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# FITTING POPULATION MODELS TO MULTIPLE SOURCES OF OBSERVED DATA

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**Abstract:** The use of population models based on several sources of data to set harvest levels is a standard procedure most western states use for management of mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and other game populations. We present a model-fitting procedure to estimate model parameters from multiple sources of observed data using weighted least squares and model selection based on Akaike's Information Criterion. The procedure is relatively simple to implement with modern spreadsheet software. We illustrate such an implementation using an example mule deer population. Typical data required include age and sex ratios, antlered and antlerless harvest, and population size. Estimates of young and adult survival are highly desirable. Although annual estimates are desirable, the procedure also can be applied—with less precision—to data sets with missing values in any of the data series. The model-fitting procedure adjusts input estimates and provides estimates of unobserved parameters to achieve the best overall fit of the model to observed data. Rigorous, objective procedures such as those described here are required as a basis for wildlife management decisions because diverse stakeholder groups are increasing the intensity with which they scrutinize such management decisions.

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**Key words:** AIC, Akaike's Information Criterion, *Cervus elaphus*, elk, least squares, maximum likelihood, model fitting, mule deer, *Odocoileus hemionus*, parameter estimation, population modeling, spreadsheet software.

Modeling populations to set harvest levels and other management strategies has become the norm in wildlife management (Bartholow 1992, White 2000). For example, the Colorado Division of Wildlife builds or modifies such models annually for each of the data analysis units (DAU) in the state. The division uses these models to project the population and determine harvest objectives for the upcoming hunting season. To develop these models, data are collected on the DAU population (White and Bartmann 1998a, Bowden et al. 2000). In Colorado, measured attributes have included young:female and male:female ratios, either pre-harvest or postharvest (Czaplewski et al. 1983, Bowden et al. 1984, Pojar et al. 1995); harvest (White 1993, Steinert et al. 1994); survival with radiocollars (White et al. 1987, Bartmann et al. 1992, White and Bartmann 1998b); neckbands (White and Bartmann 1983) or mortality transects (Bartmann 1984, Bartmann and Bowden 1984); population size from quadrat counts (Kufeld et al. 1980, Bartmann et al. 1986, Pojar et al. 1995); mark-resight (Bartmann et al. 1987, Bear et al. 1989, Neal et al. 1993, Bowden and Kufeld 1995); line transects (White et al. 1989, Pojar et al. 1995); change-in-ratio (Otis 1973), catch-effort (Laake 1992), and pellet group counts (Bowden et al. 1969, Freddy and Bowden 1983a,b).

Typically, biologists who build models based on data collected from a DAU population align or otherwise match the model predictions to the observed values manually in an ad hoc and subjective fashion. They do this by changing model parameters until the predictions match some prior expectations or visually appear to approximate the data (e.g., Bartholow 1992). However, this actually is a statistical parameter estimation problem and more formal solution methods are available. We describe a statistically rigorous, objective, yet relatively easy-to-implement procedure for estimating parameters of population models from multiple types of population data. We use a mule deer example from the Piceance Basin in northwest Colorado, USA, to illustrate the procedure. Despite the emphasis on game management, the technique generally is applicable to fitting any wildlife population model to multiple types and sources of data. More mechanistic models that relate population responses to environmental or management variables also can be fit with this approach, although data requirements for such applications are higher.

## METHODS

### Data Collection

Age and sex ratios for the Piceance Basin mule deer population were estimated with helicopter surveys conducted during December or early Jan-

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uary prior to antler drop each biological year from 1981 to 1997 (except 1987 and 1996). Estimates were based on  $\bar{x} = 1,041$  deer classified/year (SD = 249, min = 759, max = 1,539). Survival estimates for 1981–1995 (White et al. 1987, Bartmann et al. 1992, White and Bartmann 1998b, Unsworth et al. 1999) of fawns were based on  $\bar{x} = 106$  collars/year (SD = 45, min = 45, max = 161), and survival estimates of adults were based on  $\bar{x} = 51$  collared females/year (SD = 27, min = 8, max = 93). This assumed that survival of males >1 year old was the same as for adult females. We radio-collared deer in November or early December and computed survival for a 1-year interval. We developed estimates of harvest from telephone surveys of 5% of the license holders for over-the-counter antlerless licenses, and from 20 to 50% of limited antlerless licenses (Steinert et al. 1994). Population estimates for 1981–1985 and 1988 were developed from 120 0.25-mi<sup>2</sup> (0.67-km<sup>2</sup>) quadrats surveyed by helicopter following Kufeld et al. (1980). Surveys were conducted during January or February. We estimated sightability of deer on quadrats as 0.67 following Bartmann et al. (1986), meaning that each deer counted on a quadrat represented 1.5 deer. We will refer to the entire set of direct field estimates for parameters as  $\tilde{\theta}_i$  (where  $i$  references all years and field measurements sequentially) and their estimated standard errors as SE( $\tilde{\theta}_i$ ).

### Population Model

The model must be kept simple to economize the amount of input required to estimate model parameters from observed data. However, the model must adhere to biological authenticity to be useful in projecting population status. For illustration purposes, we develop a model for mule deer to correspond with an example data set. Mule deer population dynamics are much more complicated than the model portrays. However, routine measurement of a wider array of inputs required for a more complicated model is unrealistic. Thus, the model presented here is a reasonable trade-off between what can be measured practically and what is needed to predict mule deer populations for management purposes. Even this simplified model will have more potential parameters than the data can support. Consequently, we compare a family of related models with additional simplifying assumptions and select the most parsimonious using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). We begin by defining the most

general model; reduced parameter variants are described in the section on Model Fitting.

We model the population in annual time steps referenced to the time of annual surveys in December, following harvest. Our model includes only 2 age classes: fawns and adults. We chose to not distinguish yearlings from older animals because survival data were not collected to support this additional complication. The gender of fawns is not differentiated until they are counted in December, at which point a constant proportion,  $r$ , is added to adult males. Thus, we define 3 population segments: fawns (labeled Juveniles or  $J$ ), does (labeled Females,  $F$ ), and bucks (labeled Males,  $M$ ). Fawn, female, and male population segments survive the year according to specific annual rates,  $S_J(t)$ ,  $S_F(t)$ , and  $S_M(t)$ . New fawns are recruited into the population in December in proportion  $R_J(t)$  to each year's December adult female population. Due to harvest and aging, does present in December do not match the does that gave birth, however, we define recruitment relative to the December does to match the age ratio data collected in the field. Annual harvest mortality is modeled separately for males,  $H_M(t)$ , and females,  $H_F(t)$ ; is additive and independent of natural mortality; and is applied to the population following natural mortality and prior to the next December count. Thus, the equations to project the population from December of year  $t$  forward to December of year  $t + 1$  after natural mortality, harvest, and recruitment are:

$$\begin{aligned} N_F(t+1) &= r S_J(t) N_J(t) + S_F(t) N_F(t) - H_F(t+1), \\ N_M(t+1) &= r S_J(t) N_J(t) + S_M(t) N_M(t) - H_M(t+1), \\ \text{and} \\ N_J(t+1) &= R_J(t+1) N_F(t). \end{aligned} \tag{1}$$

Total population size ( $N_T$ ) in early December in year  $t$  is thus

$$N_T(t) = N_J(t) + N_F(t) + N_M(t). \tag{2}$$

The M:F ratio,  $R_M(t)$ , is also computed in the model for comparison to values measured in the field

$$R_M(t) = N_M(t) / N_F(t). \tag{3}$$

Because we collected no explicit data on adult male survival, separate annual estimates of male and female survival are not identifiable, so they must be modeled using fewer parameters. One plausible simplifying relationship assumes that

male survival follows the same pattern through time as female survival,  $S_M(t) = \gamma S_F(t)$ . That is,  $\gamma$  could be included as a parameter to be estimated. Although either a constant recruitment sex ratio,  $r$ , or  $\gamma$  could be estimated with our data, estimation of both, or time-specific values of either would require a more elaborate data collection operation. In preliminary model runs, we tested the value of adding sex differences and found it explained a negligible amount of variation. Therefore, we chose to use the simplest model possible by setting  $r = 0.5$  and  $\gamma = 1$  so that adult male and female natural recruitment and survival rates are equal. Thus, differences between the sizes of the adult sex class are only due to harvest.

For each year, the model contains values for 10 parameters:  $N_T(t)$ ,  $N_M(t)$ ,  $N_F(t)$ ,  $N_J(t)$ ,  $H_M(t)$ ,  $H_F(t)$ ,  $S_F(t)$ ,  $S_J(t)$ ,  $R_M(t)$ ,  $R_J(t)$ . However, 5 relationships impose biological structure on these parameters given in Equations 1–3, leaving 5 unknowns to be measured each year. In addition to these, adult male and female population size must be measured in at least 1 additional year (typically initial values,  $N_M(0)$  and  $N_F(0)$ ) for the model to be identifiable. Thus, for a model of  $T$  years, a minimum of  $5T + 2$  values must be observed to fit this model. If fewer values were measured than the number of unknowns in the model, additional assumptions to simplify the model would be required.

**Model Fitting**

It is important to distinguish between the set of estimated model parameters (referred to collectively as  $\hat{\theta}_i$ ) versus estimates made directly from field observations (collectively,  $\tilde{\theta}_i$ ). Of the 10 annual values included in our model,  $\hat{\theta}_i$ , we collected field data to estimate 6 [ $H_M(t)$ ,  $H_F(t)$ ,  $S_F(t)$ ,  $S_J(t)$ ,  $R_M(t)$ , and  $R_J(t)$ ] in most years (with occasional missing values) plus measurements of  $N_T(t)$  in 6 years. These field estimates constitute the set  $\tilde{\theta}_i$ . Notice that in this example, more annual field measurements (6) were made than the number of unknowns (5) in the model, providing additional degrees of freedom for statistical estimation.

If, as in our example, all of the unknown parameters in the population model,  $\hat{\theta}_i$ , can be estimated directly from field data (i.e., by setting  $\hat{\theta}_i = \tilde{\theta}_i$ ), then the population model can be used directly (without fitting) to project the population. The population for the first year is taken as the population estimate from quadrat surveys for the same year multiplied by the sightability factor (Bartmann et al. 1986) of 1.5. Population seg-

ments are then initialized by using estimated age and sex ratios to partition the estimated population. Survival and recruitment rates are then used to project subsequent annual populations. However, this approach does not use all of the population- and age-ratio data after the first year and, thus, is inefficient. Small errors in survival rates can accumulate over time, resulting in large errors (either positive or negative) in the projected population size in later years. This method also requires direct estimates of survival and harvest every year. We make such a projection to demonstrate its poor performance.

Because we have more measurements than unknowns, an improved parameter estimation strategy that uses all of the data is to treat each of the parameters directly estimated from field data,  $\tilde{\theta}_i$ , as an observation and then select corresponding values for each model parameter,  $\hat{\theta}_i$ , so that the sum of weighted squared errors between field- and model-based estimates of all parameters

$$\varepsilon_i^2 = [(\tilde{\theta}_i - \hat{\theta}_i) / SE(\tilde{\theta}_i)]^2 \tag{4}$$

is minimized. The weight of each of the field measurements is taken as the reciprocal of its variance. Each parameter may have been estimated with field measurements but has an associated (often large) error,  $SE(\tilde{\theta}_i)$ , and so better estimates can be developed using all of the data. Any change in a model-based estimate from its original field-based estimate increases the size of the error, and thus penalizes the optimization for the change. The resulting fit of the model balances the fit to each of the independently estimated field parameters based on the relative precision of each. By using  $SE(\tilde{\theta}_i)$  to weight the difference  $\tilde{\theta}_i - \hat{\theta}_i$ , the resulting residual error is approximately a standardized normal variable with mean zero and standard deviation 1. Thus, the varying scales of the observed data are standardized to have the same relative scale. The  $\varepsilon_i$  can be viewed as a sample of size  $n$  from a Normal(0, 1) distribution with joint log likelihood

$$\log \mathcal{L} = -\frac{n}{2} \log(2\pi) - \frac{1}{2} \sum_{i=1}^n \varepsilon_i^2, \tag{5}$$

because  $\sigma$  is assumed to be 1 in the usual normal log likelihood. Hence,  $\sigma$  is not estimated as part of the likelihood. The sample size  $n$  is the total number of  $\varepsilon_i^2$  summed in the objective function. To maximize the log likelihood function, only the term  $\sum_{i=1}^n \varepsilon_i^2$  needs to be optimized, and this process can be done easily with the optimizer

function of spreadsheet software. This estimator is termed an ordinary least squares estimator (OLS; Seber and Wild 1989) because covariances of the  $\epsilon_i$  across the different types of field measurements are assumed to be zero.

We fit a family of models to the field measurements using the OLS procedures described above. Models in this series differed only in the amount of temporal (annual) variation allowed for each of the survival and age ratio parameters. Year-specific harvest was assumed to be known— $SE[\hat{H}_i(t)] = 0$ ;  $\hat{H}_i(t) = \tilde{H}_i(t)$ —and thus not modified in the model fitting. All models in this series require estimating initial sizes for adult male and female population segments. We first consider Model 1 with constant recruitment and adult and fawn survival across years, with 5 parameters estimated. Next, Model 2 with a linear trend in age ratios, but constant adult and fawn survival is considered, with 6 parameters estimated. Models 3–7 include year-specific estimates for various combinations of the recruitment rate and adult and juvenile survival rates. Each of these models has 15 year-specific fawn survival parameters estimated for the 18-year period (1981–1998) with 3 missing values in each. Like Model 2, Models 4 and 5 assume a linear trend in recruitment. Model 7, the most general, adds 45 year-specific estimates of recruitment and survival to the 2 initial population segment size estimates for a maximum of 47 parameters.

We used model selection based on information theory (Burnham and Anderson 1998) to select among these various models using the  $AIC_c$  value

$$AIC_c = -2\log\mathcal{L} + 2K + \frac{2K(K+1)}{n-K-1}, \quad (6)$$

where  $K$  is the number of parameters estimated via optimization to minimize  $\sum_{i=1}^n \epsilon_i^2$ . Note that  $-2\log\mathcal{L}$  is equal to  $\sum_{i=1}^n \epsilon_i^2$  plus a constant, so that only the  $\sum_{i=1}^n \epsilon_i^2$  term needs to be included in the calculation of  $AIC_c$  for model selection, which is based only on relative values. Standard errors of parameter estimates can be obtained by inverting the negative of the information matrix of the log likelihood function. The information matrix is the matrix of second partial derivatives of the log likelihood with respect to each of the parameters estimated.

The OLS estimator is not fully efficient (Seber and Wild 1989) because the covariances of the  $\epsilon_i$  across the different types of field measurements are incorrectly assumed to be zero. Although serial autocorrelation is not likely to be a problem with the direct field estimates because the surveys

are performed independently across time, the fact that many of the model parameters being estimated are shared across equations and affect several model predictions (e.g., adult survival affects both the population size and age and sex ratios) may induce covariances. The residuals in year  $i$  can be considered a vector,  $\underline{\epsilon}_i$ , with  $k$  elements corresponding to each different type of measurement. The  $\underline{\epsilon}_i$  vectors each can be considered to be a multivariate normal sample with covariance matrix  $\underline{\Sigma}$ . The log likelihood then becomes

$$\log\mathcal{L} = -\frac{nk}{2}\log(2\pi) - \frac{n}{2}\log(|\underline{\Sigma}|) - \frac{1}{2}\sum_{i=1}^n \underline{\epsilon}_i' \underline{\Sigma}^{-1} \underline{\epsilon}_i, \quad (7)$$

where  $|\underline{\Sigma}|$  is the determinant of  $\underline{\Sigma}$ .

Theory for estimating  $\underline{\Sigma}$  and fitting such a model (termed seemingly unrelated regressions, SUR) is provided by Gallant (1987), and implemented in PROC MODEL (SAS Institute 1988) only for data sets where measurements for each of the field observations are all taken each year. Gallant (1987) and Seber and Wild (1989) also discuss more elaborate estimators that iteratively estimate  $\underline{\Sigma}$  and the parameters being estimated simultaneously, again implemented in PROC MODEL (SAS Institute 1988). The advantage of these more elaborate estimation schemes is to improve efficiency, but this is accomplished at some cost due to the increased number of parameters that must be estimated for the covariances of the field measurements. More importantly, the complexity of these more advanced procedures discourages their adoption for most wildlife management purposes. Note that the OLS estimates are a special case of the SUR estimates with  $\underline{\Sigma}$  defined as an identity matrix.

## RESULTS

Data collected on the Piceance mule deer herd in northwestern Colorado (Table 1) exhibit high year-to-year variation in fawn survival, and a gradual decline in fawn:doe ratios from 1981 to 1997. In addition, quadrat population estimates demonstrate high sampling variation, i.e., large standard errors. In contrast, standard errors of age and sex ratios are small relative to population estimates, and survival estimates are the most precise of all the estimated parameters.

We first built a naive 2-age class model (fawns, adults) with sex-specific classes for adults from these data using direct field estimates of the parameters (i.e., with no additional model fitting). The initial population was computed as 1.5 times

the 1981 population estimate using the assumption that 67% of the animals were counted on the quadrats sampled due to sightability limitations, based on the work of Bartmann et al. (1986). Age and sex structure of the initial 1981 modeled population was computed from the 1981 age and sex ratios. Years (1987, 1996, 1998) with missing fawn:doe ratios were replaced by the mean of the series (however, these values are not used later for parameter estimation in the model fitting procedure). Although a downward trend exists in the fawn:doe ratios, using the mean value for these years should increase the population size for this model's predictions. Nevertheless, with these inputs, the buck:doe ratio becomes negative and the population declines to zero (Fig. 1). Although the population had been thought to be declining during the 1990s (i.e., see population estimates for a portion of the area modeled here in White and Bartmann 1998*b*), the decline was not that severe. Sampling variation in the parameter estimates and the resulting inconsistencies cause the model to predict extirpation. Most notably inconsistent are the population estimates for 1981, 1982, and 1983. The 1982 estimated population appears to be much too low, in that biologically the population likely could not grow from the estimated low point in 1982 to the higher estimate in 1983 (Table 1, Fig. 1).

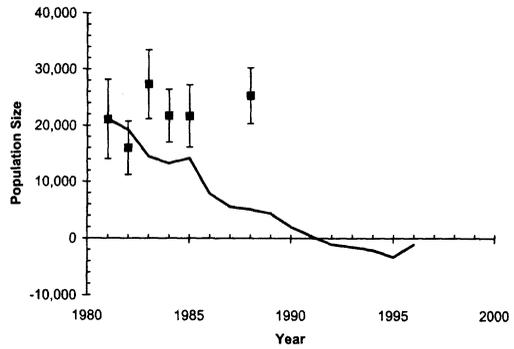


Fig. 1. Estimates and 95% confidence intervals for observable (uncorrected for sightability) mule deer population (squares) based on quadrat counts from helicopter surveys in the Piceance Basin, Colorado, USA, plotted with a naive population projection (line) based on direct field estimates of initial population size by age and sex class and annual survival rates and harvest. Population projections were not fitted to annual age ratio data. Model predictions were multiplied by the sightability factor of 0.67 so that predicted and observed population values are comparable.

Model fitting using the OLS estimation procedure for the series of models indicated that, based on AIC<sub>c</sub>, the most appropriate model in this sequence is Model 4, with a linear trend on age ratios, year-specific fawn survival, but constant adult survival (Table 2). The Akaike weight

Table 1. Estimates of fawn and adult survival, fawn:doe and buck:doe ratios, and population size for the Piceance mule deer herd, northwestern Colorado, USA, 1981–1995. Missing data are shown as blank entries.

Year	Fawns:100 does		Bucks:100 does		Fawn survival		Adult survival		Population size		Buck harvest		Doe harvest	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1981	77.7	5.78	13.8	1.95	0.48	0.068	0.86	0.049	21,103	3,592	2,293		19	
1982	75.5	4.34	11.4	1.34	0.36	0.044	0.81	0.048	16,004	2,425	3,072		10	
1983	78.8	4.83	11.4	1.45	0.05	0.021	0.83	0.045	27,309	3,129	3,512		64	
1984	70.2	4.49	7.4	1.16	0.19	0.039	0.88	0.040	21,723	2,387	2,017		12	
1985	72.5	5.57	7.2	1.38	0.41	0.039	0.92	0.038	21,657	2,822	1,849		30	
1986	63.5	4.11	14.0	1.62	0.42	0.038	0.76	0.068			931		21	
1987					0.15	0.033	0.88	0.083			1,326		24	
1988	74.2	3.76	13.9	2.04	0.35	0.064	0.83	0.108	25,248	2,517	1,449	75	585	19
1989	65.7	2.72	12.4	1.90	0.77	0.049	0.90	0.051			2,227	95	1,512	59
1990	61.2	3.32	16.2	2.09	0.32	0.069	0.94	0.035			1,822	92	1,691	48
1991	46.4	2.26	11.9	1.45	0.49	0.072	0.77	0.052			1,917	92	1,238	45
1992	45.5	2.85	10.5	1.74	0.14	0.029	0.71	0.048			1,310	68	1,296	70
1993	42.6	3.04	10.1	2.30	0.65	0.038	0.84	0.038			1,041	63	777	53
1994	46.1	2.86	7.8	1.67	0.76	0.034	0.88	0.035			1,210	65	221	17
1995	47.6	3.03	10.7	2.24	0.70	0.038	0.93	0.029			1,489	68	182	16
1996											1,631	69	206	18
1997	46.1	3.00	11.5	1.80							1,194	60	442	39
Mean	60.9	3.73	11.3	1.74	0.42	0.045	0.85	0.051	22,174	2,812	1,782	75	490	38
SD	13.7		2.6		0.23		0.07		3,886		698		589	

Table 2. Sequence of models fit to the field measurements reported in Table 1. The number of parameters for each component are included in parentheses.

Model	Age ratios	Fawn survival	Adult survival	Initial population	K <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>
1	Constant (1)	Constant (1)	Constant (1)	Buck & Doe (2)	5	1009.1
2	Linear trend (2)	Constant (1)	Constant (1)	Buck & Doe (2)	6	900.1
3	Constant (1)	Year-specific (15)	Constant (1)	Buck & Doe (2)	19	366.1
<b>4<sup>c</sup></b>	<b>Linear trend (2)</b>	<b>Year-specific (15)</b>	<b>Constant (1)</b>	<b>Buck &amp; Doe (2)</b>	<b>20</b>	<b>203.0</b>
5	Linear trend (2)	Year-specific (15)	Year-specific (15)	Buck & Doe (2)	34	268.3
6	Year-specific (15)	Year-specific (15)	Constant (1)	Buck & Doe (2)	33	227.4
7	Year-specific (15)	Year-specific (15)	Year-specific (15)	Buck & Doe (2)	47	413.3

<sup>a</sup> K is the number of estimated parameters in each model.

<sup>b</sup> AIC<sub>c</sub> is the Akaike Information Criterion calculated as  $\sum_{i=1}^n \epsilon_i^2 + 2K + \frac{2K(K+1)}{n-K-1}$  (see text for full definition).

<sup>c</sup> Best (lowest AIC<sub>c</sub>) model is shown in bold.

for Model 4 is >0.9999, indicating that this model is by far the most appropriate of the 7 considered. Results from Model 4 produce a much more consistent fit of the model to the quadrat estimates of population size (Fig. 2) than the original naive model projection (Fig. 1). The predicted decline in the population is now consistent with other observations of population size estimated on a small portion of the study area modeled here (White and Bartmann 1998b). The fit of the model predictions to the estimated buck:doe ratios is reasonable (Fig. 3) and involves only small adjustments to fawn:doe ratios (Fig. 3) and fawn survival estimates (Fig. 4). Adult survival rates are assumed constant, and thus 14 parameters are saved in this model compared to Model 5, where this rate is year-specific. Modeling the linear trend in recruitment saves an additional 13 parameters relative to the most general model. The strong selection of this model indicates that most of the year-to-year variation in observed adult survival rates is due to sampling error rather than process variation in the actual survival rate. The decline in recruitment also is clearly distinguished from other explanations for the decline in this population.

Two subtle, but critical, differences between the original estimates and those from the best fitted model account for the dramatic differences in predictions. First, adult survival rate in the fitted model is estimated to be 0.88, whereas the geometric mean of the direct field estimates of adult survival rate was 0.85. This small difference is enough to change the projection from population extirpation to a more modest decline. Second, the estimated observable (adjusted for sightability)

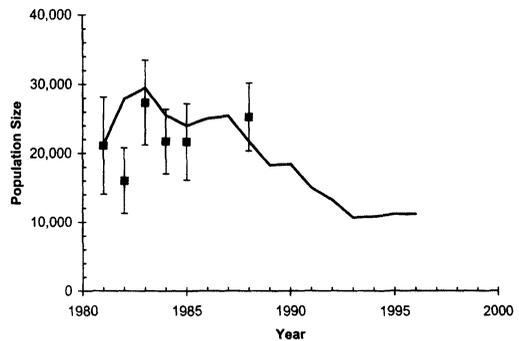


Fig. 2. Estimates and 95% confidence intervals for mule deer population (squares) based on quadrat counts from helicopter surveys in the Piceance Basin, Colorado, USA, plotted with the best (AIC<sub>c</sub>) fitted model (Model 4) predictions (line) which include constant adult survival, a linear trend in recruitment, and year-specific juvenile survival rates. Model predictions were multiplied by the sightability factor of 0.67 so that predicted and observed population values are comparable.

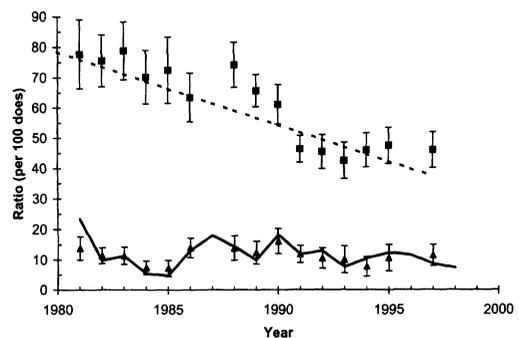


Fig. 3. Estimates and 95% confidence intervals for buck:doe (triangles) and fawn:doe (squares) ratios from helicopter surveys in the Piceance Basin, Colorado, USA, plotted with the best (AIC<sub>c</sub>) fitted model (Model 4) predictions (solid and broken lines, respectively) which include constant adult survival, a linear trend in recruitment, and year-specific juvenile survival.

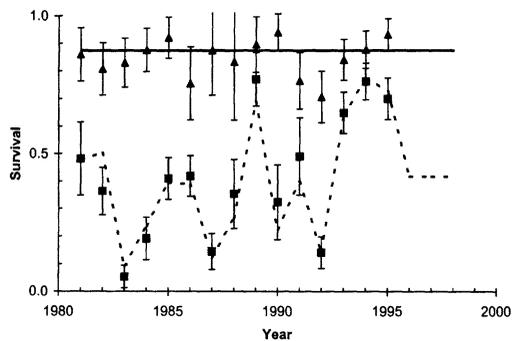


Fig. 4. Radiocollar estimates of fawn (squares) and adult female (triangles) survival rates from the Piceance Basin, Colorado, USA, compared to best (AIC<sub>c</sub>) fitted model (Model 4) predictions (broken and solid lines, respectively) which include constant adult survival, a linear trend in recruitment, and year-specific juvenile survival.

starting population in 1981 from the fitted model, based on all available data, is 24,203 as opposed to the 1981 direct field estimate of 21,103.

Excel<sup>®</sup> Version 5/7 and Quattro Pro<sup>®</sup> Version 8 spreadsheets with the Piceance mule deer example are available from the Internet at <http://www.cnr.colostate.edu/~gwhite>. Although this spreadsheet model is specific to the example presented here, it can be used as an example from which other population models can be easily implemented by making appropriate changes.

## DISCUSSION

The procedure described here for model fitting to observed data is a least squares estimation approach. If the statistical errors in the estimates are assumed to be normally distributed, then the procedure gives maximum likelihood estimates. Because survival estimates from radiocollars might be more appropriately treated as binomial variables, the objective function could be changed for these estimates to be a binomial log-likelihood. In the example presented here, this was not done because the survival estimates were computed with a staggered-entry Kaplan-Meier procedure with some observations that were censored. Therefore, a binomial log-likelihood estimator would not be appropriate.

One extension that should be considered is to incorporate the sampling covariances of estimates taken in the same year. For example, the fawn:doe and buck:doe ratio estimates have a sampling covariance because both are estimated from the same classification data. Other param-

eters might have sampling covariances depending on the estimation approach used, e.g., fawn and adult survival rates would be correlated if estimated from band recoveries (White and Bartmann 1983) instead of radios. An appropriate technique to handle this within-year covariance would be to use matrix algebra to weight the pair of estimates by the inverse of their variance-covariance matrix. Mathematically, the entire optimization process could be formulated as a matrix equation equivalent to the SUR procedure described, although such an elegant presentation would not likely benefit the understanding of the procedure by most biologists, nor would it be likely to change the modeling results enough to alter management decisions in the field.

The procedure presented here is similar to the one described by Lipscomb (1974) where we consider the weights in his nonlinear programming formulation as the inverse of the variance of the estimates. The power of modern spreadsheet software facilitates rapid implementation of this approach, whereas previously, problem-specific software, often written in FORTRAN code at substantial expense, was not as robust and easy to adapt to new problems as the spreadsheet approach. The availability of PROC MODEL (SAS Institute 1988) provides the flexibility to use more elegant estimation procedures, but does not permit missing values, thus requiring that all field measurements be taken every year. Other approaches to population model fitting involving Bayesian and Kalman filtering methods have been suggested (Schnute 1994, Zheng et al. 1998, Miller and Meyer 2000, Trenkel et al. 2000) but are sufficiently complex to discourage most management agencies from adopting them. We believe that the simpler methods outlined here are a sufficient improvement over previously available methods. Relatively small effort is required to apply them, whereas the cost of more advanced techniques may not be justified by the incremental improvement in efficiency.

The applicability of model fitting and selection procedures presented here is not limited to the structure or features of the example mule deer model that we used for illustration. There are no restrictions on linearity, continuity, functional complexity, or parameterization. The structure of the most general model considered should depend on the complexity of the data available, the prior knowledge about the biology of the species, and the research or management questions of interest. With sufficient data, it is a sim-

ple matter to include additional complexity such as additional age classes or separate survival rates by sex. Density feedback from population size to vital rates can be modeled as a simple linear relationship, or using a nonlinear function with a more appropriate shape such as the logit, to enforce biological constraints. Common harvest complexities encountered for some species (e.g., elk), such as wounding losses, illegal kill, and differential harvest mortality due to antler point regulations, can be modeled by constant, proportional, or more complex functions. When precise harvest records are unavailable, unlike in our example, harvest itself can be considered a parameter to be estimated. Our modeling of juvenile survival as a function of time illustrates how all of these additional biological and management mechanisms can be implemented.

One desirable objective of more complex, mechanistic models of a population is their ability to project forecasts of the relevant covariates. The model in our example modeled recruitment as a function of time and adult survival as a constant. Only the fawn survival rate was year-specific. Therefore, population projections can be made using this model by adding additional assumptions only about the future fawn survival rate. Using a mean value is one such assumption that facilitates projections. However, a model that could predict future fawn survival as a function of more easily forecast variables would be an improvement and should be the focus of future research. For example, a particularly valuable class of extended models incorporate explanatory variables into the population dynamics. Covariates can be used to provide estimates of winter severity or drought (McCulloch and Smith 1991). Furthermore, juvenile survival or recruitment might be modeled as a function of commonly available weather covariates such as seasonal temperatures, precipitation, or snow depths. These relationships need not be linear. To accommodate severe winters, an approach that works reasonably well is to compute survival each year as  $S_i = s^{W_i}$ , where  $W_i$  represents a winter severity index with  $W_i = 1.0$  representing an average winter, values of  $W_i > 1$  are more severe than normal, and  $0 \leq W_i < 1$  less severe than normal. The values of  $s$  and each  $W_i$  are additional parameters that must be estimated to fit the data to the model. The value of such models is that they aid researchers in understanding causes of population change and managers in anticipating the future effects of current and forecast environmental conditions.

Numerical considerations can cause problems with the optimization required to determine the maximum likelihood estimates. Some models require more effort to find the optimal solution than other models. A useful option available with many spreadsheet optimization programs is to allow automatic scaling of the optimization variables. Otherwise, the several orders of magnitude difference of parameters (e.g., survival rates vs. population sizes) will cause numerical difficulties with the optimizer, and no solution will be achieved. When data are sparse (many missing values) or the model is overparameterized, these problems can prevent convergence of the optimization or cause it to converge to a local minimum. For difficult models, a good approach is to begin by optimizing only the parameters that have the most variation while fixing the others at the values of the field estimates. In the Piceance mule deer example, we started the optimization process with just the population estimates, holding age ratios, fawn survival, and adult survival constant. After we calculated this intermediate solution, we progressively added the linear trend on age ratios, year-specific fawn and adult survival, and age ratios, to the optimization, using the prior solution as initial values. At each step, all parameters estimated by optimization at the previous step were reestimated simultaneously using the added parameters, so that each solution was globally optimized.

For some problems, particularly ones with sparse or imprecise data, the optimizer can be given numerical constraints on any combination of parameters to ensure that they remain within biologically reasonable limits. This should be done sparingly to avoid biasing results with preconceived notions of the values of parameters. Typically, it should be necessary only to constrain parameters to the range of biologically feasible values, such as  $0.0 \leq S \leq 1.0$ . If biologically unreasonable results are obtained even with these minimal constraints, this suggests that the data set is inadequate and probably should be abandoned or supplemented with additional data, or the model should be simplified by removing some parameters.

We emphasize that all field estimates are assumed to be unbiased and accompanied by appropriate (and unbiased) measures of precision. Because the estimated precision of each measured value is used to weight that value in the model fitting, parameters with overestimated precision, due to either bias or improper methods of

estimation, will be given greater consideration than they deserve. When such a situation is suspected and cannot be corrected, the suspect data can either be discarded or given less weight by inflating the precision estimate, both of which are ad hoc approaches that we discourage.

In the example presented here, data were available for almost every parameter estimate for most years, with quadrat population estimates being the notable exception. Because our data set was nearly complete, the most general models we could examine included those with annual variation in various vital rates. However, when data are more sparse, as is common, stronger assumptions must be made to simplify models by, for example, considering only average survival or simple trends. Typically, survival estimates from radiocollars are not available for most mule deer DAU in Colorado. Also, many of the mule deer DAU and almost all elk DAU lack field-based estimates of population size, adding another complication to the model-fitting procedure. Model fitting with field estimates of only age and sex ratios, in the absence of survival and population data, often results in driving the population size projections to infinity. Statistically, this is a parameter identifiability problem. Biologically, this behavior is exhibited because the larger the population, the less impact is produced when estimated harvest is subtracted from the model population, allowing more flexibility to fit the observed age and sex ratios. For these DAU, assumptions must be made about the population's size at some point in time. Although no specific minimum data set is required to apply this technique, sparser and less precise data sets require more subjective assumptions, can be expected to yield less precise results, and may even fail to converge on a biologically reasonable solution at all. Caution in the interpretation of such inadequate data sets is strongly advised. Addition of subjective constraints to the optimization process, in such cases, also is strongly discouraged because this will lead to subjective conclusions that are not supported by the data.

## MANAGEMENT IMPLICATIONS

The model-fitting procedure presented here provides a rigorous, objective model alignment procedure that is easy to implement with standard PC spreadsheet software. Most wildlife investigations lack the necessary data with which to estimate all the required parameters before a model is built. Even if data are plentiful, inconsistencies in the data will likely cause the perfor-

mance of the model to be unsatisfactory. Thus, a model-fitting procedure is required to decide which estimates to adjust, and by how much, to achieve the best alignment. However, spreadsheet models should be used neither to legitimize subjective opinions nor as a substitute for good field data (see Unsworth et al. 1999 for recommended data requirements). As population models are increasingly used to manage wildlife populations, more rigorous and objective methods should be used to build these models, so that they can withstand the public scrutiny of an increasingly involved and diverse set of stakeholder groups.

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