A BAYESIAN APPROACH TO MOOSE POPULATION ASSESSMENT AND HARVEST DECISIONS

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ABSTRACT: Assessments of ungulate populations need to be expressed in probabilistic terms to convey uncertainty about key parameters and the consequences or "risks" of alternative policies for harvest. The use of Bayesian estimation and risk assessment is described and applied to a declining moose (*Alces alces*) population in north-eastern British Columbia. A simple balance model was used to calculate posterior distributions of probability for population size of adults at the start of the assessment period and recruitment rate of calves. Model inputs included two mid-winter surveys of absolute abundance, a herd-composition survey and a harvest/effort index for adult bull moose. Calf recruitment was positively density dependent at moderate to high densities of moose. Probability distributions were estimated for moose population size in 1988 (95% CI's: 7,655 - 10,550) and 1995 (95% CI's: 3,805 - 5,980). Risk functions were used to determine the probability of obtaining various adult sex ratios after 3 years of additional bull harvest. Some of the limitations of the moose assessment were that not all of the model parameters were treated as uncertain, that deterministic assumptions about population dynamics were used, and that the behaviour of this predator-ungulate system at low densities of moose was poorly understood. This can bias the degree of certainty in estimates of parameters and risk associated with various harvest policies.

ALCES VOL. 34(1): 47-58 (1998)

Key words: *Alces*, Bayesian estimation, key parameters, modeling, population assessment, risk functions

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Wildlife managers routinely use population models to assess the dynamics of hunted populations, and to evaluate the consequences or "risks" of harvest policies (Pojar 1981). A key limitation of most models for ungulates, however, is that they neither explicitly incorporate uncertainty into the population assessments, nor do they quantify the risks associated with different harvest policies. If the parameter estimates are uncertain, then prescriptions for harvest to achieve desired management objectives may either be too conservative or overly optimistic. If they are too conservative, additional opportunities for harvesting will not be realized, whereas if they are overly optimistic, harvests will not be sustainable. Several recent failures in renewable resource management, such as the collapse of the Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador, are testimony to the danger of not explicitly incorporating uncertainty and risk into population assessments (Hilborn *et al.* 1992, Hutchings and Myers 1994).

Bayesian estimation has been recognized as an appropriate statistical method for producing probability distributions for population parameters, including population abundance (Hilborn and Walters 1992). By incorporating probability distributions, rather than point estimates of parameters, the probability of achieving various harvest management objectives can be quantified. While Bayesian approaches have received considerable attention in fisheries and marine mammal management (e.g. Hoenig *et al.* 1994, McAllister *et al.* 1994, Walters and

Ludwig 1994, Raftery *et al.* 1995), they have received only limited attention in managing ungulate harvests (Pascual and Hilborn 1995). In this paper, I provide a case study for using Bayesian estimation to assess the uncertainty of several parameters for a moose population in north-eastern British Columbia, based on relatively simple procedures that can be implemented on a Microsoft Excel® spreadsheet (Walters and Ludwig 1994). I also develop risk functions which incorporate the uncertainty of key parameters to assess the impact of future bull harvest levels on mid-winter bull/cow ratios.

STUDY AREA

I studied a declining moose population located within Wildlife Management Unit (WMU) 7-42 of north-eastern British Columbia (ranging from 57°14'N, 122°42'W to 57°45'N, 124°47'W). This 6,057-km^2 area comprised the southern portion of the Muskwa project area (17,900 km^2) and has been the site of ongoing studies on wolf-ungulate interactions (Elliott 1989). Although many of the moose wintering within WMU 7-42 are migratory, most of their annual movements occur within the WMU, hence population closure was assumed.

Objectives for harvest management include maintaining the adult sex ratio at $\geq$30 bulls/100 cows post-season (J. P. Elliott, B.C. Environment, Fort St. John, *pers. comm.*). To meet the objective for this adult sex ratio, hunter harvests have been restricted to bull moose during an autumn hunting season (Aug. 15 to Sept. 30 and Oct. 16 to 31). In 1994, the "any bull" season in WMU 7-42 was replaced with a "spike-fork" (moose with a spike or fork antler) and "tripalm" (moose with 3 or more tines on at least one brow palm) regulation in an attempt to further reduce the bull harvest, and improve the bull/cow ratio. Regulations prohibited the harvest of antlerless moose.

Predation by wolves (*Canis lupus*) appears to be the primary factor regulating this moose population, although grizzly bears (*Ursus arctos*) and black bears (*U. americanus*) also may be important predators (Elliott 1989). Predation on moose is thought to be characterized by a density-dependent (regulatory) phase at low moose densities and an inverse, density-dependent (nonregulatory) phase at moderate to high moose densities (the predation model of Messier 1994:479). Other ungulate prey that inhabit this area included caribou (*Rangifer tarandus*), mountain sheep (*Ovis dalli stonei*), mountain goat (*Oreamnos americanus*), bison (*Bison bison*), elk (*Cervus elaphus*), and deer (*Odocoileus hemionus* and *O. virginianus*).

The biogeoclimatic zones of the area were described by Krajina (1965) and the physiography by Holland (1976). The climate is typical of the subarctic with long, cold winters and a short growing season. The 4,104 km^2 survey area for moose occupied the lower two-thirds of WMU 7-42, and spanned the Muskwa Ranges of the northern Rocky Mountains, the Muskwa Foothills and the adjacent lowlands of the Alberta Plateau.

METHODS

Hunter Harvest

Harvest statistics, including total harvest, sex-age composition, and kill per unit effort (KPUE), have been estimated annually since 1976. These variables were derived from a harvest questionnaire mailed to a random sample of hunters, with a follow-up second questionnaire sent to non-respondents. KPUE was calculated as the number of adult bulls killed by resident hunters/100 hunter days. I assumed that KPUE was a nonlinear function of bull moose abundance (Fryxell *et al.* 1988), and could be described by a power function

(Cooke and Beddington 1985):

$$KPUE_t = q_1 B_t^{q_2},$$

where $KPUE_t$ is the annual bull kill per unit effort in year t, B_t is the pre-season estimate of adult bulls, q_1 is a scaling parameter and q_2 is the power parameter. Note that only when $q_2 = 1$ is KPUE a linear index of absolute abundance.

Moose Population Surveys

Surveys of Absolute Abundance. - Surveys of absolute abundance were conducted during February-March in 1989 and 1993 based on stratified random sampling designed for aerial moose surveys (Gasaway *et al.* 1986). A sightability correction factor (SCF) for undercounting bias was conservatively assumed to be 1.05 (Boertje *et al.* 1996). This assumption was based on the extensive use by moose of subalpine habitats where visibility was excellent, the high search effort (~2.3 min/km^2) employed, and use of helicopters (Bell 206) to count and classify moose. The rate of population change between the two surveys, and its associated 95% confidence interval, was calculated following the procedure of Gasaway *et al.* (1986:66-70). The survey estimates were extrapolated to all of WMU 7-42 by assuming a similar density and composition of moose outside the survey area.

Survey of Herd Composition. - An aerial survey of herd composition was conducted during February 1994 to classify moose. Transects were uniformly spaced straight lines through WMU 7-42, modified where necessary for feasibility in rough topography. This pattern was assumed to be random relative to the animals and thus produced unbiased ratios of bulls/100 cows and calves/100 cows.

Bayesian Estimation of Key Parameters

Procedures for Bayesian estimation were used to calculate posterior probability distributions for two key parameters (Walters and Ludwig 1994). The first key parameter was the number of adult moose in mid-August 1988 (N_{88}), or just before the hunting season. The second parameter was the intercept (R_0) of the recruitment slope (R_1) for calf recruitment (R_t, calves/adult), which was assumed to change linearly with the abundance of adult moose, i.e. $R_t = R_0 + R_1 N_t$. N_{88} was considered a key parameter as 1988 was the start of the assessment period, and the initial number of animals is critical in balance models that fit population parameters using an "observation error" estimation procedure (Walters 1986:136, Eberhardt 1987, Hatter and Janz 1994). R_0 was also considered a key parameter since it affected calf recruitment, an important parameter in determining population growth rate (Bergerud 1992).

Bayes' Theorem was used to calculate the probability distributions of the key parameters. The theorem defines the link between the likelihood of the data given the parameter values and the probability to place on the parameters (Walters and Ludwig 1994):

The "probability of the parameter values (N_{88}, R_0) given these data" is called the

$$\left(\text{Probability of } N_{88}, R_0 \text{ given the data}\right) = \frac{\left(\text{Probability of the data given } N_{88}, R_0\right) \times \left(\text{Prior probability of } N_{88}, R_0\right)}{\text{Total probability of the data}}.$$

Bayes posterior probability for those values. Here, data refers to other information used in the population assessment including harvest data, survey data and known population parameters. The "probability of these data given the parameter values" is called the likelihood function. The "total probability of the data" is the sum of the numerator over all parameter values. The "prior probability of the parameter values" represents a non-scientific (i.e., based on judgement and past experience rather than the data) degree of credibility assigned to the parameter values.

Bayesian estimation of the key parameters involved four steps: (1) choice of a prior probability distribution for N_{88} and R_0; (2) formulation of the likelihood functions for KPUE and the moose survey parameters; (3) development of a moose population model to calculate the likelihood function's; and (4) calculation of the Bayes probability distribution for each key parameter. Because the posterior probability does not depend on any constant multiplier terms that may appear in the prior or the likelihood function, the entire likelihood function was not required for the third step. Walters and Ludwig (1994) referred to the likelihood multiplied by the prior and stripped of such constants as the "posterior kernel."

Selection of the Prior Probability Distribution. - A uniform distribution for the prior probability was used. This assumed that that all parameter values should be equally weighted. With a uniform prior, specified over a "reasonable" range of parameter values, the Bayes posterior probability calculation reduces to the following simple formula:

$$\left(\begin{array}{l}\text{Bayes posterior}\\ \text{probability for}\\ \text{parameter values}\end{array}\right) = \frac{\text{(Likelihood of the parameter values)}}{\left(\begin{array}{l}\text{Sum of the likelihoods over all parameter values}\\ \text{admitted}\end{array}\right)}$$

Formulation of the Likelihood Functions. - The equation used to calculate the likelihood credibility kernel for KPUE (L_1) was:

$$L_1 = \left[\frac{\sum(Z_t - z')^2}{n-1}\right]^{-(n-1)/2}$$

where

$$z' = \frac{\sum Z_t}{n},$$

and

$$Z_t = \ln(KPUE_t) - q_2 \ln(B_t),$$

(Walters and Ludwig 1994:718-719). Here, n is the number of years of KPUE. This procedure allows for the estimation of q_1 as a "nuisance parameter" without its direct solution. The power parameter q_2 also was treated as a nuisance parameter and was estimated by nonlinear estimation with Microsoft Excel® Solver, as the conditional maximum likelihood value for each combination of N_{88} and R_0 (C. J. Walters, Univ. of BC, *pers. comm.*). Potential values for q_2 ranged between 0.00 - 1.00. Thus, the model considered cases where harvesting was either random ($q_2 = 1$) or nonrandom ($q_2 < 1$). In nonrandom hunting, hunters would be expected to concentrate their effort in areas where moose were most abundant.

The equation used to calculate the likelihood credibility kernel for the survey-based population estimates (L_2) was:

$$L_2 = \exp\left[-\sum \frac{(Y_i - U_i)^2}{2V_i}\right]$$

(Walters and Ludwig 1994:716), where Y_i is the mid-winter estimate of moose of a given sex and age class in the model ($i = 1$ for adult bulls, 2 for adult cows, and 3 for calves), and U_i and V_i are the extrapolated population mean and variance from the survey estimate. The survey variance underestimated the population variance because neither the sightability of moose, nor the variance associated with extrapolating U_i to WMU 7-42 was incorporated. Because of this, a more reasonable estimate of the population variance was obtained by doubling the survey coefficient of variation (CV) (C. J. Walters, *pers. comm.*), i.e.

$$V_i = (2 \cdot CV_i \cdot U_i)^2$$

The multinomial distribution was used to calculate the likelihood credibility kernel for the 1994 herd composition survey (L_3):

$$L_3 = \prod_{i=1}^{3} \left[\frac{Y_i}{Y} \right]^{n_i}$$

(Hilborn and Walters 1992:220-221), where Y is the mid-winter model estimate of moose, and n_i is the number of moose of a sex and age class$_i$ counted during the survey. The total likelihood required to calculate the Bayes posterior probability distribution was the product of the individual likelihood's, i.e. the likelihood for all survey and KPUE data $(L_{1\text{-}3}) = L_1 L_2 L_3$.

Moose Population Model. - A simple balance model was used to calculate the likelihood kernel's. The population was partitioned into adult bulls (B), adult cows (C), and calves (Ca). The model consisted of the following interdependent equations, starting with the pre-season population in 1988:

$$B_{t+1} = [B_t - H(B)_t]Sa + 0.5Ca_t Sj,$$

$$C_{t+1} = C_t Sa + 0.5Ca_t Sj,$$

$$Ca_{t+1} = R_0 N_{t+1} - R_1 N_{t+1}^2$$

where $H(B)_t$ were the adult bull harvests, Sa was the adult (≥1-year-old) nonhunting survival rate, and Sj was the survival rate of calves from autumn to the following hunting season. R_1 was estimated as a nuisance parameter, using the same procedure for q_2. I assumed that 50% of the nonhunting mortality occurred between the end of the hunting season and mid-winter. If either the number of bulls or cows were eliminated during the population projection then calf recruitment was zero. Sa was assumed to be 0.85 for adult moose, which was the value estimated for an adjacent moose population displaying a similar rate of decline (Hatter and Bergerud 1991). Sj was likely less than Sa (Larsen *et al.* 1989) and was assumed to be 0.80. An equal calf sex ratio was also assumed (Boer 1992). Harvest totals were revised upwards by 20% to incorporate additional losses due to wounding (Fryxell *et al.* 1988).

The model was used to reconstruct population trends from 1988-89 to 1994-95. I used the 1989 mid-winter survey, the assumed winter mortality, and the 1988 harvest to back-calculate an initial adult sex ratio for N_{88}. Because the model was parameterized for moderate to high moose densities (>0.65 moose/km²), where the calf recruitment rate declined when moose density was lowered, only short term population trajectories were projected within this density range. I did not attempt to model long term maximum sustained yields, because the calf recruitment rate would be expected to increase once moose density was sufficiently low to reduce the wolf predation rate (Messier 1994, 1996).

Calculation of the Joint and Marginal Bayes Probability Distributions. - Following the recommendation of Walters and Ludwig (1994), both N_{88} and R_0 were represented at >40 discrete levels between a minimum and maximum value on a parameter grid. Potential values for N_{88} were determined through trial and error, by iterating over a range of values that produced likelihood's that were essentially zero for the minimum and maximum values. I considered a limited range of negative values for minimum R_0 in the parameter grid because a linear approximation of recruitment rate with moose abundance, at moderate to high densities, could have a negative intercept (C. J. Walters, *pers. comm.*). The resulting likelihood value for each combination of parameters was stored in a "joint likelihood table". After all the likelihood values were calculated, the table was scaled as each individual likelihood divided by the sum of all likelihood's to calculate the "joint Bayes posterior probability table." The maximum likelihood or "maximum *a posteriori*" estimate for the key parameters was the parameter combination that had the highest posterior probability value. The marginal posterior probability for each key parameter was the probability of each discrete level of one parameter summed over all other levels admitted for the other parameter. For example, the marginal distribution with respect to R_0 was:

$$\left(\begin{array}{l}\text{Probability of } R_0 \\ \text{given the data and } N_{88}\end{array}\right) = \sum_{N_{88}}(\text{Probability of } [N_{88}, R_0] \text{ given the data}).$$

The 95% confidence or "credibility" intervals (CI's) were calculated by excluding values $\leq$2.5% and $\geq$97.5% of the cumulative marginal probability distribution (Hilborn and Walters 1992:224).

Estimating Probability Distributions for Population Abundance. - The grid of posterior probabilities for the key parameters was used to estimate the probability distribution for the pre-season number of moose in 1988 and 1995. This involved setting up a grid of discrete population ranges ("bins") for each year and then finding the total probability that the population size was within each of these ranges (Walters and Ludwig 1994:717-718). Thus, for each point in the (N_{88}, R_0) grid, I computed the model population size for 1988 and 1995. The posterior probability associated with the key parameters was then placed in the appropriate bin for each year. After completing all combinations of (N_{88}, R_0), each bin was summed to estimate the total probability that the population size occurred within the range represented by the bin.

Risk Function for Harvest Decision

Harvest management for moose limited by predation in Alaska, Yukon and northern B.C. has primarily been restricted to hunting bull moose, since "male-only" harvests do not affect the population growth rate in the mid- to long-term (Van Ballenberghe and Dart 1982). However, a concern or "risk" of "any bull" only harvests is that excessive skewing of bull/cow ratios may lead to impaired productivity (Crete *et al.* 1981, Crete 1987). A risk function was used to determine the probability of obtaining mid-winter bull/100 cow ratios ranging from $\geq$10/100 to $\geq$30/100, after 3 additional years of harvest (cf. Walters and Punt 1994). To calculate the risk function, the model was projected forward from 1995-96 to 1997-98 for each (N_{88}, R_0) combination on the parameter grid, and for each harvest level. Harvest levels ranged from 0 to 300 moose, in increments of 25. The 1998 mid-winter bull/cow ratio was stored in a "post-season bull/cow risk performance table". If the parameter combination failed to meet the mid-winter bull/cow objective, then the associated probability from the Bayes posterior probability table was stored in a "masked probability table." Finally, the entries in the masked probability table were summed and subtracted from 1 to calculate the probability that a given harvest level achieved a desired adult bull/cow ratio.

RESULTS

Survey Estimates of Moose and Hunter Harvest

Numbers of moose in the 4,104-km^2

survey area declined significantly ($t = 2.58$, 39 df, $P < 0.05$) from 5,538 ± 1108 (95% CI) in 1989 to 3,423 ± 1301 moose in 1993, for an annual finite rate of change (λ) of 0.89 (95% CI's: 0.80 - 0.98)(Table 1). During this period, adult bulls declined from 1,138 ± 414 to 519 ± 190, and adult cows declined from 3,351 ± 747 to 2,377 ± 942. The adult sex ratio dropped from 34 ± 14 bulls/100 cows to 22 ± 9 bulls/100 cows, and mid-winter calf ratios dropped from 31 ± 7 calves/100 cows to 22 ± 5 calves/100 cows. In 1994, 15 calves/100 cows were observed. The extrapolated survey estimates for WMU 7-42 (6,057 km^2) were 6,808 and 4,208 moose in 1989 and 1993 respectively.

During the "any bull" hunting seasons, moose harvests increased from 376 bulls in 1989 to 489 in 1991 and then declined to 370 in 1993 (Table 2). In 1994, the bull harvest was reduced to 229 under the selective bull harvest strategy. KPUE also declined during the 1989 to 1993 period when harvest regulations were constant (Table 2).

Estimates of Parameters

The maximum *a posteriori* estimates for the marginal distributions of the key

Table 1. Moose mid-winter estimates (N) from absolute abundance surveys for 1989 and 1993, and sample size (n) for herd composition survey for 1994 in WMU 7-42, north-eastern B.C.

	1989		1993		1994
	N	CV	*N*	CV	*n*
Adult Bull	1138	15.4	519	16.4	41
Adult Cow	3351	10.7	2377	19.0	191
Calf	1049	16.1	527	25.0	28
Total	5538	9.6	3423	18.2	260

Table 2. Annual hunter harvest including assumed 20% wounding loss, and kill per unit effort (KPUE) for adult bull moose in WMU 7-42, northern British Columbia.

	1988	1989	1990	1991	1992	1993	1994
Harvest	429	376	405	489	425	370	229
KPUE	7.00	6.55	6.34	5.74	5.29	5.16	n/a

parameters were N_{88} = 7,250 (95% CI's: 6,125 - 9,250) (Fig. 1) and R_0 = 0.02 (95% CI's: -0.30 - 0.30) (Fig. 2). R_1 ranged from -0.0001 to 0.00005, q_1 from 0.02 to 0.45, and q_2 from 0.34 to 0.78. The maximum *a posteriori* estimate for the joint probability distribution was N_{88} = 7,375 and R_0 = -0.06. For this parameter combination, the extrapolated survey results were similar to the model mid-winter estimates (1989: 7,713 moose, 35 bulls/100 cows and 30 calves/100 cows; 1993: 5,635 moose, 22 bulls/100 cows and 20 calves/100 cows; 1994: 18 bulls/100 cows and 16 calves/100 cows). Probability distributions for the pre-season number of

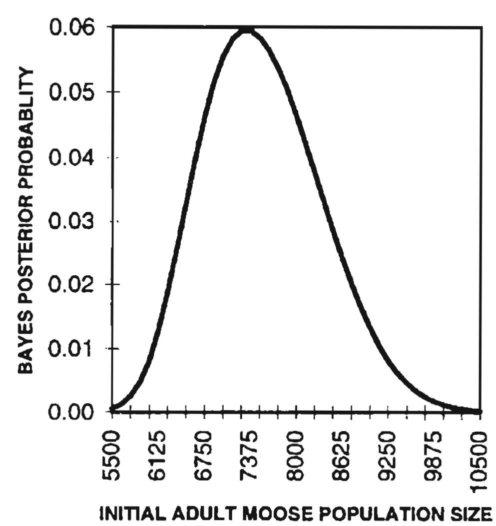

Fig. 1. Marginal Bayes posterior probability distribution for the 1988 pre-season number of adult moose (N_{88}) in WMU 7-42, based on KPUE and population surveys.

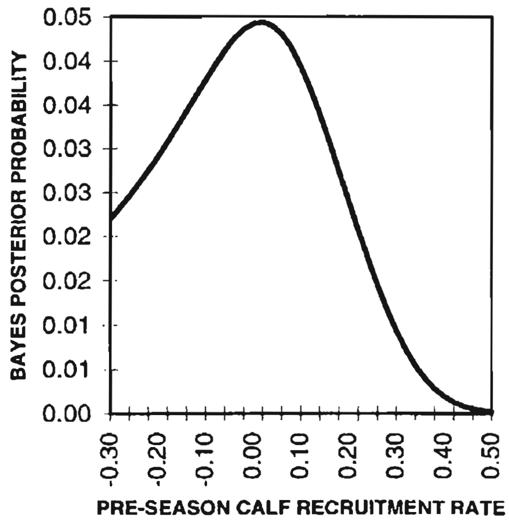

Fig. 2. Marginal Bayes posterior probability distribution for pre-season calf recruitment rate (R_0) in WMU 7-42, based on KPUE and population surveys.

moose in 1988 (median = 8,980; 95% CI's: 7,655 - 10,550) and 1995 (median = 4,590; 95% CI's: 3,805 - 5,980) showed almost no overlap (Fig. 3).

The KPUE parameters q_1 and q_2 were highly correlated (r = -0.94), as were the recruitment parameters R_0 and R_1 (r = 0.97). The "parameter confounding" and truncated distribution of R_0 implied that these data could be fit with a wide range of hypotheses about population size and recruitment. Dropping information on KPUE had little effect on the probability distribution for N_{88} (6,625; 95% CI's: 6,000 - 8,500). Conversely, dropping the survey information and using only KPUE data for the likelihood function resulted in a relatively flat probability distribution for this parameter. This indicated that KPUE, without survey data, had little capability for defining posterior probabilities.

Risk Assessment

The population model was used to estimate annual harvest levels for bulls that would meet various adult sex ratio objectives for mid-winter 1998 (Fig. 4). The risk function indicated there was only a 53% chance of obtaining ≥30 bulls/100 if har-

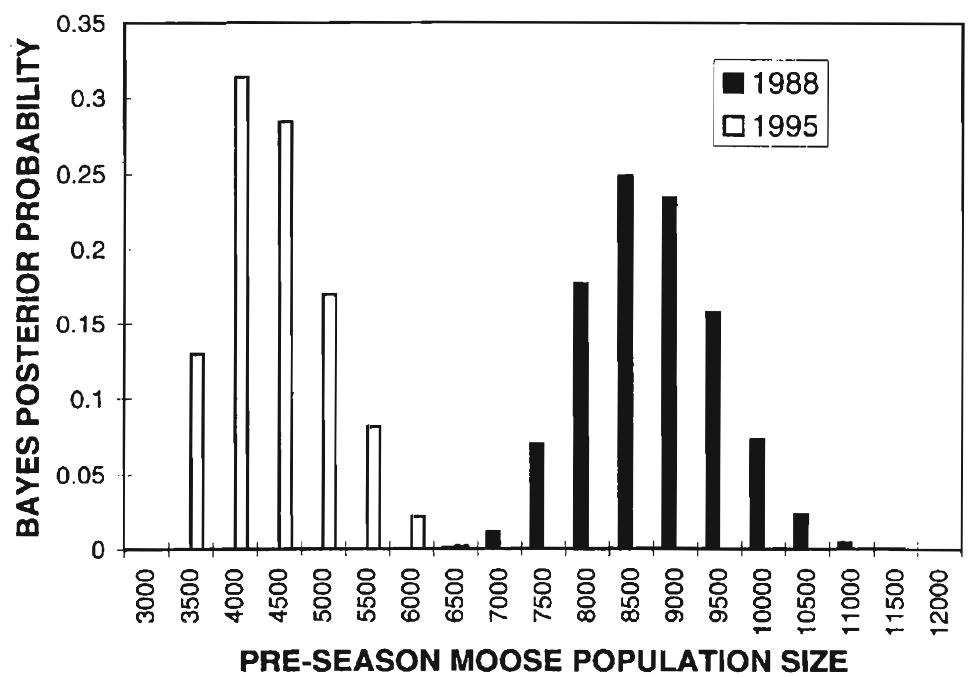

Fig. 3. Bayes posterior probabilities for pre-season number of moose in WMU 7-42 for 1988 and 1995.

vesting was terminated. If 100 bulls were harvested annually, there was only a 12% chance of obtaining this sex ratio, and < 1% chance if 200 were harvested annually. Thus, with continued harvesting, it was apparent the adult sex ratio objective for this population (≥30 bulls/100 cows) would probably not be realized, at least over the short-term.

DISCUSSION

The primary advantage of Bayesian estimation over more traditional modeling approaches is its ability to assess, in probabilistic terms, uncertainties for population parameters, and to incorporate this uncertainty into risk functions when determining annual allowable harvests. Nonetheless, Bayesian methods can be just as misleading as more traditional modeling approaches, if data used to calculate the likelihood functions are biased. Likelihood functions in this case study were calculated from two mid-winter stratified random block surveys, a herd composition survey, and a time series of KPUE. Stratified random block surveys corrected for sightability should provide the most accurate estimates of absolute abundance, bull/cow, and calf/cow ratios (Gasaway *et al.* 1986). Herd composition surveys may provide additional information on sex and age ratios. Van Ballenberghe (1979) warned, however, that surveys of moose composition may produce biased sex and age ratios, particularly if an appropriate survey design and adequate search effort are not employed. KPUE may provide a useful index of population trend if a nonlinear relationship between KPUE and density is accounted for, as might result from interference among competing moose hunters (Fryxell *et al.* 1988). Ideally, surveys of absolute abundance or the number of moose seen per hour flown during annual surveys (e.g. Ballard *et al.* 1991), rather than KPUE, should be used to monitor population trends.

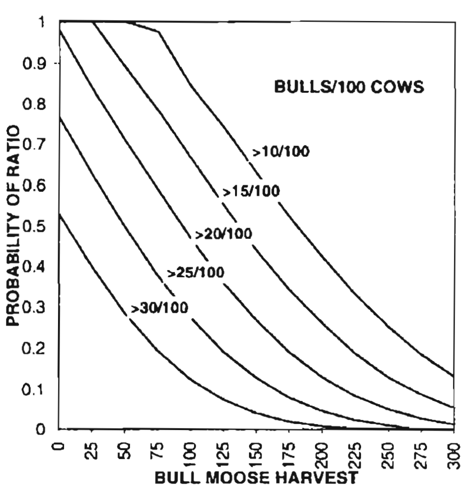

Fig. 4. Risk function for bull only harvest policy in WMU 7-42 required to achieve various post-season bull/cow ratios, under positive density-dependent calf recruitment.

The model structure employed in Bayesian estimation is equally important as the data used. I assumed calf recruitment changed linearly with adult moose population density. However, one reviewer suggested that a more realistic model structure might be to relate calf recruitment to the density of females (*sensu* McCullough 1979). The model estimated the uncertainty associated with two key population parameters (N_{88} and R_0), and treated R_1, q_1 and q_2 as nuisance parameters. By incorporating R_1 and q_2 directly into the assessment, the posterior probability distribution for R_0 was substantially flattened over that obtained when these parameters were not included. Other parameters were assumed known. The adult nonhunting rate of survival is one of the most important factors affecting rate of increase of ungulate populations (Fowler and Smith 1973, Nelson and Peek 1982, Eberhardt *et al.* 1982). Similarly, calf sex ratios are known to have a marked impact on rate of increase (Van Ballenberghe 1983, Boer 1992). Because both of these parameters were assumed known without error, the degree of certainty in the key parameters was probably overestimated, whereas the risks associated with a given level of harvest were underestimated. Thus, both these parameters should be measured when monitoring moose populations. Alternatively, another reviewer suggested the uncertainty of these parameters, as well as other unknown parameters, could be estimated using Gibbs sampling (Tanner 1993, Gilks *et al.* 1996). Nonetheless, to be effective, a more extensive data set than used here would be required.

An advantage of using a simple model structure, as opposed to a more complex age-structured model for moose within WMU 7-42, was that it minimized the number of parameters that must be estimated, or assumed known. A disadvantage was that this approach may have over-simplified the population dynamics of moose in this area. For example, the model neither directly incorporated interactions between moose and their habitat, nor did it allow for stochastic variation in recruitment or temporal variation in age-specific survival of adults. Walters and Ludwig (1994) suggested that the best strategy for evaluating model structure is to test a sequence of increasingly realistic models to see what each has to say about the data. While misleading results may be obtained from models that are too simple, detailed models that emphasize realism can also fail badly if they require estimation of too many parameters (Walters 1986).

In this example, KPUE appeared to contribute little information for defining probability distributions for moose population size and the KPUE parameters were highly correlated. The relationship between KPUE and moose abundance was also poorly understood. Consequently, KPUE may not be useful for Bayesian estimation and risk assessments of moose populations.

MANAGEMENT IMPLICATIONS

A common complaint by wildlife managers is that hunters do not realize the consequences of what they want (McCullough 1984). The risk functions provided a simple method for displaying the consequences of various short-term bull harvests on adult sex ratios, and could be extended to display the trade-offs between various other harvest policies and opportunities to the public (e.g. the impact of bull-only hunting versus harvesting both bulls and cows on adult sex ratios and moose population growth). Although the risk functions cannot answer the important question "what is an acceptable level of risk", they do provide an objective method for displaying uncertainty. Client groups, whose recreation and livelihood depend on hunting, would likely become better informed on the consequences of various harvest options if risk functions were used. It would also enable these groups to provide more constructive input for formulating harvest decisions, based on the level of risk they may be willing to accept.

ACKNOWLEDGEMENTS

I thank J. P. Elliott and B. Webster for providing the moose survey data for 1993 and 1994. Special thanks to C. J. Walters for introducing me to Bayesian estimation and risk functions, for advice on constructing Bayesian models, and for encouragement and support of this work. The manuscript was substantially improved with helpful comments by J. Fryxell and five anonymous reviewers.

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