

OPTIMAL HARVESTING OF MOOSE IN ALBERTA

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ABSTRACT: We developed a stage/sex matrix model for quota-harvest management of moose (*Alces alces*) populations in Alberta, and believe that the model structure has general applicability for harvesting of large mammal populations. The model includes density dependence in stage/sex-based vital rates and allows for estimation of carrying capacity and herd composition at carrying capacity from limited population survey data and harvest data. The model allows a biologist to evaluate optimal harvest strategies with the aim to optimize either the yield of the number of bulls harvested (goal B) or the yield of the total number of moose harvested (goal TY). The model predicted that to optimize yield of bulls, hunting of calves should be avoided because male calves recruit into the bull population the following year. If optimizing total yield, calves should be subject to intense harvest; harvesting for calves was predicted to be more intense than for bulls if female harvesting was not allowed, otherwise less intense. Bull harvest was less intense when trying to optimize yield of bulls than optimizing total yield. Small quotas of females could increase optimal yield substantially. The model also predicted that predation on calves and females reduced long-term optimal harvest intensity and calf predation reduced optimal total yield more than it influenced the optimal harvest of bulls. Reductions in moose abundance caused by predation and stochastic weather events can potentially cause severe consequences to harvest policy, challenging wildlife managers who must balance moose conservation, predator control, and hunter harvests. We believe that our model can facilitate harvest management, but vigilant monitoring of herd population size and composition will be necessary to ensure balance between predation and hunter harvests.

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Key words: Alberta, *Alces alces*, density dependence, harvesting, moose, predation, stage/sex population model, stochasticity, wildlife management.

Ungulate population dynamics are influenced by the combined effects of density dependence (Eberhardt 2002, Owen-Smith 2006), harvesting (Solberg et al. 1999, Coulson et al. 2004), predation (Nilsen et al. 2005, Varley and Boyce 2006), and stochastic environmental factors (Sæther et al. 2001). General patterns of density dependence in ungulate populations are reasonably well understood with both survival and reproduction changing inversely with population density (Fowler 1987, Eberhardt 2002, Owen-Smith 2006). Environmental stochasticity influences fluctuations in ungulate populations through effects on mortality and fecundity (Gaillard et al.

2000, Boyce et al. 2006). Density-dependent limitation and influence of environmental factors co-occur in most populations (Sinclair 1989) so that the impact on population growth of environmental factors such as a severe winter and winter ticks (*Dermacentor albipictus*) typically increases with population density (Milner et al. 1999, Samuel 2007).

For ungulates, predation can be an important limiting factor (Van Ballenberghe 1987). Studies on predator-moose (*Alces alces*) relationships in North America suggest that predators (mainly grizzly bear [*Ursus arctos*], black bear [*U. americanus*], and wolf [*Canis lupus*]) were a major cause of calf mortality

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in many moose populations, removing 3–55% or more calves annually (Ballard and Van Ballenberghe 1998). Ungulate populations also are harvested for meat, hides, and antlers worldwide (Gordon et al. 2004). Excessive exploitation, especially when combined with uncertainty associated with predation, may risk severe reductions in local populations and even local extinction. Therefore, how to efficiently manage and harvest wild ungulates in the presence of environmental stochasticity and predation becomes critical to ungulate managers.

Harvests of ungulates are typically highly selective with quotas often established by sex and age/stage (Sæther et al. 2001, Clutton-Brock et al. 2002). Data for management of ungulate populations is usually limited, and consequently harvest quotas are usually set with insufficient and incomplete information (Milner-Gulland et al. 2004).

Harvest modeling is widely used for the management of ungulate populations (Pojar 1977, 1981, Getz and Haight 1989, White and Lubow 2002, Cooper et al. 2003). Wildlife biologists are often frustrated, however, because of the large number of unknown parameters required for many of these demographic models. Furthermore, density dependence is a fundamental requirement for the existence of optimality in any model of sustainable harvest (Mendelsohn 1976, Boyce et al. 1999) and demographic book-keeping models without density dependence such as ONEPOP, POP50 and PopII (Pojar 1981) cannot identify optimal harvest levels. Another model, the Sex-Age-Kill model (Skalski and Millspaugh 2002, Skalski et al. 2005) has untenable assumptions of a stationary age distribution; this assumption cannot be met if there are any fluctuations in population size (Millspaugh et al. 2009).

Ungulate populations are structured according to age and sex (Gaillard et al. 1998, Nilsen et al. 2005), and consequently their dynamics are best explained when including age- and sex-specific vital rates. Similar to

life-table models (Caughley 1977, Taylor et al. 2000), projection matrix models such as the Leslie (1945) matrix are well suited to studying how changes in vital rates affect ungulate population growth rates (Caswell 2001). In these models, the starting point is a certain number of individuals in each age and sex class in the first year. The individuals are then transferred to the next class by rates defined by the elements of a transition matrix (Leslie 1945, 1948, Caswell 2001) representing age- and sex-specific birth and survival rates. In practice, because population and harvest data are usually stage-based, animals often are categorized by developmental stage rather than age. Therefore, generalized transition matrices (Lefkovitch 1965, Caswell 2001) that contain the number of individuals in different stage and sex classes can be used to update the model populations.

We developed a model for quota-harvest management of moose populations in Alberta that includes 1) stage and sex structure as typically monitored in the field, 2) estimation of carrying capacity and herd composition at carrying capacity from limited population survey and harvest data, 3) stage-structured density dependence following the general patterns documented in ungulate populations (Fowler 1987, Eberhardt 2002, Owen-Smith 2006), and 4) environmental stochasticity. The model thereby was designed to use data typically available to field biologists.

We investigated optimal harvest strategies for moose populations in Alberta with the aim either to optimize the yield of bulls (i.e., the number of harvested males of yearling age and older; goal B) or alternatively to optimize total yield (i.e., the total number of harvested calves, females, and bulls; goal TY) within Wildlife Management Units (WMU). We investigated optimal bull harvesting in addition to optimizing total yield because of hunter interest in bulls, and the perception that bulls could be harvested without reducing herd size. First, we examined the differences between the 2 goals

in terms of yield, optimal harvest intensity of different sex/stages, and post-harvested population abundance and composition; then we studied how environmental stochasticity influenced the results. Finally, because predators killed mostly calves and predation varied in time and space, we examined the effects of predation on optimal harvesting for different harvesting targets and predation scenarios.

METHODS

Study Area and Data Sets

WMUs selected for detailed investigation were in central Alberta east of the Rocky Mountains at the southern edge of the boreal forest (Fig. 1). The vegetation was mixed wood (Beckingham et al. 1996) with the predominant tree species being white spruce (*Picea glauca*), black spruce (*P. mariana*), and aspen (*Populus tremuloides*). Predators of moose included abundant black bears and wolves, and relatively low densities of grizzly bears and cougars (*Puma concolor*). Hunting was managed primarily by limited quota permits issued by the province of Alberta.

Moose population estimates in Alberta were made by aerial survey when snow conditions permitted, usually January–March, using a modified Gasaway method (Gasaway et al. 1986, Lynch and Shumaker 1995). Herd composition was recorded as the number of calves, cows, and bulls. A major moose population survey was completed in the winter of 1993–94, when 46 WMUs were surveyed by air and the total moose population was estimated at 81,000. Follow-up aerial surveys typically were done in high-priority WMUs; WMU 346, WMU 350, and WMU 358 had the longest data sets available from 1993–1994 to 1996–1997 (WMU 346) or to 1997–1998 (WMU 350 and WMU 358) and were chosen for this study. The population estimate for WMU 358 in 1993–94 was about two-fold less (≈ 1200 animals less) than in 1994–95 and thereafter, which was unrealistically low and identified as an outlier. Therefore, only data from the

remaining 4 years were used for WMU 358. Moose population density and composition in WMU 346 during 1997–1998 were approximated by density and composition available in WMU 351 nearby.

Population Model

We used a generalized transition matrix \mathbf{A}_t (Lefkovitch 1965, Caswell 2001) to update the model population from \mathbf{n}_t to \mathbf{n}_{t+1} by:

$$\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t \quad (1)$$

where \mathbf{n}_t contains the number of animals in different stage and sex classes at time t .

Moose population and harvest data were usually recorded in 3 classes: 1) young/calves (including both female and male calves), 2) females/cows (including female yearlings and adults), and 3) males/bulls (including male yearlings and adults); therefore, we tailored the vector \mathbf{n}_t to consist of 3 stages: calves, females, and males as defined above. In other words, the transition matrix followed both male and female calves as a lumped calf group and then differentially recruited them into different rows for males and females. Moose

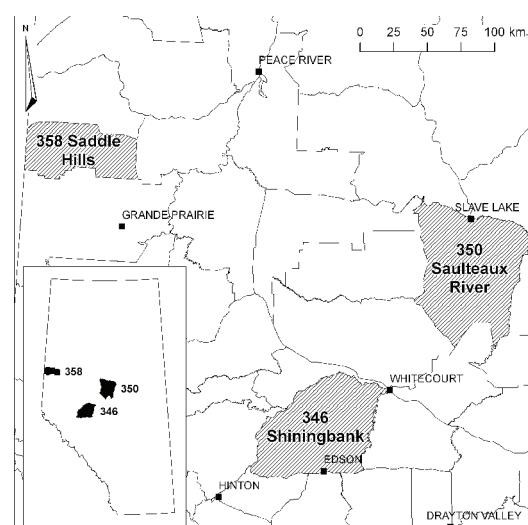


Fig. 1. Location of the 3 Wildlife Management Units (WMUs) in Alberta, Canada from which data were obtained for illustrating the performance of our harvesting model.

in Alberta breed in late September and early October (Stelfox 1993) with calves born the following spring; calves must survive summer and autumn to be included in winter counts. Harvesting typically begins in late September, continuing through November. Aerial surveys of population size and composition are usually done January–March depending on snow conditions.

Based on this information, equation (1) with harvest included can be written more specifically as:

$$\begin{pmatrix} n_{y,t+1} \\ n_{f,t+1} \\ n_{m,t+1} \end{pmatrix} = \begin{pmatrix} 0 & R_t & 0 \\ \delta S_{CF,t} & S_F & 0 \\ (1-\delta)S_{CM,t} & 0 & S_M \end{pmatrix} \begin{pmatrix} n_{y,t} \\ n_{f,t} \\ n_{m,t} \end{pmatrix} - \begin{pmatrix} H_{y,t} \\ H_{f,t} \\ H_{m,t} \end{pmatrix} \quad (2)$$

where R_t is the density-dependent recruitment rate at time t (early to mid-winter), δ is the proportion of females among calves at recruitment, $S_{CF,t}$ and $S_{CM,t}$ are density-dependent survival for calves to yearlings at time t , where subscripts CF and CM represent female and male calves. S_F and S_M are survival rates of females and males which we assumed to be density independent (see Demographic Parameters). $H_{y,t}$, $H_{f,t}$, and $H_{m,t}$ refer to harvest mortality of calves (sexes combined), females, and bulls, respectively. R_t , $S_{CF,t}$, and $S_{CM,t}$ are given as follows, with biological details explained in the following subsection:

$$R_t = \alpha_0 \exp\left(p \left[1 - \left(\frac{N_t}{K}\right)^{\gamma_0}\right]\right) \quad (3)$$

$$S_{i,t} = \frac{S_i}{\exp\left(\alpha_i \left(\frac{N_t}{K}\right)^{\gamma_i}\right)} \quad (i = CF, CM) \quad (4)$$

where $R^* = \alpha_0 \exp(p)$ is the maximum recruitment, S_i ($i = CF, CM$) are survival rates of female calves and male calves at low population density when no density effect occurs, N_t is the population size at time t , K is the carrying capacity, γ_i ($i = 0, CF, CM$) is the density dependence exponent in recruitment

and survival, and α_i ($i = 0, CF, CM$) are coefficients relating to the relative abundance of 3 stages at carrying capacity. Constraints on α_i ($i = 0, CF, CM$) are provided in Appendix 1. This model structure permits stage-specific differences in density dependence that are prevalent in ungulate populations (Eberhardt 2002, Owen-Smith 2006).

Demographic Parameters

Recruitment - Recruitment rate was determined from juvenile survival (measured from birth to winter census), fecundity (or litter size, measured by the number of offspring produced per female), and the proportion of females that breed (Schwartz 1992). Calf survival of ungulates has been reported to be very sensitive to limiting factors (Gaillard et al. 1998, Eberhardt 2002). In a review of temporal variation in fitness components of large herbivores, Gaillard et al. (2000) suggested that preweaning and postweaning survival were generally low (\bar{X} of 0.638 and 0.697) and varied markedly over time and space (CV of 0.265 and 0.279). Likewise, studies have shown year-to-year variation (Gaillard and Yoccoz 2003) and density dependence (Sand et al. 1996, Ferguson et al. 2000) in fecundity. As for the breeding proportion of females, studies indicate that relatively few yearling cow moose have calves, and few 2-yr-old and older cows have twins when population density is high (Schwartz and Franzmann 1998). Due to the uncertainty in estimation of the components of recruitment, 3 estimates [respectively, the 3/8, 4/8 (2nd), 5/8 quartiles of a normal distribution with mean of 0.75 and variance of 0.182², i.e., $N(0.75, 0.182^2)$ for juvenile survival; $N(1.88, 0.207^2)$ for fecundity; and $N(0.765, 0.206^2)$ for breeding proportion] for each component were used based on empirical data from *Ecological Archives* E084-089-A1 and Gaillard et al. (2000). These estimates were targeted for the maximum recruitment, R^* , so they were adjusted higher compared to empirical data from the literature because empirical data

were estimated under the influence of various limiting factors such as density dependence and predation. Consequently, the recruitment rate at low population density was calculated by $R^* = (\text{juvenile survival}) \times (\text{fecundity}) \times (\text{breeding proportion of females})$, when no density dependence occurred. To account for the density effect in recruitment, we used a density-dependent function given by equation (3). Although the precise shape of the density dependence relationship (fecundity and mortality) in moose was poorly documented, empirical data suggested that there was little density dependence at low-moderate population densities, but the response became stronger as density approached carrying capacity (Fowler 1987, Gaillard et al. 1998, Nilsen et al. 2005).

Survival - Survival of calves has been demonstrated to be more sensitive to density dependence than survival of adult animals (Bonnenfant et al. 2009). We used equation (4) to account for the density effect in calf survival. To keep the model relatively simple and analytically tractable, we assumed that the survival of adult females and males remained unchanged with population abundance. Previous studies of moose have shown that survival rates of females and bulls varied from 0.85–0.94 (Bangs et al. 1989, Larsen et al. 1989, Ballard et al. 1991); we used this range of values in our model fitting.

Carrying Capacity

Estimating K - Carrying capacity K was estimated according to the Θ -logistic model (Gilpin and Ayala 1973). Under harvesting the rate of change of a population with logistic growth takes the form:

$$dN/dt = \ln\lambda_0 \cdot N \left[-(N/K)^{\theta} \right] - H \quad (5)$$

where N is the total population size, $\ln\lambda_0$ is the potential growth rate, with λ_0 being the dominant eigenvalue of the matrix in equation (2) with no density dependent effects, i.e., in

the limit as $N \downarrow 0$ [equations (3) and (4)], Θ shapes the nonlinearity of density dependence, and H is the total annual moose harvest (Xu et al. 2005). When the population achieves an equilibrium population size N^* , which is less than K and could be approximated by the mean value of observed population size, we have:

$$K = \frac{N^*}{(1 - H / (\ln\lambda_0 \cdot N^*))^{1/\theta}} \quad (6)$$

Studies in different moose populations suggest that potential λ_0 with no density dependence typically varies from 1.10–1.41 (*Ecological Archives* E084-089-A1). For ungulate populations, Θ is typically >1.0 giving the rate of change in population size a skewed shape with a maximum somewhere above half- K (Crete 1987, Boyce 1989). Here, we used the average value of γ_i (>1 , see below) ($i = 0, CF, CM$) to approximate Θ . This degree of nonlinearity is insufficient to result in exaggerated overcompensation (Getz 1996) but appropriately captures the biological process of density dependence characteristic of ungulate populations (Fowler 1981, 1987, Eberhardt 2002, Owen-Smith 2006).

Estimating herd composition at K -

Herd composition at carrying capacity was represented by the number of females per calf, o_{fy} , and the number of bulls per calf, o_{my} (see Appendix S1), which was estimated by conditional least squares (CLS) (Dennis et al. 2001; detailed in Appendix 2). Further, $\alpha_0, \alpha_{CF}, \alpha_{CM}$ can be obtained from equations (S2)–(S4) (Appendix 2). Because data sets were limited, we set predetermined combinations of other model parameters to estimate o_{fy} and o_{my} . We set δ at 4 plausible values of 0.3, 0.4, 0.5, and 0.6, γ_i ($i = 0, CF, CM$) was chosen between 1.5–4.0, $S_{CF} = S_{CM}$ were fixed to some certain value (Table 1), S_F, S_M were chosen between 0.85–0.94 (as described in **Demographic Parameters**), and R^* was chosen from the 3 estimates mentioned previously. Finally, the

Table 1. Definitions and parameter values in the population model for each of the 3 WMUs in Alberta, Canada.

Parameter	Value			
	WMU 346	WMU 350	WMU 358	
Recruitment rate at low population density [†]	R^*	1.3066	1.0787	0.8774
Survival rate of calves at low population density [†]	$S_i (i = CF, CM)$	0.90	0.90	0.90
Survival rate of females	S_F	0.85	0.91	0.92
Survival rate of males	S_M	0.85	0.90	0.89
Finite rate of increase	λ_0	1.3017	1.2266	1.1297
Carrying capacity	K	3488	3856	3298
Number of female per calf at carrying capacity [‡]	o_{fy}	1.3990	2.5162	2.9556
Number of male per calf at carrying capacity [‡]	o_{my}	2.4040	3.7482	4.8895
Coefficients regulating relative abundance of different stages at carrying capacity [@]	α_0	0.7148	0.3974	0.3383
	α_{CF}	0.7628	0.4636	0.1326
	α_{CM}	0.2215	0.3651	0.1582
Recruitment coefficient #	p	0.6032	0.9985	0.9529
Variance-covariance matrix of error vectors ^{&}	Σ	Σ^1	Σ^2	Σ^3
Proportion of female calves at recruitment	δ	0.5	0.4	0.3
Density dependence exponent	γ_0	1.5	2.0	1.5
	γ_{CF}	1.5	3.0	4.0
	γ_{CM}	3.0	4.0	4.0

† Numerical values based on Ecological Archives E084-089-A1, Gaillard et al. 1998, 2000, and Northern Moose Management Progress Report, 2002 (web resource).

‡ Estimated by CLS (Appendix 2).

@ Calculated from equations (S2)-(S4) (Appendix 1).

Calculated from $R^* = \alpha_1 \exp(p)$.

$$\& \quad \Sigma^1 = \begin{pmatrix} 0.0563 & 0.0155 & 0.0037 \\ 0.0155 & 0.0233 & 0.008 \\ 0.0037 & 0.008 & 0.0029 \end{pmatrix}, \quad \Sigma^2 = \begin{pmatrix} 0.0303 & 0.0009 & 0.0211 \\ 0.0009 & 0.0084 & 0.0128 \\ 0.0211 & 0.0128 & 0.035 \end{pmatrix},$$

$$\Sigma^3 = \begin{pmatrix} 0.051 & 0.0264 & 0.0055 \\ 0.0264 & 0.014 & 0.0015 \\ 0.0055 & 0.0015 & 0.0062 \end{pmatrix}, \text{ for calculation details see Appendix S2.}$$

λ_0 Calculated as the dominant eigenvalue of the matrix in equation (2) with no density dependent effects, i.e., in the limit as $N \downarrow 0$.

K was calculated from equation (6).

combination that produced the smallest total sum of squared errors, $\sum_{i=1}^3 Q_i$, as well as positive $\alpha_i (i = 0, CF, CM)$ was chosen for each WMU (Table 1).

Harvesting and Predation

Hunting seasons for moose in Alberta open as early as September, but most harvest

is in October-November. Telephone surveys were conducted by Alberta Sustainable Resource Development and the Alberta Fish and Game Association shortly after the close of the hunting season to estimate the number of calves, females, and bull moose harvested in each WMU (Stelfox 1993). Besides harvest mortality, moose also are subject to predation by wolf, black bear, grizzly bear, and cou-

gar; calves account for the bulk of predator kills (Ross and Jalkotzy 1996, Ballard and Van Ballenberghe 1998, Munro et al. 2006). When fitting the model, we assumed that approximately 40% of calves were subjected to predation annually before winter aerial surveys (see Ballard and Van Ballenberghe 1998), and considered female and bull mortality by predation or aboriginal harvest to be part of natural mortality.

Elasticity Analysis and Model Simulations

Given the uncertainty in parameter estimation based on a limited data set, elasticity analysis was conducted to examine how sensitive the population growth rate [as measured by λ , the dominant eigenvalue of the matrix in equation (2)] was to the estimated parameters. Elasticity analysis is a variation of sensitivity analysis where elasticities (e_{ij}) of the matrix elements (a_{ij}) were scaled (ln) sensitivity values (s_j) that summed to 1.0 (Caswell 2001):

$$e_{ij} = \frac{\partial (\ln \lambda)}{\partial (\ln a_{ij})} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (7)$$

The matrix elements R_p , $S_{CF,p}$, and $S_{CM,t}$ were comprised of several demographic parameters. Elasticity of λ to these parameters was evaluated by taking the partial derivatives of the matrix with respect to these parameters (Caswell 2001):

$$e_x = \frac{x}{\lambda} \frac{\partial \lambda}{\partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \quad (8)$$

where e_x is the elasticity of λ to a proportional change in a demographic parameter (x) as listed in Table 2. The higher the elasticity, the more sensitive λ is to changes in parameters.

In the model simulations a deterministic model [equations (S5)-(S7), Appendix 2] and a stochastic model [equations (S8)-(S10), Ap-

pendix 2] were used to project moose populations in the 3 WMUs. A preliminary evaluation of the model was conducted by plotting the observed data and the model predictions represented by the mean value and the 5th and 95th percentiles of the one-year ahead predictions (i.e., use model to update the population for one year ahead) from the stochastic model [equations (S8)-(S10), Appendix 2]. For the deterministic case, yield at equilibrium is examined. For the stochastic case, however, we simulate the process over a large number of years by using stochastic equations (S8)-(S10) (Appendix 2) and then examined mean annual yields. Model parameter estimation and simulations were implemented using the free software environment R.

RESULTS

The vital rates model of equations (3) and (4) predicted that recruitment and survival rates of calves had a negative relationship with population abundance (Fig. 2a). The corresponding population growth rate predicted from equation (1) decreased with increasing population size (Fig. 2b).

The elasticity values for the demographic parameters suggested that λ was most sensitive to changes in 4 parameters: survival of females (S_F) ranked first, survival of female calves (S_{CF}), sex ratio at recruitment (δ), and α_0 ranked second (Table 2). Other parameters would contribute little to future changes in λ (Table 2). These results were consistent for all 3 WMU's (Table 2). The preliminary evaluation of the model demonstrated that even with few data, survey counts fell within the 5th and 95th percentiles of model predictions (Fig. 3 and 4).

Model simulations indicated substantial differences in optimal harvest intensity of different sex/stage classes, yield, post-harvested population abundance, and composition between goal B and goal TY. To maximize yield of bulls, hunting of calves should be avoided (Table 3, Fig. 5a). In contrast, if optimizing

Table 2. Elasticities for parameters of the matrix model for populations from the 3 WMUs in Alberta, Canada. Elasticities were calculated for 2 levels of population abundance (i.e., in the limit as $N \downarrow 0$ and $N = K/2$, K is the carrying capacity). The top 4 ranked parameters are in bold.

Parameter	WMU 346		WMU 350		WMU 358	
	0	$K/2$	0	$K/2$	0	$K/2$
S_{CF}	0.253	0.209	0.202	0.173	0.154	0.126
S_{CM}	0.000	0.000	0.000	0.000	0.000	0.000
S_F	0.491	0.583	0.597	0.655	0.694	0.754
S_M	0.000	0.000	0.000	0.000	0.000	0.000
K	0.000	0.000	0.000	0.000	0.000	0.000
α_0	0.253	0.209	0.202	0.173	0.154	0.126
α_{CF}	0.000	-0.056	0.000	-0.010	0.000	-0.001
α_{CM}	0.000	0.000	0.000	0.000	0.000	0.000
p	0.158	0.084	0.212	0.135	0.154	0.080
δ	0.253	0.209	0.202	0.173	0.154	0.126
γ_0	0.000	0.045	0.000	0.057	0.000	0.043
γ_{CF}	0.000	0.057	0.000	0.019	0.000	0.003
γ_{CM}	0.000	0.000	0.000	0.000	0.000	0.000

Table 3. Optimal harvesting for the 3 WMUs under 2 management targets (goal B, maximizing bull harvests; goal TY, maximizing total harvests) predicted by the deterministic model [equations (S5)-(S7), Appendix 2]. Variables p_c , p_f , and p_m are the optimal proportions of calves, females, and males to be harvested, respectively. Y_m is the optimal yield of male moose at equilibrium, Y is the optimal total yield at equilibrium, X is the post-harvest population size at equilibrium, and $X_c : X_f : X_m$ represents the number of calves and males per 100 females after harvest. Other parameters are as in Table 1. No predation is considered here.

	Optimizing bull yield at equilibrium (goal B)			Optimizing yield at equilibrium (goal TY)		
	WMU 346	WMU 350	WMU 358	WMU 346	WMU 350	WMU 358
I. No cow harvest						
p_c	0	0	0	0.40	0.50	0.35
p_m	0.35	0.30	0.35	0.45	0.45	0.40
Y_m	219	194	200	--	--	--
Y	--	--	--	460	446	323
X	3488	3856	3298	2553	2911	2445
$X_c : X_f : X_m$	71:100:37	40:100:28	34:100:28	54:100:23	31:100:16	31:100:24
II. W/cow harvests						
p_c	0	0	0	0.40	0.35	0.35
p_f	0.004	0.100	0.004	0.001	0.050	0.001
p_m	0.35	0.35	0.35	0.45	0.45	0.40
Y_m	219	223	200	--	--	--
Y	--	--	--	460	480	323
X	3488	2717	3298	2553	2551	2445
$X_c : X_f : X_m$	71:100:37	66:100:51	34:100:28	54:100:23	45:100:25	31:100:24

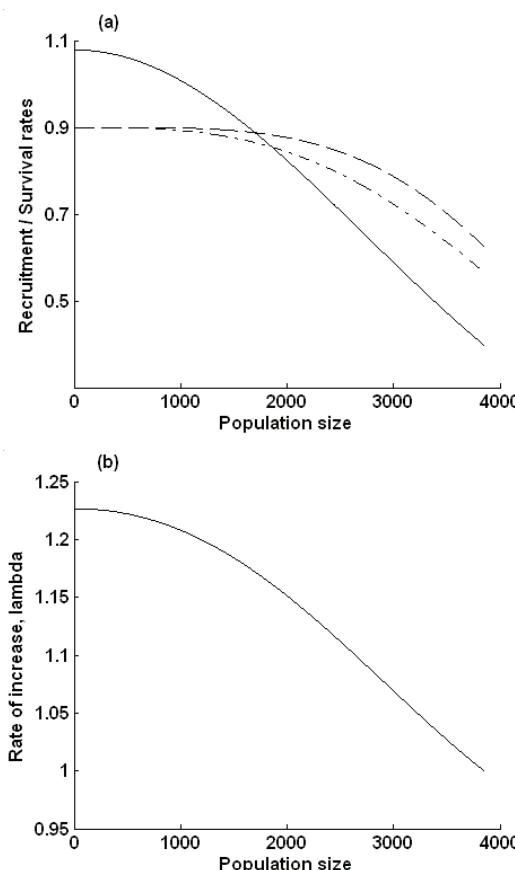


Fig. 2. Moose harvesting model including a) density-dependent recruitment (solid line), survival from calves to yearlings (dotted line, female calves; dashed line, male calves) as a function of population size, and b) rate of population increase λ as a function of population size.

total yield, calves should be subject to intense harvest (Table 3, Fig 5b). Bull harvest was suggested to be less intense for optimizing yield of bulls than for optimizing total yield (Table 3). Both goal B and goal TY needed small quotas of females. If only bulls were harvested, moose populations could attain carrying capacity (Table 3). Harvesting calves, females, or both substantially reduced the post-harvest population size, but increased harvest yields (Table 3). The post-harvest abundances of calves and bulls/100 cows were larger when attempting to optimize yield of bulls because optimizing total yield involved intense harvest of calves which would not be available to

recruit to bulls (or cows) (Table 3).

Stochasticity did not change the general results except that populations could not reach the carrying capacities when only bulls were harvested (Table 4). By comparison of Y (optimal total yield) in Table 3 with \bar{Y} (optimal mean annual total yield) in Table 4, we found that stochasticity reduces optimal total yield in each of the 3 WMUs.

In general, optimal harvest intensity decreases with predation on calves for both goals, regardless of predation on females (Fig. 6). In the presence of predation on females,

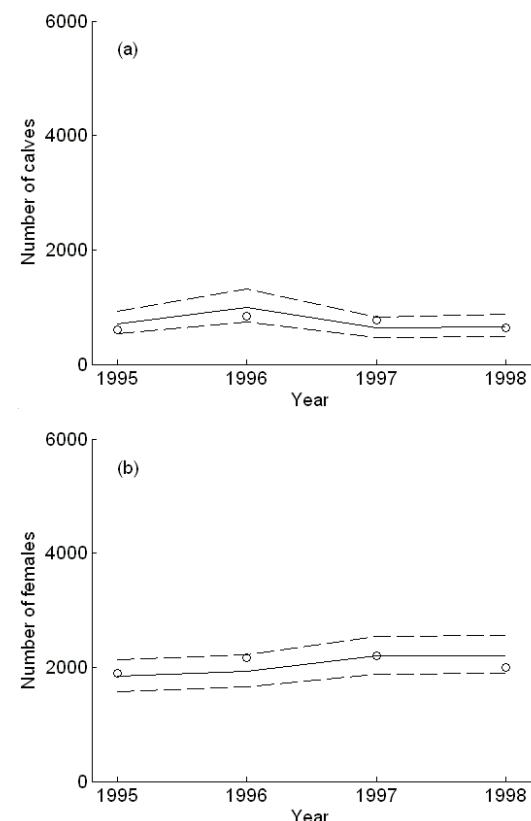


Fig. 3. Moose population survey data (circles) for WMU 350 in Alberta, Canada and predictions (lines) from stage/sex-based stochastic population model [equations (S8)-(S10), Appendix 2]: a) calves, b) females, c) males, and d) total population size. Solid lines are the mean values of model predictions, and dashed lines the 5th and 95th percentiles of model predictions. Model parameters are as in Table 1. (Continued on next page.)

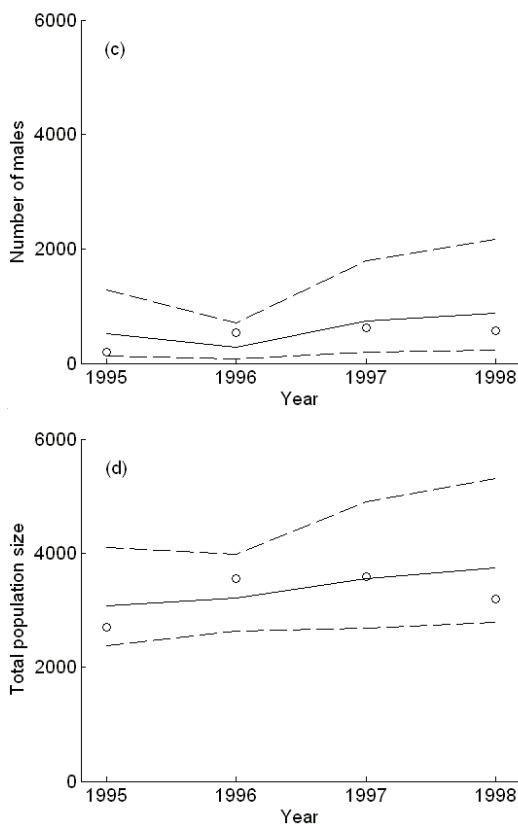


Fig. 3 (continued). Moose population survey data (circles) for WMU 350 in Alberta, Canada and predictions (lines) from stage/sex-based stochastic population model [equations (S8)-(S10), Appendix 2]: a) calves, b) females, c) males, and d) total population size. Solid lines are the mean values of model predictions, and dashed lines the 5th and 95th percentiles of model predictions. Model parameters are as in Table 1.

optimal harvesting for calves, females, and bulls were predicted to be less intense, especially when the predation rate on calves was high. For example, if calves were subject to 40-60% annual predation, optimal harvesting should involve only the harvest of bulls, leaving calves and females untouched (Fig. 6b). In this situation, optimal harvesting for goals B and TY became the same. However, in the absence of predation on cows and calves, optimal harvesting should include calves as well as bulls for goal TY (Fig. 6a).

Likewise, both the total yield and yield of bulls had a negative relationship with the rate

of predation on calves (Fig. 7). Optimal total yield decreased much faster with increasing predation on calves than did the optimal yield of bulls (Fig. 7a). The difference between optimal total yield and optimal bull yield decreased with calf predation regardless of predation on females (Fig. 7a). If predation on females was present, optimal yield of bulls and optimal total yield became the same as the rate of predation on calves increased to 40%, and dropped to a very low value when the rate of predation on calves increased to 60% (Fig. 7a). Optimal total yield of moose declined in the presence of predation on females, and the amount of decline almost remained unchanged with increasing predation on calves, whereas

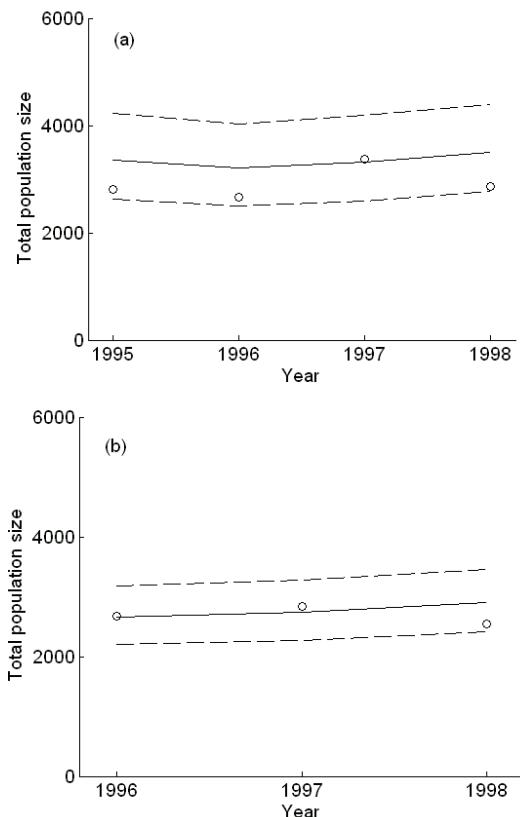


Fig. 4. Moose population survey data (circles) and model predictions (lines) [equations (S8)-(S10), Appendix 2] for a) WMU 346 and b) WMU 358 in Alberta, Canada. Solid lines are the mean values of model predictions, and dashed lines the 5th and 95th percentiles of model predictions.

Table 4. Optimal harvesting under goal B and goal TY predicted by the stochastic model [equations (S8)-(S10), Appendix 2] for the 3 WMUs in Alberta, Canada. \bar{Y}_m is the optimal mean annual male yield, \bar{Y} is the optimal mean annual yield, \bar{X} is the post-harvest mean annual population size, and $\bar{X}_c : \bar{X}_m : \bar{X}_f$ represents the mean number of calves and males per 100 females after harvest. Simulations were run for 5,000 years. Variables p_c , p_f , and p_m and other details are as in Table 3.

	Optimizing mean annual yield of bulls (goal B)			Optimizing mean annual total yield (goal TY)		
	WMU 346	WMU 350	WMU 358	WMU 346	WMU 350	WMU 358
I. No female harvesting						
p_c	0	0	0	0.35	0.45	0.40
p_m	0.35	0.35	0.30	0.45	0.45	0.45
$\bar{Y}_m + \text{sd}$	210 ± 20	190 ± 28	189 ± 22	--	--	--
$\bar{Y} + \text{sd}$	--	--	--	449 ± 56	435 ± 17	310 ± 43
$\bar{X} + \text{sd}$	3446 ± 730	3814 ± 506	3261 ± 649	2784 ± 651	3104 ± 464	2507 ± 759
$\bar{X}_c : \bar{X}_f : \bar{X}_m$	69:100:34	40:100:24	33:100:32	55:100:22	31:100:16	27:100:17
II. With female harvesting						
p_c	0	0	0	0.4	0.4	0.4
p_f	0.004	0.100	0.004	0.001	0.050	0.001
p_m	0.35	0.30	0.35	0.45	0.45	0.45
$\bar{Y}_m + \text{sd}$	209 ± 19	224 ± 38	189 ± 26	--	--	--
$\bar{Y} + \text{sd}$	--	--	--	456 ± 65	469 ± 49	307 ± 44
$\bar{X} + \text{sd}$	3450 ± 722	2737 ± 420	3275 ± 673	2671 ± 693	2385 ± 425	2512 ± 716
$\bar{X}_c : \bar{X}_f : \bar{X}_m$	69:100:34	65:100:64	33:100:26	51:100:21	43:100:25	28:100:20

the optimal yield of bulls declined as predation on calves increased (Fig. 7a).

Predation on females also reduced the post-harvest population size, which was further reduced by predation on calves (Fig. 7b). If predation on female moose occurred, post-harvest population size decreased as predation on calves increased, whereas in the absence of predation on females, no decreasing trend was observed in post-harvest population size as predation on calves increased (Fig. 7b). When females were subject to predation, the difference in post-harvest population size between the 2 goals decreased to the same value as calf predation increased (Fig. 7b).

Post-harvest abundance of calves per female generally decreased as predation on calves increased regardless of predation on females (Fig. 7c). Whereas for bulls, the abundance decreased if predation on females was absent; but if predation on females was

present, bull abundance per female generally increased or remained unchanged as predation on calves increased, depending on whether optimizing bull yield or optimizing total yield (Fig. 7c).

DISCUSSION

We developed a stage/sex demographic population model and investigated optimal harvest strategies for moose populations in Alberta with respect to 2 harvest goals (goal B - optimizing the yield of bulls; goal TY - optimizing total yield). Substantial differences were found in yield, stage/sex-specific optimal harvest intensity, post-harvest population abundance, and composition between the 2 goals. Stochasticity and predation reduced total yield as well as yield of bulls, and predation also reduced post-harvest population abundance. These results have important implications for moose management in Alberta

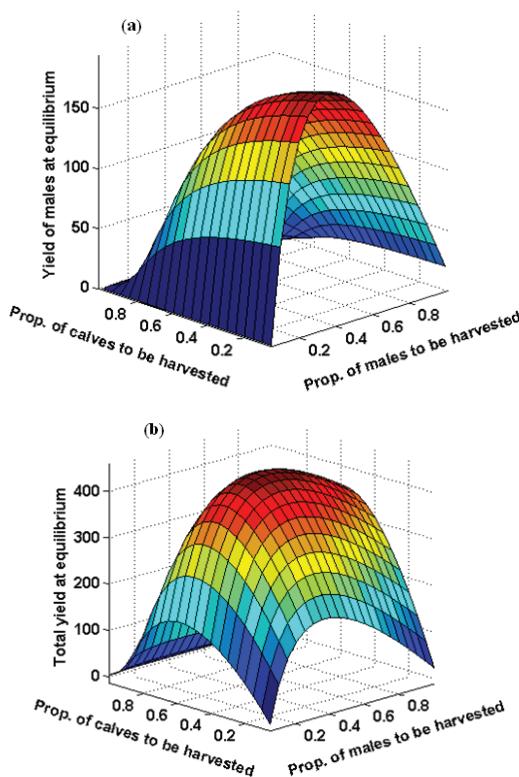


Fig. 5. Yield of a) males and b) total yield at equilibrium as a function of the proportion of calves and males to be harvested. Yield plotted for WMU 350 uses the deterministic model [equations (S5)-(S7), Appendix 2]; patterns were consistent in all 3 WMUs.

and boreal moose in general.

The results indicated that the optimal harvest quotas differed strongly among different stage/sex classes with respect to goal B and goal TY. Maximum sustainable total yield involved intense harvesting of calves and males but a low harvest rate of females, which was in agreement with Sæther et al. (2001). In contrast, optimal harvesting for bulls was found to involve no calf harvest, low cow harvest, and high harvest rate of bulls. The bull harvest rate, however, should be lower than when optimizing the annual total yield. This is mainly because harvest of calves and cows contributes to total yield and their removal stimulates density-dependent responses in survival and recruitment, and therefore in population growth rate and abundance (Boyce

and Daley 1980, Boyce et al. 1999).

Our results indicated that optimal moose harvests were influenced substantially by the existence of predation on cows and calves, and suggested that conflicts might occur between human exploitation and predation by wolves, bears, and cougars as has been stated previously (National Research Council 1997). This presents challenges for wildlife managers who must manage for moose conservation and

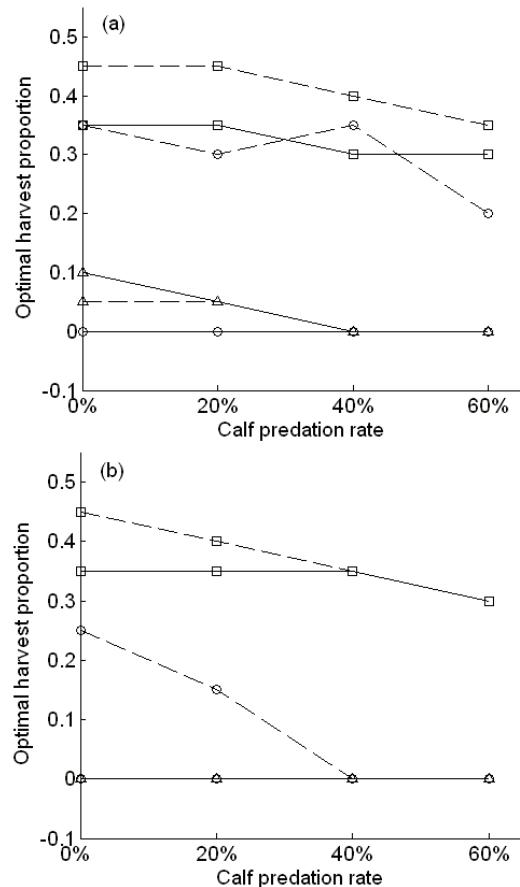


Fig. 6. The effect of calf predation on the optimal harvest proportions for calves (circles), females (triangles), and males (squares). Solid lines correspond to optimization of male yield (goal B), and dashed lines correspond to optimization of total yield (goal TY): a) no predation on females, and b) females subject to predation at rate of 10%. Plots for WMU 350 use the deterministic model [equations (S5)-(S7), Appendix 2]; patterns of predation effect were consistent for all 3 WMUs. Model parameters are as in Table 1.

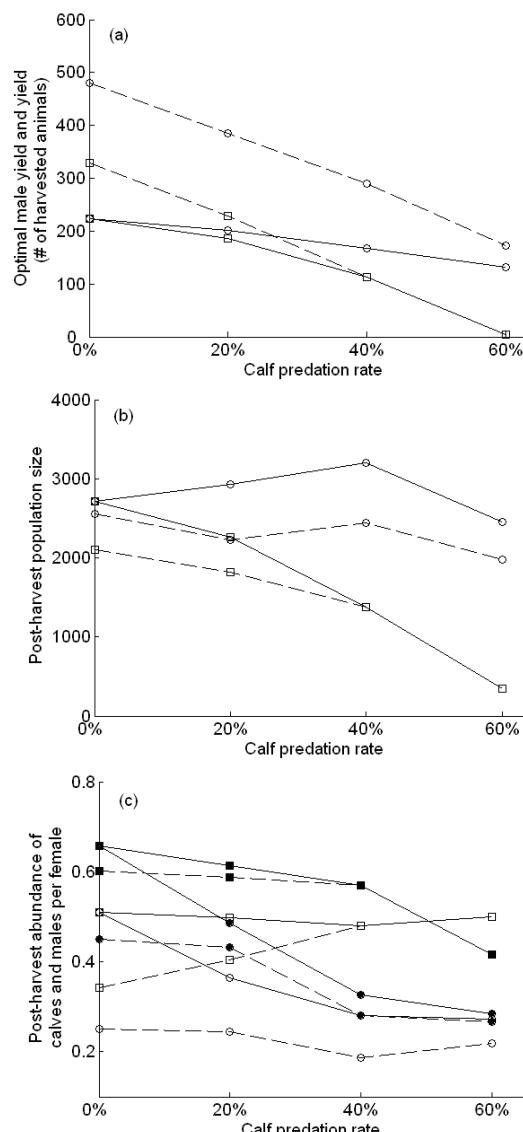


Fig. 7. The effect of calf predation on the optimal yield of bulls and a) total yield, b) post-harvest population size, and c) post-harvest abundance of calves and males per female for the case of no predation on females (circles) or 10% annual female predation (squares). Solid lines correspond to yield of bulls, and dashed lines correspond to total yield. Filled circles and squares represent calves and unfilled males in c). Other details are as in Fig. 6.

hunter harvests in the presence of abundant predators (Hayes et al. 2003). Nilsen et al. (2005) suggested that with the recolonization of wolf populations in Scandinavia, the size

of moose harvest quotas should be reduced to avoid reduction in prey abundance.

Besides predation, stochasticity was found to negatively influence the total yield as well as the optimal yield of bulls, a result consistent with the theoretical predictions by Xu et al. (2005). These results have important implications for harvest policy and boreal moose management. Because predation and stochasticity increase the likelihood that a harvest policy might unintentionally drive an animal population to undesirably low levels (Lande et al. 1995, Kokko et al. 1997, Caswell 2001), care should be taken when setting harvest quotas. We recommend using population models and to set harvest levels based on the mean results from numerical simulations over a large number of years. This caveat is especially important in context of increasing variability in vital rates associated with climate change (Boyce et al. 2006).

Our matrix population model was based on the assumption that a shortage of bulls did not influence moose reproduction. This appears to be true unless the ratio of cows to bulls becomes excessively skewed. Most North American moose management strategies selectively harvest bulls (Stewart 1985, Schwartz 1992), resulting in a skewed sex ratio toward females (Markgren 1969, Bubenik 1987). In this case, extreme sex ratios >10 cows/bull may influence mating success (Thomson 1991, Stephenson et al. 1995, Laurian et al. 2000). Solberg et al. (2002) found that the pregnancy rates among young females were reduced in populations with a severely female-biased sex ratio, and Saether et al. (2003) found delayed parturition dates and subsequently reduced body mass of calves during the subsequent winter.

Several model parameters were obtained by model fitting. Because our data sets spanned only a few years, the precision of parameter estimation was generally low. Nevertheless, our model worked well for the 3 WMUs that we studied with moose survey data lying be-

tween the 5th and 95th percentiles of the model predictions. As additional data are accumulated on these populations, confidence in the performance of the models would be expected to improve (Walters 1986, Milner-Gulland et al. 2004, Varley and Boyce 2006). We note some differences in parameter estimates among WMUs, which were possibly attributable to variation caused by undocumented predation or aboriginal harvest, or simply small sample size.

Our intent in developing this model was to provide a tool for moose management in Alberta where data are limited to those that we incorporated as inputs into this model. We have constructed this model as an algorithm that can be interfaced with the Alberta Fisheries and Wildlife Management Information System (FWMIS) to facilitate easy application by managers who are responsible for setting moose harvest quotas. The software can be modified easily for applications elsewhere. Further work could explore management for trophy bulls. We also encourage further research on error propagation and sampling designs for reliable prediction.

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APPENDIX 1

This appendix is to derive the relationships between some of the model parameters using the condition that the modeled population represented by equation (2) will stay at carrying capacity with stable age distribution when there is no harvesting. The transition matrix at carrying capacity then becomes:

$$\mathbf{A}_t \equiv \mathbf{A} = \begin{pmatrix} 0 & \alpha_0 & 0 \\ \delta S_{CF} e^{-\alpha_{CF}} & S_F & 0 \\ (1-\delta)S_{CM} e^{-\alpha_{CM}} & 0 & S_M \end{pmatrix} \quad (\text{S1})$$

where the dominant eigenvalue is equal to 1.0. n_y^* , n_f^* , n_m^* are abundances of calves, females, and males at carrying capacity. Because $\mathbf{A} \begin{pmatrix} n_y^* \\ n_f^* \\ n_m^* \end{pmatrix} = 1 \begin{pmatrix} n_y^* \\ n_f^* \\ n_m^* \end{pmatrix}$, we designate $o_{fy} = n_f^* / n_y^*$ and $o_{my} = n_m^* / n_y^*$ have the following constraints for α_i ($i = 0, CF, CM$):

$$\alpha_0 = 1/o_{fy} \quad (\text{S2})$$

$$\alpha_{CF} = \ln \left(\frac{\delta S_{CF}}{(1-S_F)o_{fy}} \right) \quad (\text{S3})$$

$$\alpha_{CM} = \ln \left(\frac{(1-\delta)S_{CM}}{(1-S_M)o_{my}} \right) \quad (\text{S4})$$

α_i ($i = 0, CF, CM$) should be positive, otherwise populations go through positive density dependence in recruitment or survival.

APPENDIX 2

This appendix presents the equations (deterministic as well as stochastic) derived from equation (2) which we use to estimate model parameters and conduct model simulations. Rewrite equation (2) as:

$$n_{y,t+1} = \alpha_0 \exp \left(p \left[1 - \left(\frac{N_t}{K} \right)^{\gamma_0} \right] \right) n_{f,t} - H_{y,t} \quad (\text{S5})$$

$$n_{f,t+1} = \delta \frac{S_{CF}}{\exp \left(\alpha_{CF} \left(\frac{N_t}{K} \right)^{\gamma_{CF}} \right)} n_{y,t} + S_F n_{f,t} - H_{f,t} \quad (\text{S6})$$

$$n_{m,t+1} = (1-\delta) \frac{S_{CM}}{\exp \left(\alpha_{CM} \left(\frac{N_t}{K} \right)^{\gamma_{CM}} \right)} n_{y,t} + S_M n_{m,t} - H_{m,t} \quad (\text{S7})$$

To connect the deterministic model with time-series data and estimate model parameters, we add noise on a logarithmic scale. The noise structure is realistic and corresponds to environmental-type fluctuations (Dennis et al. 1991, 1995). The variability component due to environmental fluctuations is expected to outweigh the component due to demographic fluctuations at large population sizes (Dennis and Costantino 1988). The corresponding stochastic model becomes:

$$n_{y,t+1} = \left\{ \alpha_0 \exp \left(p \left[1 - \left(\frac{N_t}{K} \right)^{\gamma_0} \right] \right) n_{f,t} - H_{y,t} \right\} \exp(E_{y,t}) \quad (\text{S8})$$

$$n_{f,t+1} = \left\{ \delta - \frac{S_{CF}}{\exp \left(\alpha_{CF} \left(\frac{N_t}{K} \right)^{\gamma_{CF}} \right)} n_{y,t} + S_F n_{f,t} - H_{f,t} \right\} \exp(E_{f,t}) \quad (\text{S9})$$

$$n_{m,t+1} = \left\{ (1-\delta) \frac{S_{CM}}{\exp \left(\alpha_{CM} \left(\frac{N_t}{K} \right)^{\gamma_{CM}} \right)} n_{y,t} + S_M n_{m,t} - H_{m,t} \right\} \exp(E_{m,t}) \quad (\text{S10})$$

Take a logarithmic transformation and substitute equations (S3)-(S4) into equations (S9)-(S10), to yield the following stochastic model after rearrangement:

$$\ln(n_{y,t+1}) = \ln \left\{ \alpha_0 \exp \left(p \left[1 - \left(\frac{N_t}{K} \right)^{\gamma_0} \right] \right) n_{f,t} - H_{y,t} \right\} + E_{y,t} \quad (\text{S11})$$

$$\ln(n_{f,t+1}) = \ln \left\{ \delta - \frac{S_{CF}}{\exp \left(\ln \left(\frac{\delta S_{CF}}{(1-S_F) \rho_{fy}} \right) \left(\frac{N_t}{K} \right)^{\gamma_{CF}} \right)} n_{y,t} + S_F n_{f,t} - H_{f,t} \right\} + E_{f,t} \quad (\text{S12})$$

$$\ln(n_{m,t+1}) = \ln \left\{ (1-\delta) \frac{S_{CM}}{\exp \left(\ln \left(\frac{(1-\delta) S_{CM}}{(1-S_M) \rho_{my}} \right) \left(\frac{N_t}{K} \right)^{\gamma_{CM}} \right)} n_{y,t} + S_M n_{m,t} - H_{m,t} \right\} + E_{m,t} \quad (\text{S13})$$

thereby producing a nonlinear, multi-variable autoregressive model. Development of statistical methods for nonlinear autoregressive models has received much attention in recent years (Tong 1990). $\mathbf{E}_t = [E_{y,t}, E_{f,t}, E_{m,t}]'$ is a random noise vector and is assumed to have a trivariate normal distribution with a mean vector of $\mathbf{0}$ and a variance-covariance matrix of Σ . Diagonal elements of Σ are represented by variances of $\mathbf{E}_y = [E_{y,1}, E_{y,2}, \dots]$, $\mathbf{E}_f = [E_{f,1}, E_{f,2}, \dots]$, and $\mathbf{E}_m = [E_{m,1}, E_{m,2}, \dots]$. Off-diagonal elements of Σ are represented by covariances among \mathbf{E}_y , \mathbf{E}_f , and \mathbf{E}_m . E_1 , E_2 , and $E_{..}$ are assumed to be uncorrelated.

Conditional least squares (CLS) was used to estimate the parameters o_{my} and o_{fy} and in equations (S12) and (S13). CLS methods relax many distributional assumptions about the noise variables in the vector \mathbf{E}_t (Klimko and Nelson 1978, Tong 1990). CLS estimates are consistent (converge to the true parameters as sample size increases), even if \mathbf{E}_t is non-normal and autocorrelated, provided the stochastic model [equations (S11)-(S13)] has a stationary distribution.

CLS estimates are based on the sum of squared differences between the value of a variable observed at time t and its one-year ahead forecast value, given the observed state of the system at time $t-1$. To estimate o_{my} and o_{fy} there are 2 such conditional sums of squares:

$$Q_2(o_{fy}) = \sum_{t=1}^T E_{f,t}^2 = \sum_{t=1}^T \left(\ln(n_{f,t+1}) - \ln \left\{ \delta \frac{S_{CF}}{\exp \left(\ln \left(\frac{\delta S_{CF}}{(1-S_F) b_{fy}} \right) \left(\frac{N_t}{K} \right)^{\gamma_{CF}} \right)} n_{y,t} + S_F n_{f,t} - H_{f,t} \right\} \right)^2 \quad (\text{S14})$$

$$Q_3(o_{my}) = \sum_{t=1}^T E_{m,t}^2 = \sum_{t=1}^T \left(\ln(n_{m,t+1}) - \ln \left\{ (1-\delta) \frac{S_{CM}}{\exp \left(\ln \left(\frac{(1-\delta) S_{CM}}{(1-S_M) b_{my}} \right) \left(\frac{N_t}{K} \right)^{\gamma_{CM}} \right)} n_{y,t} + S_M n_{m,t} - H_{m,t} \right\} \right)^2 \quad (\text{S15})$$

Here $n_{f,t+1}$ and $n_{m,t+1}$, $t = 1, \dots, T-1$ are the observed census counts for the female and male stages. Parameters δ , K , S_{CF} , S_{CM} , S_F , S_M , λ_{CF} , λ_{CM} are prefixed, correspondingly:

$$Q_1 = \sum_{t=1}^T E_{y,t}^2 = \sum_{t=1}^T \left(\ln(n_{y,t+1}) - \ln \left\{ \alpha_0 \exp \left(p \left[1 - \left(\frac{N_t}{K} \right)^{\gamma_0} \right] \right) n_{f,t} - H_{y,t} \right\} \right)^2 \quad (\text{S16})$$

The noise variances and covariance (diagonal and off-diagonal elements in the variance-covariance matrix Σ of \mathbf{E}_t) were estimated using the conditional residuals (Dennis et al. 1995).

If the time-series of observed census counts are long enough (roughly over 30 yr), it is possible to estimate all model parameters that appear only in 1 of the 3 equations [(S11)-(S13)] by using CLS. Unfortunately, our census counts are very short (5 yr for WMU 346 and 350). When data are limited, as in our examples, we recommend estimating as many model parameters as possible using empirical data collected from demographic studies, and to leave those parameters that are difficult to estimate for estimation by model fitting.