

# A Stochastic Model of Population Dynamics for the Rocky Mountain National Park Elk Herd

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## Background

The National Park Service plans to substantially reduce the abundance of elk wintering in Rocky Mountain National Park by culling animals within park boundaries. Population reductions will occur adaptively. Each year, the size of the population will be assessed relative to objectives and, based on this assessment, the following year's removal efforts will be adjusted to assure that the trajectory of the population remains within acceptable limits. Essential to the success of this adaptive approach is a model of elk population dynamics that allows managers to forecast the effect of alternative management actions on the elk population. This model should provide a framework for continuously updating estimates of the current size of the population using all of the data at hand, including census, harvest and culling data, and observations of sex and age composition. The model should base each year's forecasts on data from the current year as well as from previous years. The model must plainly show all sources of uncertainty in its predictions; it must explicitly consider uncertainties arising from natural variation in population processes (emigration, immigration, natality, survival) as well as those caused by errors in observations of the population and uncertainty about the harvest. The model must improve as the data improve.

The foundation for such a model exists in the work of Lubow and colleagues (2002), who used data from 1965 – 2001 to develop an age and sex structured model of elk population growth inside and outside of the park. Before their model can be used to guide efforts to guide current park management, it must be updated with data accumulated during 2001-2006. In addition, the analytical procedures used by Lubow and colleagues can be improved using more modern techniques. The likelihood approach used by Lubow (2002) assumed that all uncertainty resulted from errors in observations. Variance in population processes was not explicitly included in estimates of the model's parameters. Failure to include process variance as well as observation error in estimates of model parameters can cause misleading results (Carpenter et al. 1994, De Valpine and Hastings 2002, Dennis et al. 2006, Freckleton et al. 2006). Thus, there are two needs. First is to use the most recent data to estimate model parameters and second is to develop a modeling framework that includes additional sources of uncertainty in parameter estimates and model predictions.

## Data

There are three data sets that can be used to estimate parameters in an updated population model. The park elk population has been censused almost continuously since the mid 1960's (Figure 1). Before 1994, the census data include total counts unadjusted for sightability; thereafter, population estimates were adjusted to account for animals that were not observed using a multiple regression model (Figure 1). Until the 1990's, the population appeared to be regulated by density dependent feedback to population growth rate, producing a clear,

asymptotic trend in the data. However during the last decade, the population has appeared to decline substantially, resulting in a hump-shaped relationship between population size and time (Figure 1).

In addition to estimates of total population size, observations of the sex and age composition of the population composition were made during 1969-1978 and 1992-2008. Animals were classified as bulls (males older than 1.75 years), spikes (males approximately 1.75 years old), cows (females 1.75 years old and older) and calves (males and females approximately 8 months of age). Conversations with park staff and census observers led us to conclude that bulls were strongly under-represented in classification counts. Therefore we chose to include only cows and calves in the classification data used in parameter estimation.

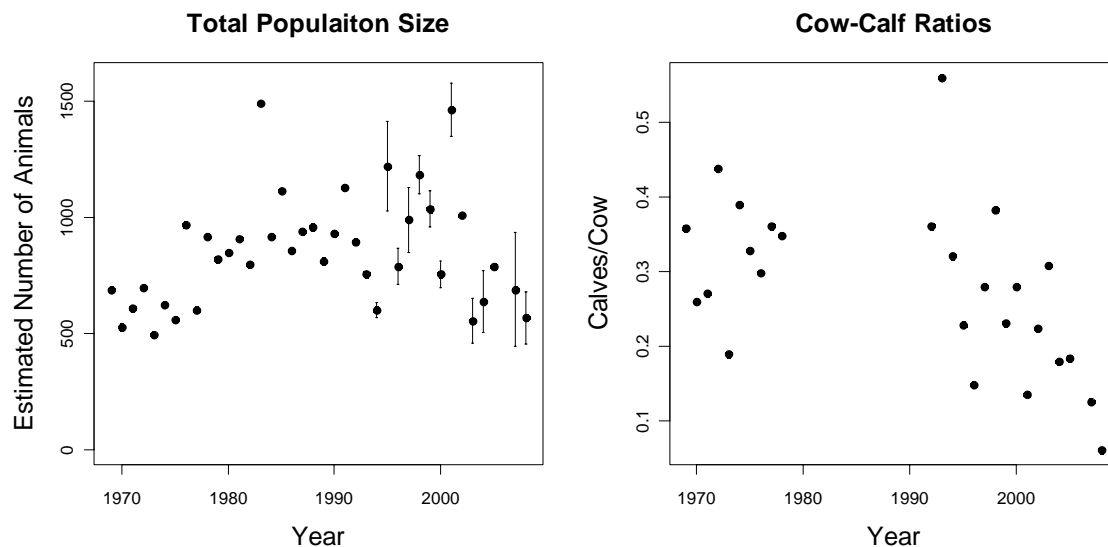


Figure 1. Data on abundance and composition of the Rocky Mountain National Park Elk herd. Vertical bars show  $\pm 1$  standard deviation of the mean estimate.

Data are also available on annual harvest for the Colorado Division of Wildlife Game Management Unit 20 for 1969-2008 (Figure 2). These data are assembled over an area roughly four times as large as the area of the park east of the continental divide. Thus, while it is plausible that a certain fraction of the elk harvested in GMU 20 spend the winter in Rocky Mountain National Park, that fraction remains unknown. The boundaries of GMU changed in 1988, expanding the unit east and south to increase its area by approximately 340 square miles. This implies that differences in the impact of harvest on RMNP elk population before and after 1988 must be accounted for in the model.

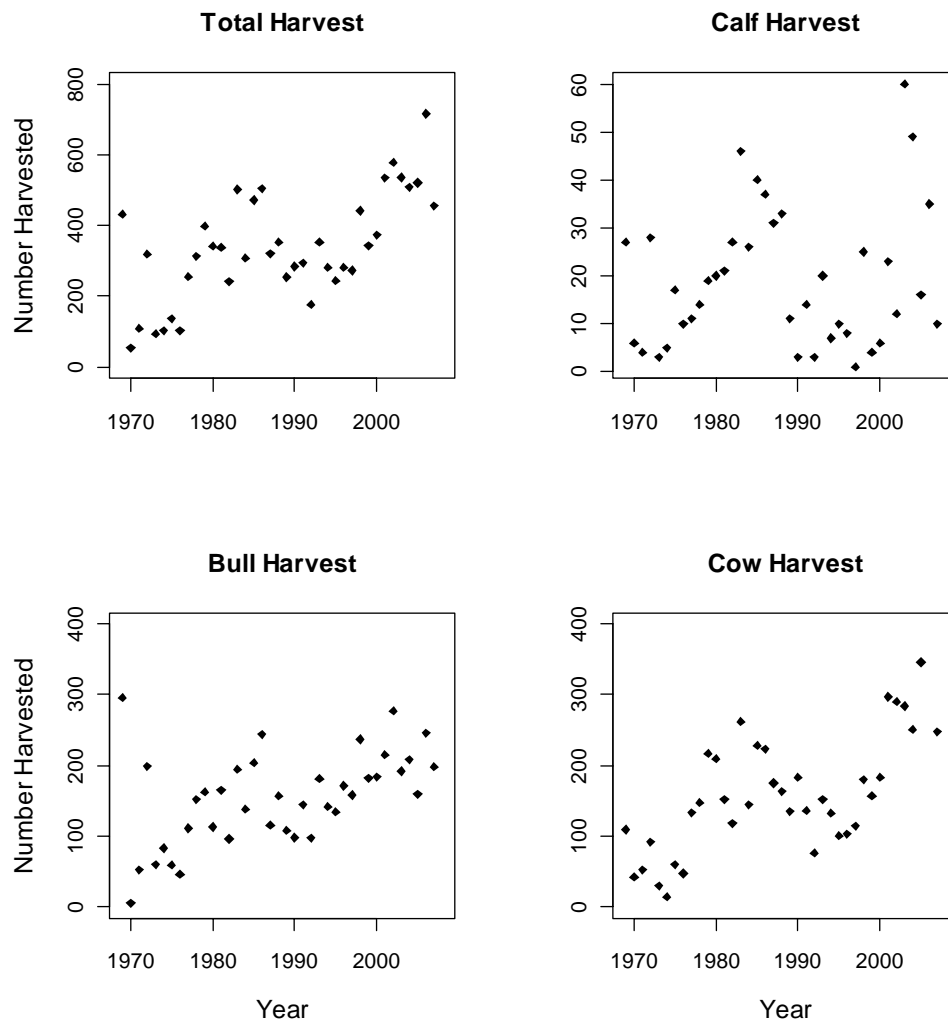


Figure 2. Number of elk harvested from Game Management Unit 20 during 1970 – 2008. An unknown number of animals in this harvest come from the park herd.

### Trends in the Data

There are three notable trends in the data. The first is the apparent decline in population size that has occurred since the mid 1990's. Earlier modeling efforts focused on the asymptotic trends in estimated population size that were evident during 1970-1995, and invoked density dependent feedbacks from population size to juvenile recruitment and survival as the primary control on the populations dynamics. However, the current data suggest a hump-shape trend over time (Figure 1) rather than the s-shaped pattern seen earlier.

A second notable trend is the dramatic, linear increase in harvest that has occurred outside the park boundary. Since 1970, total harvest and cow harvest have grown by a factor of four, from fewer than 100 animals harvested per year to almost 400. The model of Lubow et al. 2002 lumped harvest mortality with other sources of mortality and assumed, implicitly, that mortality from harvest was constant over time. Thus, although harvest was largely ignored in earlier

population models, the strong temporal trends in the number of animals harvested from GMU 20 suggest it must be included here.

The third trend of note is a linear decline in cow calf ratios that occurred from 1990 to 2008. Over this time interval, observed ratios of calves per cow declined from approximately 0.35 to 0.10. The fact that these trends occurred concomitant with declines in population size argues against density dependent feedback in calf recruitment. That is, if recruitment were strongly density dependent, we would expect increases in the number of calves per cow during 1995 – 2008 because population numbers appeared to be declining over this interval.

### **State Space Modeling**

State-space models (Calder et al. 2003, Newman et al. 2006) are ideally suited for representing the dynamics of populations when there is uncertainty about the processes that control the dynamics and when observations of the population are made with error. Failing to use the state space approach can lead to erroneous conclusions about the factors that control population growth and decline (Dennis et al. 2006, Freckleton et al. 2006). In particular, unless errors in observations can be separated from variance arising from the failure of the model to perfectly represent the population process, time series of data will show strongly density dependent dynamics even when the density dependent signal may be weak or absent (Freckleton et al. 2006).

State space models include two components, the process model and the data model (Calder et al. 2003, Newman et al. 2006). The process model represents the true state of the population and any uncertainty that results because the model is unable to portray all of the sources of variation in the population's dynamics. The data model relates the true state of the population to the observations of the state and associated uncertainties arising from our inability to observe the true state perfectly.

In the remainder of this document, we develop and implement a state space model in the Bayesian framework following approaches described by Millar and Meyer (2000b, 2000c, 2000a) and Brooks et al. (2004).

### **Organization of this Document**

In the next section, we describe a highly general process model that will serve as base for constructing a candidate set of more detailed models. We then describe the data model that we used to link the predictions of the process model to data on total population size and population composition. Next, we show how we bring the data and process models together in a hierarchical Bayesian framework. We describe alternative process models and then discuss the results of parameter estimation and model selection. We close by drawing conclusion from the modeling results.

## Process model

Here, we develop and implement a state space model in the Bayesian framework following approaches described by Millar and Meyer (2000b, 2000c, 2000a) and Brooks et al. (2004). We represent the Rocky Mountain National Park using a discrete time, stage structured model portraying dynamics of three age/sex classes: juveniles, adult males, and adult females. Our choice of model structure is based on the following biological reasoning. We assumed that there were no differences in survival of male and female juveniles, allowing use to lump them into a single class. Moreover, although, virtually all offspring are produced by females that are older than two years, we decided to include a single female age classes in the model for two reasons. First, it is not possible to differentiate adult from yearling females in sex and age classification counts, which requires these segments of the population to be pooled in the data. Second, and most importantly, the harvest data did not distinguish between adult and yearling females.

Equations in our model assume that a birth pulse occurs in June and that census occurs in February. As is traditional for models of this type, the time step is one year. We define recruitment as the number of calves produced per cow that survive from birth to their first census and we define juvenile survival as the proportion of calves alive at census that survive to become yearlings. We assume that the preponderance of adult mortality occurs after census and before the next birth pulse, that is, during the interval between February and June.

We first describe the general formulation of a base process model, a formulation that will serve as a foundation for more specific models discussed in a later section. Thus, all of the more specific models will start with the equations we offer here. The general model includes juveniles, defined as male and female animals aged 8 months at the time of census and adult males and females, aged 1.75 years and older at census.

We define the three element vector  $\mathbf{N}_t = (N_{1,t}, N_{2,t}, N_{3,t})$  as the abundances of each age class at time  $t$  indexed by  $i=1$  for juveniles, 2 for adult females, and 3 for adult males. Thus, in our notation,  $N_{1,t}$  gives the number of juveniles at time  $t$ . The estimate of total population size at time

$t$  is given by  $N_{total,t} = \sum_{i=1}^3 N_{i,t}$ .

We define three time invariant survival rates:  $s_1$  is the probability of survival of juveniles from age 8 months to age 1.75 years;  $s_2$  is the probability of survival of females aged 1.75 years and older, and  $s_3$  is the probability of survival of adult males 1.75 years and older. We define recruitment ( $r$ ) as the number of offspring that survive to their first census produced per adult female. Thus, recruitment includes the number of offspring born per adult female and survival between birth and approximately 8 months of age. Let  $m$  be the proportion of newborns that are female.

We assume that the true population size for the  $i$ th age/sex class at time  $t$  can be represented as a lognormal distribution with shape parameters  $\mu_{i,t}$  and standard deviation  $\sigma_i$ , where  $\mu_{i,t}$  is the mean and  $\sigma_i$  is the process standard deviation on the log scale for age class  $i$  at time  $t$ . In the following, the posterior distribution of the total population size will be denoted

by  $N_{total,t} = \sum_{i=1}^3 N_{i,t}$ .

The base process model is given by

$$N_{1,t+1} \sim \text{lognormal}(\mu_{1,t+1}, \sigma_1),$$

where  $\mu_{1,t+1} = \log(s_2 r N_{2,t})$  is the deterministic estimate of the mean number of juveniles,

$$N_{2,t+1} \sim \text{lognormal}(\mu_{2,t+1}, \sigma_2),$$

where  $\mu_{2,t+1} = \log(m s_1 N_{1,t} + s_2 N_{2,t})$  is the mean number of adult females, and

$$N_{3,t+1} \sim \text{lognormal}(\mu_{3,t+1}, \sigma_3),$$

where  $\mu_{3,t+1} = \log[(1-m)s_1 N_{1,t} + s_3 N_{3,t}]$  is the mean number of adult males.

We assume that this model, or its elaborations described below, represents the “true” model and that the observed data are generated from this model. We model the observations as follows.

### Observation model

In the observation model we incorporate the observed data. We have data on the total population size for  $n$  years contained in the vector  $\mathbf{O} = (O_1, O_2, \dots, O_{40})$ . So  $O_1$  is the observed population size in 1969 and  $O_{40}$  is the observed population size in 2008 (left panel of Figure 1). 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 census data during 1994-1998, which include estimates of observation uncertainty, that the variance of the counts is greater than the mean and is 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:

$$\lambda_t \sim \text{gamma}\left(\frac{N_{total,t}^2}{\sigma_o^2}, \frac{N_{total,t}}{\sigma_o^2}\right),$$

$$O_t \sim \text{Poisson}(\lambda_t),$$

where  $N_{total,t}$  is the model’s estimate of the posterior distribution of the true population size and  $\sigma_o$  represents the estimate of observation error. We obtained two separate estimates for observation error. Census data before 1994 lacked annual estimates of standard deviations of counts. For these data (years 1-25), we estimated  $\sigma_o$  from the census data alone. After 1994 (years 26-40) we assumed that the measured standard deviations were random effects drawn from a gamma distribution,

$$se_t \sim \text{gamma}(\alpha, \gamma),$$

where  $se_t$  is the observed census data standard error for year  $t$ . The mean of this distribution was used to estimate  $\sigma_o$ , so  $\sigma_o = \alpha / \gamma$ .

We also have classification data which include estimates of sex and age composition for juveniles and cows. To use the classification data in estimating model parameters, we composed the following likelihood. Let  $T_t$  be the total number of adult females and juveniles classified at time  $t$  and  $C_t$  be then number of juveniles classified (thus  $T_t - C_t$  is the number of adult females classified). Because there are years with missing data for classification, we will simplify notation below by assuming that that the elements of the vectors of classification data are properly

aligned in time with the elements of the prediction vectors (i.e, the subscripts on  $O$  and  $T$  are aligned in time with the subscripts on the  $N$ ) . For the years in which we had classification data, we compose a binomial likelihood,

$$C_t \sim \text{binomial}\left(\frac{N_{1,t}}{N_{1,t} + N_{2,t}}, T_t\right)$$

where  $N_{1,t}$  is the process model prediction of the number of juveniles in the population at time  $t$  and  $N_{2,t}$  is the process model prediction of the number of adult females in the population at time  $t$ .

### Hierarchical, state-space model

Let  $\theta$  be a vector of the parameters in the process model, excluding the variances. Thus,  $\theta$  will include the parameters describe above (survival rates and recruitment) as well as any additional parameters that are needed to implement more detailed, specific process models described subsequently. Let  $\sigma$  be the vector of process standard deviations, so  $\sigma = (\sigma_1, \sigma_2, \sigma_3)$ . Let  $\eta$  be a vector containing the estimates of the initial conditions for each age class. We need a model that expresses the probability of observing the ensemble of the observed and “true” values. We say “true” because in the state-space framework, we assume that the process model gives rise to the observations. Thus, it is “true” because it quantifies the deterministic prediction of the model and the associated uncertainty created by process variance, that is, all of the factors that influence the value of state variables but that are not included in the deterministic prediction. Recall that the vector  $C$  includes the number of juveniles counted in classifications and the vector  $T$  is the corresponding total number of juveniles and adult females counted. The vector  $O$  contains the census data across all years for which we have classification data.

The fully stochastic, Bayesian model is specified by:

$$\begin{aligned}
p(\sigma, \sigma_o, \theta, \eta, N | O, C, T, se) &\propto p(N_1 | \theta, \eta, \sigma) \times \\
&\prod_{t=2}^n p(N_t | N_{t-1}, \theta, \sigma) \times \\
&\prod_{t=1}^{10} p(C_t | N_{1t}, N_{2t}, T_t) \times \\
&\prod_{t=23}^{40} p(C_t | N_{1t}, N_{2t}, T_t) \times \\
&\prod_{t=1}^{25} p(O_t | N_{total,t}, \sigma_o) \times \\
&\prod_{t=26}^n p(O_t | N_{total,t}, se_t, \alpha, \gamma) \times \\
&\prod_{t=26}^n p(se_t | \alpha, \gamma) \times \\
&p(\sigma) p(\theta) p(\eta) p(\alpha) p(\gamma)
\end{aligned}$$

Given the assumptions on distributions above, we have:

$$\begin{aligned}
& p(\sigma, \sigma_o, \theta, \eta, N | O, C, T, se) \propto \log normal(N_1 | \eta, \theta, \sigma) \times \\
& \prod_{t=2}^n \log normal(N_t | N_{t-1}, \theta, \sigma) \times \\
& \prod_{t=1}^{25} Poisson(\lambda_t | N_{total}, \sigma_o) \times gamma\left(\frac{N_{total}^2}{\sigma_o^2}, \frac{N_{total}}{\sigma_o^2}\right) \times \\
& \prod_{t=26}^n Poisson(\lambda_t | N_{total}, \alpha, \gamma, se_t) \times gamma\left(\frac{N_{total}^2}{(\alpha/\gamma)^2}, \frac{N_{total}}{(\alpha/\gamma)^2}\right) \times \\
& \prod_{t=26}^n gamma(se_t | \alpha, \gamma) \times \\
& \prod_{t=1}^{10} binomial\left(C_t | \frac{N_{1,t}}{N_{1,t} + N_{2,t}}, T_t\right) \times \\
& \prod_{t=23}^{40} binomial\left(C_t | \frac{N_{1,t}}{N_{1,t} + N_{2,t}}, T_t\right) \times \\
& p(\sigma) p(\sigma_o) p(\theta) p(\eta) p(\alpha) p(\gamma)
\end{aligned}$$

The prior distributions  $[p(\boldsymbol{\sigma}) \times p(\sigma_o) \times p(\boldsymbol{\theta}) \times p(\boldsymbol{\eta}) \times p(\alpha) \times p(\gamma)]$  were chosen as conjugates whenever possible. Prior distributions and their parameters are summarized in Table 1.

Table 1. Prior distributions for model parameters. (Some of the parameters listed here are defined in the next section).

Parameter	Prior and parameters	Notes
$s_1$ , juvenile survival	beta(1.49, 2.7)	weakly informative <sup>1</sup>
$s_2$ , adult female survival	uniform(.85, .98)	weakly informative.
$s_3$ , adult male survival	uniform(.85, .98)	weakly informative
$m$ , sex ratio at birth	beta(49.5, 49.5)	informative
$r$ , number of offspring surviving to 8 months of age produced per adult female in absence of density dependence	uniform(.1, 1)	uninformative
$a_1$ , proportion of harvest from GMU 20 that comes from the park before 1988	uniform(0, .5)	uninformative



Parameter	Prior and parameters	Notes
$a_2$ , proportion of harvest from GMU that comes from the park during and after 1988	uniform(0, .5)	uninformative
$a_3$ , the proportion of calves whose mothers were harvested from the park who die as a result of cow harvest.	uniform(0, .5)	uninformative
$\beta_0$ , intercept of logit relationship for density dependent effects on recruitment, the number of offspring surviving to 8 months of age produced per adult female	uniform(0.847, 3.0)	weakly informative
$\beta_1$ , slope of logit relationship for density dependent effects on recruitment, the number of offspring surviving to 8 months of age produced per adult female	uniform(-0.5, 0)	weakly informative
$\tau = 1/\sigma^2$ , the reciprocal of the process variance	gamma(0.001,0001)	uninformative
$\sigma_0$ , the standard deviation for observation uncertainty	uniform(0,500)	uninformative
$\alpha$ , hyperparameter for observation uncertainty	gamma(0.001,0.001)	uninformative
$\gamma$ , hyperparameter for observation uncertainty	gamma(0.001, 0.001)	uninformative

<sup>1</sup> Based on data in Raithel(2007)

### Alternative Models

We composed eight alternative models (Table 2) representing effects of density dependence, harvest, weather, and their combinations. The density dependent models assumed that recruitment was an inverse logit function of the total population size, i.e.,

$$r_t = \frac{e^{\beta_0 + \beta_1 N_t}}{1 + e^{\beta_0 + \beta_1 N_t}}$$

so in equation (1) the mean becomes  $\mu_{1,t+1} = s_2 r_t N_{2,t}$ .

We also examined effect of winter weather. Winter weather was represented as the departure of annual temperature measurements from the long term average, calculated as the observation of the temperature for a given year minus the mean temperature across all years divided by the mean temperature. Defining this quantity as  $x_t$ , we modeled the combined effect of density and weather on recruitment as:

$$r_t = \frac{e^{\beta_0 + \beta_1 N_t + \beta_2 x_t}}{1 + e^{\beta_0 + \beta_1 N_t + \beta_2 x_t}}.$$

To investigate the impact of harvest outside the park, we considered several harvest models. In the harvest models the estimated number of animals in each age class was reduced by the estimate of the proportion of the total harvest that came from the park population. Let  $h_{i,t}$  be the estimated number of animals in age class  $i$  harvested from game management unit 20 during time  $t$  and  $a$  be the estimated proportion of the harvest taken from the park population. Then the means in equations (1)-(3) become

$$\begin{aligned}\mu_{1,t+1} &= \log(s_2 r N_{2,t} - a h_{1,t}), \\ \mu_{2,t+1} &= \log(m s_1 N_{1,t} + s_2 N_{2,t} - a h_{2,t}), \\ \mu_{3,t+1} &= \log\left[(1-m)s_1 N_{1,t} + s_3 N_{3,t} - a h_{3,t}\right].\end{aligned}$$

We allowed for observation error in harvest rates as follows. Let  $H_{i,t}$  be the observed number of animals harvested from age class  $i$  at time  $t$ . Using the method of moments, we estimated harvest rates as

$$\mathbf{h}_t \sim \text{gamma}\left(\frac{\mathbf{H}_t}{\sigma_H^2}, \frac{\mathbf{H}_t}{\sigma_H^2}\right)$$

where  $\mathbf{h}_t$  is a vector of 3 harvest rates, one for each age class;  $\mathbf{H}_t$  is the corresponding vector of observed harvest rates, and  $\sigma_H$  is the estimate of the observation uncertainty.

During years before 1988, there were no data on the observation error of the harvest, so we estimated a coefficient of variation using

$$cv.h \sim \text{uniform}(0,1)$$

From 1988 forward, we used observed, age specific standard deviations on harvest rates to estimate  $\sigma_H$  for each age class. So, for example, to estimate the number of juveniles harvested incorporating the measured observation error for juvenile harvest (*se.calves<sub>t</sub>*):

$$h_{i,t} \sim \text{gamma}\left(\frac{H_{i,t}^2}{se.calves_t^2}, \frac{H_{i,t}}{se.calves_t^2}\right)$$

We created two harvest models. Harvest model 1 estimated two values for the parameter  $a$ ;  $a_1$  is the estimated proportion of harvest taken from park residents for the years before 1988, and  $a_2$  is the estimation proportion for the years including and after 1988. We reasoned that the proportion of the harvest taken from park likely became smaller as the area of GMU 20 increased in 1988. Harvest model 2 represents additional juvenile mortality that resulted because mothers were harvested, leaving juveniles orphaned. This model was the identical to the harvest model above, except that it included an additional proportionality term,  $a_3$  to represent the juvenile mortality that added to adult female mortality. So in equation (1) the mean juvenile population at time  $t$  is given by

$$\mu_{1,t+1} = s_2 r N_{2,t} - a_i h_{1,t} - a_3 (a_i h_{2,t}).$$

where  $i$  indexes the time period for differences in GMU boundaries. We used annual data on the standard deviation of harvest estimates for each age class to estimate  $\sigma_H$ .

Table 2. Alternative models of dynamics of the Rocky Mountain National Park elk population.

Model name	Description
Density dependence	Base model + density dependent feedback on juvenile recruitment.
Density dependence + weather	A suite of 4 models that included different independent variables explaining effects of winter weather on recruitment.
Harvest 1	Base model + harvest with two estimates of $a$ , one before the boundary change for GMU 20 and one after.
Harvest 2	Same as harvest 1, but with additional term to represent mortality of juveniles resulting from harvest of adult females.
Density dependence + harvest	Harvest model 2 + density dependent feedback on juvenile recruitment.

### Model Implementation

Before any parameters were estimated with the empirical data, we conducted exhaustive model tests using simulated data to assure that our estimation procedures were able to accurately estimate known, generating parameter values.

We estimated the posterior distribution for each parameter and for derived quantities of interest using Monte-Carlo Markov Chain (MCMC) methods implemented in WinBUGS (Lunn et al. 2000) and R (R\_Development\_Core\_Team 2007). MCMC chains were initialized with five different sets parameter values chosen within biologically plausible bounds for each parameter. After an initial burn-in period of 20,000 iterations, we obtained 50,000 iterations of each of the five chains, thinning each by 10, thereby providing a sample of 25,000 observations across the 5 chains. Gelman-Rubin-Statistics were used to assure convergence (Brooks and Gelman 1988). We used the Deviance Information Criterion (DIC) to evaluate models (Spiegelhalter et al. 2002).

Derived quantities of interest included the probability that the current population exceeds or falls below management targets. These probabilities were calculated empirically from MCMC output using the `ecdf ( )` function in R.

## Results

### Model Selection

Harvest model 2 emerged as the best approximating model based the Deviance Information Criterion (Table 3, Figure 1). Models that included harvest parameters were strongly supported in the data, while density dependence alone and density dependence + weather had virtually no support relative to the best harvest model. Although Harvest model 1 was also supported relative

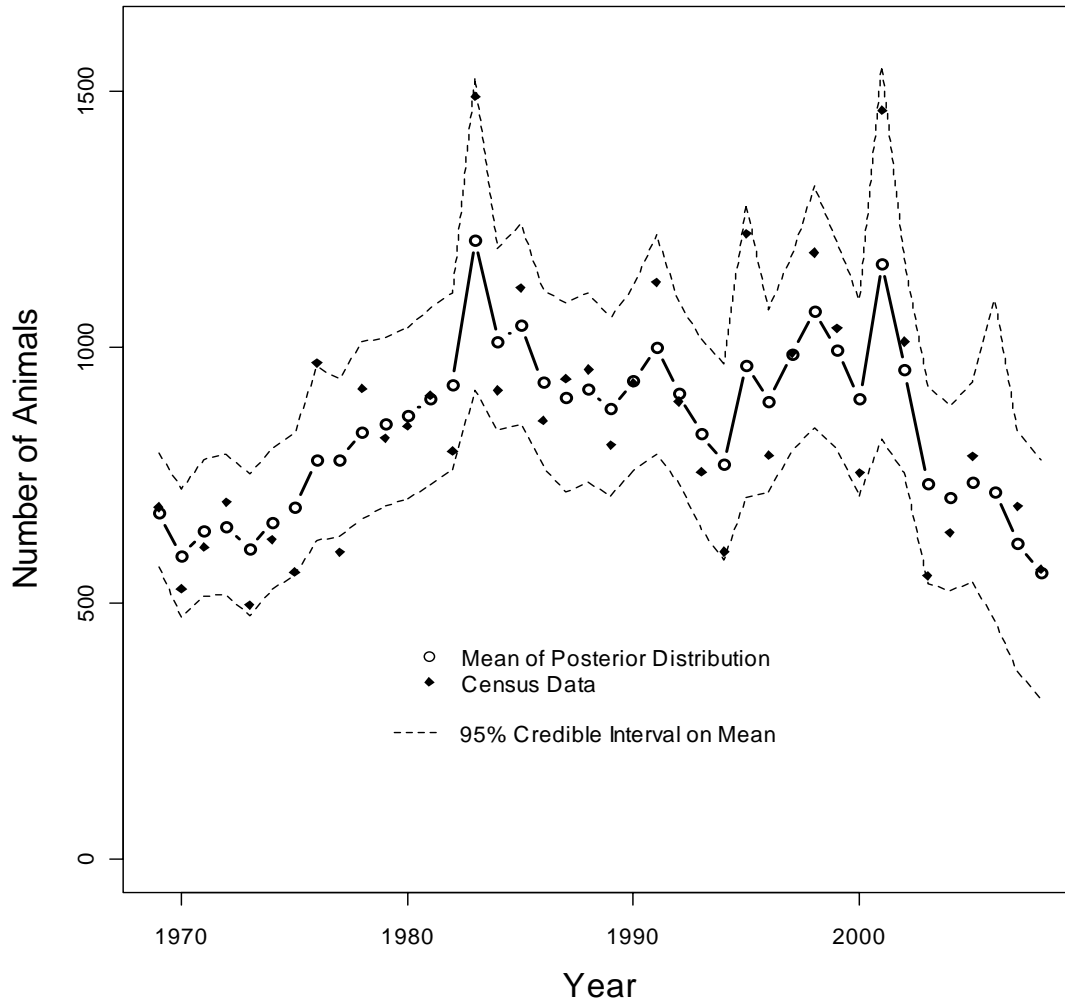


Figure 1. Model estimates of the elk population size in Rocky Mountain National Park during 1969 – 2008.

Table 3. Results of model comparisons

Model	Mean deviance	DIC
Harvest 2	712	774.7
Harvest 1	713	776.6
Density dependence + harvest	716	778.4
Density dependence	717	781.0
Density dependence + weather		$\geq 781$

to Harvest 2, its predictions were similar. Averaged over the last 5 years (2003-2008), there was only a 5% difference in the predictions of the two models (mean Harvest 2 = 668 animals, 95% credible interval = 508, 827, mean Harvest 1 = 705, 95% credible interval = 564 , 866). Hereafter, we will make inferences using Harvest 2.

#### *Parameter Estimates*

Vital rates estimated from Harvest model 2 were consistent with current knowledge of elk life history (Table 4). Adult survival for males and females was greater than 90% and juvenile survival (i.e., the proportion of animals 8 months old that survive to 1.75 years) averaged 63%. Recruitment rates were .35 juveniles per adult female. As expected from previous work (Gaillard et al. 1998), process variance was greatest for juveniles and adult males and lowest for females.

We estimated that approximately one quarter of the animals harvested from GMU 20 came from the park population during 1967 to 1987 ( $a_1$  in Table 4). During 1988-2008, about a tenth of the harvest from GMU 20 included park animals ( $a_2$  in Table 4). We estimated that 40% of juveniles whose mothers were harvested failed to survive to their first census ( $a_3$  in Table 4). Credible intervals on all of these proportions were broad.

Table 4. Parameter estimates for Harvest 2 model of dynamics of the Rocky Mountain National Park elk population.

Parameter	Mean	95% credible interval
Juvenile survival ( $s_1$ )	0.62	0.29-89
Adult female survival ( $s_2$ )	0.94	0.87 – 0.98
Adult male survival ( $s_3$ )	0.94	0.860 – 0.98
Neonate sex ratio ( $m$ )	0.50	0.40 – 0.59
Recruitment rate ( $r$ )	0.34	0.27 – 0.40
Proportion of harvest from park, pre-1988 ( $a_1$ )	0.24	0.11 – 0.47

Proportion of harvest from park, 1988 and after ( $a_2$ )	0.089	0.0052 – 0.22
Additive calf mortality resulting from cow harvest ( $a_3$ )	0.39	0.16 – 0.49
Observation uncertainty for census, pre 1994 ( $\sigma_0$ )	133	65 – 210
Observation uncertainty for census, 1994 and after ( $\sigma_0$ )	147	80 – 231
Process uncertainty <sup>1</sup> for juveniles	75.6	12.2 – 163
Process uncertainty <sup>1</sup> for adult females	47.8	8.8–95
Process uncertainty <sup>1</sup> for adult males	99.7	10 – 317

<sup>1</sup>Mean of estimates of standard deviation of lognormal, posterior distribution at a mean population size = 300 animals in each age class.

### *Population Predictions*

The estimate of the current population size was 560 animals (95% credible interval = 312 – 778).

### *Population Predictions Relative to Management Objectives*

The RMNP Elk and Vegetation Management Plan calls for maintaining the elk population between a 600 and 800 animals, an interval we will call the target range. Because our model incorporates process variance and observation error in our estimates of the population size, we are able to make statements about the probability that the population is currently within this range. We are also able to estimate the probability that the population will be outside the target range in the future given hypothetical management actions.

We constructed an empirical, cumulative distribution function for the 2008 population size based the posterior distributions of the park population size (Figure 2). Using this cumulative distribution, we estimated that the there is a 36% chance that the current population falls within of the target range. There is a 63% chance that the current population is below 600 animals and a 1% chance that the population exceeds 800 animals.

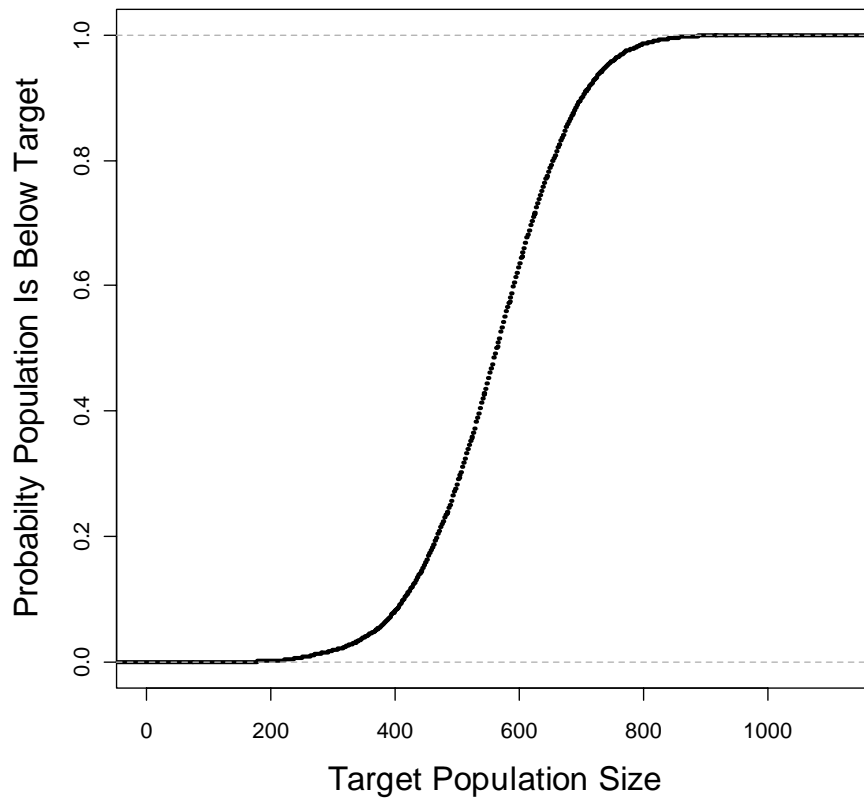


Figure 2. The probability that the Rocky Mountain National park elk population was less than a given target population size during 2008.

We constructed four scenarios for future removals and estimated cumulative distributions for the 2009 population size based on these scenarios. Scenario 1 assumed that the harvest from GMU 20 for 2008 will be identical to the harvest for 2007 and that no culling will occur in the park. Scenario 2 assumed 2007 harvest levels would be maintained in 2008 and that there would be an additional culling of 40 cows. Scenario 3 assumed the same harvest and culling of 100 cows. Scenario 4 assumed harvest at half 2007 levels and culling of 40 cows. Under all scenarios, there was a very substantial probability that the 2009 population size target would be less than the lower bound of the target range.

Table 3. Probability that the RMNP elk population is within the target range during 2009 given different assumption on culling and harvest.

Scenario	P( $N \leq 600$ )	P( $600 < N \leq 800$ )	P( $N > 800$ )
Harvest same as 2007, no culling	.72	.27	.02
Harvest same as 2007, cull 40 females	.81	.17	.01
Harvest same as 2007, cull 100 females	.91	.08	.00
Harvest $\frac{1}{2}$ 2007, cull 40 females	.77	.21	.01

## Discussion

We developed a state-space model of the dynamics of the Rocky Mountain National Park elk population, a model that incorporates multiple sources of uncertainty in its predictions. The model offered plausible estimates for all parameters, although some of these estimates, (for example, juvenile survival) were not estimated precisely. These imprecise estimates simply point to the fact that the data used to estimate the model parameters are quite variable.

Harvest outside the park emerged as a strong influence on the abundance of elk within park boundaries. Previous models (Lubow et al. 2002) subsumed estimates of harvest effects within the estimate of survival. This was a reasonable approach as long as harvest levels were relatively low and the population was increasing toward an asymptote. In this case, density dependence could be invoked to explain the asymptotic trends in the data and the effects of harvest on abundance could be assumed to be time invariant. However, in the time since that work was done, census estimates have declined dramatically, from 1461 animals in 2001 to 566 in 2008 (Figure 1). Steep declines in cow-calf ratios (Figure 1) imply *reduced* recruitment in the face of declining densities. These patterns argue strongly against density dependence as the primary mechanism regulating dynamics of the park elk herd.

Instead, our results show that a relatively small contribution of the park population to the overall harvest (about 10% annually since 1988) was sufficient to cause declines in abundance when harvest, particularly harvests of adult females, was large and increasing over time (Figure 2). Harvest models without any density dependent terms were able to produce asymptotic patterns in the data prior to the year 2000. Thus, it is possible that asymptotic patterns in the data which were previously ascribed to feedbacks of increasing population density (Lubow et al. 2002) were actually caused by accelerating increasing harvest. This emphasizes the importance of collecting data to help estimate the impacts of harvest on the park population. This could be achieved by marking animals in the in the park and determining the proportion of those marks show up in the harvest.

To our knowledge, our work is the first to quantify the interactive effects of adult and juvenile survival mediated by harvest. We show that the magnitude of juvenile mortality depended on the



number of adult females harvested. The idea behind this interaction is that orphan juveniles are exposed to increased risk of mortality following harvest of their mothers. This interaction also may result, at least in part, from under-reporting of juvenile harvest by surveyed hunters.

Our work strongly suggests that the current park population may be below the lower end of the desired range established in the Elk and Vegetation Management Plan. The Harvest 2 model had the greatest support in the data and also predicted the smallest population size. Hence, it is the most conservative in terms of supporting removals. There are two kinds of errors that could be made in implementing the elk management plan. If the population is underestimated, then it may take somewhat longer to achieve management goals. However, if the population is over estimated, the managers run the risk of reducing the population to unacceptably low levels. Because this outcome has particularly undesirable political, social, and economic consequences, it is fortunate that the model that had the greatest support in the data was also the model that is most precautionary.

## **Future Work**

### *Model Refinements and Management Experiments*

There are at least two promising ways that the structure of our model might be improved. Although we did explore the effects of weather on recruitment, we have not yet explored the influence of winter weather on the proportion of harvest that comes from the park herd. It is plausible that some of the variance in the process model could be absorbed by weather covariates that help explain annual variation in the effect of harvest. It would be useful to explore adding a third age class. Although we do not believe that composition counts of bulls are reliable, the data on yearling males is likely to be more accurate. These data might improve estimates of juvenile survival. This would raise some important challenges in applying the harvest data because the data fail to discriminate among yearlings and adults. Finally, there may be a better approach to estimating the age composition data. The current estimates the proportion of calves in the population using a binomial likelihood. It is also possible to use data on individual groups to estimate this proportion assuming that each group represents a draw from a beta distribution. This approach would better represent the sampling design.

It may be possible to take advantage of any planned variation in harvest outside of the park to understand the role of harvest in regulating the population within the park. The model suggest the hypothesis that reductions in the number of cows killed in DAU 9 should translate into increases in the Park elk population and vice versa.

### *Supporting Decisions on Future Monitoring*

The model provides an ideal framework for analyzing the potential benefits of alternative tactics for population monitoring. For example, we could evaluate the relative benefits of conducting the census less frequently, but with more census points within a year. We could evaluate the relative return on composition counts versus total census. Our results strongly suggest it would be extremely worthwhile to attempt to get a better understanding of the effects of harvest on park animals, which could be relatively straightforward to accomplish using marked animals.

### *Adaptive Management*

Our model provides a basis for adaptive management as it was originally defined in the seminal work of Walters(1986). The Bayesian framework that we implemented is ideally suited to this interplay between management and research and, although it is not widely appreciated, is the approach that was originally advocated by Walters (1986). This approach is cyclic—we have a model that makes predictions relevant to management decisions; management actions are taken. We compare the models predictions with observations, and, as a result of this comparison, the model is revised and improved. As this cycle proceeds, there is continuous improvement in the model and in the quality of the model quality of management decisions. We look forward to participating in this process as the Elk and Vegetation Management Plan is implemented.

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