	0	0	0	0	0	0	0
1999	0	2	0	0	0	0	0	1	0	0	0
2000	1	2	0	0	0	0	0	0	0	0	0
2001	2	3	0	0	0	0	0	0	0	0	0
2002	2	3	0	0	0	0	0	0	0	0	0
2003	1	0	1	0	0	0	0	0	0	0	0
2004	3	4	1	2	0	0	0	0	0	0	0
2005	0	1	2	1	0	1	0	0	0	0	0
2006	2	4	2	0	0	0	0	0	0	0	0
2007	2	0	1	0	1	0	0	1	0	0	0
2008	1	0	1	1	0	0	1	0	0	0	0
2009	0	1	1	1	0	0	0	0	0	1	0
2010	0	0	1	0	0	0	0	0	0	0	0
2011	1	0	0	1	1	0	0	0	0	0	0
2012	2	1	0	0	0	1	0	0	0	1	0
2013	0	4	1	1	2	0	0	0	0	1	1
2014	1	0	0	0	0	0	0	0	0	0	0

CHAPTER 3: TRENDS IN MICHIGAN BLACK BEAR REPRODUCTION

INTRODUCTION

Reproductive characteristics of many wildlife populations are difficult to study over broad scales because such research usually involves expensive field work and visual observations that can only be accomplished for a small number of individuals. Female black bears (*Ursus americanus*), however, show signs of their reproductive past in their teeth (Coy and Garshelis 1992) and reproductive tracts (Erickson et al. 1964), which are easily collected from harvested bears. Reproductive rates are a critical driver of population growth among black bears (Beston 2011), so the extraction of reproduction characteristics from black bear teeth and reproductive tracts can be useful for assessing the status of a population.

Teeth and reproductive tracts provide insight into different aspects of black bear reproduction. The spacing of the cementum annuli (growth rings) in the teeth of female black bears indicates the years in which her body was stressed by raising cubs through a pattern of thinner (years of stress) and wider rings (Coy and Garshelis 1992). The patterns in the cementum annuli are permanent, so a tooth from a harvested bear can indicate all the years in which she produced cubs throughout her life. Although useful, the annuli patterns cannot indicate how many cubs a bear produced. Cub production may vary due to age (Bridges et al. 2011) and nutrition (Noyce and Garshelis 1994), so additional resources are necessary to understand the complete reproductive potential of a black bear population. Reproductive tracts of female bears carry the scars of 2 years of implanted embryos (Erickson et al. 1964), an indication of potential litter size. The reproductive tract of a harvested female can therefore provide information on her most recent litter. True litter size and cub sex ratios, however, can only be evaluated by direct observation.

Beginning in 1994, the Michigan Department of Natural Resources (DNR) amassed a large dataset on the reproductive histories of thousands of black bears throughout the state by collecting teeth, through 2015, and reproductive tracts, through 2011. Our objective was to combine information from the teeth and reproductive tracts with information from field studies conducted over the same time period to describe the reproductive patterns of Michigan black bears including age of primiparity, litter size, litter sex ratios, and the proportion of adult females breeding in the population. We examined the data separately from the Upper Peninsula (UP) and northern Lower Peninsula (NLP) and looked for trends over age, time, and geographic region. While other sources report results from cementum annuli patterns (Allen et al. 2017), reproductive tracts (e.g., Wooding and Bukata 1996), and direct observation (e.g., Eiler 1989, McDonald and Fuller 2001), we were unable to find any source that had similar insight into a black bear population using all 3 methods simultaneously.

METHODS

From 1994-2015 the DNR required successful Michigan black bear hunters to register their bears within 72 hours of harvest. During registration, the hunter reported the sex of the bear and the date and location of harvest and submitted a premolar from the bear. From 1994-2011 the DNR also asked hunters to submit the reproductive tract of females, although effort to collect the tracts decreased over time.

Reproductive Tracts

Laboratory staff examined the reproductive tracts of 1,006 bears harvested from 1994 through 2011 using the methods of Erickson et al. (1964) to count placental scars (indicating implantation of embryo in year of harvest and year preceding harvest). Bears may spontaneously abort fetuses prior to birth, which could lead to positive bias in the use of placental scars to estimate litter size (Erickson et al. 1964). Several studies, however, have found that litter size is insensitive to maternal nutrition (McDonald and Fuller 2001, Costello et al. 2003, and Bridges et al. 2011) and that poor maternal nutrition leads to reproductive intervals longer than the expected 2 years (Eiler et al 1989, Rogers 1976) suggesting that stress is more likely to lead to complete failure of reproduction than reduction in litter size (Costello et al. 2003). We therefore assumed we could use the counts of placental scars as an estimate of litter size of the bear in the 2 breeding seasons that preceded harvest.

We used Poisson regression to examine the effect of a categorical maternal age class (3 years old, 4 years old, 5 years old, and 6+ years old) variable, continuous year variable (year of birth 1993-2011), and a categorical region variable (UP, NLP) on the count of placental scars per bear. We excluded all 0 counts so we could use the counts as an estimate of litter size of reproducing females. To align the data with the Poisson distribution, we adjusted the scar counts by subtracting 1 to allow for a minimum count of 0. We used Akaike's information criterion (AIC) model selection (Burnham and Anderson 2002) to select among all additive combinations of age, region, and year. We then used the selected model to calculate the mean adjusted scars per adult female and added 1 to transform the result back to the scale of the true counts.

Cementum Annuli Patterns on Premolar Teeth

Laboratory staff examined the cementum annuli spacing on premolar teeth of 8,048 bears harvested from 1994 through 2015 using the methods of Coy and Garshelis (1992) to determine years in which bears showed evidence of reproduction. We excluded from analysis any data from the year of harvest because the pattern may have been obscured due to incomplete annuli. Opportunistic field observations and annuli patterns from the >8,000 teeth examined show evidence for <10 females producing cubs before they were 3 years old, so we focused our analysis on females that were at least 3 years old. Females that were >3 years old at the time of harvest had data from at least one breeding year pre-harvest.

We determined the age and breeding status of each female within each breeding year to determine the number of females breeding (narrow annuli) and not breeding (wide annuli) within each age, region, and year class. (Due to low aging error reported in Chapter 2, we assumed the age reported by lab staff based on cementum annuli aging techniques was accurate.) We calculated the proportion of adult females breeding within each class by dividing the number of females with a narrow band by the total number of females in the class with valid pattern data.

To determine whether we could pool data over region and age class, we used fixed effects logistic regression to model the proportion breeding and used AIC to compare models. To account for overdispersion in the data, we calculated $\hat{c}$ and compared models using QAIC following the recommendations of Burnham and Anderson (2002) and using the dfun function in R (R Core Team 2015) as described by Bolker (2016). The most parameterized model predicted the proportion breeding from year, region (UP or NLP), and age (3 years old, 4+ years old), and a region*age interaction, treating all variables as categorical. We fit reduced models including year alone, region+year, age+year, and age+region+year effects. We were interested in examining the temporal pattern in breeding rates and so included year in all models. Due to small sample sizes, especially in the NLP (<10 female bears in most age classes in most years), we excluded data from breeding years earlier than 1990.

To calculate the mean age of primiparity, we first investigated whether there was any relationship between the age at harvest and the age of first reproduction that could introduce bias into our analyses. We defined the age of primiparity as the age at which a female first displayed a narrow cementum annulus. Since we did not include the annulus from the year of harvest in the analysis, a female bear had to be harvested at ≥4 years old to be included. Through visual inspection, we compared the distribution of the age of primiparity within each age class of harvested females. Using R (R Core Team 2015), we calculated the mean age of primiparity by sampling *n* bears from females within each age-at-harvest class from 4 years old through 11 years old so that each age-at-harvest class was represented equally. We then calculated the median age of primiparity using the methods of Sokal and Rohlf (1969) as described in Garshelis et al. (1998).

Marked Bears

Field staff visited bear dens throughout Michigan from 1986 to 2016 for a variety of research and management purposes. Den sites were identified by locating collared bears during the denning period or by direct observations reported by members of the public. When staff encountered a female with cubs or yearlings in the den, they recorded the number, sex, and age of the offspring. We used the data from bear encounters to calculate the number of cubs and yearlings per adult female and the sex ratio of cubs and yearlings in the den. The DNR often tracked the same collared bears for several years, so den check data were biased toward older females. Given that the den checks were not conducted for the purposes of collecting reproductive data, we combined all available records over all available years within each region to provide a second broad picture of reproductive output to compare with results based on the data from reproductive tracts and premolar teeth.

RESULTS

Hunters harvested 16,787 female bears in Michigan from 1994 through 2015, and we examined the cementum annuli patterns of approximately one-third of those bears (Figure 3.1). The remainder of the harvest that we did not examine were those with no or insufficient tooth sample submitted and those that were <4 years old at the time of harvest. Collection of reproduction tracts peaked during the first year of collection and quickly declined after that (Figure 3.1). By 2011, tracts were submitted on <2% of the harvested females.

Litter Size

We estimated litter size using the number of placental scars per reproductive female. Litter size varied by age, region, and year in the top selected model with an AIC weight of 0.514 (Table 3.1). The second ranked model had more than one-third of the AIC weight, however, and excluded year. Further examination of the data showed that the proportion of 6+-year-old females in the dataset declined as year increased, so year and age were not independent. In

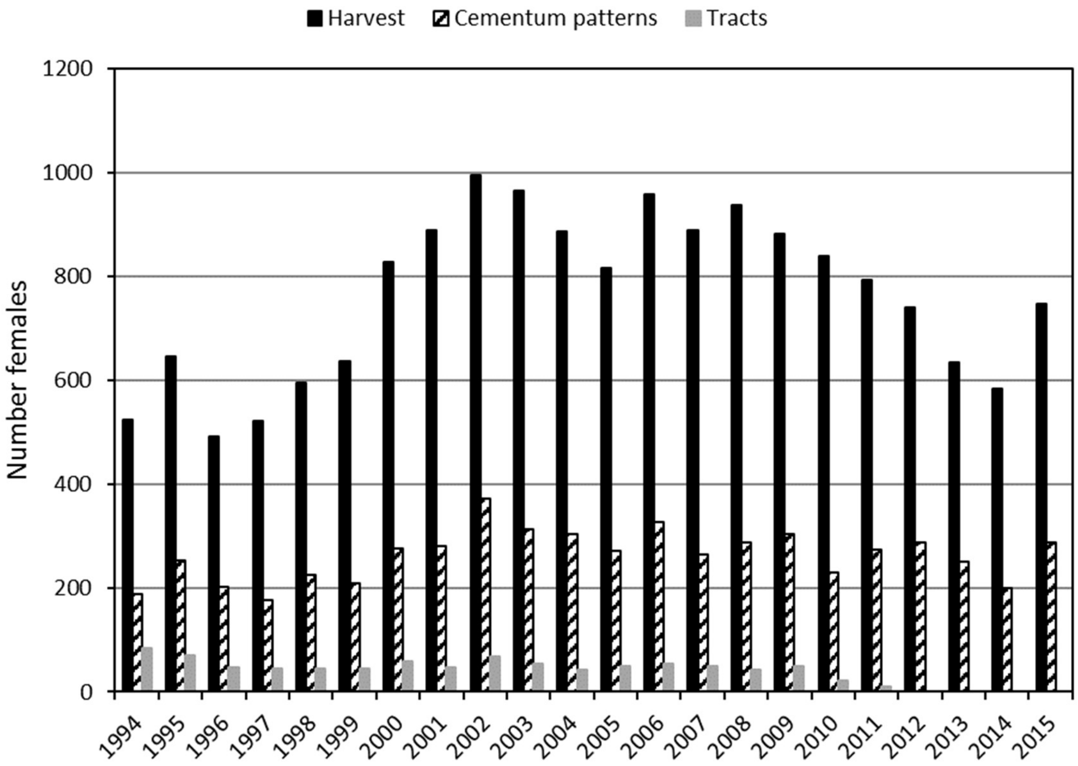

FIGURE 3.1. Number of female black bears harvested and number of cementum patterns and female reproductive tracts examined from bears >3 years old (cementum patterns) >2 years old (tracts) at time of harvest from Michigan, USA, 1994-2015.

TABLE 3.1. Poisson regression models used to predict the number of placental scars per harvested female that had scars from breeding years 1993-2011 in Michigan, USA.

Model	AIC	Δ AIC	W_i
age+region+year	1361.1	0.0	0.514
age+region	1361.8	0.7	0.362
age	1365.1	4.0	0.070
age+year	1365.6	4.5	0.054
region+year	1386.1	25.0	<0.001
year	1386.5	25.4	<0.001
region	1388.2	27.1	<0.001

response, we focused on differences among ages and regions rather than over years based on model age+region. The mean litter size, as measured by placental scars, varied between 2 and 3 cubs per litter (Table 3.2). Litter size increased as maternal age increased within both the UP and NLP, and there were larger litters in the NLP than the UP according to placental scars (Table 3.2).

Data from den visits showed a similar number of cubs per adult female between the UP and NLP, but the values were higher than those calculated from the placental scars due to the age bias of collared bears (Table 3.2). The number of yearlings per adult females was lower than the number of cubs per adult female and declined more in the NLP than the UP (Table 3.2).

Proportion Adult Females Breeding

Model selection results did not support pooling data over regions or age classes to calculate the proportion of females breeding within a year or the dropping of the interaction term from the model (Table 3.3). The proportion of 3-year-old females in the UP producing cubs each year was consistently lower than for all other adult females, around 0.1, while the proportion of older females producing cubs in the UP fluctuated around 0.5 (Figure 3.2). The NLP females showed more variability than did the UP females, and the difference between 3-year-old and older females was less for the NLP than for the UP (Figure 3.2).

Cub and Yearling Sex Ratios

The sex ratio of cubs and yearlings in the den showed a consistent bias toward males. In

TABLE 3.2. Mean litter size of black bears in Michigan, USA, as measured by the number of placental scars from reproductive tracts of hunter harvested female black bears, 1993-2011, and den checks, 1988-2016.

		Placental Scars			Den Checks, Cubs			Den Checks, Yearlings		
Region	Age (years)	N	Mean	SE	N	Mean	SE	N	Mean	SE
UP	3+				98	2.78	0.08	64	2.52	0.11
	3	52	1.92	0.11						
	4	68	2.19	0.12						
	5	61	2.35	0.13						
	6+	236	2.66	0.08						
NLP	3+				101	2.72	0.08	44	2.36	0.13
	3	34	2.13	0.13						
	4	15	2.47	0.18						
	5	16	2.67	0.20						
	6+	38	3.05	0.18						

Table 3.3. Logistic regression models used to predict the proportion of adult female black bears that produced cubs within breeding years 1990-2014 in Michigan, USA ($\hat{c}$=1.62).

Model	QAICc	Δ QAICc	W_i
age+region+year+(age*region)	460.21	0.00	1.000
age+region+year	634.06	173.85	<0.001
age+year	672.42	212.21	<0.001
region+year	1906.32	1446.10	<0.001
year	1939.02	1478.81	<0.001

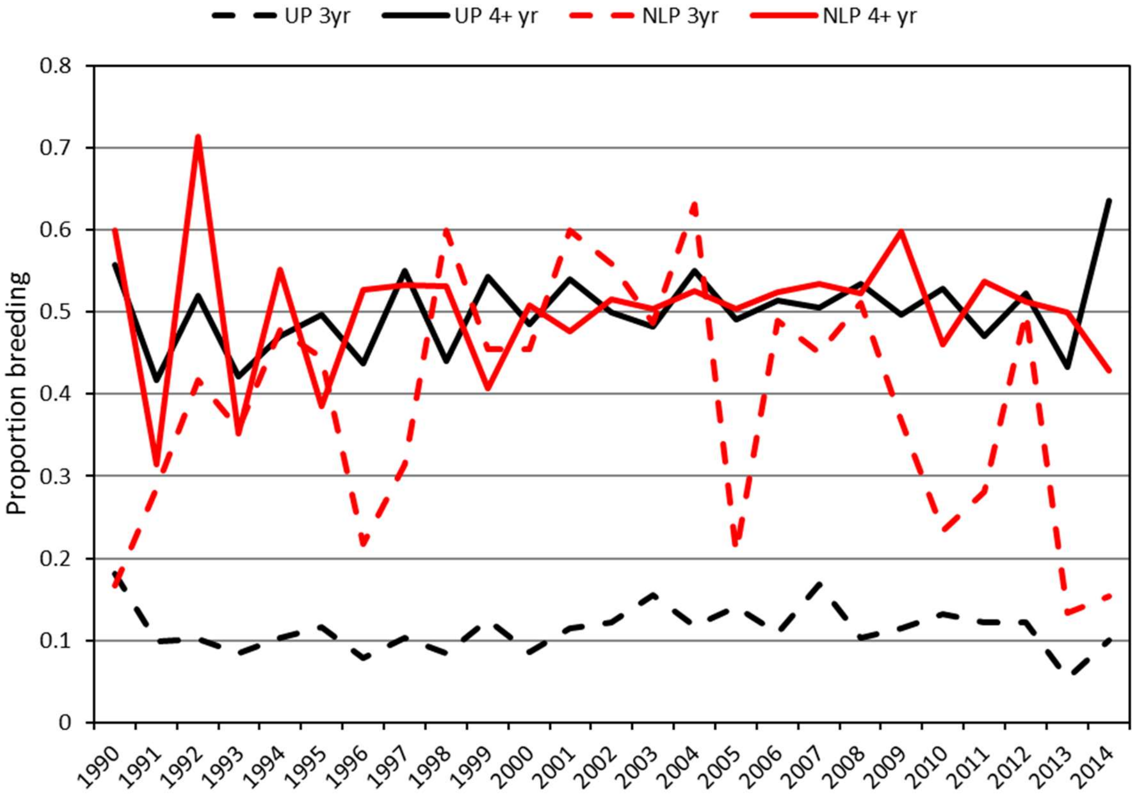

FIGURE 3.2. Proportion of females breeding in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, based on cementum annuli spacing from a premolar tooth of bears harvested from 1994-2015.

the UP, the proportion of cubs in the den that were male declined from 0.59 to 0.54 by the time the cubs were yearlings. In the NLP, the proportion of cubs in the den that were male was 0.54, lower than in the UP, but increased to 0.56 for yearlings.

Age of Primiparity

The majority of females reproduced for the first time at 4 years old or 5 years old in the UP and 3 years old or 4 years old in the NLP (Figure 3.3), which was reflected in both the mean and median age of first reproduction (Table 3.4). All bears had reproduced by 7 years old in the NLP and 9 years old in the UP. There was no consistent pattern in age of primiparity related to age at harvest (Figure 3.3). Bears harvested at an even age were more likely to have first reproduced at an odd age and vice versa (Figure 3.3).

DISCUSSION

The multiple datasets that we examined suggest that Michigan's black bear population was productive, with females breeding young and producing an average of >2 cubs per litter with some variability between regions and among maternal age class. Michigan black bear litter size was comparable to or higher than the mean litter size of states throughout eastern North America. Of the studies summarized in Bridges et al. (2011), only Pennsylvania reported a higher mean litter size. Bears in the NLP also started reproducing at a younger age than did those in most other regions of eastern North America, while primiparity of bears in the UP fell at about the midpoint of the range of ages (summarized in Bridges et al. 2011).

Garshelis et al. (1998) suggest that some field studies may report age of primiparity

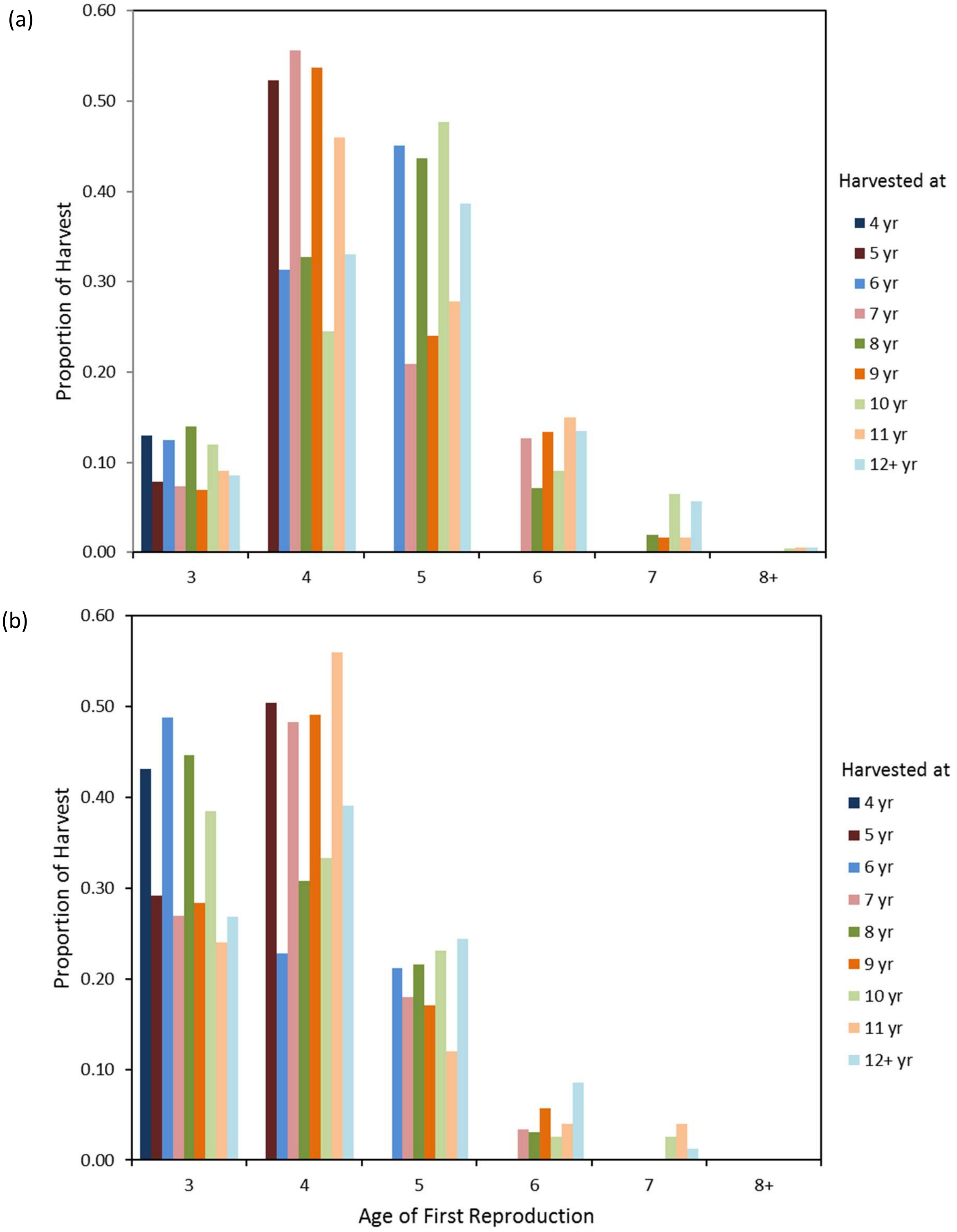

FIGURE 3.3. Distribution of the age at which harvested black bear females first reproduced in the Upper Peninsula (a) and northern Lower Peninsula (b) of Michigan, USA, results pooled from bears harvested 1994-2015.

TABLE 3.4. Mean and median age of first reproduction of black bears in Michigan, USA, calculated from cementum annuli spacing from premolar teeth of bears harvested 1994-2015.

Region	n	Mean	SE	Median
UP	800	4.19	0.032	4.31
NLP	200	3.80	0.062	3.82

biased low if no corrections are made for the loss of older bears that have not yet had the opportunity to breed. Our objective, however, was to describe the actual demographic statistics of the Michigan black bear populations, not the potential. We therefore felt it appropriate to calculate the age of primiparity from the harvested bears without considering the age at which bears could have bred had they not been harvested. There was no support that doing so biased our results because there was no pattern in the age of primiparity over the age at harvest (Figure 3.3). Because younger age classes made up a larger proportion of the harvest and because bears were protected from harvest when they were accompanied by cubs, we could have biased our calculation of the mean age of primiparity toward the status of 3-year-old bears (Figure 3.2). To remove that potential bias, we randomly selected an equal number of bears from each age-at-harvest class.

Allen et al. (2017) identified potential but unknown biases in the calculation of reproductive statistics from cementum annuli spacing depending on the treatment of annuli of indeterminate width. We excluded all indeterminate annuli (including year of harvest). Doing so could have introduced a negative bias (we could have removed more records of reproductive years than we did records of non-reproductive years). It is possible that the true proportion of bears breeding in any single year was higher than we estimated and the age of primiparity lower than we estimated. Since the annual estimated proportion of 4+-year-old females breeding fluctuated around 0.5, however (Figure 3.2), it is unlikely that any bias is substantial. Once a black bear female has started reproducing, she usually reproduces every other year, so we would expect the proportion of females breeding within the older age classes of a population to not greatly exceed 0.5 in any single year.

The consistent, steady proportion of adult females breeding over time (Figure 3.2) suggests that the massive mast failures that would be necessary to produce reproductive synchrony (Bridges et al. 2011) were either rare or bears were able to find sufficient sources of non-natural food (such as agricultural crops and bait) to supplement their diet (McDonald and Fuller 2001). We could interpret the synchronous dips and peaks in breeding in 4+-year-old females in both the UP and the NLP from 1990-1994, however, as evidence of a statewide mast failure. A mast failure in 1988 could have led to high cub mortality in 1989, leading more females than usual to give birth to cubs in 1990. The variability in the breeding of 3-year-old females in the NLP may be evidence of younger animals delaying initial reproduction in response to food abundance (Rogers 1976, McDonald and Fuller 2001) or may be due to small sample size (N=6 to 53).

Although the den check data may not be representative of the larger population, they do provide some interesting observations about cub production and survival. The den check data show some evidence of cub mortality, as the mean number of yearlings in the den was lower than the mean number of cubs, but the apparent cub survival appears higher than for other North American populations (Beston 2011). The den check data also indicated a cub and yearling sex ratio slightly leaning toward males. If such a difference were true of the larger population, Elowe and Dodge (1989) and Samson and Huot (1995) both suggest it could have been due to maternal body condition, but both emphasize the complexity of the systems that manipulate the sex ratios of mammalian young.

Both the UP and the NLP bear populations are as or more productive than those in other regions of eastern North America (Beston 2011 and Bridges et al. 2011). Beston (2011) hypothesized that the high reproductive output of eastern North American black bears may be a response to robust food abundance or shorter adult life expectancy due to harvest mortality. The higher age of primiparity (Table 3.4) and smaller litter size (Table 3.2) of the UP bear population as compared to the NLP bear population may reflect differences between the regions in these factors. The UP has a smaller human population and less agriculture than the NLP (see Study Area), which could reduce the availability of alternative food sources for black bears and increase their susceptibility to fluctuations in mast abundance.

Both food abundance or harvest pressure could change over time within each region, affecting bear reproduction. Periodic reassessments of reproductive trends would reveal if the Michigan black bear populations continue to exhibit high productivity. Evidence of decreased productivity by lower proportion of females reproducing or smaller mean litter sizes could suggest the need for decreased harvest pressure to maintain population viability. Although we detected fluctuations in the proportion of females breeding annually, the mean proportion breeding did not appear to shift rapidly (Figure 3.2), so reassessments every 10-15 years would likely be frequent enough to detect major changes.

While periodic reassessments might be sufficient to support management decisions, annual estimates of black bear reproduction such as those estimated in this chapter could be useful in validating black bear population models. Continued annual collection of bear teeth and assessment of reproduction patterns would be useful for evaluating the output of such models. In the absence of data on mast production, examination of annual trends of the proportion of females breeding can also provide evidence of frequency of mast failures (Bridges et al. 2011). Increasing frequency of mast failures could impact not only reproduction but natural survival, harvest mortality, and nuisance behavior (Rogers 1976, Elowe and Dodge 1989, Eiler et al 1989, Noyce and Garshelis 1997, Obbard et al. 2014), to which managers may want to respond with changes in habitat manipulation or harvest regulations.

CHAPTER 4: A STATISTICAL CATCH-AT-AGE ANALYSIS OF THE MICHIGAN BLACK BEAR POPULATION

INTRODUCTION

The primary goal of the Michigan Department of Natural Resources' (DNR) black bear (*Ursus americanus*) management program is to balance the often conflicting values of a diverse stakeholder base while maintaining a sustainable bear population below biological carrying capacity (Bump 2009). While the DNR's bear management objectives focus on population impacts, the DNR uses management actions to directly manipulate population abundance and distribution to achieve the desired change in impacts (Bump 2009). The DNR uses recreational harvest as the primary tool to manipulate bear population abundance and distribution and relies on a license and quota system to achieve the desired harvest and allocate the harvest throughout the state (Bump 2009).

Such a management system requires some means to monitor changes in population abundance. For many years, the management system relied heavily on capture-mark-recapture (CMR) techniques to estimate the bear population in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) every 3 to 5 years. The CMR surveys were expensive to conduct, and the resulting population estimates were not available for 1-3 years after the initial marking period. The expense, delays, and lack of detail left the DNR looking for an alternative means of monitoring the bear population.

The DNR has collected data on the age of almost every harvested bear for over 20 years. Analysis methods that could take advantage of the information contained within age-at-harvest data would provide a means to monitor the bear population without the need to expand data collection efforts. Summing the number of bears harvested over a cohort would eventually provide the total number of bears that originated in that cohort, assuming all mortality was harvest mortality. While the harvest accounts for a large proportion of bear mortality in Michigan, car kills and other sources of mortality mean some bears would never appear in the harvest data (Etter et al. 2002). Given the long lifespan of bears, waiting until a cohort has been completely harvested would also require managers to work with data that was so old as to be uninformative to current situations. A more complex methodology is, therefore, necessary to account for the complexity of bear population dynamics and to provide estimates in a more timely manner. A variety of techniques have been developed to estimate population size from age-at-harvest data under different assumptions and using different auxiliary data (Skalski et al. 2005). We explored the potential of statistical catch-at-age analysis techniques (SCAA) to monitor the bear population in Michigan.

Statistical catch-at-age analyses require data on the age composition of the harvest over several years. The techniques originated in the fisheries field (e.g., Fournier and Archibald 1982) but have recently been applied to a variety of wildlife datasets (e.g., Gove et al. 2002 and Fieberg et al. 2010). The concept that underlies the SCAA models is to estimate the demographic and harvest related parameters that led to the size and composition of the observed harvest. The age-at-harvest data are related back to the population through auxiliary data. The appeal of the SCAA for Michigan was that the DNR had estimates of hunter effort in addition to the age-at-harvest data and so would not require investment in new data collection efforts. The SCAA models could also potentially provide estimates sooner and with far greater detail, including a variety of demographic parameters, than the CMR estimates. Garshelis and

Hristienko (2006) called for more rigorous black bear population estimators to support management agencies, and SCAA models have been found to answer that call (Conn et al. 2008).

Our goal was to develop SCAA models for Michigan black bear for the DNR to use to monitor the black bear population, assess effects of past management, and support decisions on future management actions. Specifically, our objectives were to: 1) develop and evaluate SCAA models for black bears for the UP and NLP of Michigan, 2) test the sensitivity of the modeled population estimates to simplifying assumptions and available data, and 3) to build a model to project future changes in the bear population under different harvest regimes.

METHODS

Data

From 1992-2015, black bear hunters using a State of Michigan bear hunting license were required to register their kill with the DNR within 72 hours of harvest. Licensed hunters were legally allowed to take any bear that was not a cub and not a female accompanied by cubs. Hunters brought the carcass to a DNR registration station where DNR employees or authorized volunteers attached a seal to the pelt, recorded date and location of harvest, and removed a premolar for age determination. Beginning in 2008, several tribal governments also issued licenses to their members to harvest bears, and the registration requirements were unique to each tribe. Some hunters using a tribal bear license registered their harvest with the DNR, while tribal governments voluntarily shared with the DNR data on other bears harvested by their members. Tribal harvest records were available beginning in 2009 and represented an unknown, but likely majority, proportion of the actual tribal harvest. All premolars collected through the aging process were sent to the DNR lab for aging using the cementum annuli techniques of Willey (1974) and Coy and Garshelis (1992).

We summarized the registration numbers in data matrices representing the total number of male and female bears harvested and registered by state and tribal hunters from 1992 through 2015 from age 1 year old through age 20+ years old. We took advantage of all harvest registration records by assuming that records of unknown sex and age represented the same sex and age composition as bears where sex and age were recorded within the same harvest year (Appendix 4A). After allocating the unknown sex and age bears to the appropriate categories, we adjusted the corrected sex and age matrices for sexing and aging error using the methods we report in Chapter 2. Due to the multiple older age classes with no harvested bears, we chose to pool the older bears into a multi-age 7+-year-old category for the UP and 6+-year-old category for the NLP. The NLP model required a lower pooling age due to the smaller population, smaller harvest, and thus sparse data among the older age classes. The resulting data matrices represented the composition of the known annual bear harvest.

Following the close of the black bear seasons in 1990-2015, the DNR surveyed a random sample, stratified by bear management unit (BMU), of bear hunters, defined as people who were successful in the license lottery (1990-1998) or purchased their license (1999-2015) (e.g., Frawley and Boon 2016). Survey recipients were sent an initial questionnaire and up to 2 additional questionnaires, if the DNR had not yet received a response. Beginning in 2007, all bear license buyers had the option of completing the questionnaire online. Those who completed the questionnaire before the DNR identified the randomly sampled hunters were combined in a separate stratum. The questionnaire asked license buyers to indicate whether or not they hunted bears, the primary method by which they hunted bears, the number of days spent pursuing bears, and the counties in which they hunted. We used domain estimation methods described in Cochran (1963) to estimate the number of hunters and the number of hunter days within a region (UP and NLP) from the responses that were stratified by BMU (Appendix 4B).

In addition to the harvest-related data collected through the registration stations and the survey questionnaire, capture-mark-recapture (CMR) estimates were also available for both the UP and NLP bear populations. The DNR conducted intermittent CMR studies of the UP population using tetracycline as a biomarker beginning in 1990 for a Lincoln-Petersen estimator (Garshelis and Visser 1997) and using genetic marking techniques in the NLP beginning in 2003 for a closed capture estimator (Dreher 2007). Following the recommendation of Belant et al. (2011a), we used 3 years of recovery data to estimate the UP population using the Lincoln-Petersen estimator. The field methodologies of both studies were designed to exclude cubs from the marked population and to estimate pre-harvest population abundance (number of 1+-year-old individuals in the population immediately preceding the opening of the harvest seasons). The data that were available to us allowed us to use 9 CMR population estimates in the UP and 4 in the NLP.

Model

The SCAA model had 2 major components consisting of a population model and an observation model. The population model described the structure of the population and the annual changes in the population composition through recruitment, harvest, and non-harvest mortality (Figure 4.1). The observation model provided a probability distribution for observed harvest values given the actual population. We used the observation model to relate the harvest and CMR data to model parameters by using maximum likelihood estimation techniques to find the parameter estimates that best fit the data. Each region had an independent SCAA model with separate data sets. Unless we specifically describe regional differences, the model structure below applied to both UP and NLP models. We ran all models in ADMB-IDE 11.2 (Fournier et al. 2012).

In the population models, we broke the population down into 2 sexes and multiple age classes beginning with 1-year-old bears and continuing in annual increments to a 7+-year-old category for the UP and 6+-year-old category for the NLP that pooled all bears of the maximum age class and older. The model estimated as parameters the initial population (pre-harvest abundance in 1992) within each age and sex class and then advanced the appropriate number of individuals through the population according to the data and the parameter estimates. From the pre-harvest population (n_{say}), we subtracted the known state and tribal harvest and advanced the year and the age of the surviving bears in the post-harvest population, which overwintered. From the post-harvest population, we removed the non-harvest mortality as a pulse (see *Model Variants* for details) to find the pre-recruitment population. This model structure assumed no non-harvest mortality during the harvest season. Statewide, the season length was 46 days (10 September through 26 October). Due to the short season length and the low number of deaths of Michigan black bears to causes other than harvest (Etter et al. 2002), this was a reasonable approximation. Cubs were protected from harvest in Michigan so

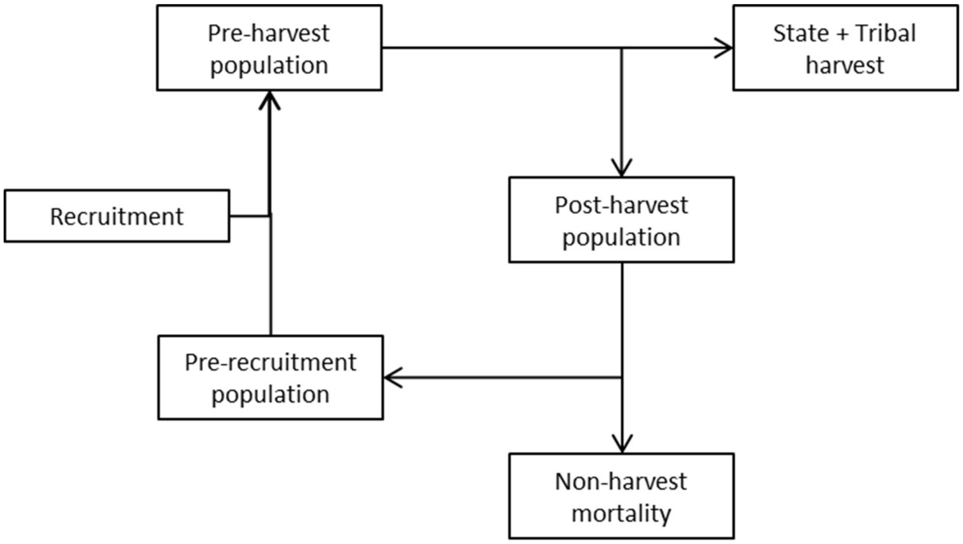

FIGURE 4.1. Schematic of the annual cycle of a population model of black bears in Michigan, USA.

the earliest age for which we had observation data was yearlings (approximately 19 months old). We, therefore, chose to define recruits as yearlings immediately prior to the first harvest season in which they were vulnerable to legal harvest. The model estimated the total number of recruits to add to the pre-recruit population in each year, and we divided those into males and females using an estimate of the proportion of male yearlings in the den from Chapter 3. Once we added the recruits into the population, the population completed a cycle and reached the pre-harvest population. The models ended with the post-harvest 2016 population. (See Table 4.1 for detailed information.)

The observation model used a catch-per-effort model (originally proposed by Leslie and Davis 1939) to predict the harvest from effort data (Table 4.1). Within the observation model, each year the bear population was subject to different harvest pressure based on the total effort (measured as number of hunters) (Appendix 4C) and allocated among the different age and sex classes based on their unique catchability parameters. The catchability parameter combined the unique vulnerability of different age and sex classes of bears to harvest due to their natural behaviors and the selectivity of hunters for different age and sex classes due to their preferences (Noyce and Garshelis 1997). Hunter days, an alternative measure of hunter effort, showed similar temporal trends (Appendix 4C).

Model Variants

Due to uncertainty in the appropriate structure for the non-harvest and harvest mortality models, we used model selection based on Akaike's Information Criteria (AIC) to find the best fit model for the data (Burnham and Anderson 2002). We anticipated little annual

TABLE 4.1. Definitions of symbols used in statistical catch-at-age models of Michigan, USA, black bears.

Index	Definition
a	Age class of bears; a=1 year to a_{max}
a_{max}	Age class pooling all bears that have attained some maximum age, defined in model descriptions
s	Sex index of bears; s = m (male) or f (female)
y	Year index; y = 1992 to 2015
Data	**Definition**
h_{say}	Number of harvested bears of sex s, age a, and year y
p_s	Proportion of recruits that are sex s
f_y	Hunter effort in year y
J_y	Desired total future harvest in year y (for use in projections)
$\widehat{N}_y$	Pre-harvest population estimate from CMR survey for year y
σ_y	Standard error of $\widehat{N}_y$
Parameter	**Definition**
n_{sa1992}	Initial (1992) pre-harvest abundance of sex s and age a, where a=1 to a_{max}
M_{sa}	Annual proportion of bears of sex s and age a dying due to all non-harvest causes of mortality
r_y	Number of 1-year-old bears recruited into the population in year y
C_{sa}	Catchability of bears of sex s and age a (see text for further explanation)
λ	Weight of the age-at-harvest component of the likelihood relative to the CMR component

TABLE 4.1 (cont’d)

Calculated Value	Definition
n_{say}	Preharvest abundance of bears of sex s, age a, in year y (where y=1993 to 2015); $\begin{cases} \mathrm{n}_{s,1,y} = \mathrm{r}_y * \mathrm{p}_s \\ \mathrm{n}_{s,a+1,y+1} = \left[\left(\mathrm{n}_{s,a,y} - \mathrm{h}_{s,a,y}\right) * \left(1 - \mathrm{M}_{s,a+1,y+1}\right)\right], \text{where } a\text{=1 to } (a_{max}\text{-2}) \\ \mathrm{n}_{s,a_{max},y} = \left[\left(\mathrm{n}_{s,a_{max-1},y} - \mathrm{h}_{s,a_{max-1},y}\right) * \left(1 - \mathrm{M}_{s,a_{max},y+1}\right)\right] \\ +\left[\left(\mathrm{n}_{s,a_{max},y} - \mathrm{h}_{s,a_{max},y}\right) * \left(1 - \mathrm{M}_{s,a_{max},y+1}\right)\right] \end{cases}$
N_y	Pre-harvest abundance of all bears in year y; $N_y = \sum_{s,a} n_{say}$
P_y	Pre-recruitment abundance of all bears in year *y* (includes bears only 2+ years old)
$\tilde{\mathrm{h}}_{say}$	Predicted number of harvested bears of sex *s*, age *a*, and year *y*; $\tilde{\mathrm{h}}_{say} = \left(1 - e^{-\mathrm{C}_{sa}*\mathrm{f}_y}\right) * \mathrm{n}_{say}$
g	Negative log-likelihood of the SCAA models (described in the text)
j_{say}	Number of bears of sex *s*, age *a*, and year *y* harvested in projected future years
S_{sa}	Annual proportion of bears of sex *s* and age *a* that survive all non-harvest causes of mortality

variation in non-harvest mortality due to previous studies that found that the harvest makes up the largest component of bear mortality (Etter et al. 2002), so we modeled non-harvest mortality rates that varied by sex and age and were constant over time. We anticipated higher mortality rates for younger bears than older bears, although we were uncertain at what age the rates would become constant. To select the best non-harvest mortality structure, we included model variants where non-harvest mortality was constant from age 2 years old and older and a logistic model for non-harvest mortality over age. We considered separate mortality for 2-year-old bears and 3+-year-old bears. Since all catchability models separated 2-year-old bears from all other age bears, however, the model structure did not allow us to distinguish between non-harvest mortality and harvest mortality of 2-year-old bears. Without any additional information or constraints, non-harvest mortality of 2-year-old bears was not estimable so we did not consider any such models in our model set. In all cases we separated male and female non-harvest mortality.

We assumed catchability would also vary by sex and age classes. We modeled different catchability rates for each age class up to 3 years old for both sexes in one set of models and up to 3 years old for males and 5 years old for females in other models. Due to popular theories among hunting groups that the increasing use of GPS collars on hunting dogs and trail cameras on bait piles were increasing the efficiency of hunters, we also modeled for temporal changes in catchability. We included models with separate catchability before and after (inclusive) 2005 and a linear trend over time from 1992 to 2015. In each case, the catchability of all age classes varied independently because we thought technology may have allowed hunters to change their selectivity. The choice of 2005 was somewhat arbitrary; we only had anecdotal information to suggest that hunter behaviors had changed over time and no data to indicate the rate or timing of that change. Due to changes in management objectives, the DNR raised bear hunting license quotas throughout the 2000s (Figure 4.2). To assess whether the greater availability of licenses affected catchability, we included models with 3 periods of catchability (UP: 1992-1999, 2000-2011, 2012-2015; NLP: 1992-2002; 2003-2009, 2010-2015). We were primarily interested in the effect of license availability, so we assumed the relationships among the ages and sexes remained constant and added a separate constant to catchability for each of the second and third time periods. Our final model set included all 10 combinations of non-harvest mortality and catchability variants (Table 4.2).

Model Fitting

We estimated model parameters by defining and minimizing an objective function using AD Model Builder (Fournier et al. 2012), specifically ADMB-IDE 11.2. The objective function was primarily a χ^2 objective function in which we minimized the difference between the known legal state harvest and the harvest predicted from the observation model of the general form,

$$\sum_{s}\sum_{a}\sum_{y}\frac{\left(h_{say}-\tilde{h}_{say}\right)^2}{\tilde{h}_{say}}.$$

We also explored the use of a log-normal objective function but found the models were consistently unable to converge on a solution. We incorporated a second component into the objective function based on the available CMR population estimates. Although some CMR data can be used in an integrated population model to share parameters with an SCAA population model (Conn et al. 2009), the Michigan CMR surveys were implemented in a single season

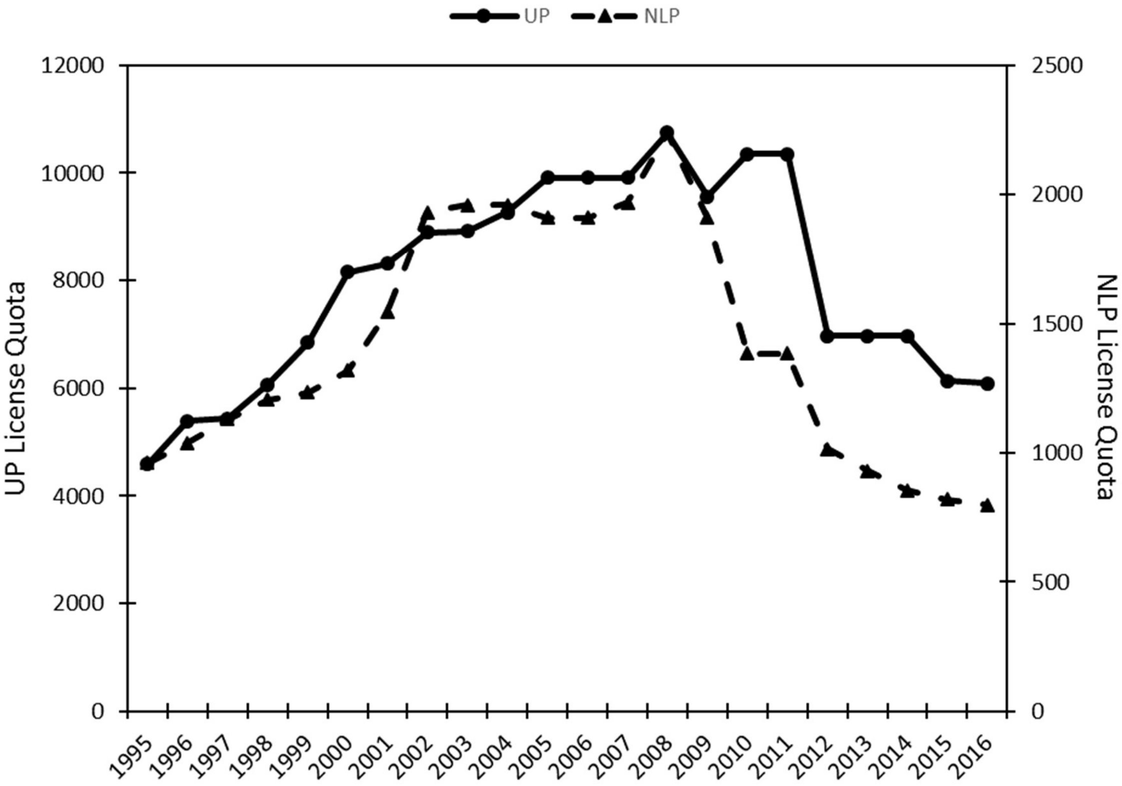

FIGURE 4.2. Number of bear licenses available for sale in Michigan, USA, 1995-2016.

TABLE 4.2. Demographic models tested in a statistical catch-at-age analysis of black bears in Michigan, USA.

Model Name	Non-harvest mortality description	Non-harvest mortality rate parameters	Catchability description	Catchability parameters
MC_3	Constant over time; separate by sex; constant over ages 2+ years old	$S_m = (1-M_m)$, $S_f = (1-M_f)$	Constant over time; separate by sex; separate for ages 1 year old, 2 years old, and 3+ years old	C_{m1}, C_{m2}, C_{m3}, C_{f1}, C_{f2}, C_{f3}
MC_5	Constant over time; separate by sex; constant over ages 2+ years old	$S_m = (1-M_m)$, $S_f = (1-M_f)$	Constant over time; separate by sex; separate for males for ages 1 year old, 2 years old, and 3+ years old and for females for ages 1 year old, 2 years old, 3 years old, 4 years old, and 5+ years old	C_{m1}, C_{m2}, C_{m3}, C_{f1}, C_{f2}, C_{f3}, C_{f4}, C_{f5}
MC_{lin}	Constant over time; separate by sex; constant over ages 2+ years old	$S_m = (1-M_m)$, $S_f = (1-M_f)$	Separate linear trends over time for each sex and age class; separate by sex; separate for ages 1 year old, 2 years old, and 3+ years old	l_{m1}, l_{m2}, l_{m3}, l_{f1}, l_{f2}, l_{f3}, C_{m11992}, C_{m21992}, C_{m31992}, C_{f11992}, C_{f21992}, C_{f31992} $\left(C_{say} = (l_{sa} * y) + C_{sa1992}\right)$

TABLE 4.2 (cont'd)

MC$_{2005}$	Constant over time; separate by sex; constant over ages 2+ years old	$S_m = (1-M_m)$, $S_f = (1-M_f)$	Separate before 2005 (early) and for 2005 and after (late) for each sex and age class; separate by sex; separate for males for ages 1 year old, 2 years old, and 3+ years old and for females for ages 1 year old, 2 years old, 3 years old, 4 years old, and 5+ years old	$C_{m1early}$, $C_{m2early}$, $C_{m3early}$, $C_{f1early}$, $C_{f2early}$, $C_{f3early}$, $C_{f4early}$, $C_{f5early}$, C_{m1late}, C_{m2late}, C_{m3late}, C_{f1late}, C_{f2late}, C_{f3late}, C_{f4late}, C_{f5late}
MC$_{quota}$	Constant over time; separate by sex; constant over ages 2+ years old	$S_m = (1-M_m)$, $S_f = (1-M_f)$	Constant change over all sexes and ages from before heightened quotas to during (mid) and after (late) period of high quotas; separate by sex; separate for males for ages 1 year old, 2 years old, and 3+ years old and for females for ages 1 year old, 2 years old, 3 years old, 4 years old, and 5+ years old	C_{m1}, C_{m2}, C_{m3}, C_{f1}, C_{f2}, C_{f3}, C_{f4}, C_{f5}, γ_{mid}, γ_{late} ($C_{saearly} = C_{sa}$ $C_{samid} = C_{sa} + \gamma_{mid}$ $C_{salate} = C_{sa} + \gamma_{late}$)
M$_{log}$C$_3$	Constant over time; logistic curve over age	L_m, L_f, k_m, k_f, m_m, m_f $\left(M_{sa} = 1 - \frac{L_s}{1+e^{-k_s(a-m_s)}}\right)$	Constant over time; separate by sex; separate for ages 1 year old, 2 years old, and 3+ years old	C_{m1}, C_{m2}, C_{m3}, C_{f1}, C_{f2}, C_{f3}

TABLE 4.2 (cont'd)

$M_{log}C_5$	Constant over time; logistic curve over age	L_m, L_f, k_m, k_f, m_m, m_f $\left(M_{sa} = 1 - \frac{L_s}{1 + e^{-k_s(a-m_s)}}\right)$	Constant over time; separate by sex; separate for males for ages 1 year old, 2 years old, and 3+ years old and for females for ages 1 year old, 2 years old, 3 years old, 4 years old, and 5+ years old	C_{m1}, C_{m2}, C_{m3}, C_{f1}, C_{f2}, C_{f3}, C_{f4}, C_{f5}
$M_{log}C_{lin}$	Constant over time; logistic curve over age	L_m, L_f, k_m, k_f, m_m, m_f $\left(M_{sa} = 1 - \frac{L_s}{1 + e^{-k_s(a-m_s)}}\right)$	Separate linear trends over time for each sex and age class; separate by sex; separate for ages 1 year old, 2 years old, and 3+ years old	l_{m1}, l_{m2}, l_{m3}, l_{f1}, l_{f2}, l_{f3}, C_{m11992}, C_{m21992}, C_{m31992}, C_{f11992}, C_{f21992}, C_{f31992} $\left(C_{say} = (l_{sa} * y) + C_{sa1992}\right)$
$M_{log}C_{2005}$	Constant over time; logistic curve over age	L_m, L_f, k_m, k_f, m_m, m_f $\left(M_{sa} = 1 - \frac{L_s}{1 + e^{-k_s(a-m_s)}}\right)$	Separate before 2005 and for 2005 and after for each sex and age class; separate by sex; separate for males for ages 1 year old, 2 years old, and 3+ years old and for females for ages 1 year old, 2 years old, 3 years old, 4 years old, and 5+ years old	$C_{m1early}$, $C_{m2early}$, $C_{m3early}$, $C_{f1early}$, $C_{f2early}$, $C_{f3early}$, $C_{f4early}$, $C_{f5early}$, C_{m1late}, C_{m2late}, C_{m3late}, C_{f1late}, C_{f2late}, C_{f3late}, C_{f4late}, C_{f5late}

TABLE 4.2 (cont’d)

$M_{log}C_{quota}$	Constant over time; logistic curve over age	L_m, L_f, k_m, k_f, m_m, m_f $\left(M_{sa} = 1 - \frac{L_s}{1 + e^{-k_s(a-m_s)}}\right)$	Constant change over all sexes and ages from before heightened quotas to during and after period of high quotas; separate by sex; separate for males for ages 1 year old, 2 years old, and 3+ years old and for females for ages 1 year old, 2 years old, 3 years old, 4 years old, and 5+ years old	C_{m1}, C_{m2}, C_{m3}, C_{f1}, C_{f2}, C_{f3}, C_{f4}, C_{f5}, γ_{mid}, γ_{late} ($C_{saearly} = C_{sa}$ $C_{samid} = C_{sa} + \gamma_{mid}$ $C_{salate} = C_{sa} + \gamma_{late}$)

framework and the data were insufficient to estimate demographic parameters. Instead, we chose to incorporate the CMR population estimates in a penalized likelihood framework in which we penalized the χ^2 objective function for deviations of the modeled population from the CMR estimates using the negative log likelihood for a normal distribution. To accomplish model selection, we modified the general form of the χ^2 objective function to give us a negative log likelihood value appropriate for use in the calculation of the AIC (Appendix 4D). We added a parameter λ to the model which served to weight the relative contribution of the χ^2 (age-at-harvest) and normal distribution (CMR) negative log-likelihoods to the final objective function. The final objective function was therefore a negative log-likelihood in the form of:

$$g = -\frac{1}{2}\sum_{s}\sum_{a}\sum_{y}\frac{\lambda}{\tilde{h}_{say}} + \frac{1}{2}\lambda\sum_{s}\sum_{a}\sum_{y}\frac{\left(h_{say} - \tilde{h}_{say}\right)^2}{\tilde{h}_{say}} + \sum_{y}\log\sigma_y + \frac{1}{2}\sum_{y}\frac{\left(N_y - \widehat{N}_y\right)^2}{\sigma_y^2}.$$

We followed many of the suggestions of Skalski et al. (2012) to evaluate the SCAA models. We conducted all model evaluation steps using model $M_{\log}C_{\text{lin}}$ because it was a highly parameterized, flexible model that allowed for variability in survival over age and catchability over time, conforming to the recommendation of Burnham and Anderson (2002) that model evaluation be conducted on the global model. We plotted

$$\frac{\left(h_{say} - \tilde{h}_{say}\right)}{\sqrt[2]{\tilde{h}_{say}}}$$

against $\tilde{h}_{say}$ to look for patterns in the residuals. We also used retrospective analysis to look for evidence of temporal trends that we had not accounted for. We evaluated each peninsula's model using data from 1992-2000 for the UP and 1992-2003 for the NLP and then iteratively added successive years of data. We started the retrospective analysis at a later year in the NLP because there were no CMR estimates available before 2003 to penalize the objective function. We then plotted the pre-harvest population estimates from each iterative run to look for trends. We used the pre-harvest population estimate in the retrospective analysis because that was the quantity of primary interest to the DNR management program.

Finally, we were able to validate the model by comparing model output on reproduction to independent data. We calculated an index of reproduction by dividing the total number of estimated recruits by the total number of estimated pre-harvest females of reproductive age within a year. We set the minimum age of reproduction at 5 years old for the UP and 4 years old for the NLP (which means they would have produced cubs at 4 years old and 3 years old respectively to produce the 1-year-old recruits the following year). UP females rarely reproduced before age 4 years old and in some years a large proportion of NLP females did reproduce at 4 years old (Chapter 3). We then compared the reproduction index to estimates of the proportion of females breeding 1 year earlier that were independent of the model (Chapter 3). We assumed the proportion of adult females breeding in one year and the number of recruits (yearlings) per adult in the following year would follow similar patterns if they represented the same population. We conducted all model evaluation steps prior to model selection so we could evaluate the fit of the base model before continuing with our analysis.

Once we selected the final model, we calculated the confidence intervals for the estimated total pre-harvest abundance for each year within each region using the penalized profile likelihood methods described in Bolker (2008) and implemented in ADMB. We calculated the negative log-likelihood of the model over a range population targets, iterating from the estimated mean by 10 bears in the NLP from 600 below the mean to 3000 above the mean and iterating by 25 bears in the UP from 7500 below the mean to 10000 above the mean. We forced the model to achieve the target population values by penalizing the negative log-likelihood by the squared deviation of the estimated population and the target population. We found the upper and lower 95% confidence limit by finding the target population value whose penalized negative log-likelihood (g_{pen}) aligned with the critical value of g + 0.5*$\chi^2_{0.95}$ with degrees of freedom of (*number of model parameters-1*). Because λ is a model parameter, the model could achieve the target population by changing the scale of the estimated λ to switch between putting the majority of the weight of g_{pen} on the CMR estimates ($\lambda < 1.0$) and on the age-at-harvest data ($\lambda > 1.0$). By changing the scale of λ from that of the best fit solution, the model changed the scale of the g_{pen} so that the critical value was not contained within the range of g_{pen} from the iterations. When the model could not achieve the upper target population without changing the scale of the estimated λ parameter, we fixed λ at the estimated mean from the best fit solution to estimate the upper confidence limit. In years in which the model could not achieve the lower target population without deviating from the known harvest or could not converge on a solution at all, we calculated the Wald confidence interval of the log of the population estimate using the asymptotic standard errors reported in ADMB and back transformed to real scale. Calculating the confidence interval on the log scale maintained the asymmetry of the profile likelihood confidence intervals. For all other real and derived parameters, we report the asymptotic standard errors.

Sensitivity Analysis

During model development we made assumptions about which we were uncertain. We evaluated how robust model results were to those assumptions by examining the effect of changing the assumptions on the estimated pre-harvest population (Table 4.3). We examined the effect of <100% registration of harvested animals, different recruit sex ratios, different statistics of hunter effort, higher or lower sexing and aging error, and inclusion of CMR estimates on the total pre-harvest population estimates. We also evaluated the effects of fixing non-harvest mortality at rates based on those from published field studies. We varied each component within the range of biological realism based on our knowledge of the system and the data available to us. We tested the effects of changing only one feature at a time.

Projection Model

While we could derive estimates of past population abundance from data collected from those populations, the DNR was also interested in projecting potential future changes in the population under different harvest regimes. We built a projection model from the estimation model by assuming that future population demographics would be similar to past population demographics. We first used simple linear regression to look for signs of density dependence within each region for recruitment rate ($\frac{number\ of\ recruits}{pre-recruitm\quad population}$) as described in Dinsmore and Johnson (2012). Because we held non-harvest mortality constant and license quotas control harvest mortality, it was not appropriate to look for evidence of density dependence in mortality. If we found evidence of density dependent recruitment in a region, we used the projected pre-recruitment population to estimate the number of recruits in future years based on the fitted regression model. If we did not find evidence of density dependent recruitment in a region, we used the reproduction index to estimate the total number of recruits produced per

TABLE 4.3. Descriptions of sensitivity analyses conducted on a statistical catch-at-age analysis of black bears in Michigan, USA. The "base" scenarios were used in all analyses outside the sensitivity analyses unless otherwise noted.

Feature	Description	Scenario Number	Scenario
All registrations	All State of Michigan hunters and many tribal hunters were required to register their harvest. Compliance was likely high but was unknown and may have been biased against females or younger bears (hunters fearing consequences of harvesting a bear accompanied by cubs or hunters harvesting a small bear they feared may be a cub).	Base	100% compliance
		1	95% unbiased compliance
		2	85% unbiased compliance
		3	Age bias (85% compliance of harvested 1-year-old bears, 95% compliance of harvested 2+-year-old bears)
		4	Sex bias (85% compliance of harvested females; 95% compliance of harvested males)
Tribal registration	Registration requirements were unique to each tribe. Representation of tribal harvest in the DNR registration database was likely high but possibly <100%.	Base	100% compliance
		5	80% unbiased compliance
		6	50% unbiased compliance
Effort	Hunters pursued bears using different methodologies, some of which may have been more efficient than others. Hunters hunting over bait made up the largest proportion of bear hunters in every year, so we tested the effect of splitting hunters between bait hunters and others.	Base	Total number of hunters
		7	Number of hunters split between bait hunters and others.

TABLE 4.3 (cont'd)

Proportion of male recruits	The data on the proportion of male recruits was sparse and based on data from den checks. Although all data suggests a male bias, the data are too sparse for us to be confident the estimate was accurate. Also, because mortality of young males was likely higher than for females, the proportion of male recruits immediately prior to the harvest was likely higher than the proportion in the den.	Base 8 9	UP: 0.54 NLP: 0.56 UP: 0.50 NLP: 0.52 UP: 0.58 NLP: 0.60
Sexing error	In Chapter 2 we estimated sexing error rates. We tested the sensitivity of the model to higher or lower sexing error.	Base 10 11	See Chapter 2 Low error = Lower limit of 95% CI of Base error High error = Upper limit of 95% CI of Base error
Aging error	In Chapter 2 we estimated aging error rates. We tested the sensitivity of the model to higher or lower aging error by forcing the standard deviation (SD) of the fitted model to be lower or higher than the base.	Base 12 13	See Chapter 2 Low error, SD=0.75*Base High error, SD=1.25*Base
Fixed initial population	We fixed the initial population of age 4 male bears in the NLP at 2 to prevent model estimation problems. Since our choice was arbitrary, we tested the sensitivity of the results to other values.	Base 14 (NLP only) 15 (NLP only)	2 1 4

TABLE 4.3 (cont'd)

CMR	Capture-mark-recapture estimates were available from more years in the UP than the NLP. Because the CMR estimates were expensive to conduct, we tested the effect of reduced availability of CMR estimates on the model results.	Base	All available CMR estimates
		16	No CMR
		17 (UP only)	Early CMR (UP: 1992)
		18	Mid CMR (UP: 2004, NLP: 2003)
		19	Late CMR (UP: 2012; NLP: 2013)
		20 (UP only)	5 year CMR (UP: 1992, 1998, 2002, 2007, 2012)
		21 (UP only)	8 year CMR (UP: 1992, 2000, 2007)
Fixed survival	Preliminary review of results led to concern that the estimated non-harvest mortality rates were not realistic. We tested the effects of fixing survival at rates based on results from Etter et al. (2002), Lee and Vaughan (2005), and Tri et al (2017).	Base	Estimated parameter
		22	S=0.98
		23	S=0.94
		24	S=0.9
Uncorrected error	Because sexing and aging error rates in Chapter 2 had minimal effects on hypothetical data analyses, we tested whether incorporating the error corrections was important in the SCAA.	Base	See Chapter 2
		25	Harvest data not corrected for sexing and aging error[a]

a. When we did not correct the harvest data for sexing and aging error, the estimates of initial population abundance changed. As a result, the fixed initial population of 4-years-old males in the NLP was no longer appropriate. Therefore, in Scenario 25 for the NLP we estimated initial abundance of 4-year-old males as a parameter instead of assigning it a fixed value as in all other scenarios.

female of reproductive age for the last 5 years of the retrospective model. We then averaged the results of the 5 years to generate an estimate of fertility to project future recruitment. We also assumed that the non-harvest mortality rates estimated in the past would continue to be constant into the future.

The DNR set bear license quotas to achieve a desired total harvest, so for each projected year we fixed the harvest at the proposed desired future harvest. To project the entire population forward, however, we needed to break the harvest down into the sex and age classes used in the model. To do so, we assumed that the most recent catchability estimates would continue into the future. We calculated the number of bears harvested in each sex and age class by

$$j_{say} = J_y \frac{\left(\frac{n_{sa}}{N}\right)\left(\frac{c_{sa}}{\sum_{sa} c_{sa}}\right)}{\sum_{sa}\left(\frac{n_{sa}}{N}\right)\left(\frac{c_{sa}}{\sum_{sa} c_{sa}}\right)}.$$

Using the projection model, we projected 4 years of future harvests to align with 2 DNR bear management cycles. The projection model advanced the population forward from the post-harvest 2016 population using the same population equations as the retrospective model (Table 4.1) except that we calculated the total number of recruits using the procedures described above. We projected 3 different scenarios for each region based on the 2015 harvest: constant harvest, increased harvest (120% of the 2015 harvest), and decreased harvest (80% of the 2015 harvest).

RESULTS

Data

From 1992 through 2015, the DNR registered 36,413 bears in the UP and 6,695 bears in the NLP from state-licensed hunters (Table 4.4). Tribal harvest registrations provided an additional 179 bears in the UP and 128 in the NLP. Once we completed all assignments of unknown sex and age animals and corrected for sexing and aging error, we removed all age 0 bears in Table 4.4 from further consideration because we modeled recruits as yearlings in the pre-harvest population. The final harvest data matrix for the NLP males had no age 4 bears in 1992, but >0 male bears harvested from that cohort in 1993. To prevent model estimation problems, we fixed the initial population of age 4 male bears in the NLP at 2. We did not find that this decision affected model results (see *Sensitivity Analysis*).

Estimates of the number of hunters that pursued bears in Michigan showed a temporal pattern in both regions of more hunters during the middle years than at either end of the time period (Table 4.5). In both regions, bait hunters also made up the majority of total hunters (Table 4.5). The CMR data that were available to us allowed us to use 9 CMR population estimates in the UP and 4 in the NLP (Table 4.6).

Model Evaluation

The model evaluation suggested the basic structure of the models was appropriate for the data. The residual plots for $M_{log}C_{lin}$ for both peninsulas showed no apparent trends; they were evenly and symmetrically distributed (Figure 4.3). Both retrospective analyses showed similar annual trends in population estimates as successive years of data were added to the

TABLE 4.4. Number of harvested bears registered in the state-licensed harvest in Michigan, USA, 1992-2015. Ages and sexes are corrected as described in the text.

	Bear age (in years)										
Year	0	1	2	3	4	5	6	7	8	9	10+
Upper Peninsula males											
1992	2.1	103.8	179.9	87.4	72.0	28.8	23.1	11.9	9.1	12.0	11.0
1993	4.3	218.0	134.8	116.6	33.6	51.8	12.2	18.7	7.6	0.0	21.7
1994	4.6	141.5	249.1	54.3	94.7	28.1	14.7	20.9	12.6	6.1	4.0
1995	2.1	229.1	145.1	175.5	25.3	54.4	12.6	8.9	15.5	6.1	8.4
1996	3.2	157.9	276.8	82.4	97.8	7.4	47.2	0.0	17.3	0.0	13.6
1997	3.2	202.7	153.3	175.0	13.0	39.0	0.0	22.2	0.0	17.2	6.7
1998	5.3	213.3	238.6	114.6	107.7	4.4	42.0	0.0	28.8	0.0	13.9
1999	5.1	300.1	325.4	149.1	63.0	42.5	0.0	28.0	0.0	8.6	12.4
2000	5.9	333.9	272.0	122.7	49.5	70.9	4.3	9.7	14.3	0.0	12.7
2001	8.6	365.7	321.3	148.6	78.3	36.8	29.2	13.0	9.5	11.0	2.4
2002	8.2	314.6	314.8	174.3	63.7	43.6	1.7	39.6	0.0	9.2	10.4
2003	12.4	352.2	413.4	146.1	96.9	32.8	32.2	0.0	16.4	10.7	16.1
2004	12.7	339.6	328.3	188.9	39.7	35.8	28.4	8.5	29.0	0.0	26.1
2005	2.7	331.7	298.1	165.7	84.3	14.9	24.7	9.8	10.5	0.0	23.0
2006	14.6	422.8	402.1	161.4	58.6	82.2	9.1	14.7	15.3	10.0	19.4
2007	7.7	398.3	301.2	155.8	50.6	37.9	3.5	18.8	0.1	3.9	18.3
2008	12.5	351.7	399.5	138.4	76.1	48.9	16.3	11.6	0.0	15.3	11.8
2009	3.1	344.9	266.9	184.1	39.5	33.0	24.5	0.0	25.0	0.0	15.1
2010	10.7	356.2	336.3	173.5	71.3	26.6	28.4	3.4	31.7	0.0	3.7
2011	5.0	332.1	296.3	174.2	51.7	75.4	19.4	24.1	2.9	11.0	13.1
2012	1.9	236.0	248.2	121.4	37.4	29.2	20.5	21.3	6.2	1.9	5.3
2013	9.2	244.4	244.7	147.2	38.4	33.3	12.9	9.1	20.6	0.0	20.6
2014	3.1	201.3	283.4	152.1	62.2	26.2	14.4	7.7	7.2	2.5	6.4
2015	2.1	103.8	179.9	87.4	72.0	28.8	23.1	11.9	9.1	12.0	11.0
Upper Peninsula females											
1992	1.1	35.0	92.7	58.5	87.1	50.2	17.6	0.6	40.2	0.0	55.9
1993	1.1	70.7	55.1	101.9	30.7	78.6	0.0	32.7	0.0	35.7	36.2
1994	1.1	42.0	134.7	57.6	66.3	16.9	58.0	11.8	31.0	0.0	56.1
1995	1.1	106.1	83.5	122.6	31.3	46.4	40.1	60.8	11.3	41.1	74.6
1996	0.0	69.5	114.6	25.0	79.4	39.7	14.9	24.3	31.9	0.0	48.2
1997	1.1	78.8	86.1	79.0	51.3	35.1	7.4	31.7	0.0	31.9	50.4
1998	2.2	96.4	130.2	48.8	96.9	29.8	26.4	39.4	9.1	20.5	53.5
1999	3.4	96.0	139.5	75.5	64.1	66.3	20.2	21.4	28.9	0.0	60.3
2000	6.9	141.5	166.8	136.9	86.9	61.2	65.7	10.6	11.4	22.8	75.7

TABLE 4.4 (cont'd)

2001	0.9	159.4	209.9	123.9	61.6	55.9	50.3	37.3	39.4	0.0	76.1
2002	3.1	146.2	208.0	130.0	84.6	70.3	38.5	36.4	33.4	3.1	132.1
2003	4.2	165.3	200.2	110.0	58.4	76.3	39.3	48.4	5.4	29.6	66.8
2004	3.1	156.6	164.3	127.7	68.9	71.6	29.8	38.8	5.1	33.0	74.1
2005	5.7	169.7	178.6	92.1	89.2	16.2	58.4	22.2	33.4	0.0	78.2
2006	4.2	174.4	199.9	108.4	86.1	60.6	37.1	49.7	9.6	35.9	85.9
2007	4.8	173.9	156.8	120.3	42.4	64.1	43.9	25.2	31.1	8.3	100.2
2008	4.7	151.6	207.6	112.7	67.5	48.5	35.5	23.0	37.8	0.0	81.1
2009	1.1	137.0	171.6	108.2	65.7	61.9	7.6	52.0	6.9	8.1	90.9
2010	6.9	161.9	165.7	133.5	64.0	46.3	29.7	40.8	7.0	14.7	66.6
2011	4.5	160.5	154.2	119.1	41.7	81.1	0.0	37.4	30.0	34.0	53.3
2012	2.2	131.1	127.6	88.0	62.6	29.9	50.2	0.0	51.4	0.0	73.6
2013	1.0	73.8	127.3	99.9	59.7	14.8	42.5	31.1	13.9	6.8	57.1
2014	1.0	90.2	123.6	88.0	24.9	40.5	4.3	30.5	8.1	15.1	46.2
2015	2.1	109.7	140.5	114.1	62.7	51.0	33.6	23.8	27.8	27.4	38.0

Northern Lower Peninsula males

1992	1.1	17.8	11.8	13.9	0.0	3.4	0.9	0.0	0.2	0.0	1.2
1993	1.0	40.2	17.8	14.7	4.2	0.4	4.3	0.0	4.9	0.0	3.2
1994	0.0	14.0	14.0	15.3	6.1	2.8	0.0	4.0	3.1	0.0	0.4
1995	0.0	31.6	19.1	14.2	1.4	2.0	0.0	1.3	0.0	3.1	0.0
1996	0.0	18.2	20.0	6.2	10.3	4.2	0.0	9.5	0.0	1.5	5.0
1997	0.0	26.4	24.5	26.8	0.0	8.2	0.0	3.5	0.0	5.1	5.5
1998	0.0	46.3	34.3	14.0	11.3	0.0	5.3	0.0	1.3	0.3	3.9
1999	0.0	54.9	24.3	17.7	11.9	3.2	0.0	0.0	6.5	0.0	2.5
2000	2.1	55.2	30.7	13.4	9.2	2.1	0.0	1.0	0.0	0.8	0.0
2001	0.0	59.8	33.9	11.0	12.4	1.4	5.4	0.1	0.7	1.7	0.0
2002	2.0	63.3	43.1	20.3	17.2	11.7	7.6	2.9	0.0	0.0	3.0
2003	3.0	94.2	44.9	29.4	11.9	3.8	4.9	0.0	6.3	0.0	2.4
2004	0.7	79.9	64.6	24.4	12.2	6.6	5.1	0.0	6.8	0.0	1.9
2005	1.0	43.8	30.9	12.9	19.0	6.0	2.7	5.9	0.0	5.0	0.0
2006	2.8	60.8	85.1	29.5	19.2	9.8	4.7	5.9	0.0	8.3	2.0
2007	0.0	75.1	41.4	30.0	14.6	0.0	1.5	0.0	3.5	1.4	1.3
2008	5.0	98.9	86.8	48.3	16.6	5.6	7.2	4.7	0.0	3.4	0.0
2009	1.8	90.2	35.5	31.9	16.7	9.6	0.0	6.4	3.9	0.0	8.2
2010	1.9	52.5	60.2	31.7	16.3	7.1	0.0	3.3	6.3	0.0	0.1
2011	1.0	50.5	62.7	25.5	10.0	10.3	2.3	4.1	3.4	0.0	0.9
2012	0.9	64.1	39.2	11.9	0.0	7.3	3.0	1.6	0.0	1.5	0.0
2013	2.1	36.6	34.9	28.0	12.3	5.0	6.6	0.0	3.6	0.0	2.4
2014	3.1	41.4	35.3	11.6	19.7	6.1	4.1	0.0	0.7	0.0	0.9
2015	1.8	55.6	52.2	32.8	21.1	2.9	0.0	8.6	1.2	0.0	0.2

TABLE 4.4 (cont’d)

Northern Lower Peninsula females

1992	0.0	21.1	20.9	8.1	11.8	1.4	7.6	0.0	5.3	0.0	5.5
1993	0.0	21.6	22.3	10.3	3.4	11.9	0.0	6.6	0.0	6.4	3.8
1994	1.0	21.0	22.8	5.3	8.4	1.3	1.4	5.4	0.0	0.4	9.2
1995	0.0	16.0	12.5	13.5	11.1	0.0	8.3	0.0	2.6	0.0	4.3
1996	1.2	17.3	16.3	2.1	10.0	0.3	0.0	4.9	0.1	0.0	4.9
1997	0.0	28.2	29.4	12.8	6.9	0.0	6.3	0.0	4.6	0.0	7.0
1998	0.0	27.3	12.2	7.4	5.9	1.7	8.5	0.4	6.3	0.0	4.6
1999	0.0	16.8	32.2	21.0	3.0	2.2	7.3	0.0	2.9	0.0	7.8
2000	0.0	30.4	28.2	11.1	11.4	1.1	7.5	0.9	2.4	2.5	7.8
2001	1.1	28.3	57.5	9.0	10.4	4.0	3.0	9.4	0.0	0.0	11.9
2002	0.0	35.5	52.2	18.9	25.3	13.0	7.1	5.7	14.9	2.3	2.9
2003	0.0	46.3	71.3	26.9	13.0	24.9	0.0	11.0	0.0	12.8	16.0
2004	2.3	34.3	61.2	19.7	27.2	5.0	4.0	7.8	0.0	2.0	17.3
2005	0.0	26.0	43.9	16.1	9.7	0.6	0.5	12.9	0.0	7.4	10.5
2006	2.2	27.8	60.1	32.1	12.0	19.3	0.0	7.8	0.0	5.4	6.0
2007	1.0	56.5	47.7	25.5	10.4	12.9	5.9	10.2	0.0	0.0	10.2
2008	2.1	45.7	74.9	16.6	23.3	4.8	28.4	0.0	15.8	0.0	25.9
2009	2.3	48.3	60.3	25.3	24.9	13.4	24.6	4.9	11.2	0.0	16.6
2010	1.1	44.9	44.3	12.5	11.3	8.2	10.0	6.5	0.0	7.0	12.0
2011	0.0	25.3	36.4	19.4	5.8	9.4	5.2	10.5	0.0	2.0	17.4
2012	1.1	37.6	53.9	13.2	27.6	9.8	5.9	4.9	3.1	5.1	14.4
2013	0.0	22.4	44.3	15.5	16.2	4.6	7.4	6.9	7.5	6.9	9.9
2014	0.0	19.3	45.0	23.1	9.5	2.2	14.0	0.0	8.4	5.3	6.1
2015	2.3	38.2	36.3	17.7	14.8	0.0	12.1	1.9	4.1	3.0	7.1

TABLE 4.5. Estimates of the number of bear hunters in Michigan, USA, 1992-2015.

	UP			NLP		
Year	Total Hunters	Bait Only Hunters	Other Hunters	Total Hunters	Bait Only Hunters	Other Hunters
1992	3418	2617	801	964	774	190
1993	3525	2576	949	1029	871	158
1994	3720	2855	865	860	725	135
1995	4159	3138	1021	842	707	135
1996	4681	3722	959	904	746	158
1997	4724	3795	929	974	804	170
1998	4959	3949	1010	997	799	198
1999	5498	4399	1099	1006	836	170
2000	6301	5048	1253	1058	879	179
2001	6477	5223	1254	1247	1046	201
2002	6932	5683	1249	1626	1421	205
2003	6919	5810	1109	1695	1520	175
2004	7045	5764	1281	1653	1510	143
2005	7281	6047	1234	1567	1376	191
2006	7286	6067	1219	1608	1455	153
2007	7200	6018	1182	1653	1471	182
2008	7618	6412	1206	1888	1675	213
2009	6661	5618	1043	1592	1427	165
2010	6973	5871	1102	1123	1005	118
2011	6803	5800	1003	1142	1026	116
2012	4781	4041	740	860	762	98
2013	4870	4096	774	754	677	77
2014	4783	4032	751	715	640	75
2015	4279	3603	676	711	608	103

TABLE 4.6. Estimates of the yearling and adult black bear pre-harvest population from capture-mark-recapture surveys in the Upper Peninsula and northern Lower Peninsula of Michigan, USA, 1992-2013.

	UP		NLP	
Year	$\widehat{N}$	SE	$\widehat{N}$	SE
1992	8059	1033		
1993	7062	761		
1998	9312	1160		
2000	11514	1362		
2002	8917	845		
2003			2011	299
2004	10631	1182		
2005			1675	362
2007	10939	1376		
2009			1473	202
2010	7898	878		
2012	9879	1384		
2013			1369	270

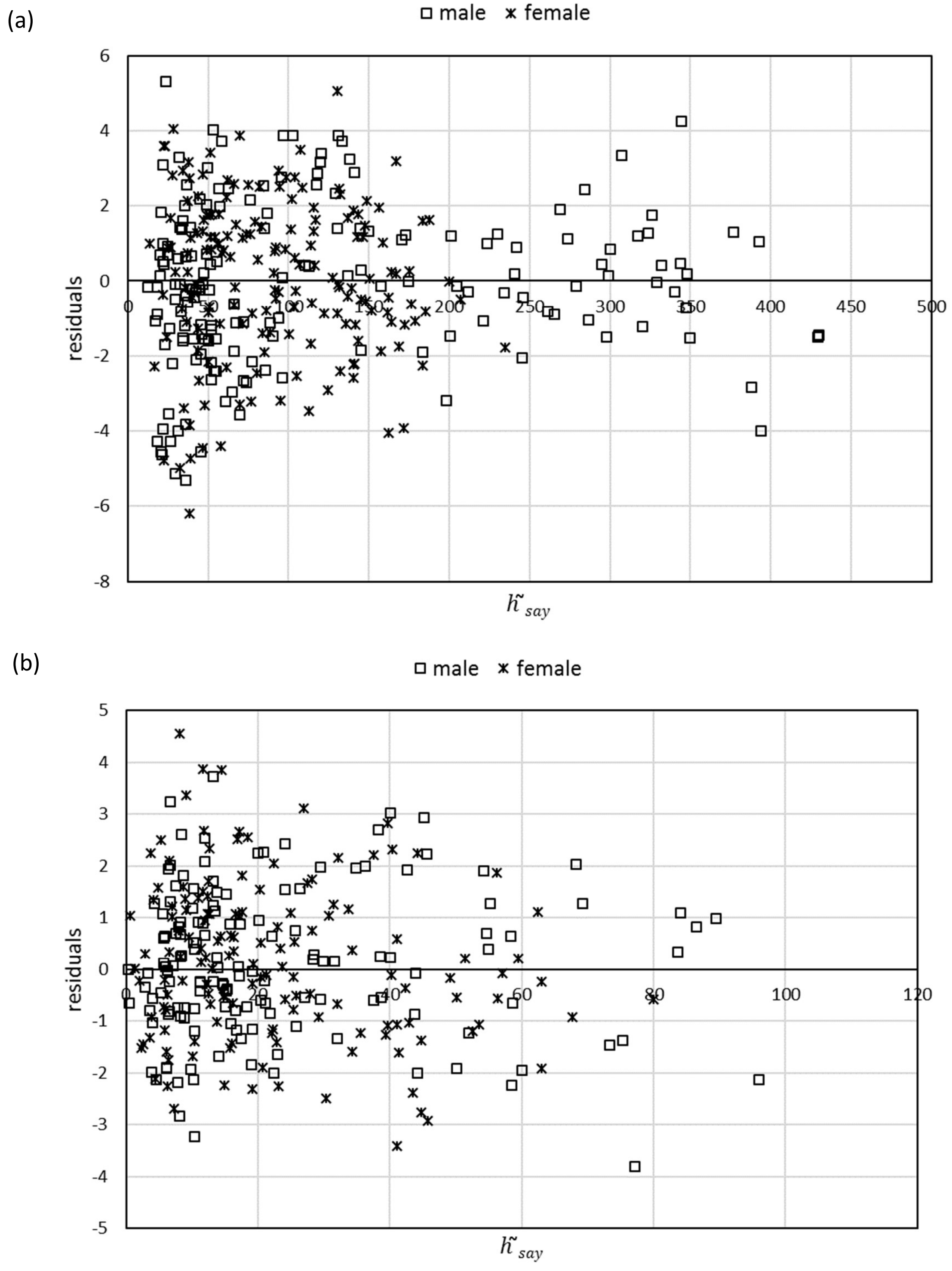

FIGURE 4.3. Residual plots from statistical catch-at-age models (model $M_{log}C_{lin}$) fit to harvest data of black bears from the (a) Upper Peninsula and (b) northern Lower Peninsula of Michigan, USA, 1992-2015.

model (Figure 4.4). The UP population estimates showed a slight tendency to increase in the beginning of the time series, and then showed similar results from 2004 and onward. The NLP population estimates showed a trend only in that the population trend shifted scale slightly as additional mark-recapture estimates became available in 2009 and 2013. In both regions, we dropped some years from the retrospective analysis because the model could not converge on a solution. The convergence failures were likely due to the highly parameterized model. Some parameters may not have been estimable when fewer data was available in earlier years.

We did not have any independent data that were directly comparable to the annual output of the model, but we assumed that the proportion of adult females breeding as estimated from cementum analysis (Chapter 3) would show a similar pattern to the estimated number of recruits per female of reproductive age if the model estimates were valid. In the UP, both values showed a generally increasing trend over time and reflected similar patterns of peaks and valley (Figure 4.5a). In the NLP, the relationship between the 2 values was less pronounced, but both showed a decline in the last few years and showed several similar peaks and valleys (Figure 4.5b). Taken together with the other model evaluation results, we concluded the model structures were sufficient to continue with further analysis.

Model Selection

In the UP, we dropped the $M_{log}C_{quota}$ model from consideration because the parameter estimation procedure could not converge on a global minimum in the objective function. Of the remaining models, there was strong support for models MC_{quota}, $M_{log}C_3$, and MC_5 (Table 4.7). There was little support for the models that incorporated changes in catchability due to

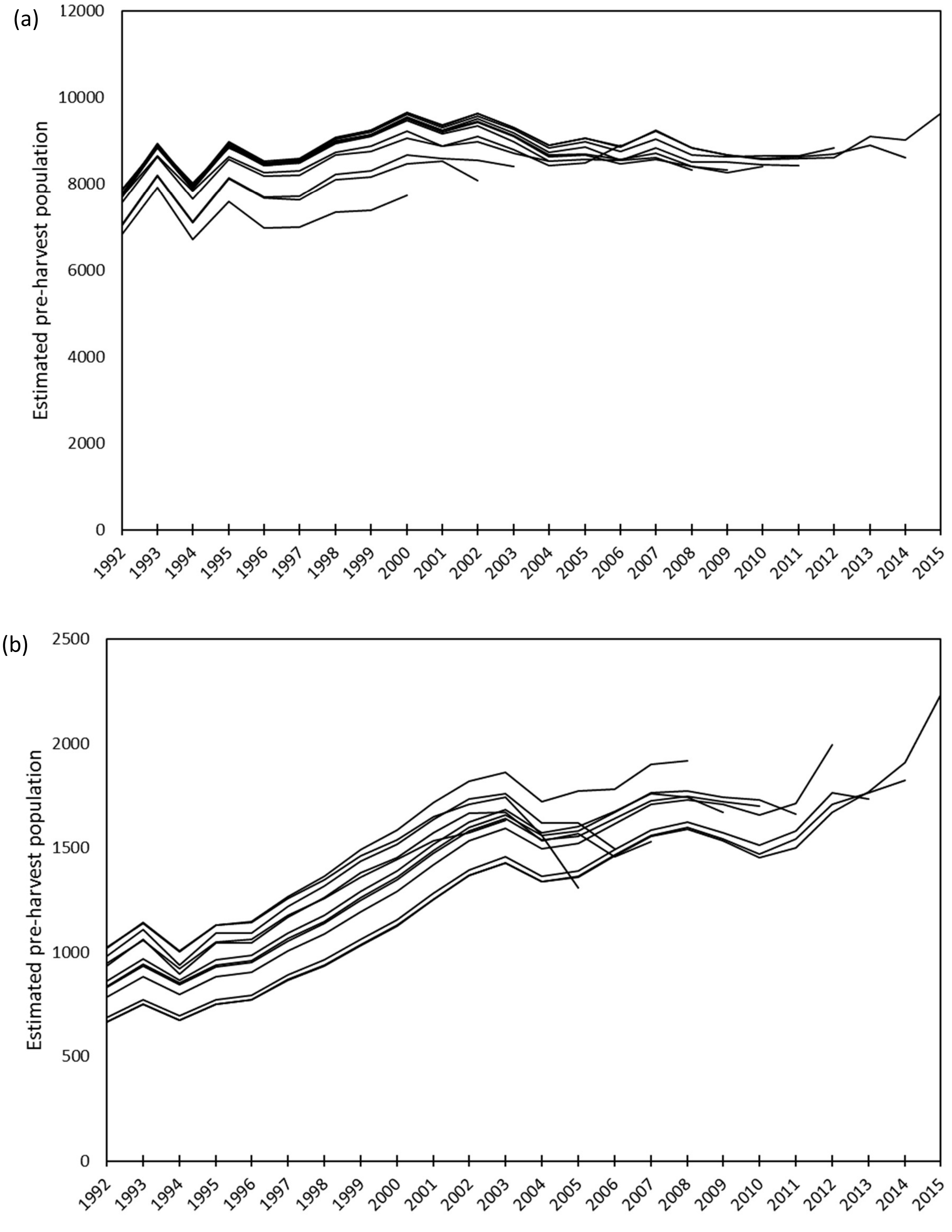

FIGURE 4.4. Retrospective plots of statistical catch-at-age analysis (model $M_{log}C_{lin}$), of black bears in the (a) Upper Peninsula and (b) northern Lower Peninsula of Michigan, USA, 1992-2015.

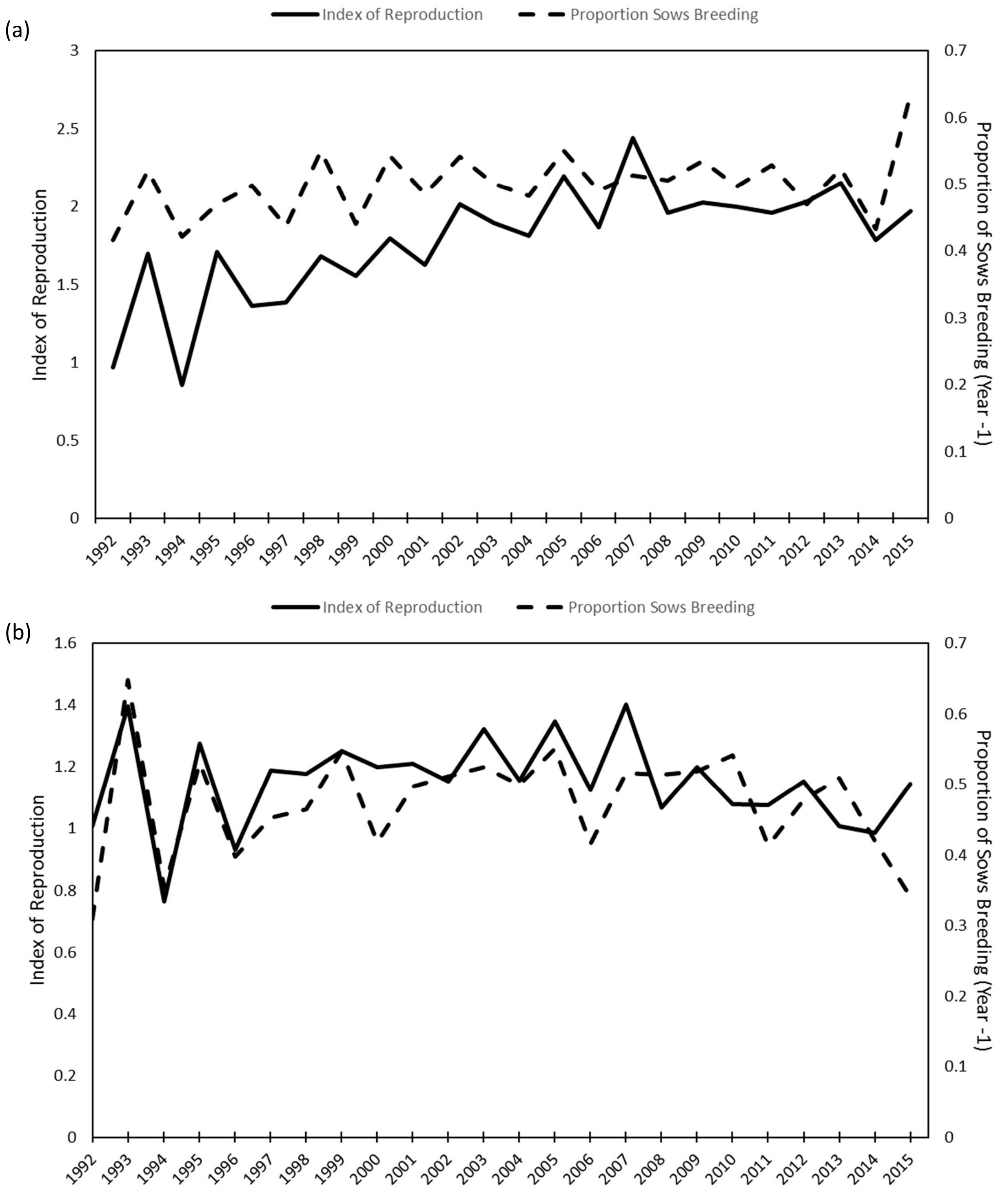

FIGURE 4.5. Comparison of an index of reproduction from a statistical catch-at-age analysis (model $M_{log}C_{lin}$) of black bears in Michigan, USA, to the proportion of adult females breeding from analysis of cementum annuli spacing in the (a) Upper Peninsula and (b) northern Lower Peninsula, 1992-2015.

TABLE 4.7. Statistical catch-at-age models of black bears of the Upper Peninsula and Northern Lower Peninsula of Michigan, USA.

Model	# parameters	AIC	ΔAIC	w_i
		Upper Peninsula		
MC_{quota}	50	2538.89	0.00	0.358
$M_{log}C_3$	50	2539.01	0.12	0.337
MC_5	48	2539.80	0.91	0.227
MC_{2005}	56	2542.65	3.76	0.055
$M_{log}C_5$	52	2545.18	6.29	0.015
MC_3	46	2546.76	7.87	0.007
$M_{log}C_{2005}$	60	2550.57	11.68	0.001
MC_{lin}	56	2555.69	16.80	<0.001
$M_{log}C_{lin}$	60	2561.06	22.17	<0.001
		Northern Lower Peninsula		
MC_{2005}	53	1438.35	0.00	0.878
MC_5	45	1443.97	5.62	0.053
$M_{log}C_{quota}$	51	1444.16	5.81	0.048
$M_{log}C_{2005}$	57	1446.35	8.00	0.016
MC_3	43	1449.44	11.09	0.003
$M_{log}C_5$	49	1451.97	13.62	<0.001
$M_{log}C_3$	47	1457.33	18.98	<0.001
MC_{lin}	53	1459.75	21.40	<0.001
$M_{log}C_{lin}$	57	1467.75	29.40	<0.001
MC_{quota}	47	1811.61	373.26	<0.001

changes in technology (C_{2005} and C_{lin} models). The results suggested that catchability was either constant over time or affected by higher number of licenses offered from 2000 to 2011. With strong support for multiple models, we could have chosen to use model averaging of results. Because we were interested in identifying one primary model and to simplify modeling procedures, we present all additional results from model MC_{quota}. Major results from models $M_{log}C_3$ and MC_5 are presented in Appendix 4E to demonstrate the sensitivity of model results to model selection.

In the NLP, Akaike weight was concentrated in the MC_{2005} model (Table 4.7), which supports constant non-harvest mortality over age and a temporal shift in catchability, which may be related to changes in technology over time. As in the UP, we were interested in identifying one primary model, so we present all additional results from model MC_{2005}.

(To ensure there were no major concerns with the fit of the final selected models, we provide model evaluation results for the UP MC_{quota} model and the NLP MC_{2005} model in the Appendix 4F).

Demographic Results

The results of the UP MC_{quota} model and the NLP MC_{2005} model show a stable to slightly increasing bear population in the UP and an increasing population in the NLP from 1992 to 2015 (Figure 4.6). The UP shows a higher proportion of females in the population than the NLP (Figure 4.7), but both show an increasing proportion of younger bears over time (Figure 4.8). The estimated total number of recruits was higher in the UP due to the larger population, but the number of recruits per female of reproductive age was higher in the NLP (Figure 4.9).

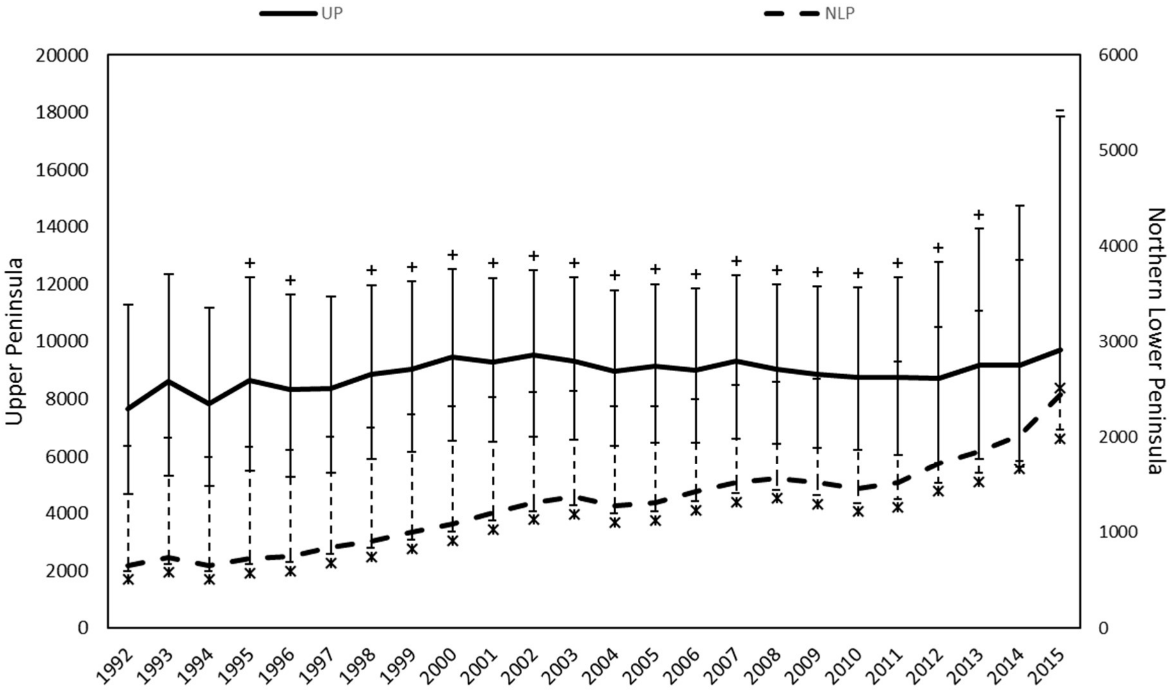

FIGURE 4.6. Estimated pre-harvest population of black bears in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, from a statistical catch-at-age model, 1992-2015. Error bars represent 95% profile likelihood confidence intervals. Error bars marked with star represent 95% Wald confidence intervals based on the asymptotic standard error. Error bars marked with a cross represent 95% profile likelihood confidence intervals conditional on a fixed λ.

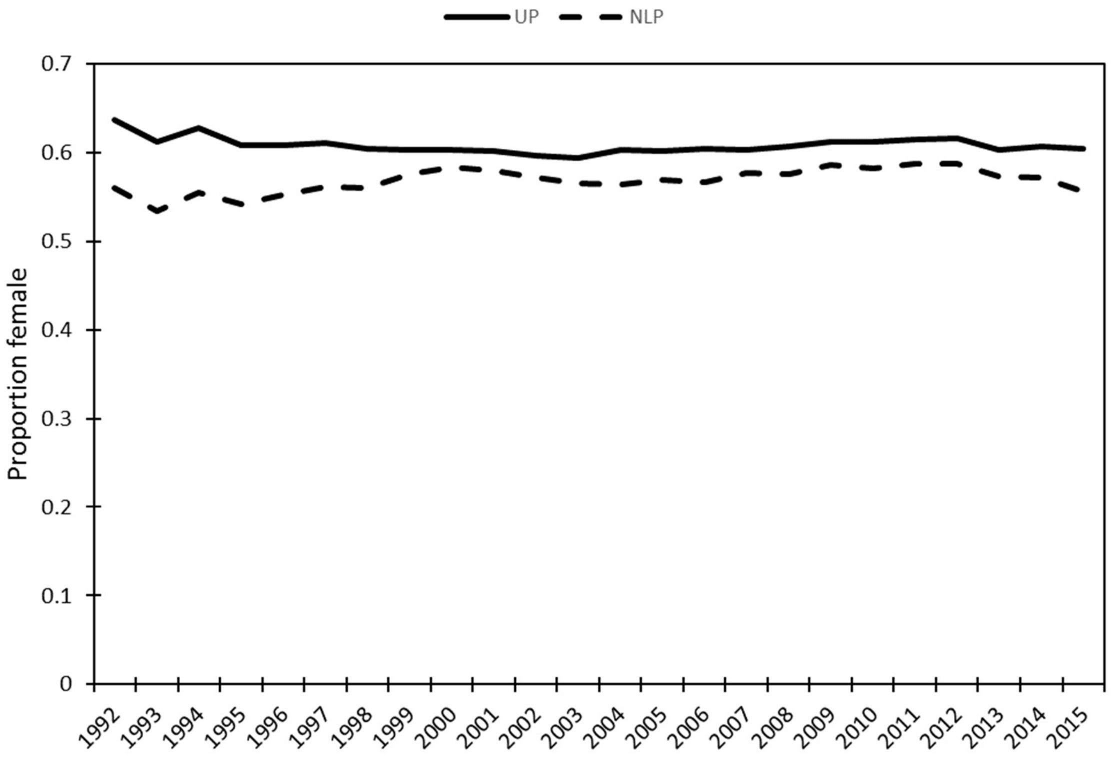

FIGURE 4.7. Proportion females in the estimated pre-harvest population from a statistical catch-at-age analysis of black bears in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, 1992-2015.

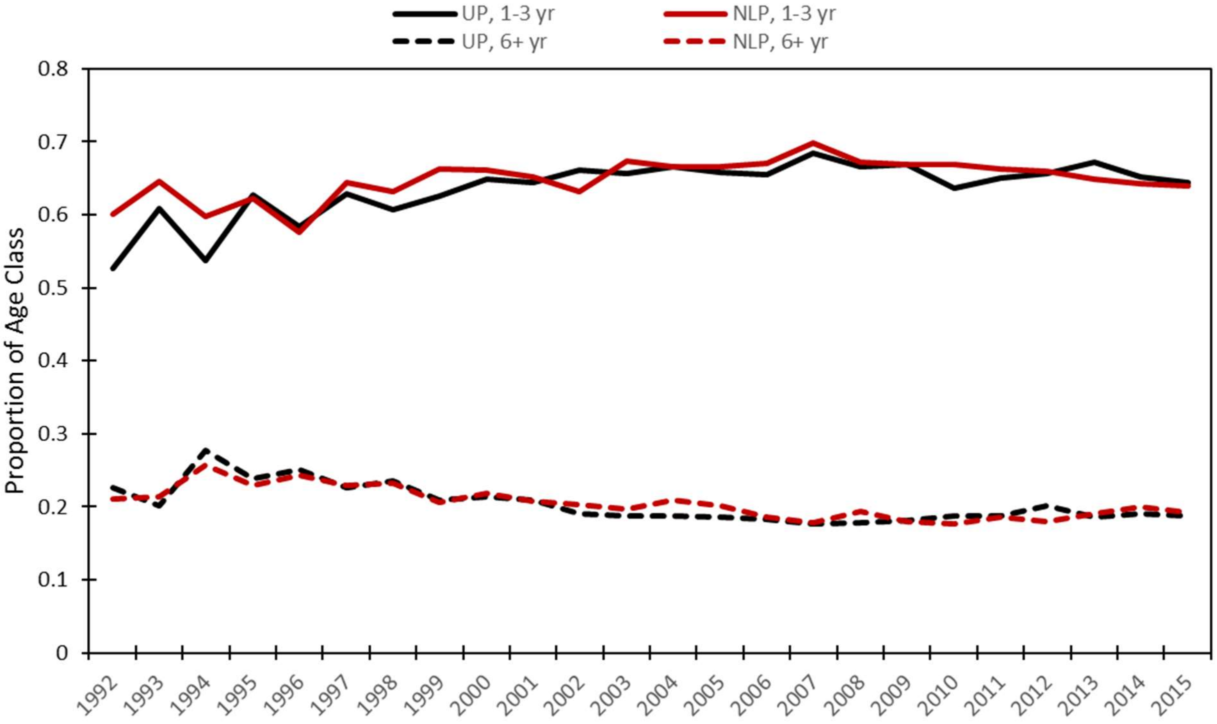

FIGURE 4.8. Proportion of 1- to 3-year-old bears and 6+-year-old bears in the estimated pre-harvest population from a statistical catch-at-age analysis of black bears in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, 1992-2015.

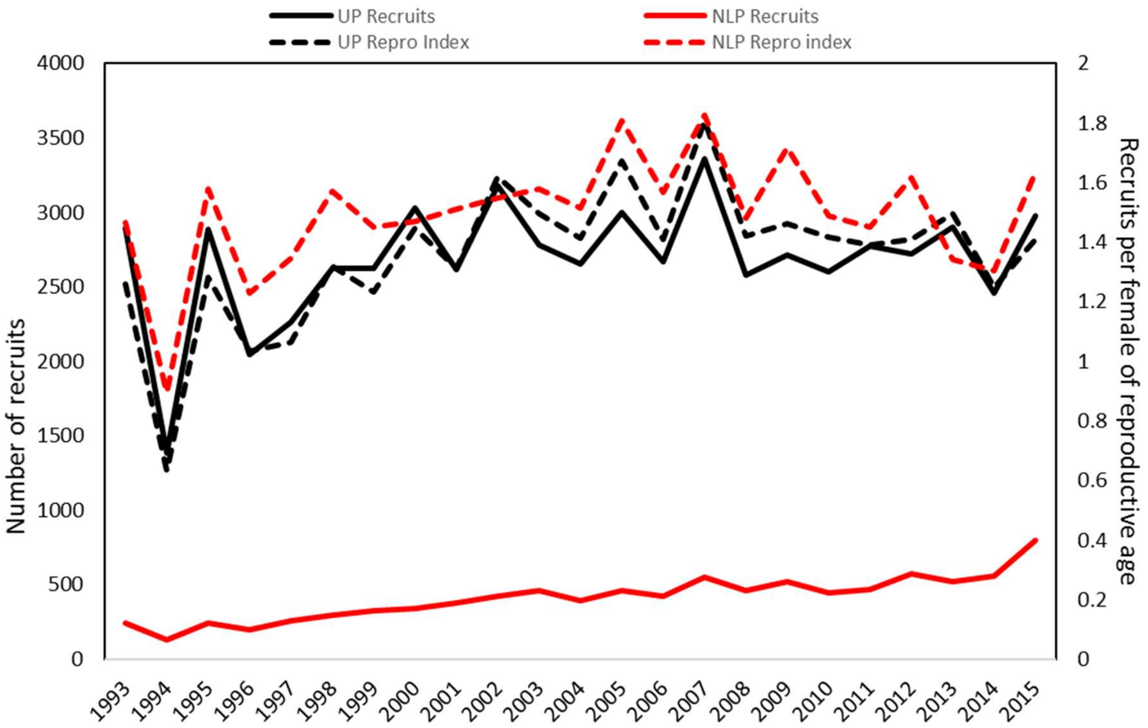

FIGURE 4.9. Estimates of recruitment from a statistical catch-at-age analysis of black bears in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, 1993-2015.

Mortality rates were also different between the 2 regions. In most cases, 1-year-old bears had lower harvest mortality rates than older bears and 2-year-old bears had the highest harvest mortality rates. The NLP harvest rates were higher than the UP harvest rates, however, and markedly so among females (Figure 4.10). In contrast the estimated NLP survival rates were higher than the UP for both males and females (Table 4.8).

Sensitivity Analysis

By modifying the data and the model structure, we were able to determine the sensitivity of the model to data uncertainty and assumptions we made throughout model development. Both the UP and the NLP models demonstrated little sensitivity to our assumptions that the registration data was complete and unbiased and to our estimates of the recruit sex ratio, sexing error, and aging error (Figure 4.11 and Figure 4.12). The NLP model also showed little sensitivity to the fixed initial population size of 4-year-old males (Figure 4.12). In all of these scenarios, the pre-harvest population estimate shifted slightly but demonstrated the same temporal trends. The temporal trend in the UP pre-harvest population estimates was slightly different between the base model and the model that differentiated between bait hunters and all other hunters (Figure 4.11). When we fixed survival rates, the NLP estimates increased in scale above the base scenario but showed similar trends (Figure 4.12). The UP population estimates differed in both trend and scale from the base, although 2 of the scenarios failed to converge. In both regions, fixing survival led to estimates of recruits per female of reproductive age that showed a steep increase over time, as compared to the more stable estimates of the base scenario (Figure 4.13). The UP model was most sensitive to the use

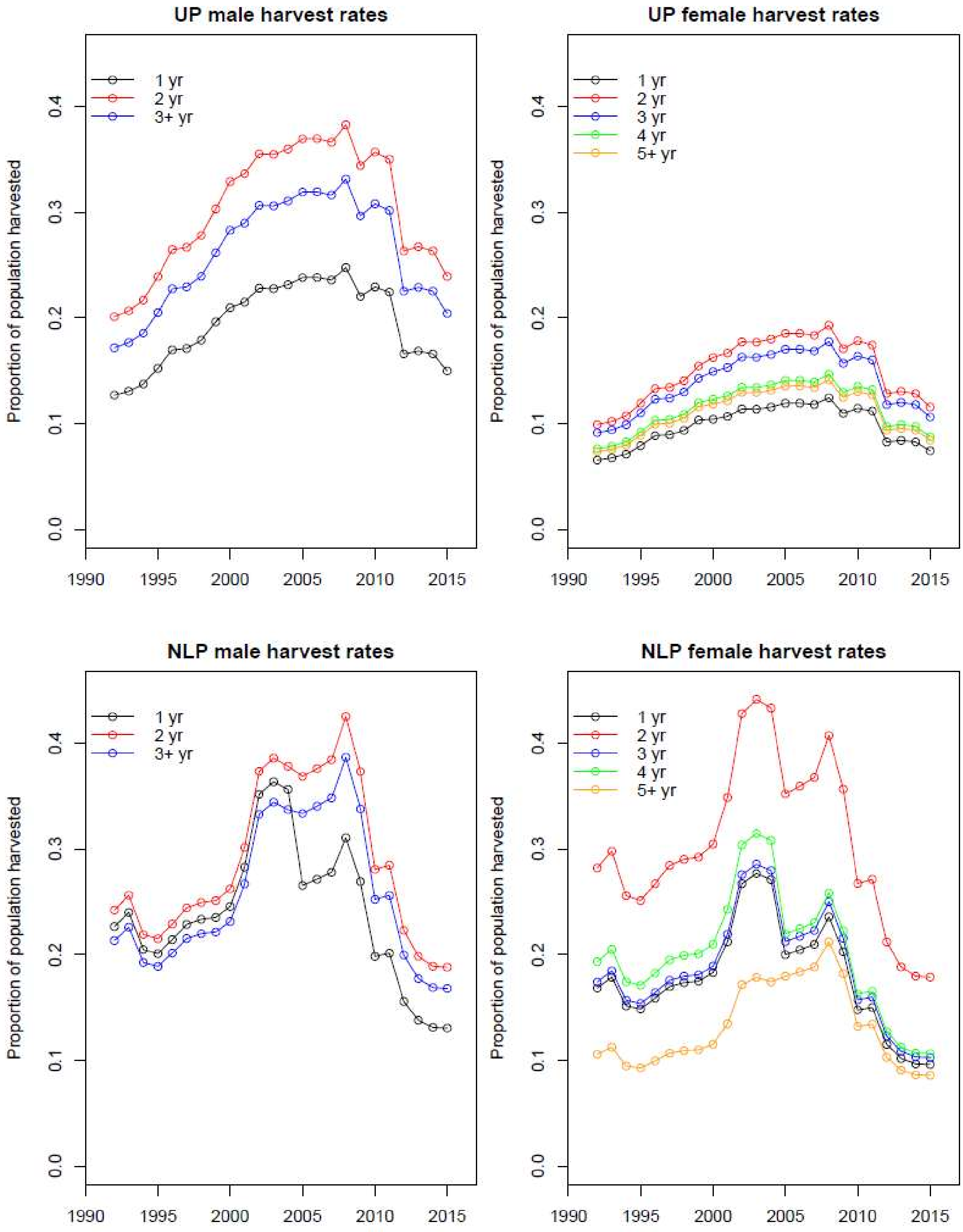

FIGURE 4.10. Estimates of harvest rates from a statistical catch-at-age analysis of black bears in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, 1992-2015.

TABLE 4.8. Estimated non-harvest survival rates from a statistical catch-at-age analysis of black bears in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, 1992-2015.

Sex	UP	NLP
Male	0.795	0.859
Female	0.886	1.0

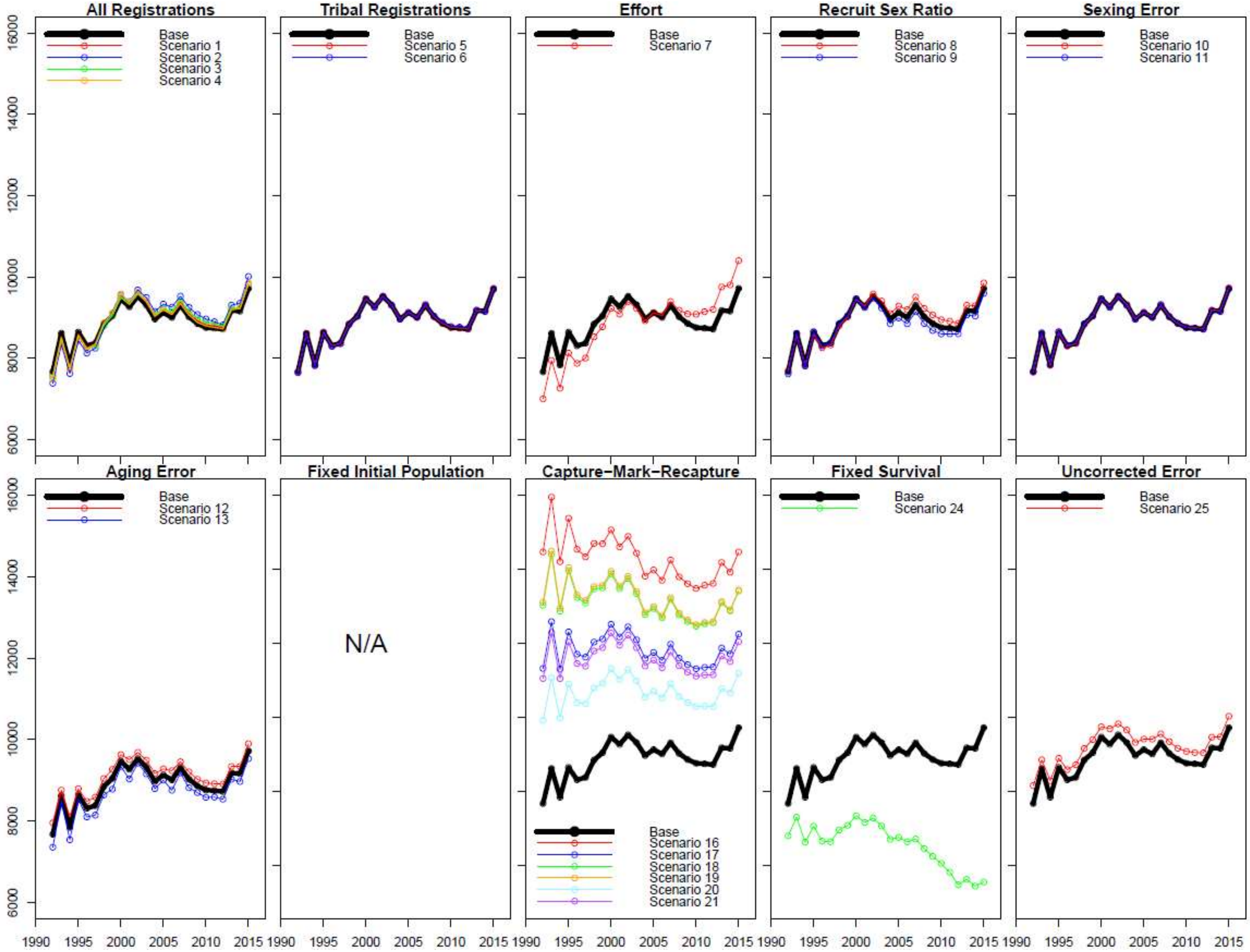

FIGURE 4.11. Estimated pre-harvest population abundance of black bears in the Upper Peninsula of Michigan, USA, 1992-2015, from a statistical catch-at-age analysis run under different scenarios (see Table 4.3 for descriptions).

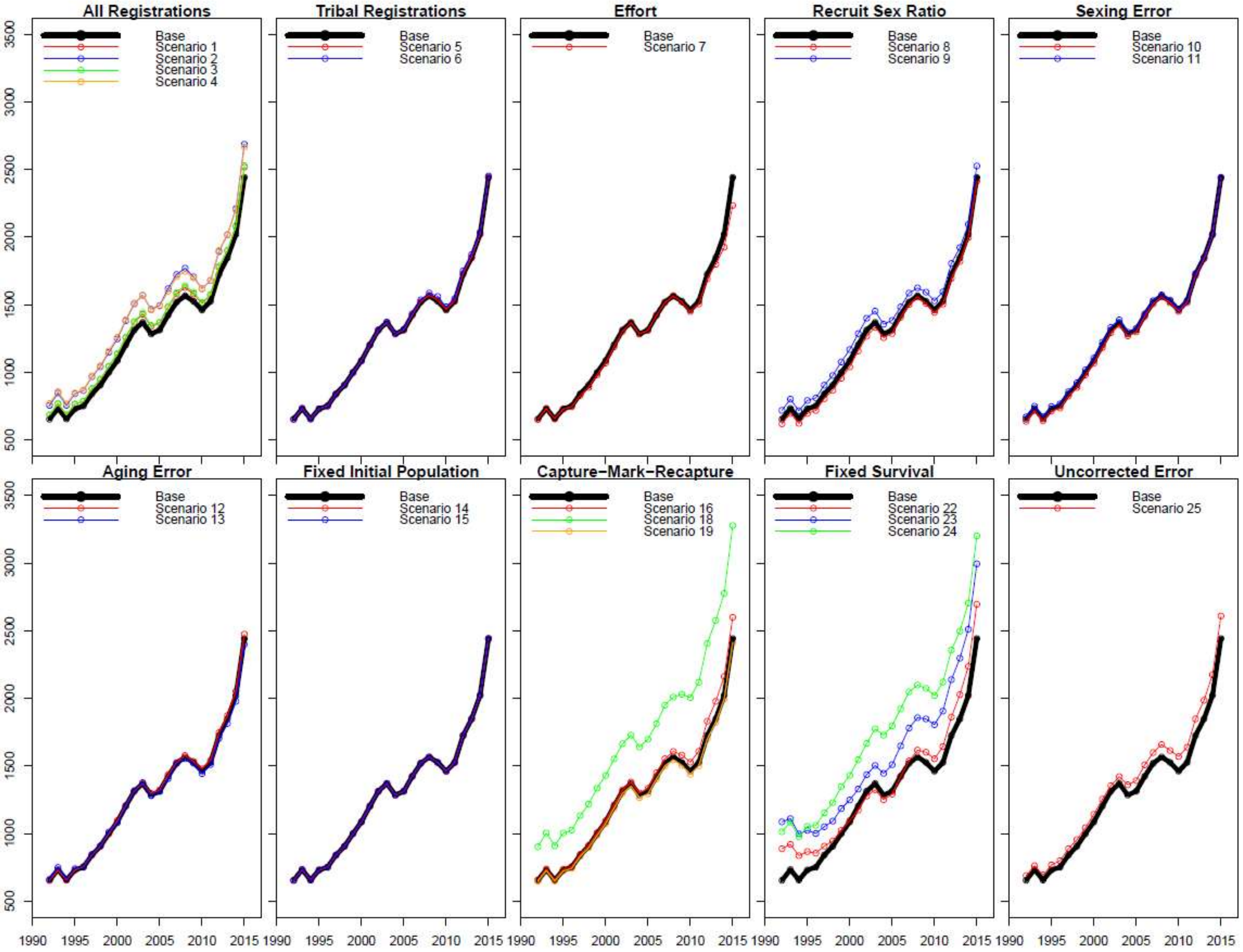

FIGURE 4.12. Estimated pre-harvest population abundance of black bears in the northern Lower Peninsula of Michigan, USA, 1992-2015, from a statistical catch-at-age analysis run under different scenarios (see Table 4.3 for descriptions).

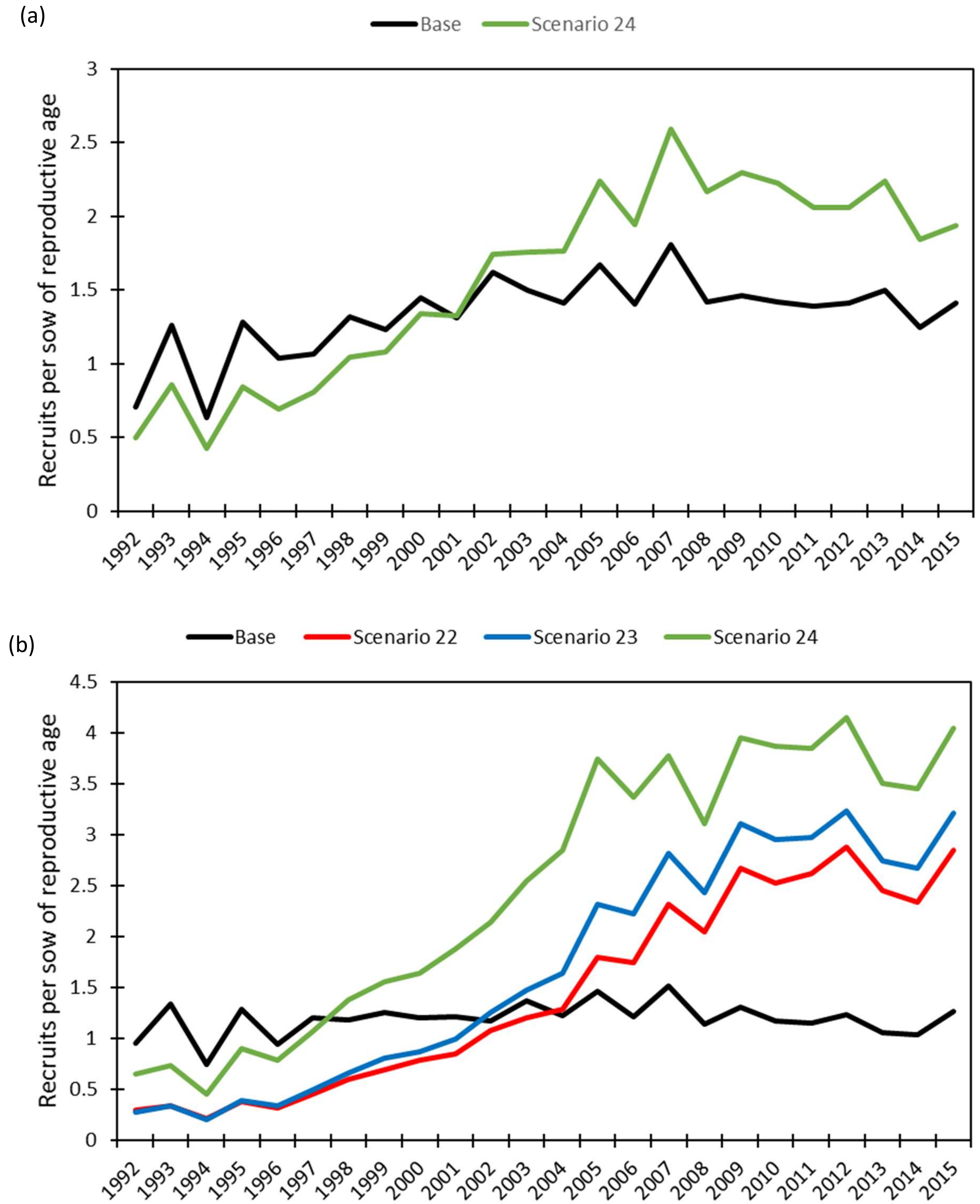

FIGURE 4.13. Estimated recruits per black bear female of reproductive age in the (a) Upper Peninsula and (b) northern Lower Peninsula of Michigan, USA, 1992-2015, from a statistical catch-at-age analysis run under different scenarios (see Table 4.3 for descriptions).

of CMR estimates to penalize the negative log-likelihood. The pre-harvest population estimates were higher than the base scenario when we used fewer or no CMR data (Figure 4.11). The NLP model showed little sensitivity to the use of CMR estimates unless we used a single estimate in the mid-point of the time period (Figure 4.12).

Projections

The UP population showed evidence of density dependent recruitment ($P = 0.02$, $R^2 = 0.24$) with recruitment rate decreasing as population increased (Figure 4.14). The NLP showed little evidence of density dependent recruitment ($P = 0.82$, $R^2 < 0.01$) with no apparent relationship between recruitment and abundance (Figure 4.14). As a result, we implemented density dependent recruitment in the UP projection model but not in the NLP model. We estimated the projection year recruits in the UP as $r_y = -0.0001261P_y^2 + 1.22P_y$ based on the best fit linear model between estimated recruitment rate and estimated pre-recruitment population (Figure 4.14).

Projected 4 years into the future, the UP black bear population showed a stable to slightly decreasing trend under the 3 harvest scenarios (Figure 4.15). The NLP population showed an increasing trend under all 3 harvest scenarios (Figure 4.15). Maintaining harvest at the level of the 2015 harvest was projected to result in a 2% decline in the bear population of the UP and a 69% increase in the NLP over 4 years. Even increasing the harvest by 20% over the 2015 harvest led to only a 4% decline in the UP population and a 57% increase in the NLP population.

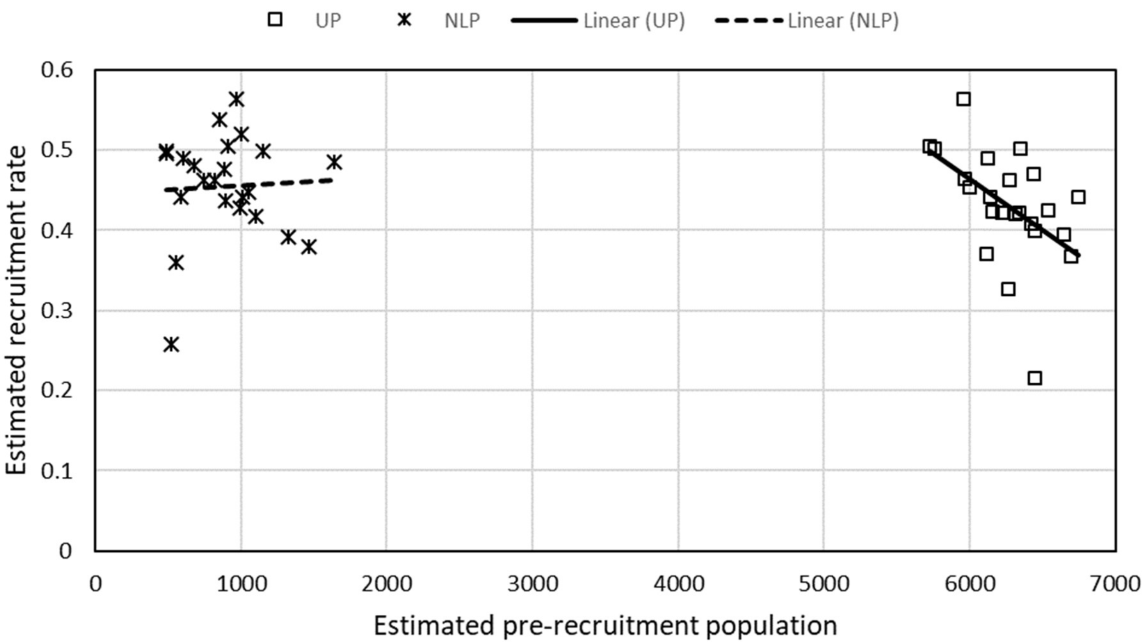

FIGURE 4.14. Annual estimated recruitment rate (number of 1-year-old bears per 2+-year-old bear in estimated pre-recruitment population) versus estimated pre-recruitment population from a statistical catch-at-age analysis of black bears in the Upper Peninsula (UP) and northern Lower Peninsula (NLP) of Michigan, USA, 1993-2015.

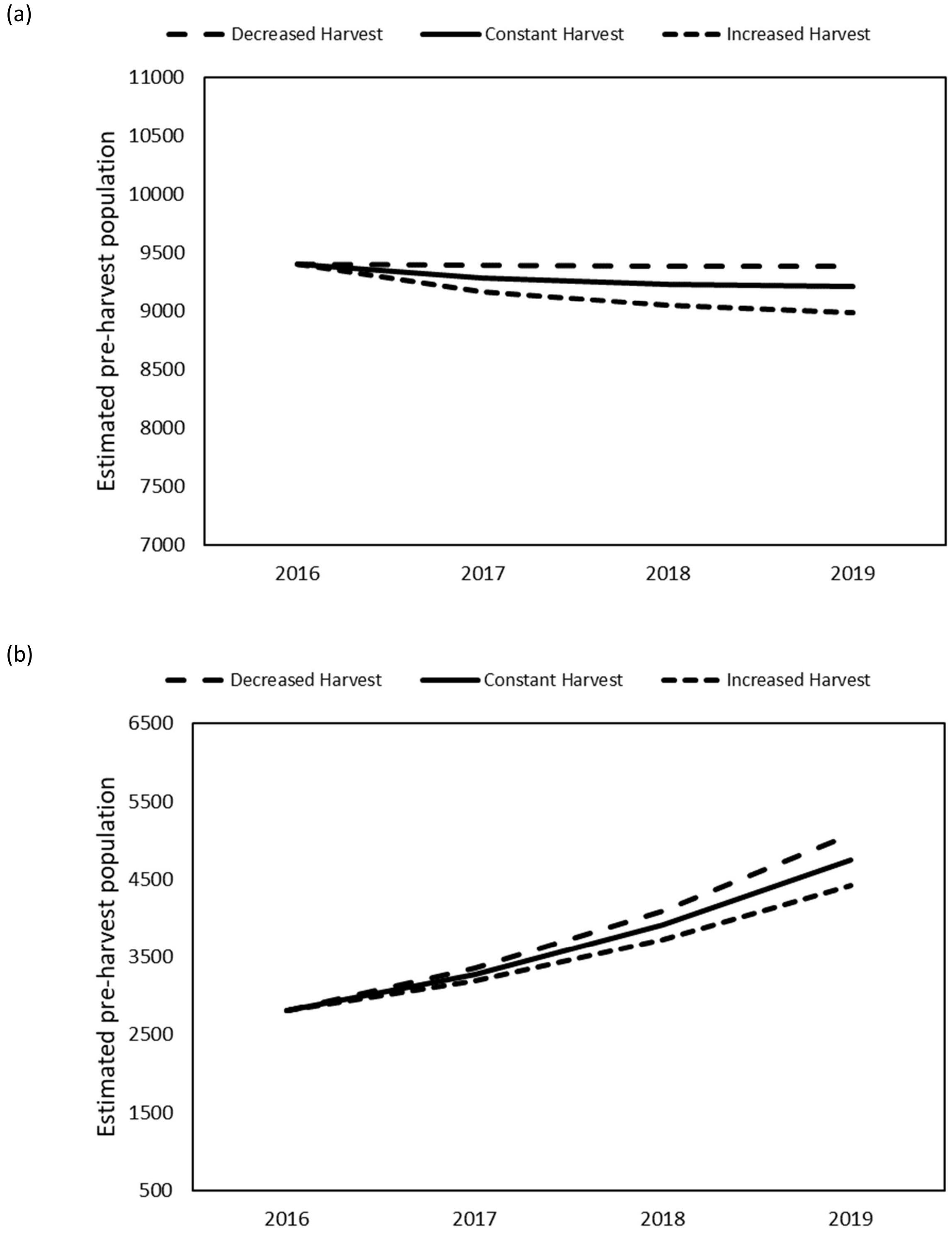

FIGURE 4.15. Projected pre-harvest population abundance, 2016-2019, of black bears in the (a) Upper Peninsula and (b) northern Lower Peninsula of Michigan, USA, under different harvest scenarios.

DISCUSSION

Model Evaluation

The estimate of primary interest from the Michigan black bear SCAA models was pre-harvest abundance due to its role in the DNR's harvest management process. We had no means to independently verify the abundance estimates from the SCAA models, but the trends over time are plausible. DNR biologists believe the NLP bear population was concentrated in the Red Oak unit during the early years of the model. Through the 1990s and 2000s, the western and southern population density increased, which would have led to an increase in the overall regional population. There is no evidence to support as dramatic a shift in the UP bear population over the same time period, however, which aligns with the slighter rising and falling UP estimates. Not only were the trends in abundance plausible given our understanding of Michigan's black bear population, they were robust to our assumptions and uncertainty (Figure 4.11 and Figure 4.12). Trends in abundance were consistent over all tested sensitivity scenarios except when we changed non-harvest survival in the UP, despite differences in scale when we made some or all CMR estimates unavailable. To maintain a consistent scale in estimated population abundance, we recommend the DNR incorporate all available CMR estimates in the SCAA models and maintain periodic CMR surveys into the future.

Most of the estimated demographic rates adhered to trends and patterns that we would expect based on published reports for other states and independent data available from Michigan. The estimated number of recruits (yearlings) per female of reproductive age fluctuated between 1.4 and 1.8 for the last 10 years of the model, with higher values in the NLP than in the UP as we found independently in Chapter 3. Since approximately 50% of females of reproductive age would produce young each year, doubling the recruits per adult female should give us an estimate of litter size. A litter size of 2.8-3.6 is slightly higher than we reported in Chapter 3, but not completely outside the range reported for other eastern North American black bear populations (Bridges et al. 2011).

Others have found that the primary cause of mortality in hunted bear populations is the harvest (Etter et al 2002, Koehler and Pierce 2005, Lee and Vaughan 2005), and the non-harvest mortality rates estimated from the SCAA models were higher than many reported for other harvested populations. Although the 1.0 survival rate for NLP females may seem biologically implausible, it is comparable to survival rates for other populations outside the hunting seasons. Etter et al. (2002) documented survival rates of 0.96-1.0 for radio-collared adult and sub-adult male and female black bears in the NLP for the months outside of the harvest season. Lee and Vaughan (2005) also documented 1.0 survival rates for 1- to 3-year-old bears during the non-harvest season in Virginia.

Harvest mortality rates differed over ages, sexes, and regions in predictable patterns. Females have some protection from harvest due to the injunction against harvesting females accompanied by cubs. Females also move less (Bunnell and Tait 1985) making them less vulnerable to harvest and have generally smaller bodies, making them less desirable to hunters. As expected, estimated harvest rates were, in most cases, lower for females than for males (Figure 4.10). This pattern has been seen before in Michigan (Etter 2002), Virginia (Lee and Vaughan 2005), Minnesota (Fieberg et al. 2010), and Pennsylvania (Diefenbach et al. 2004). The patterns in estimated harvest rates over age (Figure 4.10) can also be explained by the combination of hunter preference for larger (and therefore, likely older) bears and the higher vulnerability of 2-year-old bears that are often dispersing or exploring longer distances than adult bears (Lee and Vaughan 2003).

The models' estimated total annual mortality (combined harvest and non-harvest mortality) is approximately 40% and 45% for males in the NLP and UP, respectively, and 20% and 24% for females in the NLP and UP, respectively. The male annual mortality rates are higher than previously reported for Michigan (Etter et al. 2002) but not unprecedented for a harvested population (Sorensen and Powell 1998, Lee and Vaughan 2005, Tri et al. 2017). The female mortality rates were comparable to those reported for Michigan (Etter et al. 2002) and the Mid-Atlantic (Tri et al. 2017).

One of the benefits of the SCAA models is that they estimate all demographic parameters jointly from the same dataset, so the parameters must be consistent both with one another and with the age-at-harvest data. Thus, when we fixed the non-harvest mortality rates at lower values that were more consistent with the rates estimated in other studies, the model compensated for the lower mortality by adjusting the parameter estimates for catchability and recruitment. Estimates of recruits per female of reproductive age showed >3-fold increases over the time span of the model when we fixed non-harvest mortality and plateaued at values that suggest mean litter sizes of approximately 4 in the UP and 5-8 in the NLP (Figure 4.13). The dramatic temporal pattern and high litter sizes are biologically unrealistic and inconsistent with the reproductive data in Chapter 3, which makes the Scenario 22-24 abundance estimates (Figure 4.11, Figure 4.12) unreasonable.

Although the results of the base SCAA models were robust and reasonable, the models may potentially be sensitive to factors we could not assess. The most likely factor is the abundance of natural food (mast). Bear reproduction and vulnerability to harvest are both sensitive to mast abundance (Noyce and Garshelis 1997, Costello et al. 2003, Obbard et al. 2014). We likely see the effects of a mast failure in the peaks in reproduction (Figure 4.5) and in abundance (Figure 4.6) during the first 5 years of the model estimates in both regions. Other, less dramatic mast failures may have led to smaller peaks and valleys in the early 2000s. The models can account for mast failures in estimates of recruitment because they estimate total annual recruitment rather than mean fecundity parameters. Given the structure of the harvest rate equations, however, the models could not account for the effect of mast failures on catchability without additional data. If we could quantify mast abundance, we could modify the harvest equation (Table 4.1) by incorporating a mast index in the exponent. Fieberg et al. (2010) found that accounting for a natural food effect was important in an SCAA model of a simulated black bear population and led to more biologically plausible results when applied to data from the Minnesota black bear population.

We caution against heavy reliance on the projection models to predict effects of harvest on future populations more than a few years into the future. The projection models have some limitations. First, they assume that the future population demographic rates will be similar to those of the recent past. While this may be a reasonable assumption for the near future, unexpected events such as mast failure, significant weather events, disease outbreaks, or changes in harvest regulations or strategy could all impact the population survival, harvest mortality, and recruitment in unpredictable ways.

Second, the models assume the absolute magnitude of future harvests will be constant. We made this assumption to align the projections with the DNR's management planning strategy. The DNR sets license quotas to achieve a harvest objective. We used that desired future harvest in the projection models to facilitate evaluation of those objectives. If the size of the harvest is a function of both the size of the population and the total effort, then the harvest could not remain constant under constant effort unless the population was also constant.

Finally, we found evidence for density dependence in the UP, which allows the projection model to account for limitations of the region to support a growing population. Past populations in the NLP, however, have not demonstrated density dependence, so there is no limit to projected future growth in the projection model, which is unrealistic over the long term. Despite the limitations, the projection models should be useful for identifying the likely direction of change in the bear population over 2-4 years (1-2 management cycles) as this time frame is unlikely to be sufficient to cause gross violations in the models' assumptions or to result in major effects of habitat availability.

Management Implications

The SCAA models provide evidence of robust bear populations in both the UP and NLP. The UP population has been stable with only a 25% increase from its lowest point (in 1992) to its highest point (in 2015) (Figure 4.6). Given the evidence for density dependence in the recruitment rate (Figure 4.14), the population has limited growth potential. Czetwertynski et al. (2007) also found evidence of density dependent reproduction in black bear populations approaching carrying capacity. With stable harvest rates, the UP population is likely to remain stable into the future. In contrast, the NLP population has more than tripled from 1992-2015 (Figure 4.6) and may continue to grow at current harvest rates. The lack of evidence for density dependence suggests that the population is well below carrying capacity (Czetwertynski et al. 2007). At peak pre-harvest populations (2015 in both the UP and the NLP), the estimated bears per total area was approximately 0.23 bears per km^2 in the UP and 0.05 bears per km^2 in the NLP. While neither region is comprised entirely of suitable bear habitat, it is likely that the NLP has not yet reached its maximum bear population potential.

The Michigan bear populations have been stable to increasing despite higher annual mortality rates than average for black bears across eastern North American due to higher than average fecundity (Beston 2011). Beston (2011) suggests the large-scale tradeoff between lower survival and higher reproduction may be caused by habitat quality or anthropogenic pressures, although we have little information to assess which, or whether both, factors apply here. The same pattern does not apply at a smaller scale when comparing the UP and NLP regions, however. Averaged over age and sex classes, the UP black bear population exhibited higher mortality rates (Figure 4.10, Table 4.8) and fewer recruits per female of reproductive age (Figure 4.9) than the NLP. Local factors appear to limit the potential reproductive output of UP bears by raising the age of reproduction and lowering the litter size (Chapter 3). The lower availability of agricultural crops and other human-based food sources in the UP than in the NLP may be a factor (McDonald and Fuller 2001, Bridges et al. 2011).

The differences between the UP and NLP populations support different management approaches. The UP population has less expansion potential, higher non-harvest mortality, and lower reproductive potential and so can support lower harvest rates than the NLP to maintain a stable population. With low non-harvest mortality and high recruitment rates, the NLP population could expand rapidly if harvest rates declined and will likely continue to increase even if recent harvest rates are maintained.

Harvest is the primary tool by which the Michigan DNR manipulates the bear population to achieve its management goals. Michigan's bear management goals are to "1) maintain a sustainable bear population; 2) facilitate bear-related benefits such as recreational hunting; 3) minimize bear-related conflicts; and 4) conduct science-based bear management with socially acceptable methods. (Bump 2009)." The SCAA models we developed can play an integral role in achieving most of these goals. They provide the Michigan DNR with a science-based method to monitor bear populations and predict the effects of future harvests. The results show sustainable, and sometimes growing, bear populations in both the UP and the NLP that have offered abundant recreational hunting opportunities. The low non-harvest mortality rates and the high reproductive output of both regions allows thousands of hunters the opportunity to pursue bears each year. Continuing to collect the harvest and auxiliary data necessary to support the models and conducting periodic evaluations of model behavior will allow the Michigan DNR to continue to use the SCAA models to support bear management.

APPENDICES

APPENDIX 4A. Bears registered with unknown age and sex

Although Michigan bear hunters were required to report the sex of the bear they harvested to the DNR, hunters may not have always known the sex of the bear or registration staff may have forgotten to record the sex. When they registered their bear, hunters were also required to submit a tooth from the bear for age analysis. In some cases, registration staff were unable to collect a tooth (as when the skull was frozen), forgot to collect a tooth, or collected an insufficient tooth sample. In these cases, the age of the bear was unknown. The number of bears without a recorded sex represented at most 3.1% of the harvest and usually <2% (Table 4A.1) and the number of bears without a recorded age represents at most 10.8% of the harvest and usually <7% (Table 4A.2).

We assumed that the sex and age composition of the bears with unknown sex and age were the same as for those harvested in the same year with reported sex and age. Given the low proportion of the harvest that did not have a reported sex or age, there was little opportunity for bias, so the assumption seemed reasonable. We were able to test the assumption of the sex composition, however, by using genetic techniques to determine the sex of bears where sex was unreported at the time of registration.

From 2011-2015, DNR Wildlife Disease Lab staff extracted DNA from teeth using Qiagen DNeasy Blood and Tissue kit for bears when no sex was reported at the time of registration. Traditional PCR was then performed to determine the sex of individuals using a highly conserved mammalian zinc finger-Y-X locus and the testis-determining factor (Williams et al. 2011). Using Pearson’s chi-squared test, we compared the genetic sex breakdown of bears without a sex reported at the time of registration to the sex composition of those bears under our assumption that it would be the same as the sex composition of all other registered bears. In all but one year, the data did not refute our hypothesis (Table 4A.3).

Although we were unable to test our assumption for the unknown age bears, the most common reasons for unaged bears were frozen heads and inexperienced staff who either did not extract a tooth or extracted an insufficient tooth sample. Neither of those scenarios was likely biased toward any age class of bears, so we have no reason to believe our assumption was invalid.

TABLE 4A.1. Number of black bears harvested in Michigan, USA, with no sex reported at the time of registration, 1992-2015.

Year	Number of unknown sex bears	Unknown sex bears as % of harvest
1992	3	0.3
1993	1	0.1
1994	5	0.4
1995	7	0.5
1996	3	0.2
1997	11	0.9
1998	8	0.5
1999	13	0.8
2000	23	1.2
2001	20	1.0
2002	18	0.8
2003	18	0.8
2004	40	1.8
2005	27	1.4
2006	46	1.9
2007	24	1.1
2008	32	1.4
2009	30	1.4
2010	54	2.5
2011	42	2.0
2012	52	3.1
2013	28	1.7
2014	12	0.8
2015	11	0.6

TABLE 4A.2. Number of black bears harvested in Michigan, USA, with insufficient tooth sample submitted for aging, 1992-2015.

Year	Number of unknown age bears	Unknown age bears as % of harvest
1992	82	7.4
1993	77	6.2
1994	134	10.8
1995	89	6.2
1996	108	8.4
1997	77	6.0
1998	92	6.1
1999	116	6.7
2000	111	5.8
2001	102	4.9
2002	62	2.8
2003	77	3.3
2004	92	4.2
2005	80	4.1
2006	88	3.6
2007	212	10.0
2008	144	6.1
2009	88	4.2
2010	66	3.1
2011	103	5.0
2012	51	3.0
2013	40	2.5
2014	38	2.5
2015	35	2.0

TABLE 4A.3. Comparison of assumed sex of black bears harvested in Michigan, USA, with unreported sex by using sex ratio of bears harvested with reported sex to the actual sex determined through genetic testing.

Year	Number of bears harvested with unreported sex	Proportion male bears of those harvested with reported sex	Assumed sex of bears harvested with unreported sex		Genetic sex of bears harvested with unreported sex		χ^2 p-value
			male	female	male	female	
2011	21	0.605	13	8	11	10	0.3688
2012	46	0.549	25	21	27	19	0.5538
2013	23	0.604	14	9	14	9	1.000
2014	12	0.618	7	5	7	5	1.000
2015	10	0.566	6	4	9	1	0.0528

APPENDIX 4B. Domain estimation of hunter effort

Following the close of each bear season, the DNR conducted a survey of a stratified random sample of bear license buyers to determine hunter success, hunter effort, and determine the prevalence of different hunting methods. The survey was stratified by bear management unit and included a separate stratum for hunters who voluntarily responded to the questionnaire online before the stratified sample was identified (first available in 2007). We included a response in our analysis if the respondent answered the question “Did you hunt bear in Michigan during the [insert year] season?”. Hunters also reported the number of days they spent hunting and indicated which method they used most often. The hunting methods were “hunted over bait only,” “used dogs only (bait not used),” “used dogs started over bait,” or “used other methods not involving dogs or bait.” For each year (1992-2015) and each region (UP and NLP), we estimated the total number of bear hunters, the number of bear hunters by method, the total number of bear hunter days, and the number of bear hunter days by method using the data from each stratum (Table 4B.1). (We excluded Drummond Island hunters because we did not include the Drummond Island bear population in our model. We also excluded Pure Michigan Hunters because they represented at most 3 bear hunters and could hunt statewide and could not be assigned one specific region.)

We used domain estimation (as described in Cochran 1963) to estimate the total ($\hat{t}$) number of hunters and hunt days within a region where

$$\hat{t}_d = \sum_h \frac{N_h}{n_h} \sum_i^{n_{hd}} y_{hid}$$

and

$$SE(\hat{t}_d) = \left(\sum_h \frac{N_h^2}{n_h(n_h - 1)} \left(1 - \frac{n_h}{N_h}\right) \left(\sum_i^{n_{hd}} y_{hid}^2 - \frac{(\sum y_{hid})^2}{n_h} \right) \right)^{1/2}$$

(notation described in Table 4B.2), using *d*=1. To estimate the number of hunters or hunts days for hunters using a particular hunt method, we summed only those responses (y_{hid}) from hunters that reported that method as their primary method.

TABLE 4B.1. Number of black bear license buyers (N) and number of survey respondents who provided sufficient responses (n) in each stratum of the annual Michigan, USA, bear harvest mail survey. Web respondents self-selected by responding to the questionnaire via the internet before the stratified random sample for the mailed questionnaire was selected. (The number of web responses from a BMU is subtracted from the number of license buyers in that BMU.) We allocated web respondents to regions based on the bear management unit for which their licenses were valid.

Year	Amasa[a]	Baldwin[b]	Baraga[a]	Bergland[a]	Carney[a]	Gladwin[b]	Gwinn[a]	Newberry[a]	Red Oak[b]	Web[c]
1992	N=339 n=92		N=966 n=262	N=609 n=163	N=278 n=76		N=767 n=202	N=1007 n=270	N=1111 n=303	
1993	N=290 n=162		N=995 n=326	N=669 n=286	N=298 n=177		N=739 n=344	N=868 n=405	N=1166 n=435	
1994	N=237 n=163		N=916 n=289	N=688 n=265	N=357 n=206		N=952 n=435	N=942 n=337	N=966 n=364	
1995	N=203 n=94		N=1176 n=271	N=680 n=153	N=348 n=165		N=940 n=313	N=1247 n=225	N=960 n=398	
1996	N=322 n=114	N=30 n=26	N=1170 n=311	N=772 n=194	N=466 n=117	N=75 n=37	N=969 n=248	N=1699 n=448	N=935 n=236	
1997	N=293 n=101	N=42 n=25	N=1169 n=313	N=766 n=202	N=466 n=122	N=88 n=38	N=958 n=254	N=1807 n=473	N=1005 n=265	
1998	N=305 n=172	N=25 n=23	N=1138 n=432	N=838 n=362	N=450 n=251	N=56 n=47	N=650 n=362	N=1832 n=727	N=958 n=307	
1999	N=360 n=200	N=27 n=26	N=1356 n=391	N=1083 n=349	N=536 n=258	N=80 n=67	N=779 n=305	N=1691 n=574	N=955 n=445	

TABLE 4B.1 (cont'd)

2000	N=402 n=221	N=36 n=33	N=1651 n=395	N=1269 n=369	N=619 n=281	N=85 n=75	N=867 n=329	N=1967 n=612	N=992 n=470	
2001	N=464 n=244	N=41 n=34	N=1730 n=402	N=1218 n=357	N=717 n=301	N=179 n=164	N=905 n=338	N=1874 n=599	N=1111 n=499	
2002	N=525 n=253	N=60 n=56	N=1833 n=416	N=1274 n=382	N=888 n=322	N=152 n=131	N=986 n=337	N=1870 n=609	N=1499 n=559	
2003	N=525 n=240	N=57 n=50	N=1814 n=395	N=1316 n=376	N=900 n=306	N=158 n=129	N=983 n=332	N=1895 n=584	N=1546 n=568	
2004	N=516 n=252	N=55 n=49	N=1762 n=396	N=1303 n=353	N=1028 n=341	N=157 n=134	N=1081 n=355	N=1851 n=601	N=1525 n=561	
2005	N=519 n=236	N=57 n=52	N=1866 n=401	N=1224 n=357	N=1082 n=342	N=127 n=107	N=1113 n=338	N=1980 n=582	N=1470 n=550	
2006	N=520 n=243	N=58 n=55	N=1887 n=394	N=1226 n=356	N=1063 n=347	N=129 n=113	N=1109 n=345	N=1957 n=593	N=1483 n=553	
2007	N=492 n=234	N=62 n=56	N=1764 n=369	N=1157 n=349	N=986 n=316	N=150 n=125	N=1059 n=322	N=1906 n=570	N=1420 n=529	N_{UP}=388 N_{NLP}=108
2008	N=761 n=298	N=56 n=50	N=1983 n=396	N=1354 n=354	N=804 n=306	N=124 n=98	N=982 n=336	N=1758 n=563	N=1618 n=572	N_{UP}=545 N_{NLP}=185
2009	N=522 n=247	N=46 n=39	N=1562 n=386	N=1096 n=338	N=842 n=307	N=114 n=96	N=1040 n=325	N=1647 n=565	N=1369 n=1066	N_{UP}=548 N_{NLP}=164

TABLE 4B.1 (cont'd)

2010	N=498 n=251	N=47 n=44	N=1575 n=386	N=1349 n=330	N=808 n=306	N=103 n=82	N=1166 n=327	N=1869 n=554	N=915 n=720	N_{UP}=520 N_{NLP}=122
2011	N=495 n=262	N=39 n=33	N=1577 n=393	N=1348 n=343	N=847 n=316	N=94 n=70	N=1158 n=366	N=1866 n=615	N=948 n=744	N_{UP}=520 N_{NLP}=123
2012	N=397 n=213	N=63 n=48	N=1110 n=333	N=880 n=281	N=562 n=247	N=81 n=52	N=881 n=305	N=1119 n=461	N=684 n=468	N_{UP}=373 N_{NLP}=72
2013	N=422 n=224	N=68 n=53	N=1148 n=356	N=947 n=280	N=595 n=264	N=76 n=55	N=900 n=331	N=1167 n=447	N=604 n=442	N_{UP}=228 N_{NLP}=58
2014	N=401 n=225	N=53 n=43	N=1155 n=342	N=954 n=310	N=527 n=249	N=87 n=67	N=867 n=284	N=1141 n=476	N=542 n=311	N_{UP}=276 N_{NLP}=76
2015	N=351 n=179	N=60 n=48	N=1064 n=315	N=799 n=273	N=531 n=234	N=68 n=48	N=826 n=270	N=900 n=404	N=540 n=296	N_{UP}=257 N_{NLP}=64

a) Bear management units in the Upper Peninsula (UP).

b) Bear management units in the northern Lower Peninsula (NLP).

c) N_h=n_h for web respondents

TABLE 4B.2. Definition of notations used in Appendix 4B.

Notation
$d = \begin{cases} 0 = \text{survey respondents that did not hunt bears} \\ 1 = \text{survey respondents that did hunt bears} \end{cases}$
$\hat{t}_d = \begin{cases} \text{number of hunters} \\ \text{or} \\ \text{number of hunt days} \end{cases}$
$h = \text{stratum} = \text{bear management unit or web respondents}$ (see Table 4B.1)
$N_h = \text{number of bear license buyers in stratum } h$
$n_h = \text{number of valid responses to questionnaire within stratum } h$
$y_{hid} = \begin{cases} 1 \text{ when estimating number of hunters} \\ \text{or} \\ \text{reported number of hunt days} \end{cases}$

APPENDIX 4C. Selection of hunter effort statistic

The DNR annual hunter harvest survey asked bear license buyers to report whether or not they hunted bears, the primary method by which they pursued bears, and the total number of days spent hunting. We thus had the option of several hunt effort statistics including total number of hunters, total number of hunt days, and both hunter and hunt days broken down by primary hunting methodology. Methodologies included: hunted over bait only, used dogs only (bait not used), used dogs started over bait, and used other methods not involving dogs or bait. We classified as unknown the primary hunting method of license buyers who indicated they hunted but did not select a primary methodology.

To investigate whether we should use a hunter effort statistic that broke down the effort by methodology, we compared the reported primary hunt methodology over time using estimates as calculated in Appendix 4B. The trends in the total number of hunters and hunter days tracked each other closely within each region (Figure 4C.1), suggesting that individual hunters spent the same amount of time pursuing bears over time. The similar trends in the total days and hunters suggested that using either one as an effort statistic would result in similar results. Most bear hunters used hunting over bait as their primary hunting method, and in both the UP and the NLP the proportion of bait hunting increased over time (Figure 4C.2). Because the hunters and hunter days trends closely tracked one another in all cases, we chose to use the number of hunters as an effort statistic. To investigate whether the increasing popularity of bait hunting over time affected the harvest-effort relationship, we ran variants of the model using both total number of hunters and total hunters split between bait and other methodologies (see Sensitivity Analysis).

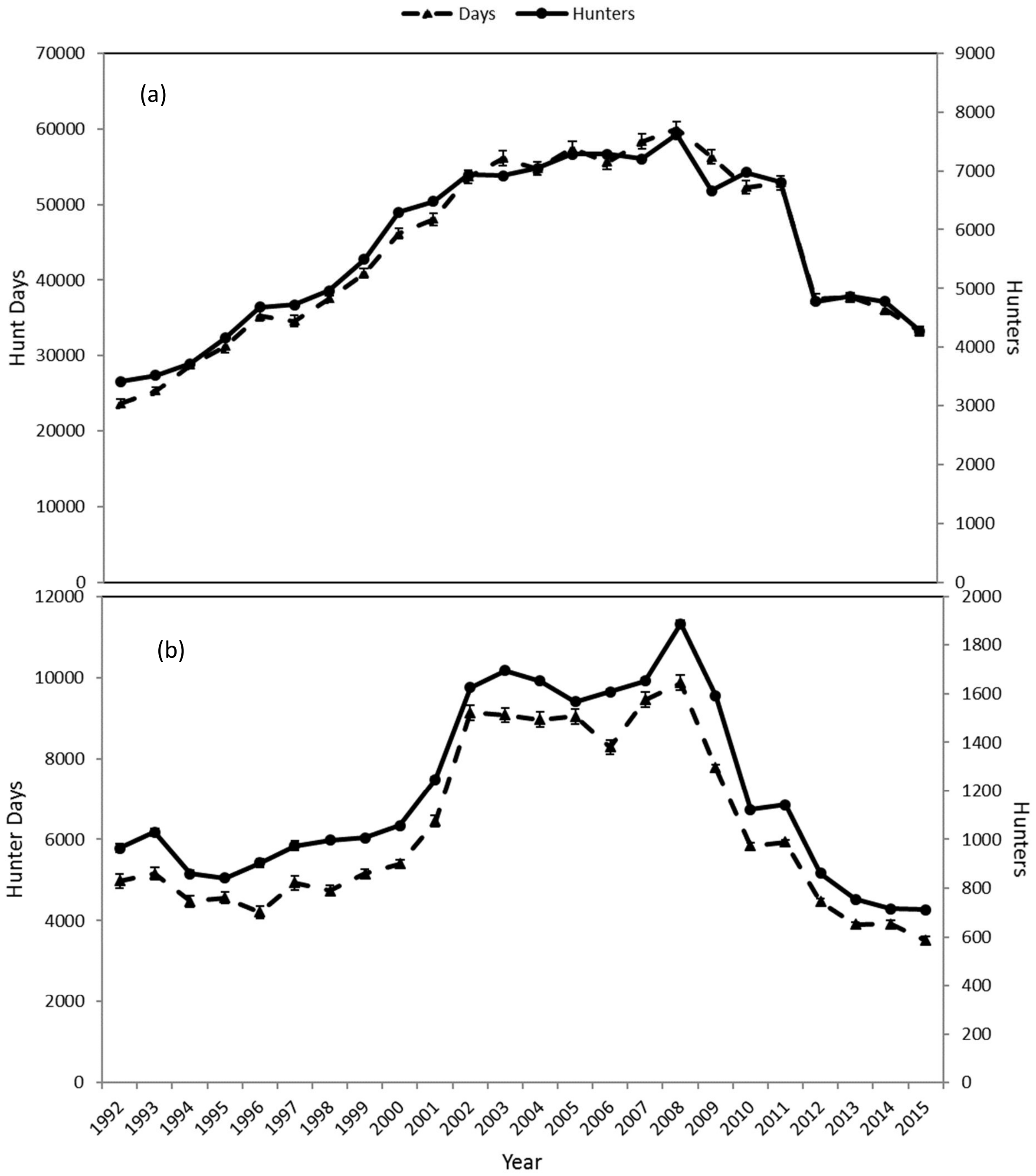

FIGURE 4C.1. Estimate (and standard error) of total number of bear hunters and bear hunter days in the Upper Peninsula (a) and northern Lower Peninsula (b) of Michigan, USA, 1992-2015.

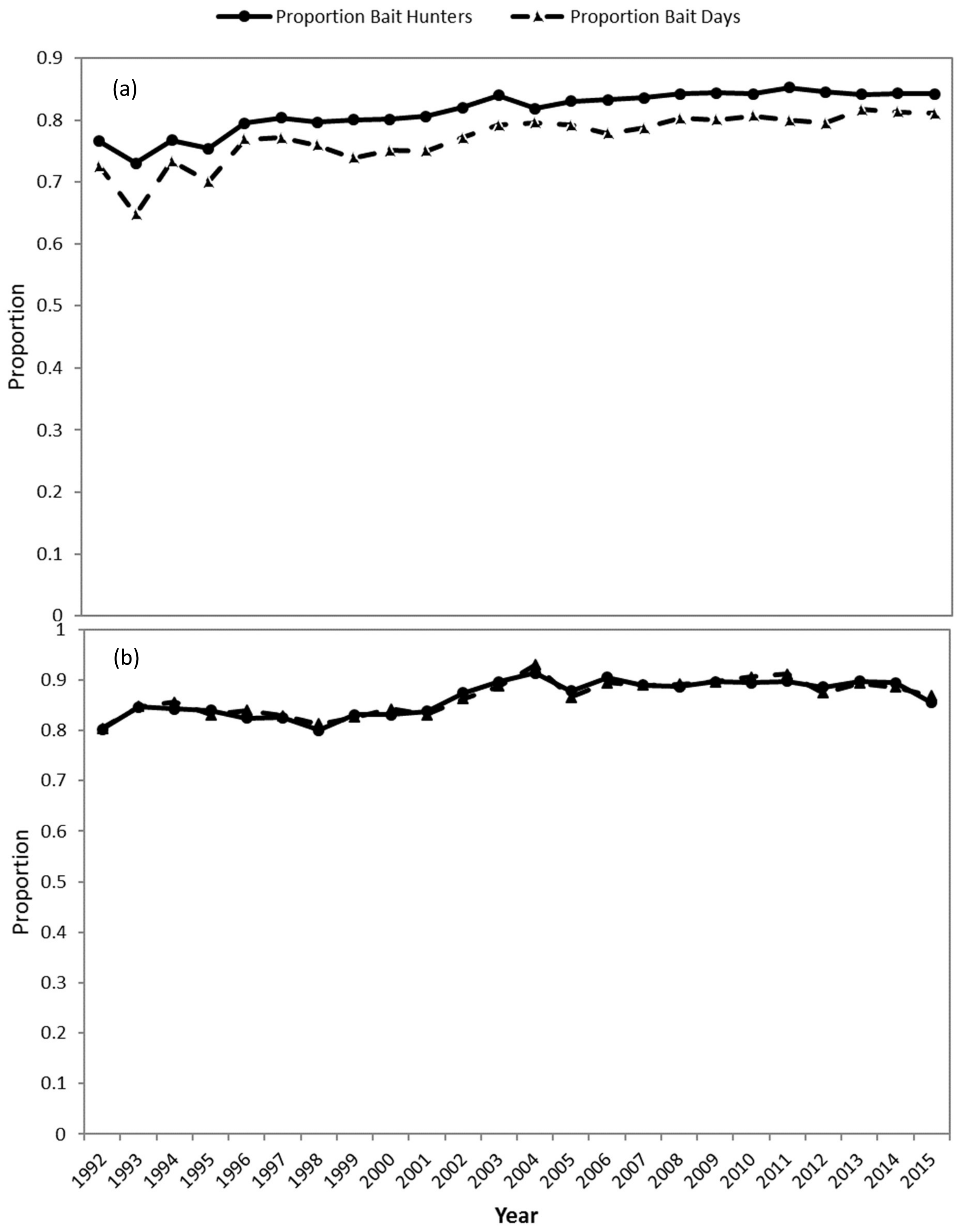

FIGURE 4C.2. Estimated proportion of bear hunters and bear hunting days where hunters reported hunting primarily over bait in the Upper Peninsula (a) and northern Lower Peninsula (b) of Michigan, USA, 1992-2015.

APPENDIX 4D. Modifying a χ^2 objective function to estimate a negative log likelihood

The general form of the χ^2 objective function is

$$g(\theta) = \sum_i \frac{\left(X_i - \hat{X}_i\right)^2}{\hat{X}_i} \qquad (1)$$

where *i* indexes the observed values and $\hat{X}$ represents the value calculated from a particular set of parameter values (θ). The general form of the normal distribution negative log-likelihood is

$$g(\theta) = constant + \sum_j \left(\log \sigma_j + \frac{\left(\frac{1}{2}\right)\left(Y_j - \hat{Y}_j\right)^2}{\sigma_j^2} \right) \qquad (2)$$

where σ^2 represents the variance. If we assume that the variance of $\hat{Y}_j$ is proportional to the predicted mean for each iteration ($\sigma^2 = \frac{\hat{Y}_j}{\lambda}$), then we could rewrite (2) to

$$g(\theta) = constant - \frac{1}{2}\sum_j \log\frac{\lambda}{\hat{Y}_j} + \frac{1}{2}\lambda\sum_j \frac{\left(Y_j - \hat{Y}_j\right)^2}{\hat{Y}_j} \qquad (3).$$

From this form, we can see that (1) is a special case of (2) where the variance is proportional to the mean and the variance is treated as known. Since we do not know the appropriate value for λ in (3), we can estimate λ as a parameter, which leads us to use (3) as the objective function to estimate θ and λ and as the negative log-likelihood for AIC calculations.

If we have auxiliary data with a normal distribution, then the combined negative log-likelihood is a combination of (2) for the normally distributed Y and (3) for the χ^2 objective function for X,

$$g(\theta) = constant - \frac{1}{2}\sum_i \log\frac{\lambda}{\hat{X}_i} + \frac{1}{2}\lambda\sum_i \frac{\left(X_i - \hat{X}_i\right)^2}{\hat{X}_i} + \sum_j \log \sigma_j + \frac{1}{2}\sum_j \frac{\left(Y_j - \hat{Y}_j\right)^2}{{\sigma^2}_j} \qquad (4).$$

We can ignore the constants in (3) and (4), because they are the same over all models, and use (3) and (4) as the objective functions for parameter estimation and as the negative log-likelihood for AIC calculations depending on whether we are using auxiliary data (4) or not (3).

APPENDIX 4E. Major results from UP models $M_{log}C_3$ and MC_5

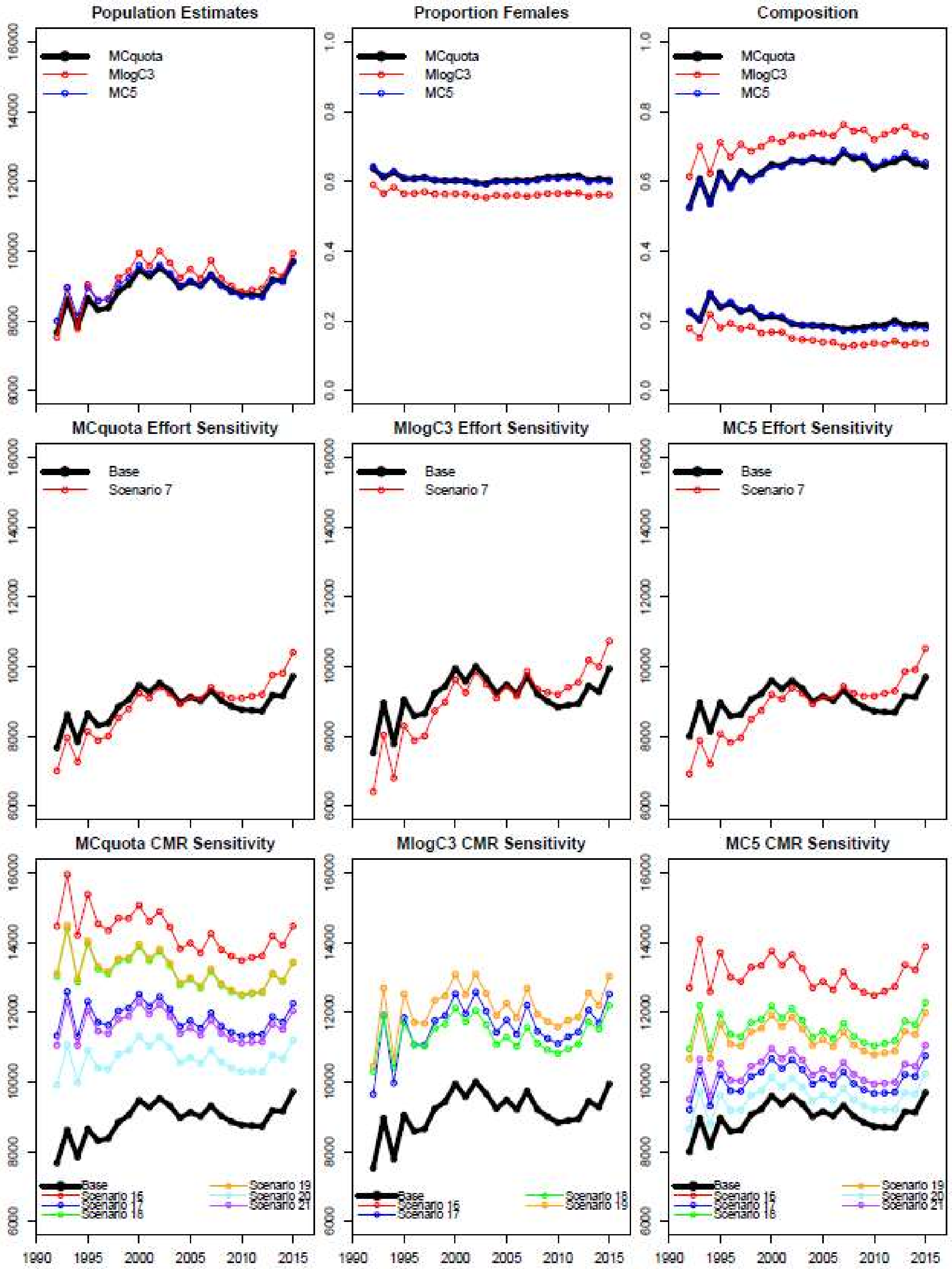

FIGURE 4E.1. Results from statistical catch-at-age models of black bears in Michigan, USA, 1992-2015. Results of models $M_{log}C_3$ and MC_5 (AIC w_i>0.2) are compared to results from top selected model, MC_{quota}. See Table 4.2 for model definitions.

APPENDIX 4F. Model evaluation results from best fit models MC_{quota} (UP) and MC_{2005} (NLP)

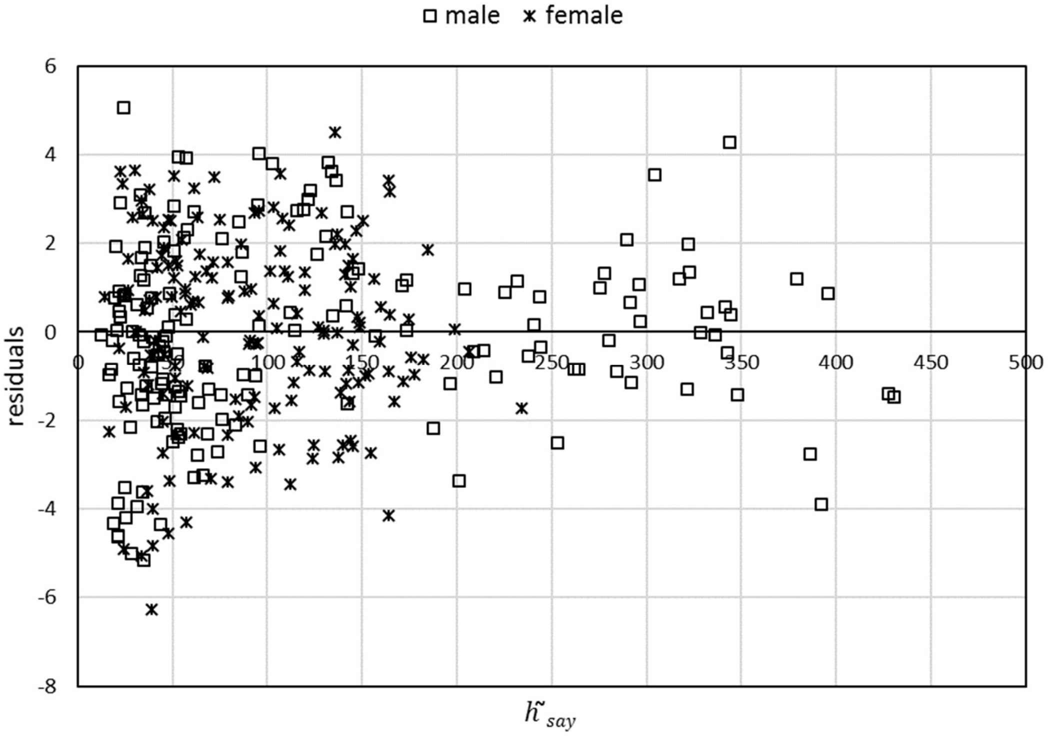

FIGURE 4F.1. Residual plot from a statistical catch-at-age model (MC_{quota}) fit to harvest data of black bears from the Upper Peninsula of Michigan, USA, 1992-2015. See Table 4.2 for model definitions.

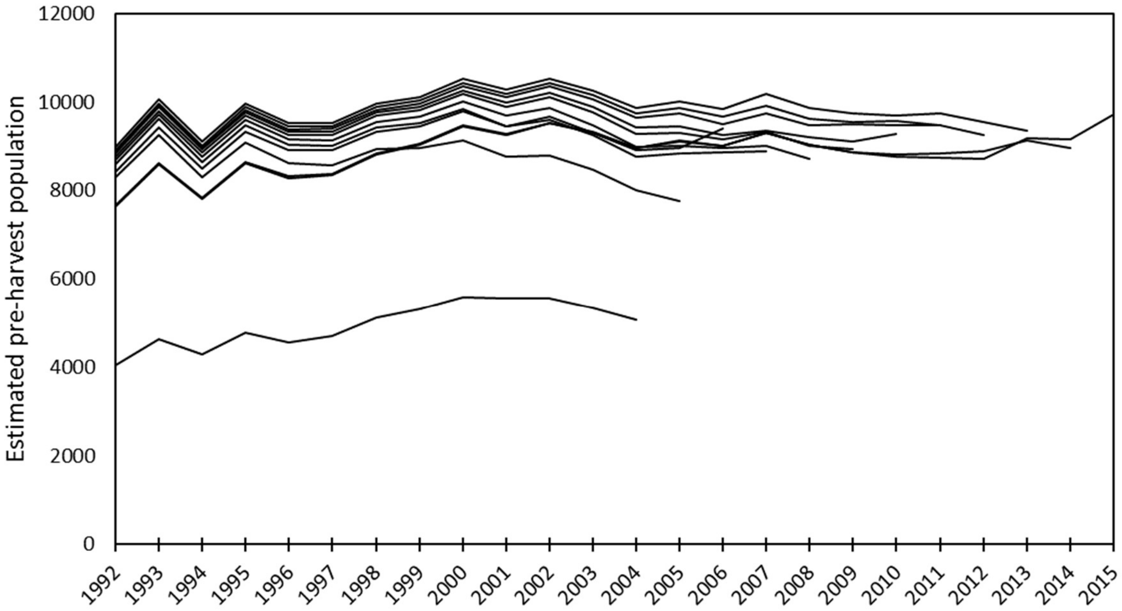

FIGURE 4F.2. Retrospective plot of a statistical catch-at-age model (MC_{quota}) fit to harvest data of black bears from the Upper Peninsula of Michigan, USA, 1992-2015. See Table 4.2 for model definitions.

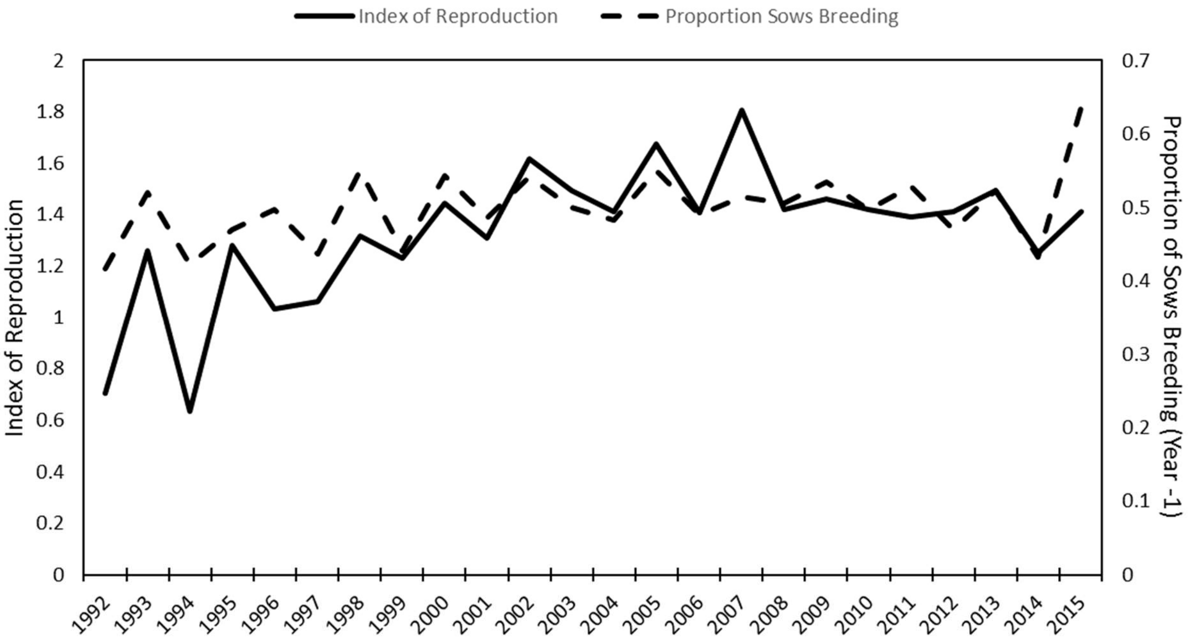

FIGURE 4F.3. Comparison of an index of reproduction from a statistical catch-at-age model (MC_{quota}) fit to harvest data of black bears from the Upper Peninsula of Michigan, USA, 1992-2015, to the proportion of females breeding from an analysis of cementum annuli spacing. See Table 4.2 for model definitions.

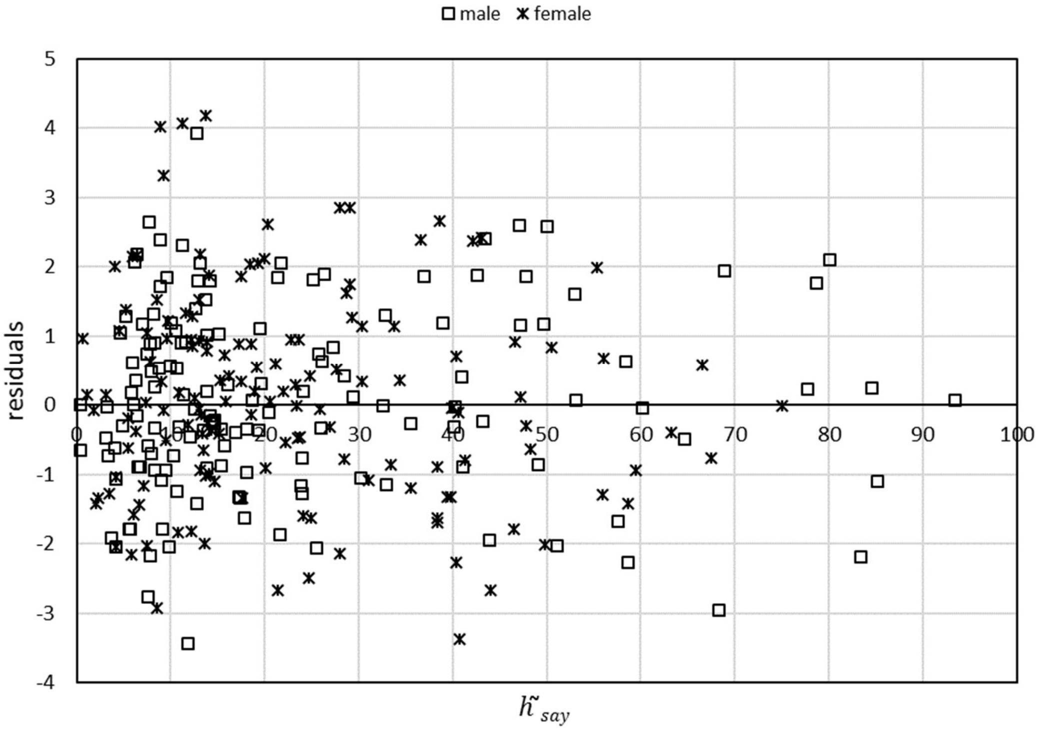

FIGURE 4F.4. Residual plot from a statistical catch-at-age model (MC_{2005}) fit to harvest data of black bears from the northern Lower Peninsula of Michigan, USA, 1992-2015. See Table 4.2 for model definitions.

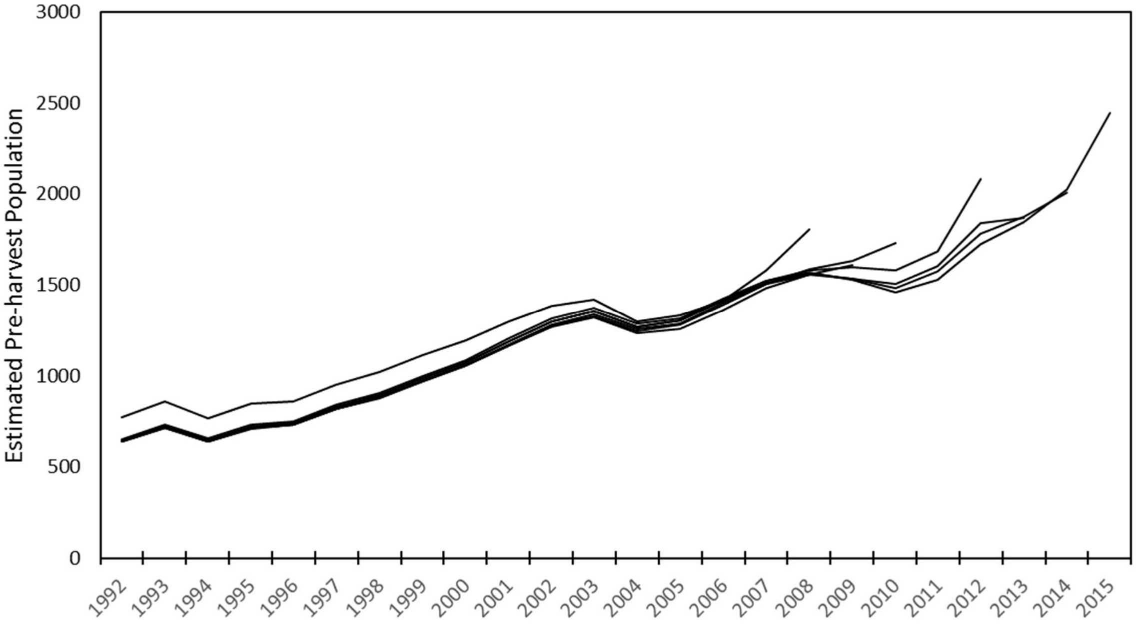

FIGURE 4F.5. Retrospective plot of a statistical catch-at-age model (MC_{2005}) fit to harvest data of black bears from the northern Lower Peninsula of Michigan, USA, 1992-2015. See Table 4.2 for model definitions.

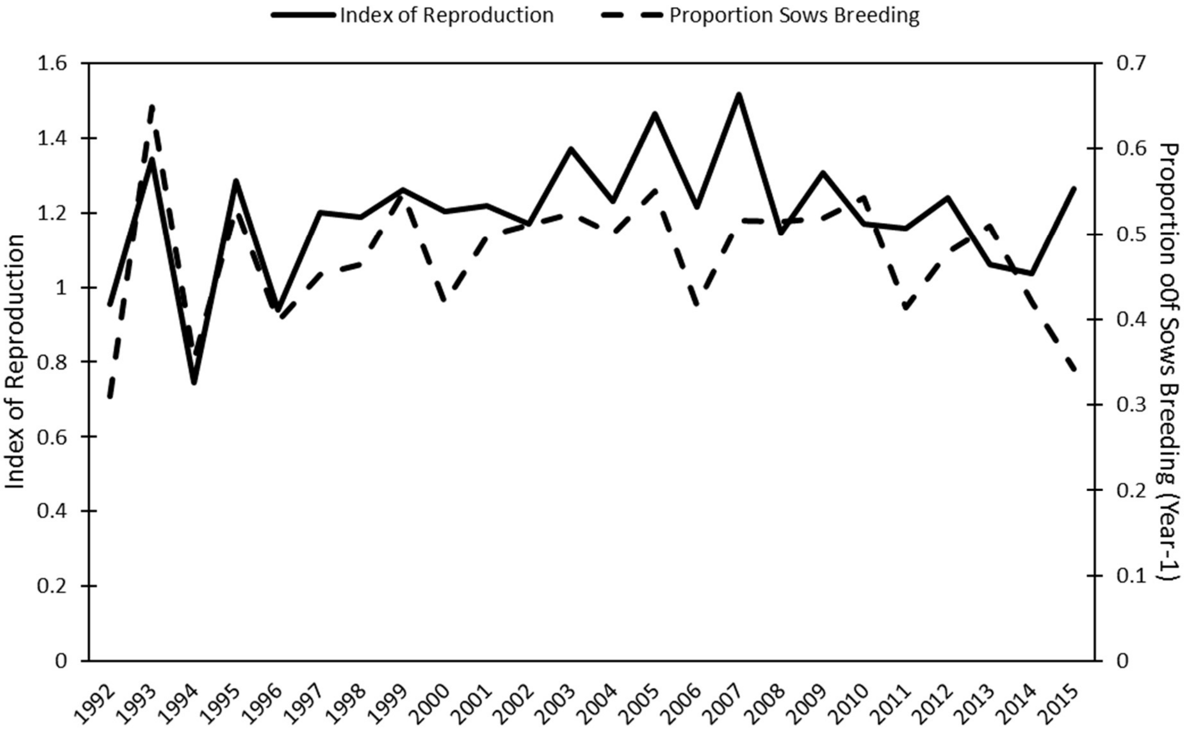

FIGURE 4F.6. Comparison of an index of reproduction from a statistical catch-at-age model (MC_{2005}) fit to harvest data of black bears from the northern Lower Peninsula of Michigan, USA, 1992-2015, to the proportion of females breeding from an analysis of cementum annuli spacing. See Table 4.2 for model definitions.

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