STATISTICAL MODELS FOR POPULATION RECONSTRUCTION USING AGE-AT-HARVEST DATA

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Abstract: Statistical analyses based on maximum likelihood methods are presented to jointly estimate harvest rates, survival, recruitment, and population abundance from age-at-harvest data. To perform the population reconstruction from the age-at-harvest data, auxiliary field data and information on harvest reporting rates are required. The statistical methods permit tests of model assumptions, goodness-of-fit, and standard errors and confidence intervals for all estimated demographic parameters. We illustrate the methods using harvest data and radiotelemetry studies of elk (*Cervus elaphus*) from northern Idaho, USA, 1988–1993. We compare results with abundance estimates using an aerial sightability survey on the same herd. The maximum likelihood methods for age-at-harvest analysis provide a comprehensive framework for population reconstruction with abundance estimates comparable to field survey techniques.

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Population analysis, as defined by Eberhardt (1971:457), is the "process of attempting to determine the structure of a population and the forces controlling past and future composition of that population." Elements of the analysis include estimating the age and sex composition of the population, survival rates, recruitment, rate of increase, and abundance. Population analysis often is the culmination and integration of many labor-intensive studies focused on various aspects of survival, fecundity, and abundance. A population analysis should be judged by how accurately it portrays the dynamics and structure of that population. Given good estimates of survival, recruitment, and abundance, "few complications of mathematics, logic, or technology are involved in understanding population behavior in general terms" (Eberhardt 1971:457–458). Unfortunately, the mathematics become increasingly more difficult, the assumptions more profound, and "all sorts of difficulties arise in trying to get along with the observations that can be obtained" (Eberhardt 1971:458).

Age-at-harvest data collected at hunter check stations is a frequent starting point for population analysis and reconstruction. Population reconstruction is a method of using such demographic data to reproduce the historical trends in animal abundance (Eberhardt 1971, Lang and Wood 1976, Downing 1980, Roseberry and Woolf 1991). Intriguingly nested within the age-at-harvest data is information on age and sex composition, survival, and fecundity rates. However, the numbers observed also are a function of hunter effort and reporting rates that might not be constant over time. Nevertheless, the information within age-at-harvest data has compelled many state agencies to collect these data. Due to the lack of better analytical methods to interpret these data, too often age-at-harvest data are collected at considerable expense, then neglected.

Assuming harvest and survival rates are known, the age-at-harvest data can be calibrated back to estimates of abundance quite readily (Downing 1980, Roseberry and Woolf 1991, Ferguson 1993). Current population reconstruction methods that use age-at-harvest data typically rely on rough estimates of survival, harvest, and reporting rates with little or no attempt to propagate the uncertainty of this information to the overall precision of the population reconstruction (Roseberry and Woolf 1991). In fisheries management, the use of survival and harvest rates in conjunction with age-at-harvest data is called virtual population analysis (VPA). See Fournier and Archibald (1982) and Deriso et al. (1985) for reviews of this literature.

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Table 1. Age-at-harvest data from cow elk harvested in Game Management Unit 4, northern Idaho, USA, 1988–1993.

	Age class																	Total reported
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	harvest
1988	21	36	15	8	7	8	6	5	3	3	4	3	2	1	1	1	2	126
1989	27	40	15	20	9	11	5	10	3	2	5	0	3	2	0	0	0	152
1990	35	42	16	19	15	14	7	7	4	5	0	3	3	3	0	2	0	175
1991	39	32	12	17	15	10	5	6	6	0	0	0	0	0	0	0	0	142
1992	27	32	25	18	13	19	5	13	5	9	2	2	1	2	1	1	2	177
1993	22	23	21	22	16	15	7	9	10	5	5	5	2	3	3	3	1	172

We present maximum likelihood approaches for analyzing age-at-harvest data from wildlife populations that explicitly incorporate auxiliary information on harvest and survival probabilities from radiotelemetry data and harvest reporting rates from compliance surveys. Traditional population reconstruction methods (Downing 1980, Roseberry and Woolf 1991) separately estimate population abundance from other demographic parameters. Our joint analysis extracts simultaneous estimates of recruitment, survival rates, harvest rates, age structure and abundance of cohorts, and reconstructs population trends over time. The maximum likelihood estimates subsequently can be used in viability analysis and estimating rates of population change. The advantages of these new techniques include (1) a single comprehensive framework for estimation, (2) the ability to avoid assumptions regarding the recruitment process, (3) maximum information extraction, and (4) the ability to estimate standard errors or confidence intervals associated with the demographic parameters. We will illustrate the statistical methods using harvest data from an elk herd in northern Idaho, USA. The generalization of this approach to other wildlife populations will be discussed.

EXAMPLE: FEMALE ELK HARVEST DATA

To illustrate the age-at-harvest analysis, data collected by the Idaho Department of Fish and Game were used. The data came from elk harvested in Game Management Unit (GMU) 4, the Coeur d'Alene River drainage in northern Idaho. Most of the harvest occurs during an October general rifle season. Either-sex elk can be harvested during a portion of this season. In northern Idaho, all successful hunters must register their animals at a check station or a department-approved checkpoint. Checkpoints are businesses, such as taxidermists and butcher shops, at which hunters can register their animal. Data such as sex of the animal, location and date of the kill, and number of days hunted are recorded. The lower jaw is collected to determine the age of the animal. Calves and yearlings are aged by inspecting tooth development (Quimby and Gaab 1957). Older animals are aged by examining cementum annuli in the I1 tooth (Klevezal and Kleinenberg 1967). Although data on both sexes were collected, we examined only the female harvest data. The elk ranged from 1 to 23 years of age. The data for elk 18 years and older were not used in this analysis because their harvest numbers were extremely few. We report the number of elk harvested by age for 1988–1993 in Table 1.

Although reporting of elk harvests is mandatory, some hunters fail to do so. Ignoring the nonreporting rate would have a negative (i.e., downward) bias on subsequent estimates of harvest rates and elk abundance. A telephone survey estimated annual compliance (R_i; $i = 1, ..., Y$) rates for the elk hunters in the panhandle region of northern Idaho that includes GMU 4. The annual estimates of reporting compliance rate were assumed to be independent of age-class and sex of the elk harvest. We present in Table 2 the sur-

Table 2. Numbers of successful hunters surveyed by telephone (a_i), numbers of hunters that registered their elk harvest (b_i), and estimated reporting compliance rate ($\hat{R}_i$) for elk hunters in the panhandle region of northern Idaho, 1988–1993. Reported counts were reconstructed from available survey records.

Year	Number of successful hunters surveyed (a_i)	Number who registered harvest (b_i)	Estimated reporting rate ($\hat{R}_i$)
1988	275	143	0.5207
1989	290	154	0.5312
1990	211	211	1.0
1991	360	272	0.7553
1992	201	201	1.0
1993	325	155	0.4768

Table 3. Results from a concurrent study of radiocollared cow elk in GMU 4 in northern Idaho, USA, 1988–1993. Numbers of total cow elk collared and their fates each year are presented (Leptich and Zager 1995).

	Number of radiotagged elk			
Year	Total	Harvested and recorded	Survived	Nonharvest mortality[a]
1988	13	1	10	2
1989	25	4	20	1
1990	25	0	24	1
1991	16	0	16	0
1992	25	4	17	4
1993	23	1	18	4

[a] Nonharvest mortality includes unrecovered wounding loss, illegal kill, and natural mortality.

vey results for the proportion of hunters who reported their elk harvest by year as reconstructed from available records.

In addition, telemetry studies of radiocollared cow elk were conducted concurrently (Table 3). The number of collared cow elk ranged from 13 to 25, and annual information on numbers that survived, were harvested, and died from natural causes were recorded (Leptich and Zager 1995). These 3 data sets constituted the information used in the population reconstruction analysis.

STATISTICAL ANALYSIS

Overview

A cohort of individuals all born during the same year forms the fundamental biological unit in this population reconstruction analysis. The change in cohort abundance from 1 year to the next is dependent on the natural survival rate and harvest probability of that cohort. The population can then be visualized as the union of the various cohorts comprising the population (Fig. 1). The observed random variables are the annual numbers of individuals of that cohort that are harvested and reported in consecutive years. The cohort data for the cow elk population are represented by harvest counts along diagonals in Table 1. However, information beyond simply the age-at-harvest numbers is needed for population reconstruction. In other words, the harvest numbers alone are insufficient to estimate abundance and differentiate the processes of survival, harvest, and reporting. In this analysis of the demographic data, parameters were estimated by max-

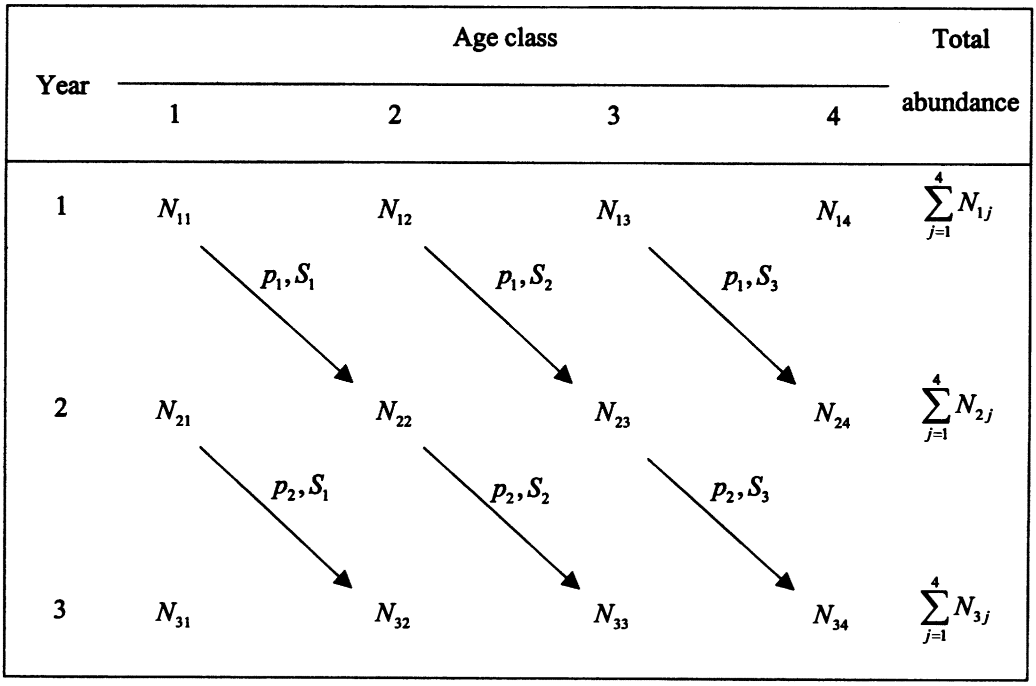

Fig. 1. Schematic of the survival and harvest processes across 3 years ($Y = 3$) and 4 age-classes ($A = 4$) based on age-specific survival ($S_j = 1,..., 3$) and year-specific harvest (p_i; $i = 1, 2$) probabilities.

imizing a joint likelihood model of the form

$$L_{\text{Joint}} = L_{\text{Age-at-Harvest}} \cdot L_{\text{Auxiliary}} \cdot L_{\text{Reporting}} \cdot \quad (1)$$

The age-at-harvest likelihood ($L_{\text{Age-at-Harvest}}$) models the observed harvest numbers as a function of recruitment and survival, harvest, and reporting rates. An auxiliary likelihood ($L_{\text{Auxiliary}}$) must be used to estimate 1 or more of the model parameters on abundance, survival, or harvest to allow the remaining parameters to be estimated. The reporting likelihood ($L_{\text{Reporting}}$) supplies information on the rates of reporting compliance to estimate the harvest reporting parameters in the model. If the reporting rate of harvested animals is 100%, this third likelihood component can be omitted from Equation 1.

The relative amounts of information in the 3 components of the joint likelihood Equation 1 can be quite different. Various investigators have suggesting tuning (Gallucci et al. 1996:38, 275) or weighting (Quinn and Deriso 1999:335, 391) the different contributions to the overall likelihood model. The perceived imbalance in information has prompted the use of a weighted likelihood model of the form

$$\ln(L_{\text{Joint}}) = f_1 \ln(\text{L}_{\text{Age-at-Harvest}}) + f_2 \ln(L_{\text{Auxiliary}}) + f_3 \ln(\text{L}_{\text{Reporting}}), \quad (2)$$

where $\sum_{i=1}^{3} f_i = 1$ and $0 < f_i < 1$. Gove (1997) investigated the use of weighted maximum likelihood analysis, but in all cases found the error mean square was less using a nonweighted versus a weighted likelihood. Therefore, we recommend a nonweighted approach to the analysis. Below, more detailed descriptions of the individual model components are presented.

Model Construction

Age-at-Harvest Likelihood.—Gove (1997) investigated 4 alternative models for the analysis of age-at-harvest data. These models differed in assumptions concerning the time varying nature of harvest and survival rates. These different models are specified as follows:

Model *MpS*: Assumes constant survival (S) over time and across all age classes, as well as constant harvest rate (p) over time and across all age classes.

Model MpS_A: Assumes age-specific survival rates (S_j) that are constant over time and a harvest rate (p) that is constant over time and across age classes.

Model Mp_YS: Assumes constant survival (S) over time and across age classes and harvest rates that vary between years (p_i) but are constant across age classes.

Model Mp_YS_A: Assumes age-specific survival rates (S_j) that are constant over time and harvest rates (p_i) that vary between years but are constant across age classes.

The 4 different models (*MpS*, MpS_A, Mp_YS, and Mp_YS_A) were selected for presentation in this paper because of their general applicability to many harvest situations. However, as many as 16 alternative classes of models can be conceptualized based on the presence or absence of either time- and/or age-dependent survival and harvest rates. Within even these model classes (e.g., Mp_YS_A), special cases also can be constructed based on the specific pattern of the time and/or age varying survival and harvest rates. For example, rather than strictly assuming age-specific survival rates (i.e., S_A), a special case would consist of a constant adult survival rate but different from subadult age classes. Hence, there is an almost unlimited variety of conceptual models from which to choose. However, as the models become more complex, the data requirements become increasingly more demanding, as shown below.

To illustrate the development of the age-at-harvest likelihood, consider the special case of age-specific survival, year-specific harvest, and year-specific reporting rates. Let

N_{ij} = abundance of animals in year $i(i = 1, \ldots, Y)$, age class $j(j = 1, \ldots, A)$;

S_j = probability that an animal in age class $j(j = 1, \ldots, A - 1)$ survives to age class $j + 1$;

p_i = probability of an animal being harvested in year $i(i = 1, \ldots, Y)$;

R_i = probability a harvested animal in year $i(i = 1, \ldots, Y)$ is reported;

x_{ij} = number of animals in age class $j(j = 1, \ldots, A)$ harvested and reported in year $i(i = 1, \ldots, Y)$.

Then, for example, the expected number of animals harvested and reported in age class $j = 1$ in year $i = 1$ can be expressed as

$$E(x_{11}) = N_{11} p_1 R_1.$$

Similarly, the expected value of x_{22} can be expressed as

$$E(x_{22}) = N_{11}(1 - p_1) S_1 p_2 R_2.$$

Here, S_i is the complement of the probability of mortality from nonhunting, natural causes. By further assuming the fates of the individuals in a cohort are independent and identically distributed, a multinomial distribution can be used to model the observed harvest numbers. A likelihood model for the first cohort in year 1 (N_{11}) harvested over 3 years with age-specific survival (S_j) rates and year-specific harvest (p_i) and reporting rates (R_i) can be written as follows

$$L(N_{11}, \underset{\sim}{p}, \underset{\sim}{R}, \underset{\sim}{S} \mid \underset{\sim}{x}) = \binom{N_{11}}{x_{11}, x_{22}, x_{33}} (p_1R_1)^{x_{11}}((1-p_1)S_1p_2R_2)^{x_{22}} ((1-p_1)S_1(1-p_2)S_2p_3R_3)^{x_{33}}$$
$$[1-(p_1R_1+(1-p_1)S_1p_2R_2+(1-p_1) S_1(1-p_2)S_2p_3R_3)]^{N_{11}-x_{11}-x_{22}-x_{33}}. \quad (3)$$

The construction of a model for the entire set of harvest data requires development of a joint likelihood to describe the expected counts for each cohort represented by the diagonals in Fig. 1. The overall likelihood model for multiple cohorts is a product of the individual cohort likelihoods. The general likelihood model with year-specific harvest and reporting rates and age-specific survival (Fig. 1) can be written as

$$L(\underset{\sim}{N},\underset{\sim}{p},\underset{\sim}{R},\underset{\sim}{S} \mid \underset{\sim}{x}) = \prod_{j=1}^{A} L(N_{1j},p_1,R_1,S_j \mid \underset{\sim}{x}) \cdot \prod_{i=2}^{Y} L(N_{i1},p_i,R_i,S_1 \mid \underset{\sim}{x}) \quad (4)$$

where A = number of age classes in the data set and Y = number of years in the data set. Model selection for this likelihood should be based on knowledge of the life history and harvest processes for the species and the best model fit to the data. In the analysis of the elk harvest data, Models *MpS* and *Mp*$_Y$*S* were considered and compared.

No stock-recruitment or fecundity relationship was used in projecting the number of recruits into the first harvestable age class. The lack of assumptions concerning the nature of the recruitment process was a major strength of these likelihood models. The models neither assume an extrinsically nor intrinsically controlled population. Instead, recruits were estimated from the history of harvest numbers and the assumptions of common harvest and/or survival processes across age classes. We avoided consideration of age-specific harvest rates by modeling only the female component of the population. By doing so, the effects of trophy hunting of larger bulls may be avoided.

Specific assumptions of the age-at-harvest analyses included the following: (1) The fate of every animal was independent of all other animals. (2) The fates of the animals were identically distributed. (3) Survival process modeled over time and across age classes was correctly formulated. (4) Harvest process modeled over time and across age classes was correctly formulated. (5) The auxiliary study was modeled correctly. (6) Harvest reporting rates were estimated unbiasedly. Assumptions 1 and 2 were necessary for modeling the data as multinomial and have little effect on point estimates but may affect variance estimates if violated. Nonindependence will cause the likelihood model to underestimate the variances because the effective sample size is smaller than perceived. On the other hand, individual heterogeneity in harvest or survival probabilities will result in the likelihood model overestimating the true variance (Feller 1968:231). Investigators have some control over Assumptions 3–6. In lieu of perfect information, post hoc analyses using goodness-of-fit statistics were used in model selection. For this reason, various approaches to model selection will be discussed below.

Reporting Rate Likelihood.—The harvest counts reported in Table 1 resulted from less than 100% hunter compliance with the mandatory registration of the elk harvest in GMU 4 of Idaho. To account for the less than perfect registration, telephone surveys, lock checks, or field checks can be used to estimate the harvest reporting rate. In this study, telephone surveys were used to estimate the annual reporting rate. The annual reporting rate was modeled as a binomial process, as follows:

$$L(R_i \mid a_i, b_i) = \binom{a_i}{b_i} R_i^{b_i}(1-R_i)^{a_i-b_i} \; ,$$

where a_i = number of successful hunters that were interviewed in the ith year ($i = 1,\ldots Y$), and b_i = number of hunters who claimed success that also had a report card on file for their kill in year i ($i = 1,\ldots Y$). The joint likelihood for the series of annual hunter compliance surveys can be expressed as

$$L_{\text{Reporting}} = \prod_{i=1}^{Y} L\left(R_i \middle| a_i, b_i\right). \quad (5)$$

An R × C chi-square contingency table test was used to test for homogeneity of the reporting rates across years and assist in the model selection process. A likelihood analogous to Equation (5) also could be used to analyze locker check or field check data for estimating compliance rates with mandatory reporting requirements.

Auxiliary Likelihood.—Because age-at-harvest data are insufficient to estimate the necessary demographic parameters required in population reconstruction, auxiliary field investigations are needed to provide the missing information. For Model *MpS*, there is 1 more model parameter than there are minimum sufficient statistics. As such, auxiliary field studies need to provide information to estimate at least 1 model parameter from the list:

$$\{N_{11}, N_{12}, ..., N_{1A}, N_{21}, N_{31}, ..., N_{Y1}, N_{1.}, N_{2.}, ..., N_{Y.}, p, S\}.$$

In other words, the investigator must supply independent field information to estimate the abundance of any cohort in year 1 (i.e., N_{1j}), recruitment in any year (i.e., N_{i1}), total abundance (i.e., $N_{i.}$) in any year, harvest rate (p) or annual survival rate (S) for estimation of the remaining parameters under model *MpS* to be feasible. A variety of techniques (Seber 1982) could be used to estimate the abundance of a specific cohort in a specific year or the total abundance (e.g., $N_{i.} = N_{i1} + N_{i2} + ... + N_{iA}$) for a specific year. Alternatively, tagging studies using release–recapture methods (Cormack 1964, Lebreton et al. 1992) or radiotelemetry methods (White and Garrott 1990) could be used to estimate survival (S) or harvest (p) probabilities. For the example of the elk herd in northern Idaho, radiotelemetry was used to estimate survival and annual harvest rates. The auxiliary study must be designed such that the sampling process can be described by a probabilistic model (i.e., likelihood) that is a function of the unknown demographic parameters of interest. Although a minimum of 1 parameter must be estimable from the auxiliary studies to use Model *MpS*, auxiliary studies could be used to provide information on 2 or more parameters with the expectation of improving the accuracy and precision of the reconstruction.

For Model MpS_A, information on 1 of the model parameters from the list:

$$\{N_{11}, N_{12}, ..., N_{1A}, N_{21}, N_{31}, ..., N_{Y1}, N_{1.}, N_{2.}, ..., N_{Y.}, S_1, S_2, ..., S_{A-1}, p\}$$

needs to be estimated from an auxiliary field study before the age-at-harvest data can be used in population reconstruction. For Model MP_YS, the auxiliary information requirements are greater. To perform population reconstruction using Model MP_YS, 2 parameters must be estimable from auxiliary studies. These 2 parameters must be chosen from among 2 of the different sets of parameters listed below:

$$\begin{array}{l}\{N_{11}, N_{12}, ..., N_{1A}, p_1, N_{1.}\}\\ \{N_{21}, p_2, N_{2.}\}\\ \vdots\\ \{N_{Y1}, p_Y, N_{Y.}\}\\ \{S\}\end{array}$$

For Model MP_YS_A, the auxiliary data requirements are similar to that of Model MP_YS. Two parameters must be estimable from the auxiliary field studies chosen from among 2 of the different sets of parameters listed below:

$$\begin{array}{l}\{N_{11}, N_{12}, ..., N_{1A}, p_1, N_{1.}\}\\ \{N_{21}, p_2, N_{2.}\}\\ \vdots\\ \{N_{Y1}, p_Y, N_{Y.}\}\\ \{S_1, S_2, ..., S_{A-1}\}\end{array}$$

As a general rule, as the population-reconstruction models become more complex, the amount of auxiliary information needed to permit population estimation increases. For each additional model parameter beyond that of Model *MpS*, auxiliary data will be required to independently estimate those additional parameters. For more complex reconstruction models, the field requirement to secure the necessary auxiliary data would likely exceed available resources. For this reason, only some of the simpler models for age-at-harvest analysis are discussed here.

Radiocollared elk with known fates each year were used to estimate survival and harvest probabilities from an auxiliary likelihood model in the Idaho elk example. Elk with collar failures were not included in the auxiliary data in the year of collar failure (i.e., right-censored). Because the elk were not aged at the time of collaring, age-specific survival rates could not be estimated. An auxiliary likelihood with year-specific harvest rates and constant survival using the radiotelemetry data (Table 3) can be written as

$$L(p_i, S \mid \underset{\sim}{n}_i, \underset{\sim}{u}_i, \underset{\sim}{v}_i) = \prod_{i=1}^{6} \binom{n_i}{u_i, v_i} p_i^{u_i} \left[(1-p_i)(1-S)\right]^{v_i} \left[(1-p_i)S\right]^{n_i - u_i - v_i}, \qquad (6)$$

where u_i = number of collared animals that are harvested in year i ($i = 1, ..., 6$), v_i = number of collared animals that die from causes other than hunting in year i ($i = 1, \ldots, 6$), and n_i = number of collared animals at risk in year i ($i = 1, \ldots, 6$). The joint likelihood model used in the reconstruction analysis is then a product of Equations 4, 5, and 6. For Model *MpS*, the annual harvest parameters p_i(i = 1, ..., 6) were replaced by a common p in Equation 6.

Parameter Estimation

Because of the complexity of the joint likelihood models, we used iterative numerical methods to calculate the maximum likelihood estimates. We used the Newton-Raphson method (Seber 1982:16–17) to obtain the estimates and standard errors using Program FLETCH (Fletcher 1970), which numerically rather than analytically calculates the first and second mixed partial derivatives. A copy of the FLETCH program written in Fortran or C can be obtained from the authors.

The program directly estimated the survival, harvest, and reporting parameters along with age-specific abundance for each cohort in year 1 (i.e., N_{11}, N_{12}, ..., N_{1A}) and the recruitment into the first age class in each subsequent year (i.e., N_{21}, N_{31}, ..., N_{Y1}). Abundance for the other age classes and total annual abundance for each year were estimated secondarily. By the invariance property of maximum likelihood estimation, the annual abundance estimates from the secondary analyses were maximum likelihood estimates as well.

The total abundance estimate for any year is the sum of the abundance estimates for the individual age classes in that year,

$$\hat{N}_{i.} = \hat{N}_{i1} + \hat{N}_{i2} + \hat{N}_{i3} + \ldots + \hat{N}_{iA} = \sum_{j=1}^{A} \hat{N}_{ij} .$$

For year 1, the total abundance is the sum of individual estimates by age class. For years 2 through Y, one must estimate the abundance of each age class from the other abundance estimates and the survival and reporting probabilities. For any age class in any year (i = 2, ..., Y), the abundance can be estimated as

$$\hat{N}_{ij} = \left(\hat{N}_{i-1,j-1} - \frac{x_{i-1,j-1}}{\hat{R}_{i-1}} \right) \hat{S}_{j-1} .$$

For the annual abundance estimates, 95% confidence intervals were calculated using profile likelihood interval estimation (Kalbfleisch and Sprott 1970). The profile likelihood confidence interval estimates generally are considered superior to interval estimates based on the assumption that MLE are normally distributed. Instead, the profile confidence intervals are based on the asymptotic properties of the likelihood ratio test (LRT), which approaches its nominal χ^2-distribution more rapidly as sample sizes increase. The LRT (Hogg and Craig 1995) is based on the difference in the log-likelihood values of Equation 1 under the alternative sets of parameter values being considered.

Model Selection and Goodness-of-Fit

We used several approaches to determine the best model for population reconstruction. One can use a χ^2 goodness-of-fit test based on the observed age-at-harvest data (x_{ij}) and their expected values under the fitted likelihood model. Under the null hypothesis of goodness-of-fit, the ratio

$$\frac{\chi^2_{\mathrm{df}}}{\mathrm{df}}$$

should have an expected value of 1 where the degrees of freedom (df) equal $A \times Y -$ (number of estimated parameters). Values greater than 1 may suggest overdispersion of the data and lack-of-model fit. In generalized linear models (GLM), this ratio is called the scale parameter (McCullagh and Nelder 1983:80–84, Aitkin et al. 1990:214).

Pollock et al. (1984) found overdispersal when fitting multinomial capture–recapture models to data from a lobster (*Homarus americanus*) population. To compensate for the lack-of-fit, they increased the maximum likelihood estimates of variance by a scale factor similar to that used in generalized linear models. We used the same approach, adjusting confidence intervals and standard errors calculated for the elk study by the factor

$$\sqrt{\frac{\chi^2_{df}}{df}}$$

When the alternative reconstruction models are nested, one also may use an LRT to compare 1 model to another (Hogg and Craig 1995). Another method for comparing models is Akaike's Information Criterion (AIC; Burnham and Anderson 1998). The AIC uses a function of the log-likelihood values (Equation 1) to rank and select among alternative model specifications. In addition to these tools, one should always use knowledge of the population and good judgment when determining which model is appropriate. For example, if one knows that

Table 4. Estimates and standard errors (SE) for the parameters that were directly estimated from Model *MpS* for the cow elk in GMU 4, northern Idaho, USA.

Parameter	Estimate	SE
N_{11}	466.18	149.75
N_{12}	424.10	137.01
N_{13}	282.57	94.16
N_{14}	225.19	76.74
N_{15}	156.34	55.75
N_{16}	152.51	54.58
N_{17}	102.78	39.29
N_{18}	64.53	27.30
N_{19}	33.92	17.28
N_{110}	60.70	26.08
N_{111}	41.58	19.85
N_{112}	41.58	19.85
N_{113}	24.27	14.44
N_{114}	14.52	11.81
N_{115}	5.70	7.97
N_{116}	9.78	14.07
N_{117}	37.95	39.12
N_{21}	448.30	146.74
N_{31}	463.01	154.61
N_{41}	499.50	172.13
N_{51}	360.17	134.61
N_{61}	417.12	186.05
p	0.0956	0.0313
S	0.9036	0.0308

hunting regulations have changed over time, the constant harvest models should be suspect.

RESULTS

Idaho Elk Analysis

The radiocollared elk provided auxiliary information used to estimate survival and harvest probabilities (Table 2). Because the elk were not aged at the time of collaring, the population reconstruction analyses were restricted to Models *MpS* and *Mp$_Y$S*. A chi-square test indicated that the annual reporting rates (Table 3) for successful elk hunters differed significantly between years ($\chi^2_5 = 328.7$, $P < 0.001$). For this reason, all modeling was based on the use of year-specific reporting rates.

Estimates Under Model *MpS*

We present in Table 4 the maximum likelihood estimates for the parameters of Model *Mp$_Y$S*. The cow elk abundance estimates by age-class and year are given in Table 5. Recruitment of 1-year-

Table 5. Abundance estimates by year and age class for cow elk in GMU 4 in northern Idaho, based on Model *MpS*.

	Age class																	Total	
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	abundance	95% CI
1988	466.2	424.1	282.6	225.2	156.3	152.5	102.8	64.5	33.9	60.7	41.6	41.6	24.3	14.5	5.70	9.8	38.0	2,144.2	1,835.0–2,352.7
1989	448.3	386.4	323.4	230.4	190.2	129.6	124.5	82.9	50.0	25.7	49.9	30.9	32.6	18.6	11.5	3.5	7.2	2,145.6	2,063.0–2,209.1
1990	463.0	362.9	286.6	268.8	176.9	157.8	99.9	104.7	59.3	40.5	20.1	37.2	27.9	24.7	13.7	10.4	3.2	2,157.6	2,012.8–2,226.8
1991	499.5	386.8	289.9	244.5	225.7	146.3	129.9	84.0	88.3	50.0	32.1	18.1	30.9	22.5	19.7	12.4	7.6	2,288.1	2,102.0–2,383.5
1992	360.2	403.7	310.4	247.3	200.2	185.6	120.0	111.3	68.6	72.4	45.1	29.0	16.4	28.0	20.4	17.8	11.2	2,247.4	2,049.0–2,369.1
1993	417.1	301.1	335.9	257.9	207.2	169.1	150.6	103.9	88.8	57.4	57.3	39.0	24.4	13.9	23.5	17.5	15.2	2,279.7	1,984.4–2,431.0

Table 6. Estimates and standard errors (SE) for the parameters that were directly estimated from Model $Mp_{\gamma}S$ for cow elk in GMU 4, northern Idaho, USA, 1988–1993.

Parameter	Estimate	SE
N_{11}	534.06	152.13
N_{12}	485.86	139.10
N_{13}	323.74	95.24
N_{14}	258.02	77.43
N_{15}	179.15	55.98
N_{16}	174.76	54.79
N_{17}	117.80	39.19
N_{18}	73.99	27.00
N_{19}	38.93	16.89
N_{110}	69.60	25.76
N_{111}	47.70	19.48
N_{112}	47.70	19.48
N_{113}	29.02	14.61
N_{114}	16.84	11.37
N_{115}	6.38	7.48
N_{116}	9.37	10.98
N_{117}	38.53	32.52
N_{21}	528.95	160.89
N_{31}	583.88	195.45
N_{41}	606.65	217.18
N_{51}	418.20	165.43
N_{61}	343.22	157.99
N_{88}	0.0984	0.0286
N_{89}	0.1158	0.0349
N_{90}	0.0674	0.0223
N_{91}	0.0673	0.0237
N_{92}	0.0654	0.0243
N_{93}	0.1331	0.0527
S	0.9037	0.0298

old cow elk into this population ranged from 360.17 ($\widehat{SE}$ = 134.6) individuals in 1992 to a high of 499.50 ($\widehat{SE}$ = 172.1) in 1991 (Table 4). The recruitment of 1-year-old elk into this population constitutes between 16.0% and 21.8% of the total abundance of cow elk each year. The chi-square goodness-of-fit statistic for this model (χ^2_{78} = 152.6771, $P < 0.001$) is highly significant. Consequently, reported standard errors and confidence intervals from this model were inflated by a scale factor of $\sqrt{152.7/78}$ = 1.3991 to account for overdispersion.

Estimates Under Model $Mp_{\gamma}S$

We report in Table 6 the demographic parameters and associated standard errors (SE) estimated with Model $Mp_{\gamma}S$. We present in Table 7 the estimates of abundance by year and age class, along with total annual abundance, reconstruct-

Table 7. Abundance estimates by year and age class for cow elk in GMU 4 in northern Idaho, based on Model $Mp_{\gamma}S$.

	Age class																	Total	
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	abundance	95% CI
1988	534.1	485.9	323.7	258.0	179.2	174.8	117.8	74.0	38.9	69.6	47.7	47.7	29.0	16.8	6.4	9.4	38.5	2,451.4	2,235.4–2,669.8
1989	529.0	446.2	376.6	266.5	219.3	149.8	144.1	96.1	58.2	30.0	57.7	36.2	37.9	22.8	13.5	4.0	6.7	2,494.4	2,416.0–2,538.3
1990	583.9	431.9	335.0	314.8	206.8	182.8	116.6	121.7	69.7	47.5	23.7	43.6	32.7	29.1	17.2	12.2	3.6	2,572.6	2,434.6–2,666.9
1991	606.7	496.0	352.4	288.3	267.3	173.3	152.6	99.0	103.6	59.4	38.4	21.4	36.7	26.8	23.6	15.5	9.2	2,770.1	2,588.4–2,877.5
1992	418.2	501.6	410.0	304.1	240.2	223.6	144.7	131.9	82.3	86.5	53.7	34.7	19.3	33.2	24.2	21.3	14.0	2,743.6	2,527.6–2,829.6
1993	343.2	353.5	424.4	348.0	258.6	205.3	184.9	126.2	107.5	69.9	70.0	46.7	29.5	16.6	28.2	21.0	18.4	2,651.9	2,311.1–2,791.6

ed from the maximum likelihood model. Harvest probabilities varied annually from 0.0654 ($\widehat{SE}$ = 0.0243) to 0.1331 ($\widehat{SE}$ = 0.0464). Total annual abundance was estimated to be lowest in 1988 with 2,451.4 (CI [2,235.4 ≤ N ≤ 2,669.8] = 0.95) cow elk and with a maximum abundance of 2,770.1 (CI [2,588.4 ≤ N ≤ 2,877.5] = 0.95) in 1991. The population estimates under Model Mp_YS are higher than those calculated under Model MpS because the common harvest rate estimated under Model MpS is greater than 4 of the 6 annual harvest rates estimated under Model Mp_YS. Overestimation of the harvest probabilities will result in negatively biased abundance estimates when the harvest counts are converted to absolute abundance by the factor $1/p$. The chi-square goodness-of-fit statistic decreased appreciably under Model Mp_YS but remained significant (χ^2_{73} = 94.2, P = 0.048). Consequently, confidence intervals and standard errors were inflated by the factor $\sqrt{94.2/73}$ = 1.1358 to compensate for overdispersion.

Comparison and Evaluation of Models

Inspection of Tables 1 and 5 illustrates that estimates of the age structure of the elk population differ depending on whether the raw harvest counts or the abundance estimates by cohort are used in the estimates of proportions. The raw harvest counts underestimate the proportion of age class 1 animals in the population and overestimate the proportion of older animals. For example, the harvest numbers would estimate that 1 year olds compose 16.7% of the population in 1988; the reconstruction model estimates 21.7%. The population reconstruction models help correct the bias that would result from the direct use of the age-at-harvest data alone in calculating the population age-structure.

For the Idaho elk data, an LRT was performed comparing Models MpS versus Mp_YS. The LRT was highly significant (χ^2_5 = 30.4186, P < 0.001), suggesting that the annual harvest rates may have indeed varied between years. During 1988–1990, the elk hunting season included a 15-day cow elk season that opened around 10 October. During 1991–1993, the cow elk hunting season was reduced to 10 days, opening on 15 October. The combination of the goodness-of-fit statistic and the LRT together with historic information suggest that Model Mp_YS was the most appropriate of the available models for this population reconstruction.

In 1990 and again in 1991, aerial surveys of the elk herd in GMU 4 were conducted (Kuck and Nelson 1991) using the sightability survey model of Unsworth et al. (1994). The sightability model estimated cow abundance at 2,873 (CI [2167 ≤ N ≤ 3,579] = 0.95) in 1990 and 2,217 (CI [1707 ≤ N ≤ 2,727] = 0.95) in 1991. Hence, the age-at-harvest model estimates compare reasonably well with the independent estimates of cow elk abundance.

DISCUSSION

The statistical models we present provide a flexible framework for analyzing age-at-harvest data and for model selection. Existing theory to analyze tagging studies (e.g., Seber 1982) can be readily used to model auxiliary data in conjunction with the age-at-harvest models presented. By applying maximum likelihood theory to the problem of analyzing age-at-harvest data, maximum information can be extracted from the available data and the limitations of the information objectively assessed. Not only can population trends be tracked, but estimates of annual recruitment as well as harvest and survival rates can be estimated along with their associated variances. This statistical approach to analyzing age-at-harvest data also provides investigators with guidance on what types and how much auxiliary information need to be collected to supplement the age-at-harvest data and reconstruct population trends. This approach also allows evaluation of alternative models and their goodness-of-fit. Most existing methods of analyzing age-at-harvest data (e.g., Downing 1980, Fryxell et al. 1988) rely on "arbitrarily selected lifetime recovery rates" or an "educated guess" (Roseberry and Woolf 1991:22–23), which preclude error estimation, formal model selection, or absolute abundance estimation. We suggest that biologists work closely with biometricians in developing the population models and performing the data analyses. These maximum likelihood methods also can provide a valuable cross-validation of survey results on large-game populations. Alternatively, these population reconstruction methods can be used to supplement information in years where large-scale and typically costly wildlife surveys are not conducted.

More effort by the statistical community needs to be focused on providing wildlife managers with the essential information needed to assess population trends and harvest strategies. The statistical methods need to be based on the types of harvest and demographic data most often collected by wildlife agencies. These data include estimates of harvest, and the age and sex composition of the population being monitored. Wildlife tagging studies need to be coordinated with the broader demographic needs of population assessment. Population reconstruction models provide a useful context for determining the relevance and contributions of such tagging studies to the overall management of a wildlife population. With the increasing demands by society to justify game harvest policies, all available information and the best analytical approaches should be used to understand the status and trends of wildlife populations.

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