Using Bayesian State-Space Models with Age-At-Harvest Data to Estimate Black Bear Abundance and Demographic Parameters

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INTRODUCTION

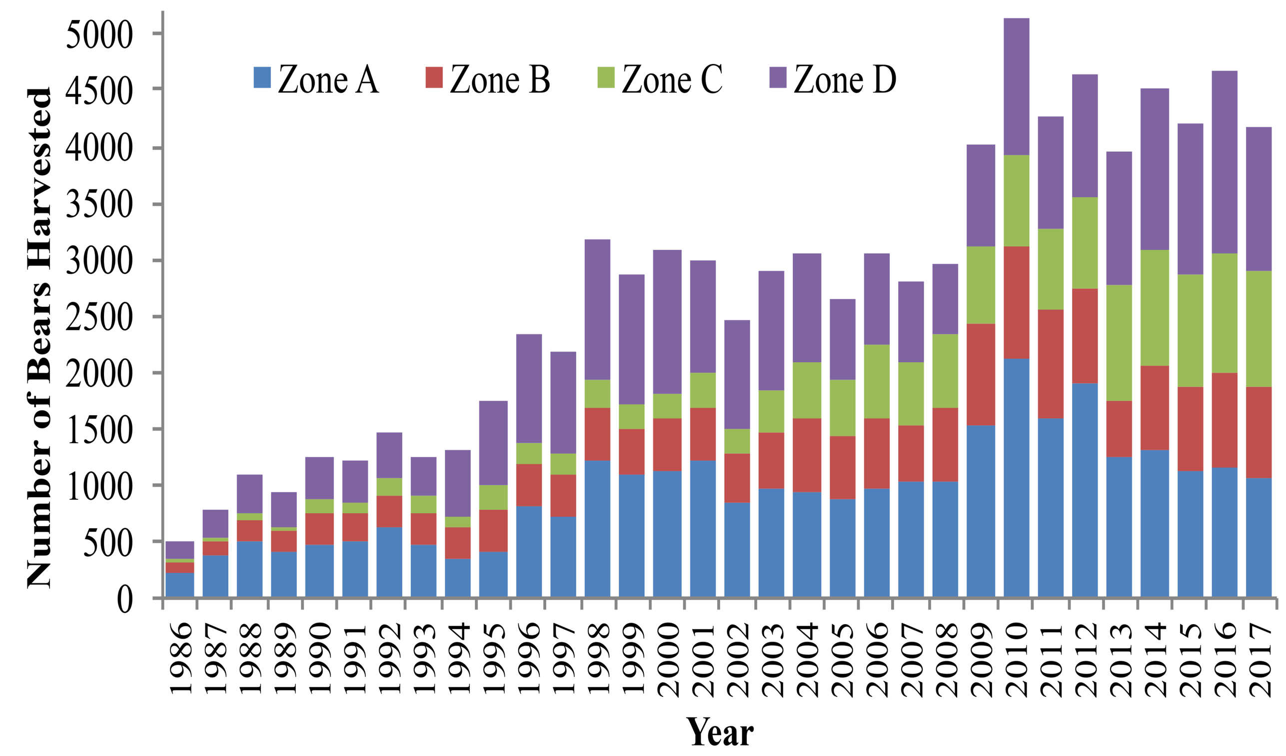
Population estimates are essential for making decisions about the management and conservation of many species, but are difficult or expensive to obtain across large geographical scales (Skalski et al. 2005). This is particularly true of mammalian carnivores, which are cryptic and difficult to count directly. Consequently, carnivore managers often base their population estimates on extrapolations from small data sets and adjust harvest quotas based on subjective opinion from the public and experts (Hristienko et al. 2007). The importance and challenges of estimating wildlife populations has led to many different estimation methods (Skalski et al. 2005). Using age-at-harvest data may be most practical across large scales (Skalski et al. 2005, Norton 2015).

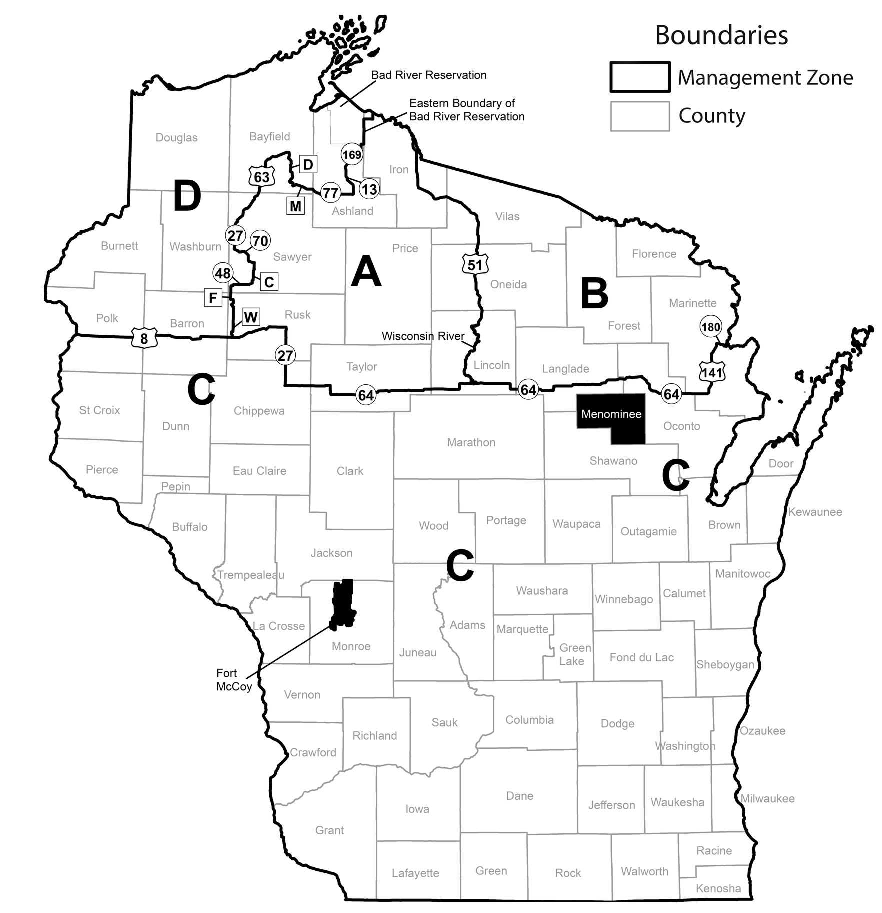
Several statistical models have been developed that use age-at-harvest data to accurately estimate populations. Models based on frequentist statistics include statistical population reconstruction (SPR) that integrate hunter effort (e.g., Skalski et al. 2011), and state-space models that integrate food availability (e.g., Fieberg et al. 2010). Models based on Bayesian statistics include data augmentation models that are similar to SPR and integrate tag recovery (e.g., Conn et al. 2008), and state-space models that integrated known-fate survival data (e.g., Norton 2015). To date there has not been a model developed that creates accurate estimates without integrating auxiliary data, which makes it necessary for large field projects to collect demographic data.

Black bears (*Ursus americanus*) are a K-selected and widely distributed solitary carnivore (Garshelis et al. 2016). In Wisconsin, black bears are a popular game animal whose population and harvest have increased over the last few decades. The Wisconsin Department of Natural Resources (WDNR) manages bear populations over a 35 day season in 4 distinct zones with unique quotas and hunting regulations. Most of the bear population resides in the northern half of the Wisconsin (zones A, B, and D). Since 1985, the WDNR has estimated bear populations using a deterministic accounting model (MacFarland 2009). However, an independent capture-recapture estimate generated from tetracycline marking found that the current model underestimated the population size by nearly 2/3 (MacFarland 2009). Independent population estimates have allowed the WDNR to more accurately assess the black bear population in the state (MacFarland 2009), but these are expensive and often conducted years apart.

Right: *The boundaries of the four black bear management zones in Wisconsin.*

Below *Annual harvest of black bears in each management zone of Wisconsin from 1986-2017.*





METHODS

Our state-space model consisted of two process models whose likelihoods were jointly modeled (Buckland et al. 2004, Norton 2015). The population process model was based on the unobserved (latent) population state process (that progresses from the initial state density to sub-state transitional densities [hunting season, non-hunting season, recruitment]), and the observation state process was based on observed harvest data (Newman et al. 2009, Norton 2015). We used Markov Chain Monte Carlo (MCMC) methods to approximate posterior distributions and based our inference on posterior summaries of the MCMC samples.

The goal of our model was to estimate abundance (*N*) of the black bear population immediately prior to the hunting season. We used black bear harvest data including total annual observed harvest (***O***), and the number of harvested animals with known age and sex (***C***) in our observation state process.

In our statewide model, we used 8 years (2009-2016) of harvest data, and based the initial population size on the WDNR estimate from 2009. In our models for each management zone, we used 6 years of harvest data (2011-2016), and based our initial population sizes on independent capture-recapture estimates generated from tetracycline marking from 2011 (N_A = 6,009, N_B = 4,468, N_C = 4,841, and N_D = 6,425). We assumed that the harvest was proportional to the population among age classes after visually assessing the harvest proportion by age class over 30 years and finding similar proportions despite increases in harvest over time.

We used reasonably informative prior distributions for the demographic parameters of the model (see table to right). Our population process model was constructed as a two-sex, ten-stage (1.5-year-olds, 2.5-year-olds, …, 9.5-year-olds, ≥10.5-year-olds; excluding 0.5-year-old cubs that cannot be harvested legally) population projection matrix (Caswell 2001). Age-specific fecundity values (as number of 1.5-year-olds entering the model, per female) were calculated as:

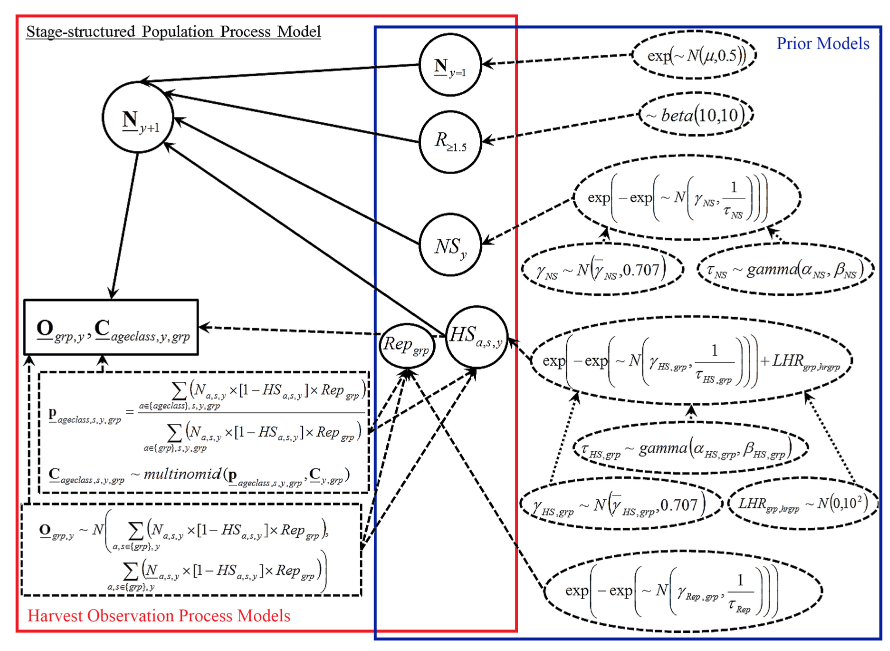
$$Fec_a = LS_a \times PR_a \times CubSa \times CubSb$$

and multiplied by the number of females in each age class of the previous year to determine the number of 1.5-year-olds entering the population and by $\boldsymbol{SP}_s$ to determine the proportion by sex. The number of 0.5-year-olds were back-calculated in the population model as:

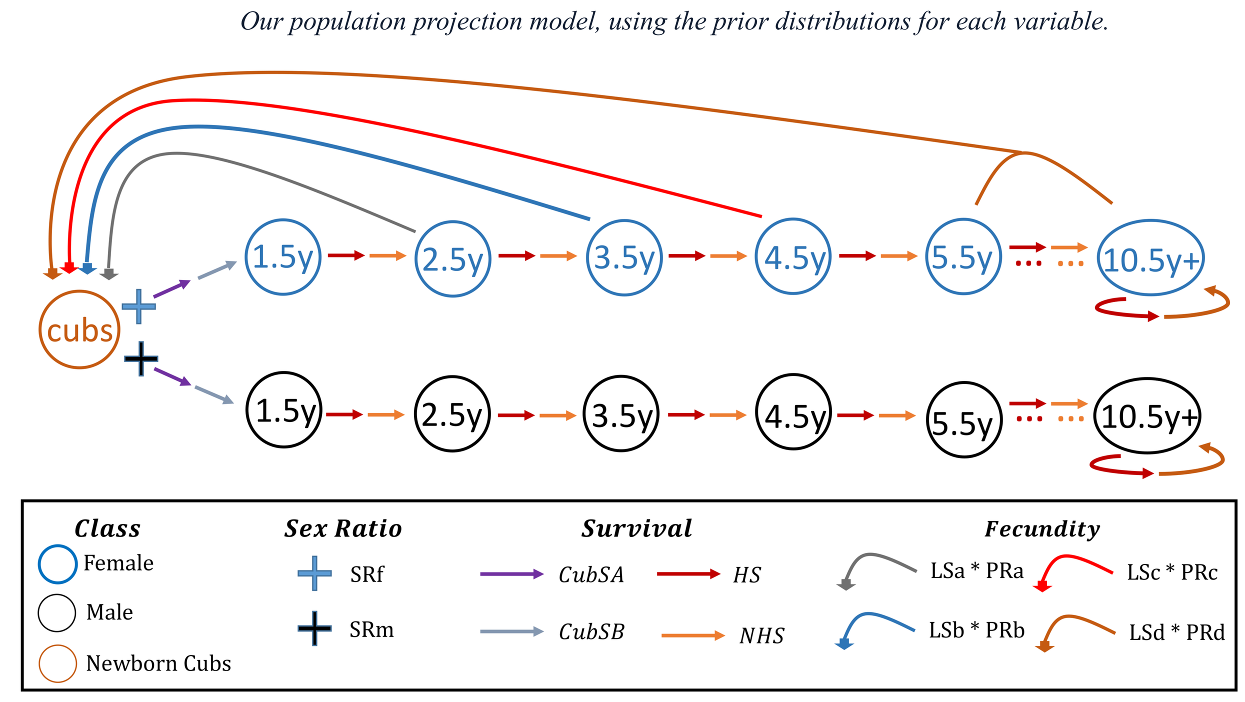
$$N_{0.5,s,y-1} = N_{1.5,s,y} \;/\; CubSb$$

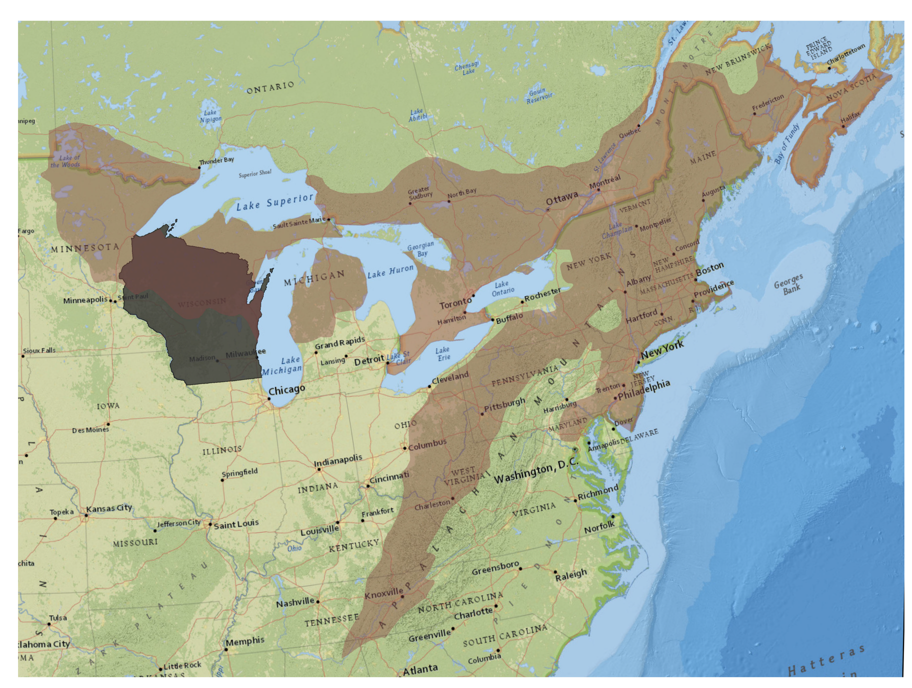
We fit our models in Program R (R Core Team 2017) using JAGS (Plummer 2003) and the R package rjags. We ran 220,000 iterations with 3 chains, a burn-in of 20,000, and a thinning rate of 4. We visually assessed the convergence and mixing of the chains, and then used Gelman-Rubin statistics on the annual abundance estimates to determine convergence.

An early draft of a Directed Acylic Graph, highlighting the prior models (population projection) in blue and the harvest observation model in red.



Our population projection model, using the prior distributions for each variable.





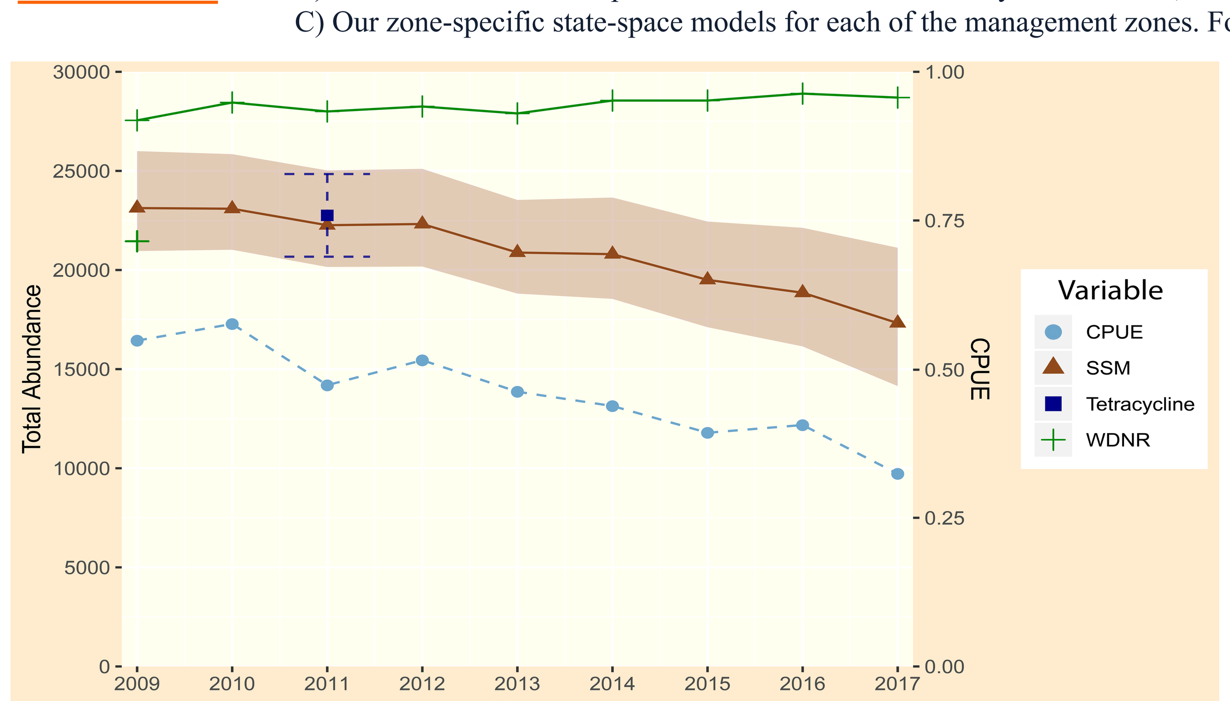
Recruitment Parameters			
Variable	Parameter	Mean	Distribution
LS-a	Litter Size 2.5-year-olds	2.00	Gamma (20,10)
LS-b	Litter Size 3.5-year-olds	2.00	Gamma (20,10)
LS-c	Litter Size 4.5-year-olds	2.00	Gamma (20,10)
LS-d	Litter Size 5.5+ year-olds	2.74	Gamma (16.4,6)
PR-a	Pregnancy Rate 2.5-year-olds	0.003	Beta (2.61,1000)
PR-b	Pregnancy Rate 3.5-year-olds	0.25	Beta (34,100)
PR-c	Pregnancy Rate 4.5-year-olds	0.53	Beta (54,48)
PR-d	Pregnancy Rate 5.5+ year-olds	0.48	Beta (47,50)
SP	Sex Proportion (female)	0.46	Beta (426, 500)

Survival Parameters				
Variable	Parameter	Mean	Long-Term Precision	Annual Precision
HSm	Male Harvest Survival	0.77	3	Gamma (20,0.5)
HSf	Female Harvest Survival	0.85	3	Gamma (20,0.5)
NS	Non-harvest Survival	0.95	4	Gamma (20,0.5)
CubSa	Cub Survival years 0.0-0.5	0.84	4	n/a
CubSb	Cub Survival years 0.5-1.5	0.71	4	n/a
Rep	Recovery Rate	0.98	2	n/a

Because demographic information from Wisconsin was sparse, we set up a quasi-study area with similar habitats across North America (above left). We then reviewed all peer-reviewed literature from this area to create the prior distributions for our model (above right).

RESULTS

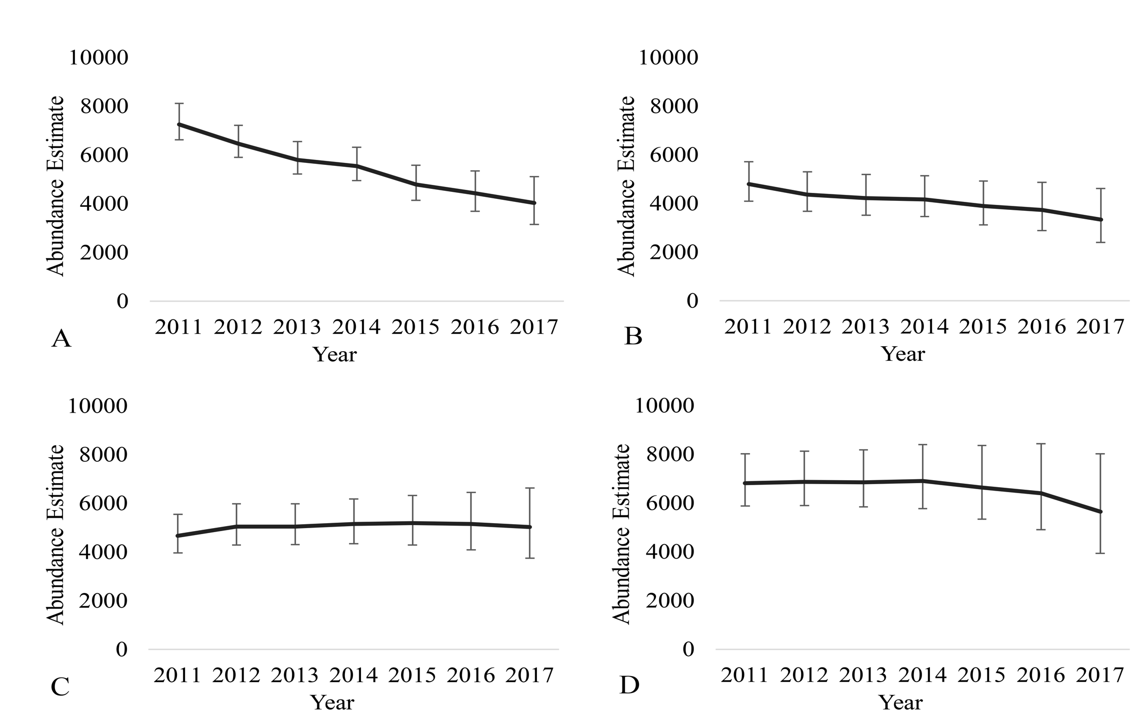
We ran models in 3 steps: A) Our statewide state-space model (as proof of concept).
B) To understand how the prior values affected the accuracy of our model, we compared the results of our statewide state-space model to models run with 10% positive and negative bias in 9 individual parameters to determine Percent Relative Change (PRC).
C) Our zone-specific state-space models for each of the management zones. For full results, including estimates of demographic parameters see Allen et al. (2018).



The statewide population estimates (from the SSM) indicated a decreasing trend in the black bear population from 2009 to 2017 and reasonable demographic parameters. The annual variation and 95% credible intervals were similar, but increased slightly in the final two years of estimation. The population abundance estimate for 2011 was visually similar to the independent tetracycline estimate for 2011. The population trend estimate had a significant and strong correlation with CPUE (df = 8, R^2 = 0.93, p <0.0001).

Variable	Description	PRC	CV
LS -10%	10% Underestimate of litter size	-0.68	0.68
LS +10%	10% Overestimate of litter size	1.09	1.09
PR -10%	10% Underestimate of pregnancy rate	-0.98	0.98
PR +10%	10% Overestimate of pregnancy rate	1.25	1.25
HSm -10%	10% Underestimate of male harvest season survival	-0.04	0.04
HSm +10%	10% Overestimate of male harvest season survival	0.02	0.02
HSf -10%	10% Underestimate of female harvest season survival	-0.43	0.43
HSf +10%	10% Overestimate of female harvest season survival	0.93	0.92
NHS -10%	10% Underestimate of non-harvest season survival	1.64	1.85
NHS +10%	10% Overestimate of non-harvest season survival	N/A	N/A
Rep -10%	10% Underestimate of reporting rate	7.33	7.26
Rep +10%	10% Overestimate of reporting rate	N/A	N/A
CubSa -10%	10% Underestimate of cub season a survival	-0.44	0.43
CubSa +10%	10% Overestimate of cub season a survival	1.30	1.30
CubSb -10%	10% Underestimate of cub season b survival	1.46	1.48
CubSb +10%	10% Overestimate of cub season b survival	-1.49	1.49
N -10%	10% Underestimate of starting population	-1.81	1.84
N +10%	10% Overestimate of starting population	1.98	2.02

Based on the PRC values, our population model estimates were most sensitive to potential bias in the reporting rates (10% underestimate = PRC of 7.33). The model was robust to potential bias in all other parameters, which had PRCs of < 2.00. Since most population models are sensitive to the initial population estimate, we also assessed the sensitivity to extreme bias in this parameter. A 50% underestimate had a PRC = -7.60%, and a 50% overestimate had a PRC = 11.88%.



The posterior estimates for abundance and demographic parameters were reasonable for each management zone. The abundance estimates indicated a decreasing trend in zone A, and a generally stable trend in B, C and D. The posterior means and distributions were improved from the prior distributions for litter sizes, initial population size, harvest season survival, and non-harvest season survival, with a notable increase in precision for the survival values.

SUMMARY

- Several rigorous statistical approaches that use age-at-harvest and auxiliary data to accurately estimate populations have recently been developed, but these are often dependent on a) accurate prior knowledge about demographic parameters of the population, b) auxiliary data, and c) initial population size. We developed a two-stage state-space Bayesian model for populations with age-at-harvest data, but little demographic data and no auxiliary data available.
- The posterior estimates for abundance and demographic parameters from our state-space models using age-at-harvest data were reasonable for our statewide estimate and for each management zone, and our statewide model estimates were also similar to an independent estimates from tetracycline marking and the trend of catch-per-unit-effort for the state.
- Our model was also robust to bias in the prior distributions for all parameters, except for reporting rate, and was robust to even extreme bias in initial population size.
- The Bayesian state-space modelling approach allows the modeler to transparently provide biologically supported information and constraints on parameters as priors, but the models use these as a starting point and the posterior values are not dependent on the prior values provided. Drawbacks of Bayesian models are that they can be more complex and difficult to comprehend and more computationally intensive to implement than simpler models.
- The Bayesian state-space models using age-at-harvest data appear effective for making zone-specific abundance estimates for the management of harvested species, and could result in better decision-making about populations and harvest quotas, and lead to more effective monitoring and management.
- Our state-space model created a precise estimate of the black bear population trend in Wisconsin based on age-at-harvest data and potentially improves on previous models by using little demographic data, no auxiliary data, and not being sensitive to initial population size.

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