

# A Stochastic Population Model of the Yellowstone Bison Population

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## INTRODUCTION

Monitoring populations and conducting research on the processes that shape their dynamics has historically been justified by the need to provide a scientific basis for decisions on population management. Population models form one of the primary tools for supporting these decisions. Models provide a way to assimilate data from many sources, including population census, observations of population composition, and detailed studies of vital rates and the ecological processes that control them. Assimilating data in population models has followed two distinct traditions: bottom-up and top-down. In the bottom-up approach, parameters are estimated from process studies, for example survival probabilities estimated by mark-recapture, and are subsequently used to predict state variables, for example population size and composition. Illustrations of this type of modeling include (Hobbs 1989, Turner et al. 1994, Moen et al. 1997, Treanor et al. 2007). In contrast, top-down modeling reverses the relationships among parameters, state variables, and data. In this approach, we attempt to estimate values of parameters from data on state variables; for example, we might use annual census and sex and age classifications to estimate survival probabilities. Examples of this approach include (Mduma et al. 1999, Lubow et al. 2002, Wang et al. 2002, White and Lubow 2002, Cooper et al. 2003).

Despite the widespread application of both approaches, the use of models to support decisions on population management has been limited by the inability of modelers to offer true forecasts—that is, to offer predictions of future population behavior that are accompanied by rigorous estimates of uncertainty. Until recently, it was impossible to place an envelope of confidence on model predictions, an envelope that responded appropriately to the multiple sources of uncertainty inherent in all ecological models.

Uncertainty arises in population models in three fundamental ways. By definition, models are abstractions that do not include all of the many influences that shape the way that populations behave. Because some of these influences remain unrepresented, there are inevitable differences between the prediction of a model and the true state of the population. This uncertainty is known as *process variance*<sup>1</sup>. A different type of uncertainty is created by our failure to observe perfectly the true state of the population. Monitoring data, no matter how carefully obtained, will always include errors arising from sampling, from the inability to count and classify accurately, and from human mistakes in recording. We will call these sources of uncertainty *observation error*. Finally, all populations are composed of individuals, each of which is unique by virtue of differences in genetics and experience. Models usually lump these individuals into groups as if they were identical. The uncertainty that arises from differences among individuals will be called *random effects*.

As recently as five years ago, these multiple sources of uncertainty were not explicitly represented in population models. Instead, the traditional approach to fitting population models to data was to lump all uncertainties into observation error. It is now well understood that this approach led to fundamental errors in inferences about populations and provided excessively optimistic conclusions about the precision of model estimates.

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<sup>1</sup>It is also called model misspecification.

Increases in computing power and, more importantly, in advances in algorithms for computation, have provided fundamentally new ways to assimilate models with data, allowing us to include process variance, observation error, and random effects simultaneously in model predictions. These new approaches provide honest forecasts of population behavior backed by statistically coherent inference.

### **A Bayesian Approach to Forecasting Bison Population Dynamics**

Here, we describe a Bayesian hierarchical approach to the problem of modeling the Yellowstone bison population. There are three reasons to use this approach. First is the ability to include prior information gained from detailed studies of bison population dynamics in a model that also responds to ongoing monitoring. Estimates of population parameters obtained from process studies become prior distributions (hereafter, priors) in a model that estimates the state of the population over time, and the estimate of the state is used to update estimates of parameters based on monitoring data. Thus, the Bayesian model represents a compromise between the “top down” influence of monitoring data and the “bottom-up” estimates of priors. If the monitoring data are noisy or sparse, then the priors dominate the results, at least until better or more comprehensive data are obtained. Alternatively, if the monitoring data are of high quality, then they adjust the values of parameters in the priors, thereby improving the estimates from process-level studies.

The second reason for using the Bayesian approach is that it provides a statistically coherent way to estimate uncertainty, both uncertainty that arises as an inherent part of the processes governing the population’s dynamics, and uncertainty that arises because we fail to observe the process without error. The framework for combining these sources of uncertainty in dynamic models is called state-space modeling and although the state-space approach is not uniquely Bayesian (De Valpine and Hastings 2002, Dennis et al. 2006, Wang et al. 2006, Lele et al. 2007), the combination of the state-space framework with data from prior, process level studies demands Bayesian estimates. The state space format can be summarized (Calder et al. 2003) as

$$\begin{aligned} y_t &= g(x_t) + \varepsilon_{obs} \\ x_t &= f(x_{t-1}) + \varepsilon_{proc} \end{aligned} \tag{1}$$

where  $y_t$  represents *data* on the state variable of interest, for example the observed population size, and  $x_t$  represents the true state of the population. The function  $g(\cdot)$  is the data model (a.k.a., observation equation) that relates the observation to the true state of the population;  $f(\cdot)$  is the process model that predicts the future, true state of the population as a function of its past state and the value of model parameters. The quantity  $\varepsilon_{obs}$  is the uncertainty that arises because of imperfect observations of the true state and the quantity  $\varepsilon_{proc}$  is the uncertainty that arises because our model cannot account for all of the variation in the trajectory of the population. By incorporating these sources of uncertainty in model estimates in a Bayesian framework, we obtain probability distributions for all of the states at each time and also obtain probability distributions for values of all model parameters.

The final reason to use the approach outlined here is that it offers the possibility of estimating unobserved quantities of interest, for example, probabilities of disease transmission that heretofore have not been estimated.

## **Objectives**

In the section below, we outline a Bayesian state space model that integrates annual observations of the bison population in Yellowstone with parameter estimates from process studies in a discrete time, stage-structured model. The objectives for model construction were to:

1. Provide a framework for assimilating data from 4 decades of monitoring and research in a way that allows those data to better inform management decisions.
2. Offer forecasts of future behavior of the population accompanied by explicit estimates of uncertainty.
3. Support decision on future monitoring and research that will enhance model predictions and their application to management decisions.

## **ORGANIZATION OF THIS DOCUMENT**

We begin by describing the data that forms the foundation for modeling. Building on that foundation, we then offer a set of equations representing the processes controlling population growth. We will refer to these equations as a process model. We will also describe how we will represent the uncertainty that arises because the process model fails to include all of the factors that shape the population's dynamics. Next we will describe how we will use the data to estimate the parameters in the process model, using what we will call data models, and we assemble these parts schematically and mathematically in a fully Bayesian, hierarchical model. We then evaluate the fit of the model to multiple sources of data and examine the estimates of its parameters. The most important part of the document comes next---an example illustrating the potential of the model to support management decisions with forecasts. We close by identifying needs for future work.

## **DATA**

We used six sets of observations as a basis for parameter estimation and forecasting. These data included total census, sex and age composition, removals and harvest, sero-prevalence, and observations of the effect of population density and serological status on birth rate. Each data set is described briefly below.

### **Total Census**

Aerial census of the Yellowstone bison population has been conducted annually for almost 40 years (1970-2008, Figure 1). Although counts were made during winter and summer, we used summer counts in this analysis because the large aggregations of bison during summer facilitate accurate counting and because summer counts were accompanied by age classifications, discussed subsequently. During almost all years, there were at least two summer counts, one taken during June and the other during July or August. Data from summer subpopulations within the park were pooled for analysis. With a single exception, census methods have been largely consistent over the 4 decades of observation. During 1970-1997 and 2002-2008, observers targeted areas where bison were known to congregate. However, during

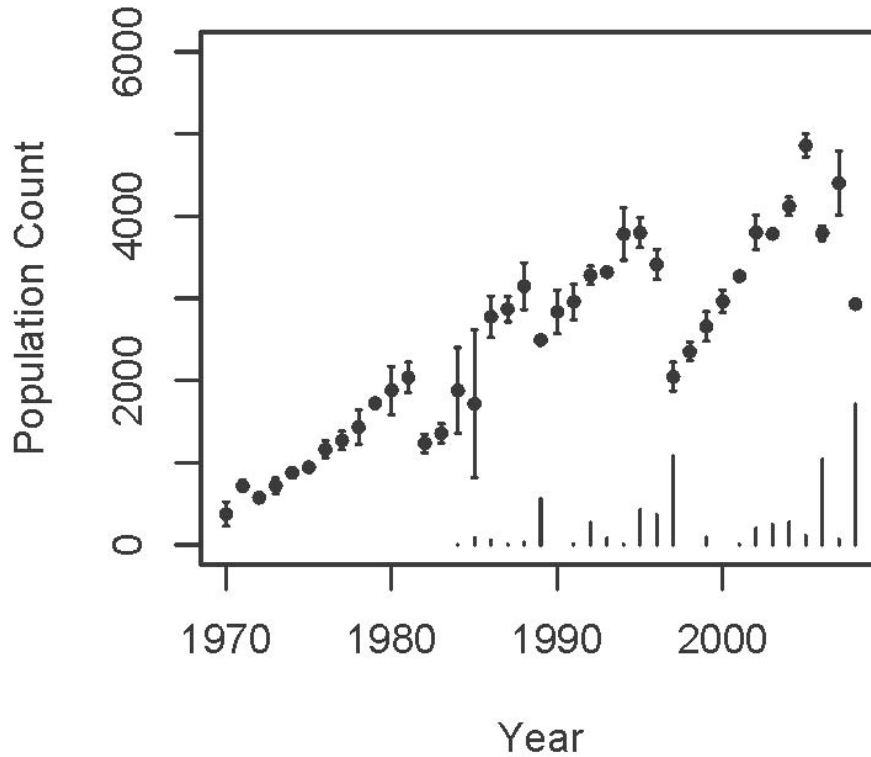


Figure 1. Census data (points) and removals (vertical lines) from the Yellowstone Bison population during 1970-2008. Bars on points are  $\pm 1$  standard deviation representing sampling error in observations.

1998-2001, observers counted bison in census blocks according to a stratified sampling design. Because the census block approach provided estimates that appeared markedly different from those of the targeted approach, we used a linear interpolation between 1997 and 2001 to estimate the data points from 1998-2000<sup>2</sup>. Replicated summer counts were used to estimate annual standard deviations in counts, and these standard deviations were used to provide an overall estimate of observation error for the census data, as described below in the section on data modeling. For years when there was only one summer count, we estimated a count standard deviation for that year as the product of the single, summer count multiplied by the coefficient of variation averaged across all years with multiple counts.

### Age and Sex Composition

Age composition of groups of bison observed during annual, aerial counts was estimated by recording the total group size and the number of juveniles (Figure 2). Each group was treated as a single observation taken from a sampling distribution of the proportion of juveniles in the population. The mean of that distribution provided the annual estimate of age composition and the standard deviation provided an accompanying estimate of observation error as described

<sup>2</sup> There are alternative approaches that could estimate a parameter correcting for the difference in census designs, but these alternatives will be pursued in future work.

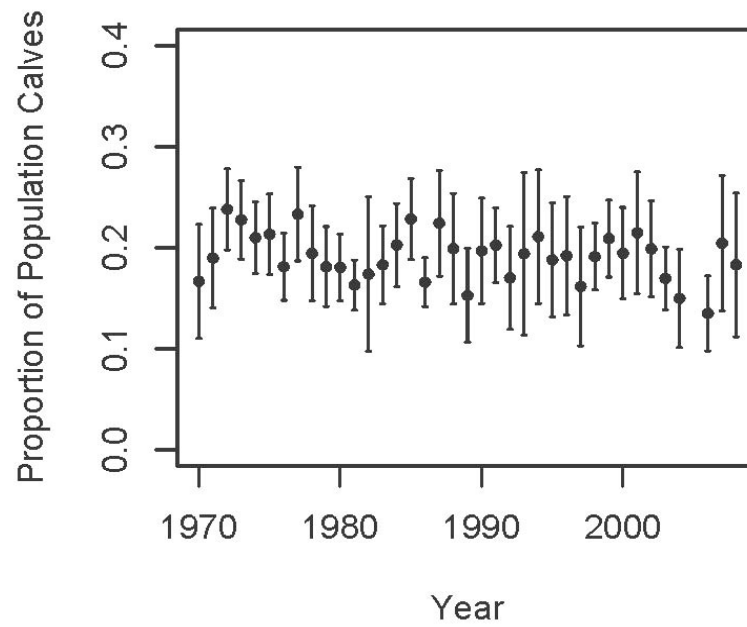


Figure 2. Observations of the average proportion of juveniles in the Yellowstone Bison population during . Vertical bars are  $\pm 1$  standard deviation.

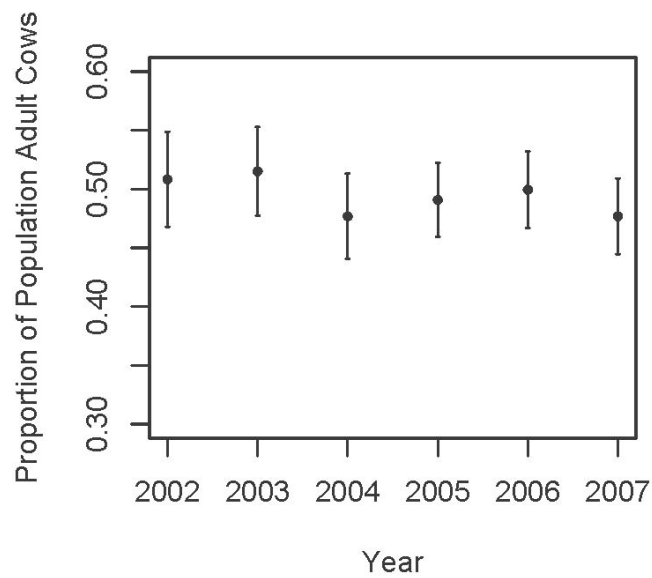


Figure 3. Observations of the average proportion of adult cows in the Yellowstone bison population during 2002-2007. Vertical bars are  $\pm 1$  standard deviation.

in the section on data modeling. During 2002-2007, age and sex composition of bison groups was observed using counts from the ground. We used these data to estimate the proportion of the population that was comprised of adult females during 2002-2007 (Figure 3). We again assumed that each group was a single observation from a sampling distribution and used the moments of that distribution to estimate sex composition and associated observation error.

### **Removals and Harvest**

We used data on removals that occurred during 1984-2008 at the west boundary near West Yellowstone, MT, and north boundary near Gardiner (Figure 1). These data were pooled and combined with estimates of the number of animals harvested by licensed hunters. It was important to adjust the removal data to correspond to the timing of events in the process model, described below. Thus, each year's total removals consisted of the post-census removals from the previous calendar year and the pre-census removals from the current calendar year. Organizing the data this way allowed the estimate of the population size at  $t + 1$  to reflect the removals that occurred during time  $t$  to time  $t + 1$ . Data on the sex and age composition of the removals was available only for years 2002-2006. These were used to estimate the composition of removals across all years, as described below.

### **Sero-prevalence**

We coalesced data collected during field immobilization of collared animals and through handling of large numbers of unmarked animals at boundary facilities to estimate age-specific serology rates of female bison. Animals were classified as sero-positive or sero-negative using serum and tested for brucellosis exposure status through field immobilization during February (1995-2001) and November-January (2002-2007), handling during February and March at the Stephen's Creek facility and handling during March and April at the Duck Creek facility. Disease status was based on the results of fluorescence polarization assay, card, buffered antigen plate agglutination, rivanol, complement fixation, standard plate, and standard tube tests performed by the Montana Department of Livestock Diagnostics Laboratory, Bozeman, Montana, USA. However, bison handled at the Duck Creek facility were classified using a trap-side card agglutination test. Animal age was recorded at the time of disease testing, so, for example, animals classified as calves were approximately 10 months old and yearlings were 22 months old. Data on sero-prevalence for adult females (age > 2 years) spanned 1985 to 2007 and formed the basis for our analysis. Age specific data were available only for 2003 to 2007. We used the data for sero-prevalence of calves to supplement the more extensive data on adult female sero-prevalence.

### **Process Studies**

The Montana Department of Fish, Wildlife, and Parks and the U.S. Geological Survey conducted a study of adult female bison in Yellowstone National Park during 1995-2001 to evaluate survival, pregnancy, and birth rates and to understand the demographic and environmental factors controlling them. The National Park Service completed a similar study during 2002-2007. Eighty bison were radio collared and monitored during 1995-2006, with animals entering the study throughout the duration of the project. Forty-one bison were radio collared and monitored during 1995-2007.

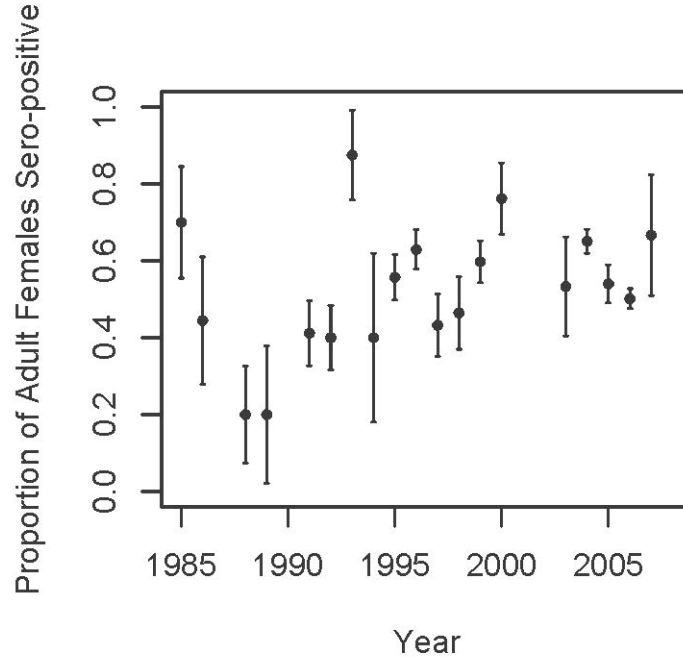


Figure 4. Average proportion of adult female bison in the Yellowstone National Park that were sero-positive for brucellosis during 1985-2008. Vertical bars are  $\pm 1$  standard deviation attributable to sampling error

We pooled data from these studies across bison subpopulations (i.e., central, northern) within the park. We used the estimated, average annual survival rate of adults,  $0.935 \pm 0.05$ , as a prior on the process model parameter for adult survival probability, as described below. We reanalyzed the data from process studies of effect of population density and serological status on birth rates (number of calves that survive for at least 2 months produced per adult female). Bayesian logistic regression provided estimates of means and standard deviations of coefficients which were used as priors on coefficients in the inverse logistic expression for recruitment in the process model.

### OVERVIEW OF BAYESIAN APPROACH

We seek to use the data described above to estimate the values of a set of states, which we for now specify as  $X$ . These states might include, for example, the number of animals in various sex, age, and disease categories over time. We will estimate these states using data models that relate observations to the true state of the system and a process model that estimates the true state. Symbolizing the data as  $Y$ , the parameters in the data models as  $\theta_Y$ , and the parameters in the process model as  $\theta_X$ , Bayes law allows us to estimate probability distributions for the states and parameters conditional on the data using

$$P(\theta_X, \theta_Y | X | Y) = \frac{P(Y | X, \theta_Y) P(X | \theta_X) P(\theta_X, \theta_Y)}{P(Y)} \quad (2)$$

Because the denominator (the probability of the data), is a normalizing constant, we can simplify this expression to

$$\begin{array}{ccccccc}
 \text{Posterior} & & & & & & \\
 \text{Distribution of} & & & & & & \\
 \text{States and} & & \text{Data Model} & & \text{Process} & & \text{Parameter} \\
 \text{Parameters} & & & & \text{Model} & & \text{Model} \\
 \hline
 P(\theta_x \theta_y, X|Y) \propto P(Y|X, \theta_y) P(X|\theta_x) P(\theta_x, \theta_y)
 \end{array}$$

The left hand side of the proportionality is the posterior probability distribution of the model's states and parameters. The right hand side consists of three parts—expressions giving the probability that we would observe the data conditional on the model's prediction (the data model or likelihood), the probability of the model's prediction conditional on the values of its parameters (the process model) and the probability of the parameters (the parameter model, i.e., the priors). We will now expand equation 2 to provide an overarching framework for the detailed discussion that follows.

We will model the population using 2 sexes, 3 ages, and 2 disease states (Figure 5). We define age classes using non-traditional notation to facilitate direct comparison with model code<sup>3</sup>, i.e, age class 1 includes animals 0-1 year old, age class 2, includes animals 1-2 years old and age class 3 is composed of animals aged 2 and older. The model will include 8 age/sex classes (Figure 5). The susceptible state (*S*) and the infected state (*I*) include 3 stages each: males and females in age class 1 and females in age classes 2 and 3. The recovered state (*R*) includes females in age class 3. The male state (*M*) includes males  $\geq 1$  years old. To obtain a simpler model, we did not keep track of the infection status of males because they are not believed to play a role in transmission.

We will use the following notation. State variables will be given in upper case letters (*S*, *I*, *R*, *M*). Subscripts on parameters will be used as needed to indicate age classes and time steps; for example,  $S_{[t,3]}$  will symbolizes the number of susceptible females at time *t* in age class 3. Parameters will be indicated in lower case English or Greek letters. Quantities to be estimated (i.e., state variables and parameters) will be italicized; data will be regular font.

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<sup>3</sup> The programming languages that we will use do not allow indexes for arrays = 0. Therefore, to allow indexing in code to be the same as age classes, we will designate juveniles as age class 1 rather than age class 0 which is more traditional notation.



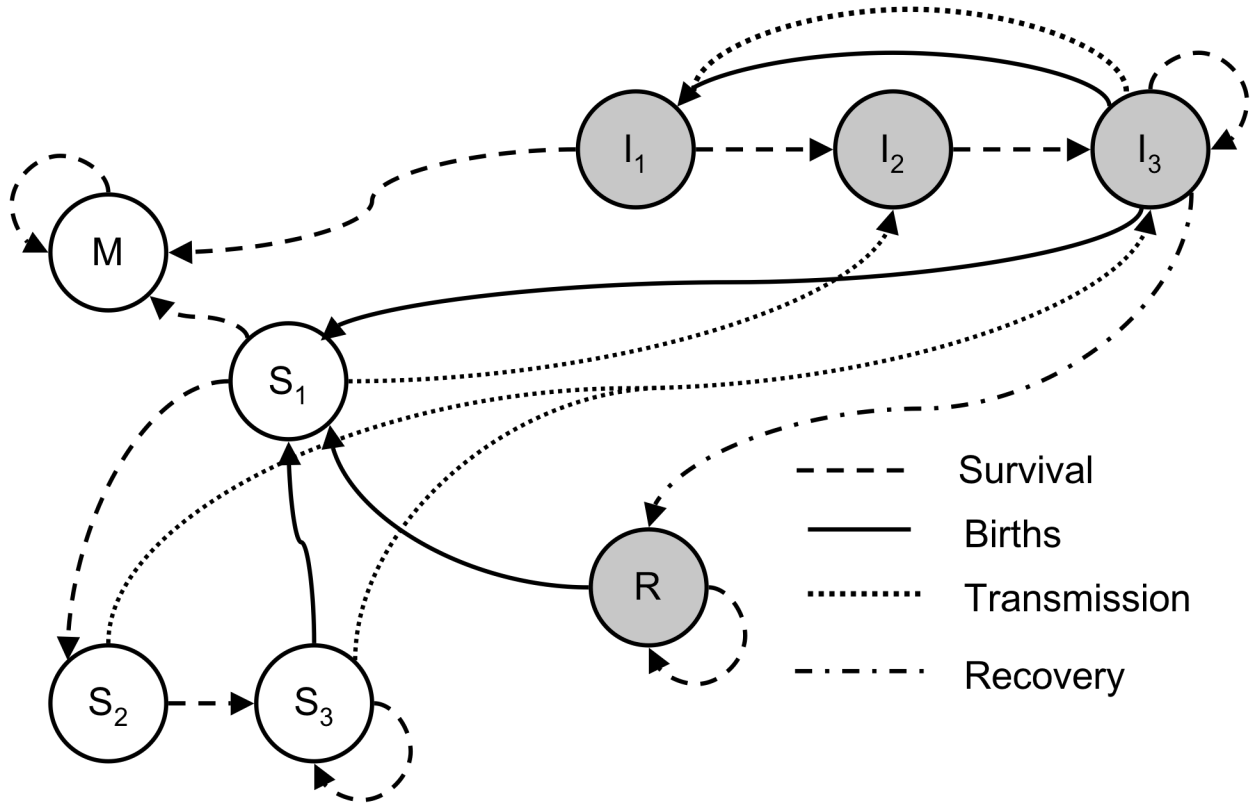


Figure 5. Node diagram of model of the Yellowstone bison population. Open circles portray sero-negative age classes. Shaded circles are sero-positive. Arrows represent survival, births, transmission of brucellosis and recovery from brucellosis. Recovery is not modeled in the traditional sense that recovered animals are not infectious. Instead, only a portion of this class sheds infectious material.

We are now prepared to specify the stochastic, Bayesian model. The model parameters are given by,  $\sigma$ , which represents error in census observations, and two vectors:  $\theta$  which are the parameters of the deterministic process model, and  $\tau$  which estimates the stochasticity in the process model. We will refer collectively to the data as  $\mathbf{Y}$ , which includes the data sets described above. The individual data sets within  $\mathbf{Y}$  include the census data ( $N_{\text{obs}}$ ), the number of calves in observed groups of bison ( $\text{ratio.calf}$ ), the number of cows in observed groups ( $\text{ratio.cow}$ ), the sero-prevalence observations ( $\text{prev.data}$ ) and records of removals ( $r$ ). To keep our notation compact here, we will omit the levels in the model's hierarchy that are needed to estimate observation error, covering these in detail in the sections that follow. We have,

$$\begin{aligned}
P(S, I, R, M, \theta_x, \tau, \mathbf{Y}) \propto & \prod_{t=1}^{39} P \left( \text{N.obs}_{[t]} \left| \sum_{i=1}^3 (I_{[t,i]} + S_{[t,i]}) + R_{[t]} + M_{[t]}, \sigma \right. \right) \times \\
& \prod_{t=1}^{39} P \left( \text{ratio.calf}_{[t]} \left| \frac{S_{[t,1]} + I_{[t,1]}}{\sum_{i=1}^3 (I_{[t,i]} + S_{[t,i]}) + R_{[t]} + M_{[t]}} \right. \right) \times \\
& \prod_{t=33}^{39} P \left( \text{ratio.cow}_{[t]} \left| \frac{\sum_{i=2}^3 (I_{[t,i]} + S_{[t,i]}) + R_{[t]}}{\sum_{i=1}^3 (I_{[t,i]} + S_{[t,i]}) + R_{[t]} + M_{[t]}} \right. \right) \times \\
& \prod_{t=22}^{34} P \left( \text{prev.data}_{[t]} \left| \frac{I_{[t,3]} + R_{[t]}}{S_{[t,3]} + I_{[t,3]} + R_{[t]}} \right. \right) \times \\
& P(S_{[1,1:3]}, I_{[1,1:3]}, R_{[1]}, M_{[1]} | \tau_{[3]}) \times \quad \left. \right\} \text{data models} \\
& \prod_{t=2}^{39} P(S_{[t,1:3]}, I_{[t,1:3]}, R_{[t]}, M_{[t]} | S_{[t-1,1:3]}, I_{[t-1,1:3]}, R_{[t-1]}, M_{[t-1]}, \theta_x, \tau_{[1:2]}, r_{[t]}) \times \quad \left. \right\} \text{process model} \\
& P(\theta_x) \times P(\tau) \quad \left. \right\} \text{parameter models}
\end{aligned}$$

We now describe each of the model's elements in detail.

### PROCESS MODEL

We assume that the northern and central herds operate as a single, intermixing unit. We assume that census occurs in mid-summer and that all births occur before census such that newborns are approximately 2 months old at the time of census. The model operates in discrete time with each state updated yearly. Because assumptions on the timing of births relative to census are critical to properly structuring the model's equations, we go over these issues in some detail in Appendix 1.

Our general approach will follow (Meyer and Millar 1999, Millar and Meyer 2000b, a). The process model will consist of two equations for each state variable,

$$\begin{aligned}
u_t &= \log f(x_{t-1}) \\
x_t &\sim \text{lognormal}(u_t, \tau_j),
\end{aligned} \tag{3}$$

where  $x_t$  is the posterior distribution of a state variable at time  $t$  and  $\sim$  indicates "is distributed as." Thus, equation 3 describes the probability distribution of the true value of the state variable  $x$  at time  $t$ ;  $f(x_{t-1})$  is the deterministic equation predicting the value of a state variable as a function of its estimated value at the previous time step, and  $u_t$  is the log of the median of the estimate of the state variable. The quantity  $\tau_{jj}$  is a vector describing the process variance<sup>4</sup>. Process variance

<sup>4</sup> Precision is often used in Bayesian analysis as a shape parameter for the normal and the lognormal distribution. In the case of the lognormal it is defined as  $1/(\text{variance on the log scale})$ . In the model code, we use precision rather than variance.

can be viewed as a term that quantifies all of the effects on the state variable that are not included in the model. There are three elements in the vector, one for the juvenile class, one for the adult females and one for the adult males. A lognormal distribution was chosen to model the stochastic process because it is well suited to a multiplicative process like population growth, because it models continuous data (which is required for the data model, below) and because it is limited to positive values. We now apply this general approach as a template for each state variable, beginning with juvenile susceptibles.

### Juvenile susceptibles

$$\mu S_{[t,1]} = \log \left( p_{[2]} f_{[t-1,neg]} S_{[t-1,3]} + p_{[2]} f_{[t-1,pos]} [R_{[t-1]} + (1-v)I_{[t-1,3]}] - \frac{q_{[t,1]} S_{[t-1,1]} r_{[t]}}{S_{[t-1,1]} + I_{[t-1,1]}} \right) \quad (4)$$

$$S_{[t,1]} \sim \text{lognormal}(\mu S_{[t,1]}, \tau_{[1]})$$

where:

$\mu S_{[t,1]}$  is the median number of susceptible juveniles of either sex (approximate age 2 months) at the time  $t$

$p_{[2]}$  is the adult survival probability;

$S_{[t-1,3]}$  is the posterior distribution of the number of adult, susceptible females in age class 3 (i.e., 2.5 years and older) at time  $t-1$ ;

$f_{[t-1,neg]}$  is the number of offspring produced per sero-negative adult female;

$f_{[t-1,pos]}$  is the number of offspring produced per sero-positive adult female;

$R_{[t-1,3]}$  is the posterior distribution of adult, recovered females in age class 3 at time  $t-1$ ;

$v$  is the probability of vertical transmission;

$I_{[t-1,3]}$  is the posterior distribution of adult, infectious females in age class 3 at time  $t-1$ ;

$S_{[t,1]}$  is the posterior distribution of the number of juvenile females;

$\tau_{[1]}$  is the process variance for the juvenile age class;

$r_t$  is data on the total number of animals harvested or removed during time  $t-1$  to  $t$ ; and

$q_{t,1}$  is the proportion of the animals removed that are juveniles.

We calculated fertility rates for sero-positive and sero-negative females as

$$f_{[t-1,x]} = \frac{\exp(b_{[1]} + b_{[2]}x + b_{[3]} N.total_{[t-1]})}{1 + \exp(b_{[1]} + b_{[2]}x + b_{[3]} N.total_{[t-1]})}, \quad (5)$$

where:

$b_{[1]}$  is the fertility of sero-negative bison at low population density;

$b_{[2]}$  is the effect of serological status on fertility;

$x$  is an indicator variable ( $x=0$  for  $S$ ,  $x=1$  for  $I$  and  $R$ );

$b_{[3]}$  is the effect of population density on fertility; and

and  $N.total_{[t-1]}$  is the total population size at time  $t-1$ .

The value of  $f$  ranges from 0 to 1. The  $b_2$  and  $b_3$  terms are expected to be negative, indicating a suppressing effect of brucellosis and population density on fertility. The final term in equation

(4),  $\frac{q_{[t,1]} S_{[t-1,1]} r_{[t]}}{S_{[t-1,1]} + I_{[t-1,1]}}$ , requires some explanation. This term estimates the number of susceptible

juveniles that are removed or harvested during the time interval  $t-1$  to  $t$ . The term has 3 components:  $q_{t,1}$  is an estimated parameter specifying the proportion of the removals that are

juveniles;  $\frac{S_{[t-1,1]}}{S_{[t-1,1]} + I_{[t-1,1]}}$  is the proportion of the juveniles that are sero-negative, and  $r_{[t]}$  is the

data on the number of animals removed or harvested. Similar terms will be found in equations for updating other state variables, below.

### Susceptible, yearling females

$$\mu.S_{[t,2]} = (1-m) p_{[1]} (1-\varphi_{[t-1]}) S_{[t-1,1]} - \frac{q_{[t,2]} S_{[t-1,2]} r_{[t]}}{S_{[t-1,2]} + I_{[t-1,2]}} \quad (6)$$

$$S_{[t,2]} \sim \text{lognormal}(\mu.S_{[t,2]}, \tau_{[2]})$$

where:

$\mu.S_{[t,2]}$  is the median number of susceptible females in age class 2 at time  $t$ ;

$m$  is proportion of males in the births;

$p_{[1]}$  is the probability of survival from age 2 months to 1 year + 2 months, assumed to be the same for male and female calves;

$\varphi_{[t-1]}$  is the probability of horizontal transmission during the time interval  $t-1$  to  $t$ ;

$S_{[t-1,2]}$  is the number of juveniles of either sex (approx age 2 months) at the time  $t-1$ ;

$q_{[t-1,2]}$  is the proportion of yearling females in the removals during time  $t$  to  $t+1$ ;

and  $\tau_{[2]}$  is the process variance for adults.

We estimated the probability of horizontal transmission,  $\varphi$ , using a discrete time variation of classical, density dependent transmission,

$$\frac{dS}{dt} = -\beta SI \quad (7)$$

For sufficiently small intervals of time, the discrete time version of equation 7 is

$$S_t = S_{t-\Delta t} e^{-\beta I \Delta t}$$

$$\frac{S_t}{S_{t-\Delta t}} = e^{-\beta I \Delta t} \quad (8)$$

The value of  $e^{-\beta I \Delta t}$  is between 0 and 1 and can be proven to be the probability that an individual that was susceptible at time  $t - \Delta t$  remains so at time  $t$ . Allowing  $\Delta t = 1$ , it follows that

$1 - e^{-\beta I}$  is the probability that an animal that is susceptible at time  $t-1$  is infected at time  $t$  and

$$\varphi_{[t-1]} = 1 - e^{-\beta I_{[t-1,3]}}. \quad (9)$$

Equation 9 provides a very flexible modeling framework. Frequency dependent transmission can be accommodated by dividing  $I_{[t,3]}$  by the model's estimate of the total population size. The effect of recrudescence can be incorporated as

$$\varphi_{[t-1]} = 1 - e^{-\beta (I_{[t-1,3]} + kR_{[t-1]})} \quad (10)$$

where  $k$  is the proportion of recovered animals that shed infectious material. Thus, there are several forms of the transmission equation that can be evaluated with model selection methods (Link and Barker 2006). Alternative models will be developed in consultation with the Yellowstone Bison Management Team and will be evaluated with the data.

### Susceptible, adult females

$$\begin{aligned} \mu.S_{[t,3]} &= p_{[2]} (1 - \varphi_{[t-1]}) (S_{[t-1,2]} + S_{[t-1,3]}) - \frac{q_{[t,3]} S_{[t-1,3]} r_{[t]}}{S_{[t-1,3]} + I_{[t-1,3]} + R_{[t-1]}} \\ S_{[t,3]} &\sim \text{lognormal}(\mu.S_{[t,3]}, \tau_{[2]}) \end{aligned} \quad (11)$$

where  $\mu.S_{[t,3]}$  is the median number of susceptible females in age class 3 at time  $t$  ;  
 $q_{[t,3]}$  is the proportion of the removals contributed by adult females;  
and other parameters and state variables are as defined above.

### Infected juveniles

$$\begin{aligned} \mu.I_{[t,1]} &= p_{[2]} v f_{[t-1, pos]} I_{[t-1,3]} - \frac{q_{[t,1]} I_{[t-1,1]} r_{[t]}}{S_{[t-1,1]} + I_{[t-1,1]}} \\ I_{[t,1]} &\sim \text{lognormal}(\mu.I_{[t,1]}, \tau_{[1]}) \end{aligned} \quad (12)$$

where  $\mu.I_{[t,1]}$  is the median number of infected juveniles at time  $t$  and other parameters and state variables are as defined above.

### Infected, yearling females

$$\begin{aligned} \mu.I_{[t,2]} &= (1 - m) p_{[1]} \varphi_{[t-1]} S_{[t-1,1]} - \frac{q_{[t,2]} I_{[t-1,2]} r_{[t]}}{S_{[t-1,2]} + I_{[t-1,2]}} \\ I_{[t,2]} &\sim \text{lognormal}(\mu.I_{[t,2]}, \tau_{[2]}) \end{aligned} \quad (13)$$

where  $\mu.I_{[t,2]}$  is the median number of infected yearling females at time  $t$  and other state variables and parameters are as defined above.

### Infected, adult females

$$\begin{aligned} \mu.I_{[t,3]} &= p_{[2]} \varphi_{[t-1]} (S_{[t-1,2]} + S_{[t-1,3]}) + p_{[2]} (1 - \rho) (I_{[t-1,2]} + I_{[t-1,3]}) - \frac{q_{[t,3]} I_{[t-1,3]} r_{[t]}}{S_{[t-1,3]} + I_{[t-1,3]} + R_{[t-1]}} \\ I_{[t,3]} &\sim \text{lognormal}(\mu.I_{[t,3]}, \tau_{[2]}) \end{aligned} \quad (14)$$

where  $\mu.I_{[t,3]}$  is the median number of infected adult females at time  $t$ , and  $\rho$  is the probability that an infected and infectious animal is recovered. Recovery probability is a latent, estimated quantity. Recovered females are those that are sero-positive but not infectious. Other parameters and state variables are as defined above.

## Recovered females

$$\mu.R_{[t]} = p_{[2]}\rho(I_{[t-1,2]} + I_{[t-1,3]}) + p_{[2]}R_{[t-1]} - \frac{q_{[t,3]}R_{[t-1]}r_{[t]}}{S_{[t-1,3]} + I_{[t-1,3]} + R_{[t-1]}} \quad (15)$$

$$R_{[t]} \sim \text{lognormal}(\mu.R_{[t]}, \tau_{[2]})$$

where  $\mu.R_{[t]}$  is the median number of recovered adult females at time  $t$  and other state variables and parameters are as defined above.

## Males

$$\mu.M_{[t]} = m p_{[1]}(S_{[t-1,1]} + I_{[t-1,1]}) + p_{[2]}M_{[t-1]} - q_{[t,4]}r_{[t]} \quad (16)$$

$$M_{[t]} \sim \text{lognormal}(\mu.M_{[t]}, \tau_{[3]})$$

where  $\mu.M_{[t]}$  is the median number of males (age 1 year 2 months and older) at time  $t$ ,  $\tau_{[3]}$  is the process variance for males and other state variables and parameters are as defined above.

Equations 4 – 16 provide a model that represents the true state of the bison population. We can say “true” because the failure of the model to predict the true state perfectly is accommodated by including stochasticity in the model—all of the processes that influence the population and that are not represented in the deterministic portions of these equations are represented in the stochastic portion. Using the state-space approach outlined in equation 1 and the Bayesian hierarchical framework shown in equation 2, we now link these process equations to the data. It will be helpful to recall that quantities that are estimated are shown in italic font and data are shown in plain text.

## DATA MODELS

Data models, also called likelihoods, predict the probability that we would observe the data conditional on the predictions of the process model, i.e.,  $P(\mathbf{Y}|\theta)$ . There are four datasets that can be used to form data models for the predictions of the process model: total census, age ratios, sex ratios, and sero-prevalence. Here, we describe a data model for each of these data sets.

### Total Census

We have data on the total population size for 39 years contained in the vector  $\mathbf{N. obs} = (N. obs_{[1]}, N. obs_{[2]}, \dots, N. obs_{[39]})$ . So  $N. obs_{[1]}$  is the observed population size in 1970 and  $N. obs_{[39]}$  is the observed population size in 2008. The model makes a prediction of the total number of animals in the population at each time step,

$$N. total_{[t]} = \sum_{i=1,3} (S_{[t,i]} + I_{[t,i]}) + R_{[t]} + M_{[t]}$$

The observations of total population size are counts, so it is reasonable to assume that they should follow a Poisson distribution. However, it is clear from the standard deviations derived from replicate counts (Figure 1) that the variance of the counts often exceeded the mean and was not constant with time. To account for this over-dispersion we treated the count data as a gamma-Poisson mixture. Using the method of moments we have:

$$\lambda_{[t]} \sim \text{gamma}\left(\frac{N_{[t, total]}^2}{\sigma^2}, \frac{N_{[t, total]}}{\sigma^2}\right)$$

$$\text{N.obs}_{[t]} \sim \text{Poisson}(\lambda_{[t]}),$$

where  $N_{[t, total]}$  is the model's estimate of the posterior distribution of the true population size and  $\sigma$  represents the estimate of the standard deviation of the observations for census resulting from sampling error. Annual observation errors were estimated from years that included replicate counts as the standard deviation calculated over the replicates,  $sd_{[t]}$ . We estimated an overall observation error by assuming that these standard deviations were random effects, modeling their distribution as

$$sd_{[t]} \sim \text{gamma}(\alpha, \nu),$$

The mean of this distribution was used to estimate  $\sigma$ , using  $\sigma = \alpha / \nu$ .

## Removals

All equations in the process model contain an element from the unobserved matrix  $\mathbf{q}$ , which contains estimates of the proportion of each age and sex class for each year when removals occurred. Thus, each row in the  $\mathbf{q}$  matrix is a vector containing the proportion of juveniles, yearling females, adult females and males in the removals. The elements of  $\mathbf{q}$  were estimated as follows. For years when composition data were available, we used the likelihood,

$$P(\text{remove\_comp}_{[t,j]} | q.d_{[t,j]}, \text{remove\_comp}_{[t,5]}) = \text{binomial}(q.d_{[t,j]}, \text{remove\_comp}_{[t,5]})(17)$$

The data are contained in the matrix `remove_comp`, indexed by  $t$  for years and by  $j$  for age / sex classes (1=juveniles, 2=yearling females, 3=adult females, 4=males, 5=total number of individuals classified). The estimated quantity  $q.d_{[t,j]}$  was our initial estimate of the proportion of the removals taken from each age and sex class. We assumed no prior information on  $q.d_{[t,j]}$  for the years where data on composition were available. For the years when composition data were unavailable, we used the data from 2002-2006 to estimate an average mean and standard deviation for a beta distribution of  $q.d_{[j]}$  averaged over 2002-2006. We used this mean and standard deviation to calculate shape parameters for the distribution for each age sex class and then used these shape parameters for priors on  $q.d_{[j,d]}$  for the 1986-2001.

Because the elements of  $q.d$  were estimated individually as beta distributed variables for each year, rather than as elements of a multinomial<sup>5</sup>, it was possible that  $\sum_{j=1,4} q.d_{[t,j]} \neq 1$ . To assure that the vector summed to 1 in the process model, we normalized the vector before using

$$\text{it in the process model, e.g. } q_{[t,j]} = \frac{q.d_{[t,j]}}{\sum_{i=1,4} q.d_{[t,i]}}$$

<sup>5</sup> The preferred approach would be to use a Dirichlet prior and a multinomial likelihood for  $\mathbf{q}$ ; However, this was not computationally feasible because it was not possible to assure that the distribution was log-convex. The approach we used is less elegant, but provides the same estimates.

### Age composition data

We have virtually uninterrupted data<sup>6</sup> on the proportion of the population that was in the juvenile stage (*ratio.calf*). Each year, >50 groups of bison were observed and the group size and the number of calves in the group were recorded. We were interested in forming a likelihood estimating the probability of the observed proportion of calves conditional on the model's prediction of the proportion of calves in the population and the error associated with the observed proportion, i.e.,

$$P\left(\text{ratio.calf}_{[t]} \left| \frac{I_{[t,1]} + S_{[t,1]}}{N_{[t,total]}}, \text{var.calf}_{[t]} \right.\right) \quad (18)$$

This could be approached using a binomial likelihood where the number of successes is the number of calves observed in a year and the number of trials is the total number of animals observed. However, this provides observations with virtually no error, because the number of animals observed is very large. Moreover, it is not consistent with the way the observations were made. Observers did not simultaneously see thousands of bison and observe the number of calves in this huge sample. Instead, they observed a series of separate groups. The size of each group could be realistically viewed as the number of trials, and the calves within a group as the number of successes. This suggests that the data should be modeled as a beta-binomial hierarchy---each group represents a “draw” from a beta distribution, and we want to estimate the mean and the variance of that distribution. The mean provides our estimate of the average ratio for the year (*ratio.calf<sub>ij</sub>*) and the variance is the estimate of the observation uncertainty. So, for each year, we estimated shape parameters for a beta distribution using data on the number of calves in a group (*calves<sub>[t,i]</sub>*) and the group size (*group.size<sub>[t,i]</sub>*):

$$P(\alpha_{[t]}, \beta_{[t]}, p.\text{ratio}_{[t,i]} | \text{calves}_{[t,i]}, \text{group.size}_{[t,i]}) \propto \prod_{i=1, \text{ngroup}} \text{binomial}(\text{calves}_{[t,i]} | p.\text{ratio}_{[t,i]}, \text{group.size}_{[t,i]}) \text{beta}(p.\text{ratio}_{[t,i]} | \alpha_{[t]}, \beta_{[t]}) p(\alpha_{[t]}) p(\beta_{[t]}) \quad (19)$$

We then calculated the mean of each year's beta distribution as

$$\text{ratio.calf}_{[t]} = \alpha_{[t]} / \beta_{[t]} \quad (20)$$

and the variance as

$$\text{var.calf}_{[t]} = \frac{\alpha_{[t]} \beta_{[t]}}{(\alpha_{[t]} + \beta_{[t]})^2 (\alpha_{[t]} + \beta_{[t]} + 1)}. \quad (21)$$

These calculations were performed externally to the overall model. The quantities *ratio.calf<sub>ij</sub>* and *var.calf<sub>ij</sub>* were read in as data for each year and were used in the likelihood for the model's predictions as follows.

For notational convenience, we define the model's estimate of the proportion of calves in the populations as

$$\mu.\text{calf}_{[t]} = \frac{S_{[t,1]} + I_{[t,1]}}{N.\text{total}_{[t]}}. \quad (1.22)$$

Next, we calculated shape parameters for a beta distribution using  $\mu.\text{calf}_{[t]}$  and the estimate of the observation error *var.calf<sub>ij</sub>*

<sup>6</sup> The only year when these ratio data were missing was 2005.



$$\begin{aligned}
shape1.calf_{[t]} &= \frac{\mu.calf_{[t]}^2 - \mu.calf_{[t]}^3 - \mu.calf_{[t]}var.calf_{[t]}}{var.calf_{[t]}} \\
shape2.calf_{[t]} &= \frac{\mu.calf_{[t]} - 2\mu.calf_{[t]}^2 + \mu.calf_{[t]}^3 - var.calf_{[t]} + \mu.calf_{[t]}var.calf_{[t]}}{var.calf_{[t]}}
\end{aligned} \tag{23}$$

We then used the shape parameters to form a likelihood for the data conditional on the model's prediction and the observation error:

$$P\left(ratio.calf_{[t]} \mid \mu.calf_{[t]}, var.calf_{[t]}\right) = \text{beta}\left(shape1.calf_{[t]}, shape2.calf_{[t]}\right) \tag{24}$$

### Sex composition data

During 2002-2007, data were collected on the sex and age composition of groups observed from the ground. Animals were classified as juveniles, yearling males, yearling females, and adult males and females. The proper way to model these data is to form a multinomial likelihood with a Dirichlet prior. However, the hierarchical approach to using individual groups as observations from a common distribution that we used above is not feasible for a Dirichlet – multinomial hierarchy. Until this approach can be implemented, we used the proportion of yearling and adult females groups in a beta-binomial hierarchy in exactly the same way as we described for the calf data, above.

### Sero-prevalence data

Data on sero-prevalance for adult females (age > 2 years) spanned 1985 to 2007 and formed the basis for the likelihood:

$$\begin{aligned}
prev_{[t]} &= \frac{I_{[t,3]} + R_{[t]}}{R_{[t]} + I_{[t,3]} + S_{[t,3]}} \\
P\left(prev.data_{[t,3]} \mid prev_{[t]}, prev.data_{[t,4]}\right) &= \text{binomial}(prev_{[t]}, prev.data_{[t,4]})
\end{aligned} \tag{25}$$

Thus,  $prev_{[t]}$  is the model's estimate of the proportion of adult females that are sero-positive. The data on prevalence are stored in a matrix with 5 columns. Column 3 contains observations of the number of adult females that were positive and column 4 contains the total number tested in year  $t$ .

## PARAMETER MODELS

The third element of our Bayesian, stochastic model (equation 2) is contributed by probability models for parameters, that is, their prior distributions (Table 1). Most of the priors were uninformative, reflecting the fact that we knew very little about the value of the parameter before this analysis was done. Other priors reflected plausible assumptions, for example that the sex ratio at birth is approximately 50/50 males to females. The remaining priors were informative based on data obtained in process studies of survival and fertility and observations of the composition of removals.

Table 1. Parameters estimated in model of the Yellowstone bison population and prior distributions used for estimation of each parameter.

Parameter	Definition	Prior distribution	Prior informative?
$b_{[1]}$	Intercept in logistic regression of birth rate on serological status and population density. Inverse logit( $b_{[1]}$ ) is the number of offspring surviving to 2 months of age produced per sero-negative female at low population density (i.e., .86)	normal(mean = 1.94, precision = 2.10)	yes
$b_{[2]}$	Sero-prevalence slope in logistic regression of birth rate on serological status and population density	normal(mean = -.70, precision = 9.8)	yes
$b_{[3]}$	Population density slope in logistic regression of birth rate on serological status and population density	normal(mean = -.0026, precision = 2.54e7)	yes
$p_{[1]}$	Juvenile survival. The probability that juveniles (aged 2 months) survive to become yearlings (aged 1 year 2 months)	uniform(.2,.95)	no
$p_{[2]}$	Adult survival. The probability that males and females aged 1.2 years and older survive from time $t$ to time $t+1$ .	beta(62.2, 4.3)	yes
$m$	proportion of births surviving to 2 months of age that are male	beta(49.5,49.5)	yes
$\beta$	Rate of transmission in continuous time (units=1/yr)	uniform(0,.1)	no
$\rho$	Probability that an infected and infectious animal becomes recovered	beta(1,1)	no
$k$	Proportion of recovered animals that shed infectious material		
$\nu$	The probability of vertical transmission	beta(1,1)	no
$\alpha_{[sd]}$	Hyper-parameter for distribution of census standard deviations	gamma(.001,.001)	no
$\nu_{[sd]}$	Hyper-parameter for distribution of census standard deviations	gamma(.001,.001)	no
$q.d_{[t,1]}$	Proportion of removals that were juveniles during $t = 1986-2001$	beta(357,1057)	yes <sup>1</sup>
$q.d_{[t,2]}$	Proportion of removals that were yearling females during $t = 1986-2001$	beta(76,1367)	yes <sup>1</sup>
$q.d_{[t,3]}$	Proportion of removals that were adult females during $t = 1986-2001$	beta(691,760)	yes <sup>1</sup>
$q.d_{[t,4]}$	Proportion of removals that were yearling and adult males during $t = 1986-2001$	beta(318,1129)	yes <sup>1</sup>
$q.d_{[t,1]}$	Proportion of removals that were	beta(1,1)	no <sup>1</sup>

Parameter	Definition	Prior distribution	Prior informative?
$q.d_{[t,2]}$	juveniles during $t = 2002-2006$ Proportion of removals that were yearling females during $t = 2002-2006$	beta(1,1)	no <sup>1</sup>
$q.d_{[t,3]}$	Proportion of removals that were adult females during $t = 2002-2006$	beta(1,1)	no <sup>1</sup>
$q.d_{[t,4]}$	Proportion of removals that were yearling and adult males during $t = 2002-2006$	bea(1,1)	no <sup>1</sup>
$\tau_{[1]}$	Variance for juvenile process equations	gamma(.001,.001)	no
$\tau_{[2]}$	Variance for adult process equations	gamma(.001,.001)	no
$\tau_{[3]}$	Variance for initial conditions	gamma(.001,.001)	no

<sup>1</sup> The proportion of removals ( $q.d_{[t,1:4]}$ ) during  $t = 1986-2001$  had informative priors that were based on the data on removals during 2002-2006. Priors were uninformative for this vector during 2002-2006 when data were available. It was necessary to estimate the composition of removals during the period when removal data were available because the total removal data contain many unclassified animals.

## IMPLEMENTATION

Posterior distributions of parameters, states, and initial conditions were estimated using Monte-Carlo Markov Chain methods implemented using the software WinBUGS (Lunn et al. 2000) and the R2WinBUGS package of the statistical computing environment, R (R Development Core Team 2007)(Appendix 3,5) . Plausible initial values were chosen at different points for chains. Initial values for state variables were randomly perturbed to values within .8 – 1.2 times the originating value. We ran 100,000 iterations of each chain, discarding the initial 25,000 values. Convergence was assured using Gelman-Rubin statistics.

## RESULTS

### What can state space models tell you?

State space models can estimate three types of quantities. First is to estimate values for the model's parameters and quantities of interest derived from them. Next is to estimate the values of past states, for example the total size of the population each year during 1970 to 2008. This might at first seem to be redundant with *data* on the states, but the model improves on the data in several ways. The models allow *all* data to influence the estimates of state variables, which usually (but not always) means that the confidence envelopes on state variables are narrower than we would obtain from the census data alone. It allows us to estimate states that are unmeasured, for example, when there are gaps in the data or for quantities that are not observed. Finally, the state space approach allows us to estimate *future* states by forecasting. All of these estimates are accompanied by confidence envelopes that quantify the uncertainties associated with the estimates. We will now report results organized in these three areas, parameter estimates, estimates of past states, and estimates of future states.

### Parameter Estimates

With a few exceptions, there was substantial uncertainty in the estimates of model parameters, particularly parameters that were associated with disease transmission (Table 2). This

uncertainty is to be expected given that the data on disease states were limited. Despite the uncertainties, we are the first to obtain rigorous estimates of transmission rates, probabilities of horizontal recovery, and probabilities of vertical transmission for the Yellowstone bison population.

Table 2. Estimates of means and 95% credible intervals for parameters in a model of the Yellowstone Bison Population.

Parameter	Definition	Mean	SD	95% Credible Interval	
				Lower	Upper
$b_{[1]}$	Intercept in logistic regression of birth rate on serological status and population density. Inverse $\text{logit}(b_{[1]})$ is the number of offspring surviving to 2 months of age produced per sero-negative female at low population density (i.e., .86)	1.314	0.381	0.519	2.025
$b_{[2]}$	Sero-prevalence slope in logistic regression of birth rate on serological status and population density	-0.59	0.285	-1.154	-0.062
$b_{[3]}$	Population density slope in logistic regression of birth rate on serological status and population density	-2.62E-04	9.29E-05	-4.34E-04	-7.06E-05
$p_{[1]}$	Juvenile survival. The probability that juveniles (aged 2 months) survive to become yearlings (aged 1 year 2 months)	.641	.144	.378	.914
$p_{[2]}$	Adult survival. The probability that males and females aged 1.2 years and older survive from time $t$ to time $t+1$ .	.954	.00286	.890	.995
$m$	Proportion of animals surviving to 1 year 2 months of age that are male	.464	.041	.385	.545
$\beta$	Rate of transmission in continuous time (units=1/yr)	2.76E-04	1.15E-04	8.93E-05	5.43E-04
$\rho$	Probability that an infected and infectious animal becomes recovered	0.106	0.067	0.008	0.263
$\nu$	The probability of vertical transmission	0.808	0.149	0.461	0.993

### Estimates of Past and Future States

**Total Population Size** Model estimates of the medians of the posterior distributions of the total population size ( $N_{total}$ ) closely tracked the data (Figure 6). Credible intervals were narrow. The seemingly tight fit between the model and the data resulted in part because the observation error in census was so low. The estimate of the posterior distribution of  $N_{total}$  for any given year is influenced by the data for that year, by the posterior distribution of  $N_{total}$  for the previous year, and by the deterministic prediction of the model. If the process error is high and the observation error is low, then model predictions tend to approach each data point. If process error is low and observation error is high, then the model's prediction tends to split the cloud of points. Our results show the simultaneous effect of both sources of uncertainty (Figure 6). The sharp declines in population size shown in Figure 6 resulted from the influence of removals, which

were based on data. Predictions of the future state of the population showed rapidly expanding credible intervals resulting from the relatively high levels of process variance (Figure 6). It appears that predicting the population size is feasible for projection intervals  $\leq 2$  years. After that, confidence in projections decreases dramatically; the forecast for the population size in

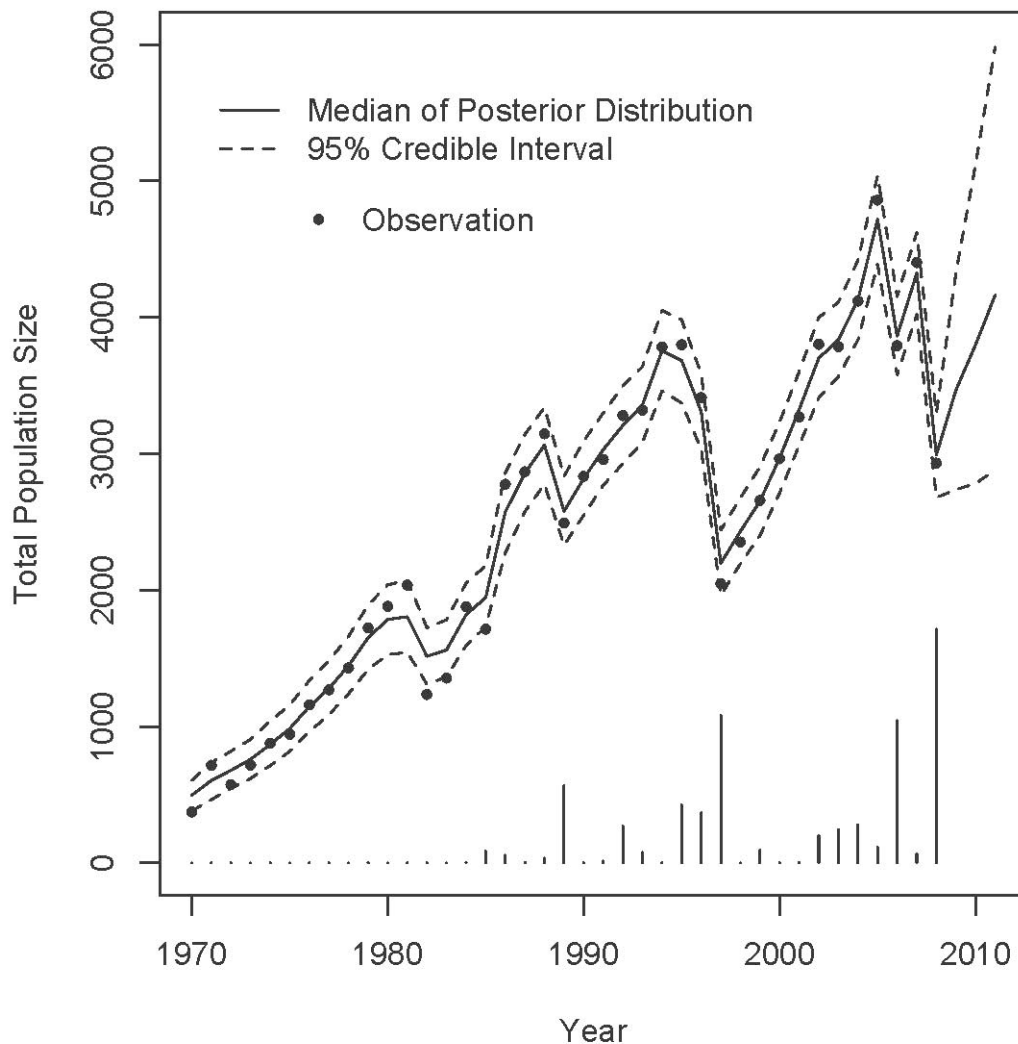


Figure 6. Estimates of the number of animals in the Yellowstone bison population during 1970 – 2008 and predicted numbers during 2009-2011. Dashed lines give 95% credible intervals on the estimate of the true and the predicted state. Vertical lines show data on harvest and removals.

2010 is 3843 with a credible interval of 2782 to 5120. However, the credible interval for the population in 2013 spans 3185 to 7692. This would appear discouraging were it not for the fact that adding future “data” on removals improves our confidence in model predictions of total abundance as will be described in a subsequent section (**Model Experiments**).

### *Population Composition*

Model estimates of the proportion of calves in the population also tracked the data closely with narrow credible intervals (Figure 7). Again, observation error for these data was relatively low because a large number of groups was classified during each year. Credible intervals on the proportion of adult females in the population spanned approximately 0.4 - 0.6, reflecting the increased observation error in the data resulting from fewer annual observations (Figure 8).

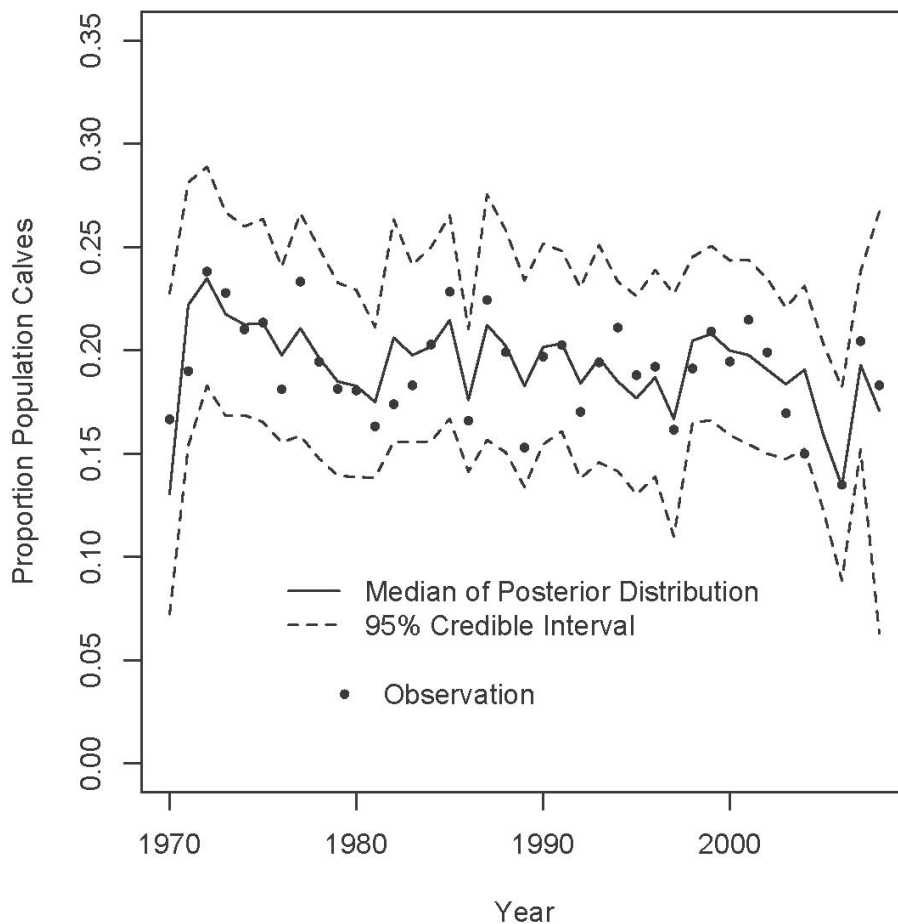


Figure 7. Estimates of the proportion of calves in the Yellowstone bison population during 1970 – 2008.

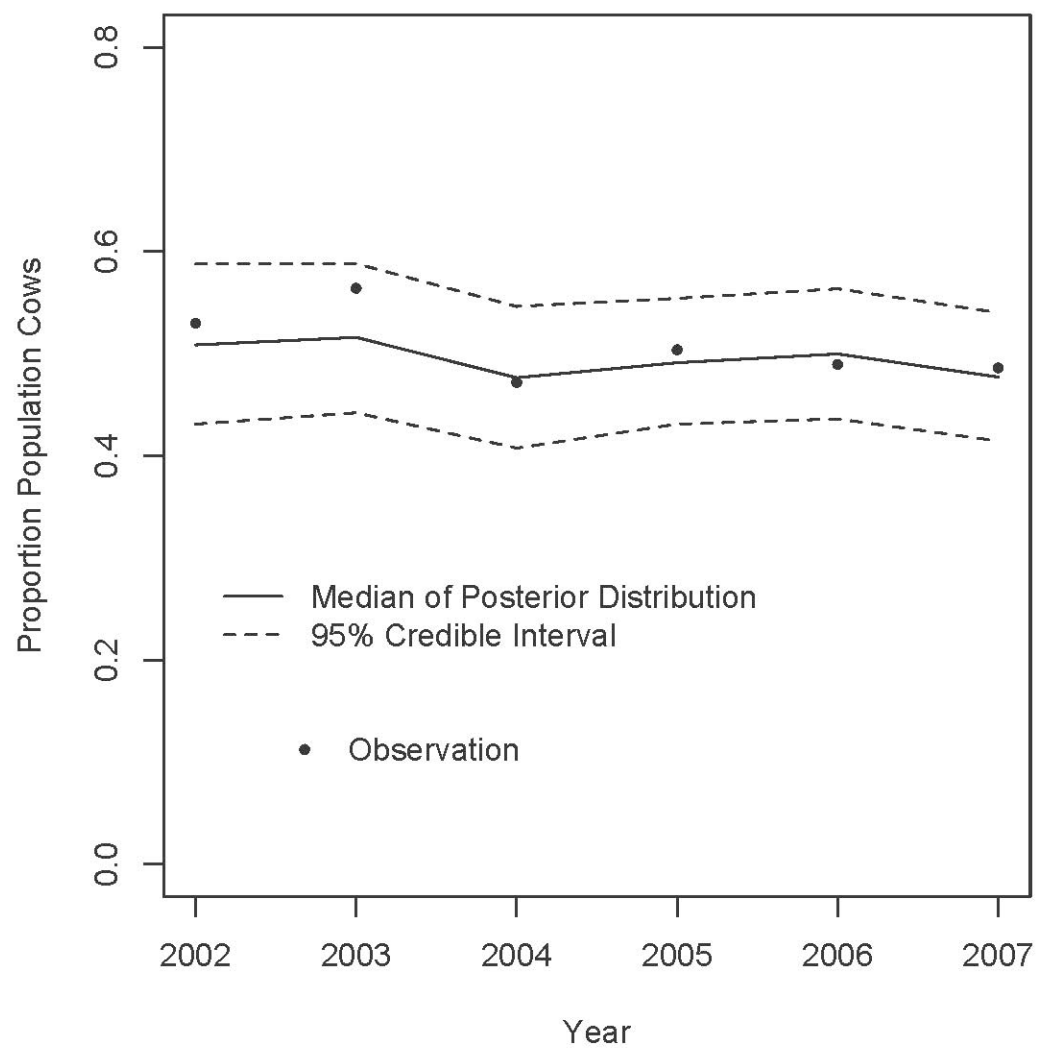


Figure 8. Estimates of the proportion of females in the Yellowstone bison population during 2002-2007.

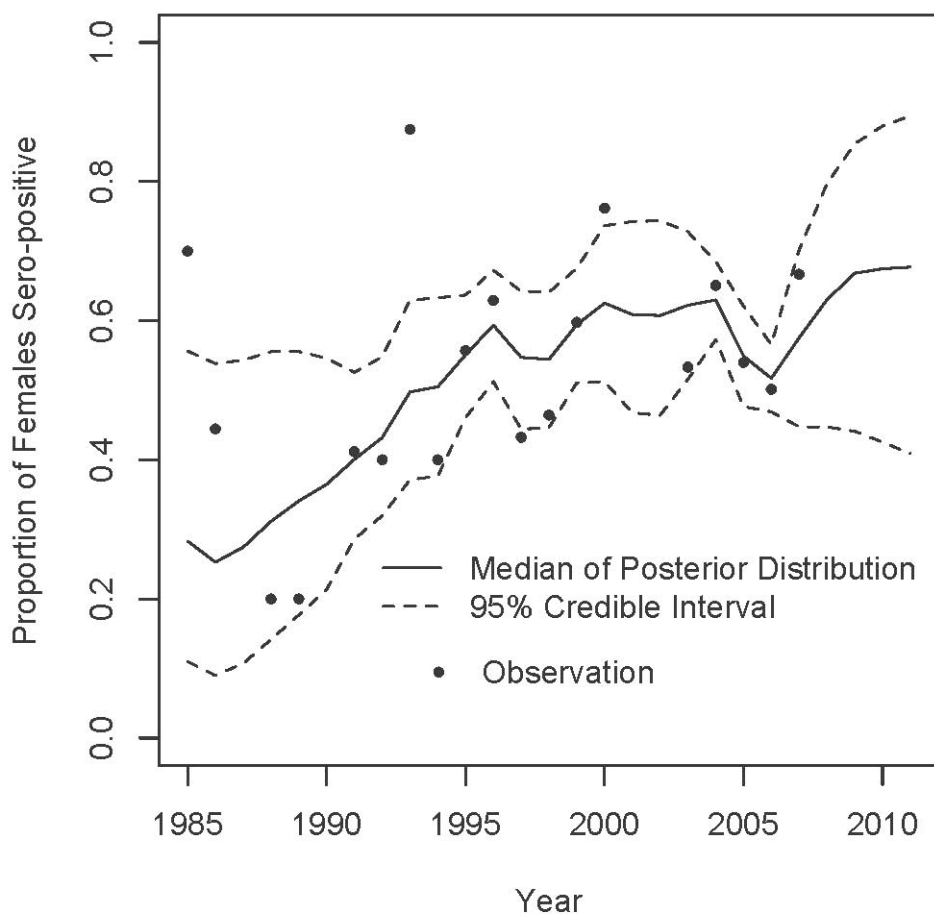


Figure 9. Sero-prevalence for brucellosis in adult cows in the Yellowstone bison population for 1985-2008 and projections of sero-prevalence for 2009 – 2011.

#### *Disease States and Processes*

Of all of the model estimates of states, uncertainty was greatest for sero-prevalence (Figure 9). This uncertainty resulted in part from observation error in the data. But it probably also reflects structural deficiencies in the model's representation of transmission. The model estimates were less sensitive to the high prevalence values in early years of the time series because these were



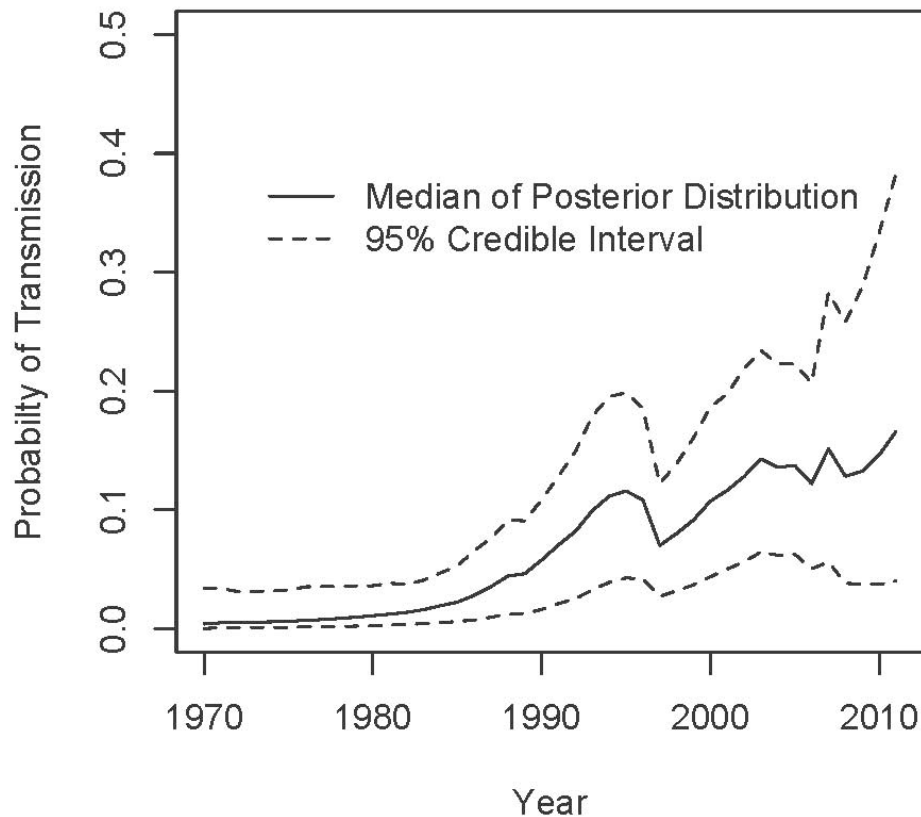


Figure 10. Model estimates and forecasts of the probability of horizontal transmission of brucellosis in the Yellowstone bison population during 1970-2011

based on very small sample sizes. The model's estimates of sero-prevalence suggest an increasing trend in the proportion of the population of adult females that is sero-positive. Again, predictions beyond the data are accompanied by broad credible intervals. Consequently, it is not possible to reliably project whether prevalence will increase or remain constant. The model's projection can rule out a steep decline in sero-prevalence in the near future.

The model estimated probability of horizontal transmission of about 0.10 during the past decade (Figure 10); that is, a female was susceptible at time  $t$  had a 1 in 10 chance that she would be infected at time  $t+1$ . Although the general predicted trend in transmission probability is upward, credible intervals cannot rule out a static trajectory. Because the model's formulation for transmission is density dependent, estimates of the probability of transmission will increase with increasing population size in this model. We will also evaluate frequency dependent transmission in future work.

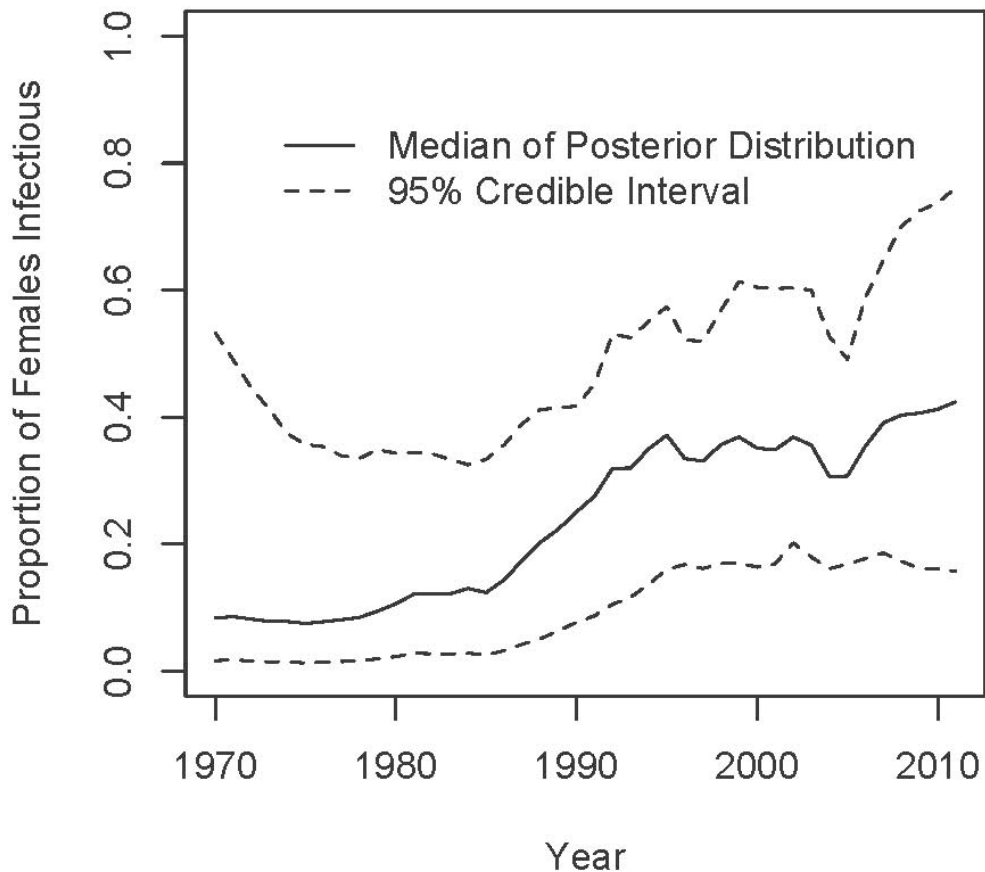


Figure 11. Model estimates and forecasts of the proportion of adult females in the Yellowstone bison Population that are infectious for brucellosis during 1970-2011.

Mirroring trends in infection probability, the model estimated that the proportion of all females that were infectious remained approximately static at about 35% during 1990 – 2008 (Figure 11). The model forecast is for no dramatic change in this proportion, although increases cannot be ruled out. Over the same time interval, model estimates and forecasts of the proportion of sero-positive bison that were infectious was about 60%.

### AN EXAMPLE APPLICATION TO MANAGEMENT

There are very few decisions about managing complex systems that are made without uncertainty. The value of models properly assimilated with data is not to eliminate that uncertainty, but rather to make it plain, to offer honest forecasts. This is the real strength of the Bayesian approach, a strength we illustrate here.

Our illustration focuses on evaluating alternatives for regulating the bison population at acceptable levels of abundance. Our model cannot specify what those levels should be. However, we *can* use the model to evaluate the probability that a given management action would result in a desired outcome. As an illustration of a desired outcome, assume that it has been decided that the bison numbers during summer should be maintained at levels between 2500 and 3500 animals within Yellowstone National Park. We can be certain that even the best managed population will fluctuate over time, and so it is sensible to choose a range as an

objective for management rather than a single, fixed population size. Once we have a clearly stated goal, we can evaluate the probability that a given management action will achieve it.

The non-random nature of culling actions has potential to adversely affect both demographic and genetic values of Yellowstone bison. Hunting as currently implemented is not expected to provide any regulatory effect due to the nature of when and where bison occupy the hunting districts outside the park. Regardless of how bison are removed from the population, culling relatively small numbers on a frequent basis would provide a mechanism to reduce social and political rhetoric, and conserve population demography and migratory patterns. For example, there is widespread concern about the large-scale removals of bison that are episodically implemented to reduce the risk of brucellosis transmission to cattle. A more attractive alternative might be using hunting by citizens outside the park to remove smaller numbers of animals regularly. The question is this: can hunting alone regulate the bison population? Or, perhaps more usefully put, how many animals must be removed annually to achieve an acceptable probability of maintaining the summer population at levels between 2500 and 3500 animals over the next five years?

Our model allows us to assess this probability in a rigorous way, based on all of the data at hand and including all of the uncertainties inherent in the data and in the model's representation of bison population dynamics (Figure 12). We can be most certain about the efficacy of different management alternatives in the near term, one or two years out. In this case, several levels of harvest give acceptable results. However, if we extend the forecast horizon to five years, then it becomes evident that only three alternatives (200, 250, and 300 animals harvested per year) have a reasonable chance to achieve the desired result in 2013 (Figure 12). The probabilities of achieving the objective are very similar for all three of these alternatives (.37 for 200, .42 for 250, and .38 for 300 animals harvested per year). The importance of including uncertainty is seen in the deterministic projections of the 200 animals/ year harvest regime, which suggest that the population would be maintained at close to 3000 animals over the entire period (Figure 13). However, despite these projections, we can only be 37% certain that this regime would meet the objectives of keeping the population between 2500 and 3500 animals. Moreover, we cannot rule out a very real chance that the population in 2013 would be well *below* its current size (Figure 13).

Thus, it would be entirely reasonable to choose to harvest 200 females per year to meet the objective of maintaining the population within the range of 2500 to 3500 animals. Even given the uncertainties in forecasting 5 years out, we have a reasonable probability of meeting that objective if we do nothing between now and then. But, we also have a window of time to make adjustments in our strategy based on new data and on revised forecasts. If the new forecasts show we are not on course to meeting our objectives, we can revise the removal strategy.

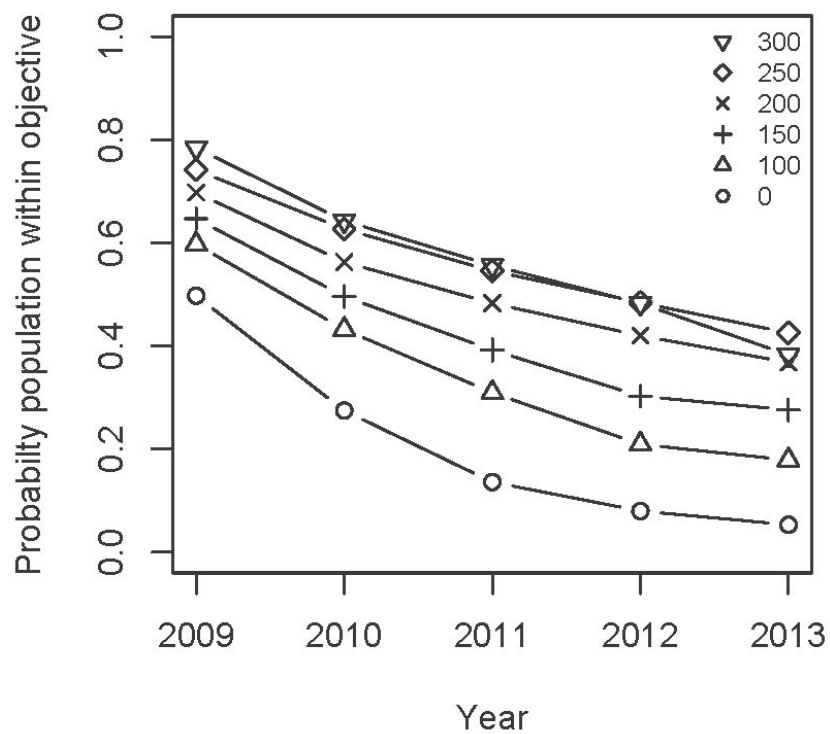


Figure 12. Probability that the Yellowstone bison population would number between 2500 and 3500 animals in 2013 under six different management regimes. Regimes are defined by the number of adult females removed from the population annually by hunting.

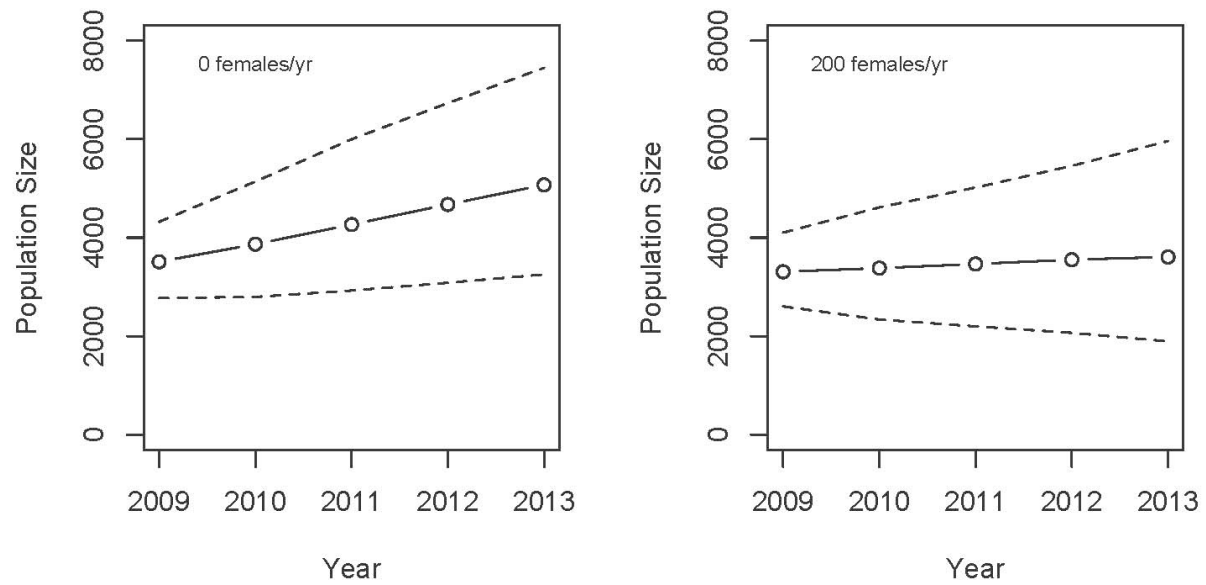


Figure 13. Forecasts of the bison population size assuming two management scenarios, no removals (left panel) and remove 200 adult females per year by annual harvest (right panel). Solid lines and open circles are predicted means of the posterior distribution and dashed lines are 95% credible intervals.

## CONCLUSION

Adaptive management (Walters 1986) has emerged as a sensible, widely used, and trusted approach for managing natural resources throughout the world. It is often overlooked that Bayesian models form a critical, central element of adaptive management as it was originally conceived by (Walters 1986). Adaptive management rightly depends on Bayesian forecasts to inform choices among a range of possible management actions. The process is cyclic. A management action (or actions) is chosen and implemented; new data are taken on the state of the system; the model forecast is updated with the new data and a new set of management actions is chosen based on the update. Thus, continuous improvement in model, management, and data are the hallmark of the adaptive management approach properly implemented. Model forecasts allow managers to make decisions based on the probability of outcomes, particularly the risks of undesirable outcomes, as illustrated above. Observing the outcomes that *do* occur allows improvement in the ability of the model to make reliable forecasts, which in turn, improves the wisdom of management decisions.

This document offers a proof-of-concept of the application of the Bayesian hierarchical approach to the problem of management of the Yellowstone bison population. We have demonstrated that the model can provide a useful tool for integrating hard-won data from a broad range of sources, including ongoing monitoring efforts and detailed studies of processes governing bison population dynamics. There remains substantial work to be done (Appendix 2). The model can be improved in the way it represents critical processes, for example, the episodic return to infectiousness of sero-positive, “recovered” individuals. The data model for total counts can be enhanced to include an estimate of the animals that are present on the summer range but are not counted. Mark-recapture studies of conversion of serological status can be used to enhance the estimate of transmission rate. There are several management experiments that remain to be conducted, including simulations to examine the effect of removing sero-negative animals on the probability of transmission. We anticipate making these improvements and updating the model annually to provide a firm, scientific basis for the adaptive management of the Yellowstone bison population.

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## Appendix 1: Assumptions on timing of births relative to census and implications for model structure.

The timing of births relative to census has important implications for the structure of model equations on recruitment. There are two issues that must be considered: which age classes contribute to offspring at the next time step (based on understanding of the biology of the species) and how to include juvenile survival and adult survival in the term for recruitment.

We assume that census occurs 1-2 months after offspring are born. Therefore age class 1 includes animals that are .1 – 1.1 years old; age class 2 includes animals that are >1.1 – 2.1 years old and age class 3 includes animals that are >2.1 – 3.1 years during their first year in the class and animals that are > 3.1 years old in subsequent years. Age class 3 is the only class that produces offspring and includes animals that give birth when they are 3 years old and older. The key point here is that the youngest animals in age class 2 at time  $t$  (age = 2.1 years) are 3 years old at the birth pulse are 3.1 years old at the next census, that is at time  $t+1$ . This is illustrated in Figure A1, below.

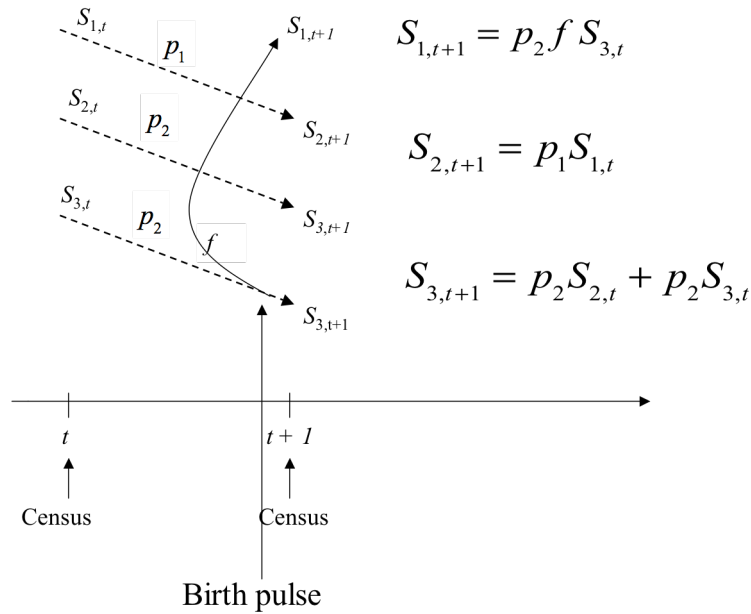


Figure A1. Relationship between assumptions on timing of events in the model and the structure of model equations using the susceptible age classes as an example. The parameter  $p_1$  is juvenile ;  $p_2$  is adult survival, and  $f$  is recruitment, defined as the number of offspring surviving to census to census produced per reproductive female.

Adult survival is included in the equation for new offspring because females must survive from census until births occur to produce offspring. We assume that all adult mortality occurs between census and births and the neonatal mortality (i.e., deaths between birth and an animal's first census) is subsumed in the term for recruitment.

## **Appendix 2: Plans for future work discussed by the Yellowstone bison management team**

### **FUTURE WORK**

#### **High Priority**

- Add infectious component to Recovered state
- Conduct model experiments on alternatives for disease control / population regulation
  - Quantify how focusing on females only relative to removal in proportion to age/sex structure may change demographics.
  - Evaluate the ability of alternative removal strategies (targeting different sero-prevalence and age classes) to reduce disease prevalence, probability of transmission, and population size.
- Examine alternative models for transmission, particularly frequency dependence
- Add data model that includes sighting probability.

#### **Low Priority**

- Add effects of summer NPP on recruitment
- Add effects of density and winter snow on juvenile survival
- Explore using sero-conversion data to improve precision of transmission rate.
- Conduct model experiments to evaluate monitoring strategies

## Appendix 3: Data Manipulation Programs

Table A.1: Summary of programs used to create data objects used to fit the Bayesian hierarchical model. Code for programs referenced in the table is found on pages 34-57. Programs are listed in the same order as they appear in the table

Data or parameter estimates needed for analysis	Source	Code, R object,	What was done
Prevalence	/Raw/boundarysero.txt /Raw/sero.txt	"/Users/Tom/Documents/YNP_Bison_Model/Data/Prevalence.R"  Prev, Prev1, and Prev2 data frames in obs in YNP_data.Rdata object	Combine age-specific prevalence into 3 age classes (1=juvenile, 2=yearling, 3=adult). Combine data for 2 herds. Create 3 data frames: Prev contains all years and age classes—used primarily for plotting. Prev1 contains data for adults only for years when these were the only observations, and Prev2 contains age specific prevalence for the few years where those data are available.
Removals	"/Users/Tom/Documents/YNP_Bison_Bin/DiseaseModel_Hobbs/Counts and Removals 1901-2008.xls"	"/Users/Tom/Documents/YNP_Bison_Model/Data/Removals.R"  Removals object in obs in YNP_data.Rdata object	The main job here was to combine the pre and post census removals into one year—the post census from the previous year (occurring during winter) and the pre-census removals from the current year. I started by making a new .csv file that contained the Lamar and Mary Mt herds and the pre and post removals. These were then worked up with the Removals.R script. The herds were summed and then the pre and post were summed for each year. The data file has 2 columns, one for year, and the other for total removals. The removals come from the year that you are predicting, i.e.  $N[t] = N[t-1] \text{ Removals}[t]$
Regression coefficients for recruitment	/raw/NR.preg.txt, /raw/CP.preg.txt	"/Users/Tom/Documents/YNP_Bison_Model/Data/Recruit.R"  "/Users/Tom/Documents/YNP_Bison_Model/Data/r.bug "  Recruits, Recruits.logr, and Recruits.bug objects in YNP_data.Rdata	Calculates mean and sd of regression coefficients for priors on coefficients used in inverse logit function for recruitment in model.  Combined data from two herds, did logistic regression to estimate recruitment (calves per female) for single adult age class ( $\geq 2$ years) using coefficients for serology, population size, SWE, and (?) Palmer drought index. It may be a good idea to break this up into 2 age classes because sero-positive converters are less likely to have a calf than sero-positive and conversion is most likely early in life.
Composition of removals	"/Users/Tom/Documents/YNP_Bison_Bin/DiseaseModel_Hobbs/Counts and Removals 1901-2008.xls"	"/Users/Tom/Documents/YNP_Bison_Model/Data/Remove_comp.R"  Remove_comp object in YNP_data.Rdata (also used below. See last line of this table)	I created a new spreadsheet (Removal composition. CSV) where I combined the yearling and adult males and also combined the know sex and unknown sex calves. This was manipulated in R to combine locations and was added to the data workspace as the "Remove_comp" object. Unknowns were omitted from the bull and cow totals.
Shape parameters for prior on removal composition (q,d vector)	Remove_comp data frame	"/Users/Tom/Documents/YNP_Bison_Model/Data/Call binom_bug_hier.R" and "/Users/Tom/Documents/YNP_Bison_Model/Data/binomH.bug"  Hard- coded values in BUGS scripts	This code finds shape parameters for 4 beta distributions, one for each proportion of an age class in the removals. The shape parameters are used to set up priors for the years when there are no data on removals and are hard-coded in the WinBUGS script.
Total count data with replicate counts	"/Users/Tom/Documents/YNP_Bison_Bin/DiseaseModel_Hobbs/Updated Count and Fecundity Data 1970-2008.xls"  "/Users/Tom/Documents/YNP_Bison_Model/Data/Updated Count Data 1970-2008.csv"	"/Users/Tom/Documents/YNP_Bison_Model/Data/Updated Counts.R"  N.obs (reps in columns, with mean, var, sd)  N.obs.plot (reps in rows for easier plotting)  in master YNP data object	Obtained data with replicate summer counts. Used these to calculate means and statistics for observation error (variance and sd) from the reps. I updated the data object to contain the new data files.

Updated calf/adult ratios	<p>"/Users/Tom/Documents/YNP_Bison_Bin/DiseaseModel_Hobbs/1970-2008 Composition Data for June and late July Aerial Counts.xls"</p> <p>"/Users/Tom/Documents/YNP_Bison_Model/Data/1970-2008 Composition Data for June Aerial Counts.csv"</p>	<p>"/Users/Tom/Documents/YNP_Bison_Model/Data/Sex and Age ver2.R"</p> <p>SexAge70_08</p> <p>CA70_08</p> <p>Cows02_07</p> <p>objects in YNP data object</p>	<p>Updated ratio data for analysis using beta hierarchical approach to deal with multiple groups. There are missing data in this file from 2005, which was the only year with no classification data from either season. Years 1971 1976 1981 1986 1998 1999 2003 2004 2006 were missing from the June data, so I used late summer values for these years. Note that the CA70_08 data are calves and group size, not calves and adults.</p> <p>Created same file structure for cows---observations of number of cows per group and group size</p>
Estimates of means and sd of calves / total	<p>input data from</p> <p>CA70_08 and Cows02_07 in YNP data object</p>	<p>"/Users/Tom/Documents/YNP_Bison_Model/Data/Ratios.Rdata</p> <p>"/Users/Tom/Documents/YNP_Bison_Model/Data/Composition_Hierarchical ver 3.R" and</p> <p>"/Users/Tom/Documents/YNP_Bison_Model/Data/CompHv3.bug"</p>	<p>These programs provide estimates of ratios and standard deviations for input to the Bayesian model. The data object Ratios.Rdata contains mean proportions of calves and cows (yearlings + adults) in the population and their standard deviations.</p> <p>Note that this Ratios data object is not included in the YNP data object</p>
Revised estimates of removals	<p>"/Users/Tom/Documents/YNP_Bison_Bin/DiseaseModel_Hobbs/Removal and Harvest 1970-2008.xls" used to make csv file</p> <p>"/Users/Tom/Documents/YNP_Bison_Model/Data/Removal and Harvest 1970-2008.csv"</p>	<p>Removals object in master data workspace</p> <p>"/Users/Tom/Documents/YNP_Bison_Model/Data/Removal_update.R</p>	<p>Simple program to replace existing Removals object with updated object.</p>
Revised estimates of removal composition reflecting new data.	<p>"/Users/Tom/Documents/YNP_Bison_Bin/DiseaseModel_Hobbs/Removal and Harvest 1970-2008.xls" used to make csv file</p> <p>"/Users/Tom/Documents/YNP_Bison_Model/Data/Removal and Harvest 1970-2008.csv"</p>	<p>"/Users/Tom/Documents/YNP_Bison_Model/Data/Remove_comp.R"</p> <p>Remove_comp object in in YNP_data.Rdata</p>	<p>Revised Remov_comp to reflect new data in updated data. Also did priors for removal composition.</p>

Pages 37 through 70 have been omitted from this draft of the report to protect the proprietary computer coding provided by the senior author while the deliberative process is ongoing. The National Park Service has a cooperative task agreement with Dr. Hobbs to collaboratively develop this population dynamics model. As the project continues the authors anticipate completion of a manuscript that will be submitted to a peer reviewed journal for publication. In the interim, the coding will not be available for distribution.