



Managing moose harvests by the seat of your pants



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ABSTRACT

Moose populations are managed for sustainable yield balanced against costs caused by damage to forestry or agriculture and collisions with vehicles. Optimal harvests can be calculated based on a structured population model driven by data on abundance and the composition of bulls, cows, and calves obtained by aerial-survey monitoring during winter. Quotas are established by the respective government agency and licenses are issued to hunters to harvest an animal of specified age or sex during the following autumn. Because the cost of aerial monitoring is high, we use a Management Strategy Evaluation to evaluate the costs and benefits of periodic aerial surveys in the context of moose management. Our on-the-fly “seat of your pants” alternative to independent monitoring is management based solely on the kill of moose by hunters, which is usually sufficient to alert the manager to declines in moose abundance that warrant adjustments to harvest strategies. Harvests are relatively cheap to monitor; therefore, data can be obtained each year facilitating annual adjustments to quotas. Other sources of “cheap” monitoring data such as records of the number of moose seen by hunters while hunting also might be obtained, and may provide further useful insight into population abundance, structure and health. Because conservation dollars are usually limited, the high cost of aerial surveys is difficult to justify when alternative methods exist.

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1. Introduction

Expenditure for wildlife monitoring is an optimization problem with costs competing for alternative conservation needs such as habitat management and protection (Nichols and Williams, 2006; McDonald-Madden et al., 2010; Possingham et al., 2012). For monitoring to be of value it should have direct consequences for resource management. One of the strongest motivations for monitoring is active adaptive management where monitoring results are used to iteratively enhance management (Nichols and Williams, 2006; Williams, 2011; Possingham et al., 2012).

Moose (*Alces alces*) populations are managed for sustainable yield throughout the species' range in North America, Europe and Asia. Moose are valued for meat, recreation, and non-consumptive use (Mattsson, 1990; Adamowicz et al., 1991). However, high moose density can lead to substantial costs to the forest industry (Hörnberg, 2001) and vehicle collisions (Huijser et al., 2009) so intermediate densities are optimal (Månsson et al., 2011). Hence there is a motivation for monitoring to identify the best current

harvest policy as well as to reduce uncertainty for future moose management decisions, i.e., “perfectly optimal active adaptive management” (Rout et al., 2009). A structured population model is required to capture the dynamics of the stage- and sex-structured population and restricted harvest quotas. Composition of the fall-season harvest can be managed by issuing hunting permits allowing a hunter to kill a calf, cow, or antlered bull. Likewise, aerial-monitoring data are recorded according to the number of calves, cows, and antlered males in the herd.

Aerial surveys are the Gold Standard for the estimation of moose populations (Ronnegard et al., 2008; Månsson et al., 2011) and the current method used in Alberta is a modified version of the Gasaway et al. (1986) method (Lynch and Shumaker, 1995). In some landscapes distance sampling (Buckland et al., 2001) from a helicopter can be more cost effective, and this method is being explored by Alaska (Nielson et al., 2006) and Alberta (W. Peters, pers. comm.). However, either of the aerial survey methods is expensive, costing on average \$60 000 for each of Alberta's 99 wildlife management units (WMUs) where population estimates are conducted (R. Anderson, Alberta Conservation Association, pers. comm.). A survey of all 99 WMUs would cost nearly \$6 million annually but staff and allocated funds are insufficient to achieve this sampling intensity, and currently only 9–11 WMUs are surveyed in any year.

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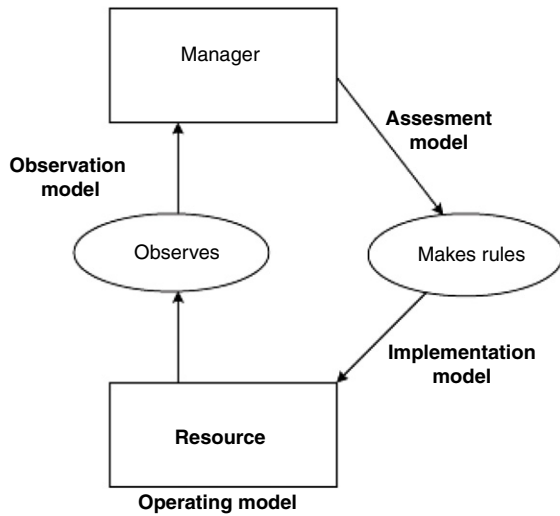


Fig. 1. A simplified Management Strategy Evaluation for Alberta moose harvests as typically used in the evaluation of fisheries. Source: Chart adapted from Milner-Gulland, 2010.

An alternative to aerial survey is to simply monitor harvests by hunters, i.e., managing by the “seat of your pants”, with no independent direct monitoring of the population (Pople, 2008; Pople et al., 2009)—a standard practice in fisheries. From harvest data we obtain a crude index of abundance based on an estimate of the probability of hunter success or the kill per unit effort (KPUE) analogous to catch per unit effort in fisheries (Crête and Dussault, 1987; Crichton, 1993; Hatter, 2001; Schmidt et al., 2005). This is measured in terms of the proportion of hunters who harvest a moose and the number of hunter days in the field to harvest a moose. Harvest data are inexpensive to obtain, in Alberta costing only \$0.60 per hunter surveyed (R. Corrigan, Alberta Fish and Wildlife, pers. comm.), but have low precision for estimating abundance or trend (Hatter, 2001; Schmidt et al., 2005). The tradeoff is obtaining infrequent observations by aerial survey versus imprecise data from harvest monitoring (Hauser et al., 2006; Pople, 2008).

Our objective is to evaluate the entire moose harvesting system including monitoring, demography, costs, and benefits, for one Wildlife Management Unit. We compare alternative harvesting strategies for their ability to achieve harvests near optimum, and we challenge the efficacy of expensive monitoring methods. We conduct a simulation study to evaluate aerial survey monitoring versus a KPUE monitoring scheme and to assess their cost effectiveness for moose population management in Alberta, Canada.

2. Model formulation

We structured our analysis around a Management Strategy Evaluation (MSE), a population simulation method developed by the scientific committee of the International Whaling Commission during the 1980s and 1990s (Boyce, 2000), and subsequently applied in a number of fisheries (Milner-Gulland, 2010). The basic structure of the MSE is illustrated in Fig. 1, containing 4 modules or subprograms. Uncertainty enters the system at each step of the process, e.g., stochastic vital rates in the population model (Boyce et al., 2006), error in estimating population parameters from sampling and error in detection probability, stochastic hunter success driven by fall weather conditions, and error in hunter-caused mortality attributable to inaccurate reporting and wounding loss (Gasaway et al., 1992; Engen et al., 1997).

The core population dynamics model is an age/sex-structured projection matrix (Lefkovich, 1965) allowing for typical moose

classification as the number of calves, $n_{y,t}$, cows, $n_{f,t}$, and antlered males, $n_{m,t}$:

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

where R_t (Eq. (2)) is the recruitment rate at time t (early to mid-winter), δ is the proportion of calves that are females, and $S_{CF,t}$ and $S_{CM,t}$ are density-dependent probabilities of survival for calves to yearlings at time t , for CF and CM female and male calves (Eq. (3)). S_F and S_M are survival probabilities for cows and antlered males. We can express Eq. (1) in matrix notation as

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

We assumed adult survival to be density independent (Eberhardt, 2002) but with density-dependent functions influencing R_t , $S_{CF,t}$, and $S_{CM,t}$ as follows:

$$R_t = \alpha_0 \exp \left(p \left[1 - \left(\frac{N_t}{K_t} \right)^{\gamma_0} \right] \right) \quad (2)$$

$$S_{i,t} = \frac{S_i}{\exp \left(\alpha_i \left(\frac{N_t}{K_t} \right)^{\gamma_i} \right)} \quad (i = CF, CM). \quad (3)$$

Here N_t is the population size at time t ; K_t is time-varying carrying capacity; the highest recruitment, $R^* = \alpha_0 \exp(p)$, occurs when there is no density dependence, i.e., $\lim N_t \downarrow 0$; S_i ($i = CF, CM$) are survival rates of female calves and male calves likewise at low population density; γ_i ($i = 0, CF, CM$) is the density-dependence exponent for recruitment and survival; and α_i ($i = 0, CF, CM$) are coefficients relating to the relative abundance of the 3 stages at K_t (Xu and Boyce, 2010). Justification for the density-dependent functions comes from the literature (Boyce et al., 1999; Eberhardt, 2002; Bonenfant et al., 2009; Xu and Boyce, 2010); the form of the survival function is that used by Clutton-Brock et al. (2002).

In density-independent models, sensitivity and elasticity analyses indicate how the asymptotic population growth rate λ can change as different parameters are perturbed (de Kroon et al., 1986; Caswell, 2001), and form the basis for efficient population management decisions when costs are included (Baxter et al., 2006). For stable density-dependent models, however, the asymptotic growth rate is $\lambda_0 = 1$ and perturbation analysis might focus usefully on other indicators of population change. For example, meaningful perturbation analysis can be performed by focusing on the sensitivity and elasticity of the invasion exponent (λ_t) to changes in the matrix elements. For density-dependent models with attractors that are stable equilibria (as here), it holds that

$$\log \lambda_t = \log \lambda(\mathbf{A}_n^*) \quad (4)$$

where (\mathbf{A}_n^*) indicates the dominant eigenvalue of \mathbf{A} calculated at the equilibrium population (Caswell and Takada, 2004). Furthermore, for long-lived iteroparous species such as moose, the elasticities of the density-dependent matrix at equilibrium are reliable estimates of the elasticities of the invasion exponent (Caswell and Takada, 2004). For our moose harvesting system we calculated an elasticity matrix at equilibrium to identify where harvests might have the most serious consequences for population resilience.

Process variance in the model enters the system through inter-annual variability in carrying capacity, which is consistent with ecological processes in moose populations (Bowyer et al., 1999; Brown, 2011). Therefore, stochasticity influenced vital rates through its effect on Eqs. (2) and (3) and we iterated through different variances in K until the variance in modeled vital

rates aligned closely with the process variance in vital rates reconstructed for this moose herd (Xu and Boyce, 2010).

A column vector of harvests is subtracted from the right-hand side of Eqs. (1)/(1a), giving:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t - \mathbf{h}_t \quad (5)$$

where

$$\mathbf{h}_t = (H_{y,t}, H_{f,t}, H_{m,t})^T \quad (5a)$$

and $H_{y,t}$, $H_{f,t}$, and $H_{m,t}$ refer to harvest mortality of calves (sexes combined), cows, and antlered males, respectively. These $H_{i,t}$ are random variables that are the sum of hunter kill and wounding loss (estimated by Gasaway et al., 1992) in the t -th year. Hunter kill is the product of the purchased quota of licenses and hunter success; only a single moose may be harvested by a hunter each year.

Potential yields for licensed moose hunters are reduced by aboriginal harvests (Lynch, 2006) and wolf (*Canis lupus*) predation. In our simulations we assumed non-selective aboriginal harvests averaging 4% of population size, and wolf predation was modeled using a Holling Type III (sigmoidal) functional response (Varley and Boyce, 2006) with wolf densities and diets estimated based on recent studies of wolf predation in Alberta (Webb et al., 2008; Latham et al., 2011).

Monitoring data form the basis for the observation model (Fig. 1), and we use estimates of population size and herd composition data from aerial survey (Lynch and Shumaker, 1995; Nielson et al., 2006) for stage-structured monitoring data, or harvest data (Schmidt et al., 2005) from an e-mail survey of hunters for “seat of your pants” monitoring. In Alberta harvest surveys are performed by IBM (also contracted by the provincial government to issue hunting licenses). Hunter compliance in harvest monitoring has been remarkably high (~90%), but as of 2011 only 60% of the hunters have e-mail addresses recorded in IBM’s database (Jim Allen, *pers. comm.*). Whereas monitoring by aerial survey is done on average only once every 10 years, harvest monitoring occurs annually.

Wildlife biologists working for Alberta’s Ministry of Sustainable Resource Development are charged with interpreting the results of the population model and the observation data to establish a harvest quota, which is the maximum number of moose hunting licenses issued for each WMU. We have modeled this process as an assessment model that sets the harvest rule (Milner-Gulland, 2010, Fig. 1). To complete the MSE, this then feeds into the harvesting vector (Eq. (4)) where harvest quotas ultimately determine $H_{i,t}$. Finally, to achieve learning in the adaptive management process (Varley and Boyce, 2006; Williams, 2011), estimates of vital rates or other model parameters are updated when justified based on data collected during the previous year. Ultimately this entire process would be conducted for each of 99 monitored WMUs in the province; we focus here on one large representative WMU for demonstration purposes.

2.1. Model analysis

To evaluate alternative monitoring schemes, the MSE process was conducted for simulated aerial survey estimates assuming 90% confidence intervals of $\pm 20\%$ as typical for moose data collected by the Alberta Conservation Association that conducted the surveys during 2008–2011. We assume unbiased estimates of true population size once every 10 years, and we apply the harvest rule to this estimate maintaining the same quota until the next aerial survey is conducted after 10 yrs. This harvest rule naturally creates temporal autocorrelation in the sampling error.

For our “seat of your pants” model for harvest management, we record only the kill of moose by stage class as registered by the IBM hunter survey without estimating abundance or herd composition

using aerial survey. IBM’s hunter survey obtains estimates of the proportion of hunters who kill a moose (hunter success) and the number of days spent hunting per kill which is a measure of kill per unit effort (KPUE). Hatter (2001) and Schmidt et al. (2005) note that KPUE underestimates declines in abundance so adjustments to harvest based on KPUE will fluctuate less than population size. This is partly attributable to a hunter’s effort being terminated with the harvest of a moose (Schmidt et al., 2005). KPUE is correlated with moose abundance but error is high, e.g., in Newfoundland only 32% of the variance in KPUE could be attributed to abundance (Fryxell et al., 1988). However, the relationship is almost certainly nonlinear (Crête et al., 1981; Fryxell et al., 1988) and much of the variation can be modeled using time-to-event Weibull regression with covariates including hunter density, mode of transportation, weather, use of guiding services, density of roads, and landscape characteristics (Schmidt et al., 2005).

We have simulated the moose population, monitoring, and harvesting system for WMU 544 in north-central Alberta, a large area (7177 km²) in the center of the distribution of moose in Alberta. We modeled the MSE to match closely the actual moose harvesting system considering (1) the current system of aerial monitoring with surveys conducted once every 10 years, (2) quotas for hunting licenses issued proportional to the change in hunter success from 2 years previous to last year, (3) ramping up harvest rate during the first 10 years to about 30% below MSY followed by proportional changes in quota following approach #2 above, and (4) constant quota set to harvest 50% of all bulls—the optimal economic harvesting strategy determined by Xu and Boyce (2010).

We evaluated the outcome of alternative monitoring schemes based on costs and benefits with data obtained from respective government organizations.

3. Results

For our model (ignoring hunting) the equilibrium population vector is (484, 1143, 2106)^T (calculated by iteration; the superscript ^T indicates the transpose of a vector). The dominant eigenvalue of the matrix at this equilibrium is $\lambda(\mathbf{A}_{\mathbf{n}^*}) = 1$ as expected, and the elasticity matrix is

$$\begin{pmatrix} 0 & 0.0909 & 0 \\ 0.0909 & 0.8182 & 0 \\ 0 & 0 & 0 \end{pmatrix}. \quad (6)$$

The elasticity matrix indicates that the survival of adult females has the greatest effect on the population’s return to equilibrium. Although antlered male survival is indicated to have zero effect on the population, very low bull densities may give rise to a degree of frequency-dependence (see Caswell, 2008) or reduced recruitment (see Section 4).

The concave yield curves shown in Fig. 2 illustrate how yield can decline precipitously if harvests and the composition of the harvests deviate much from the optimum. Nevertheless, density dependence in vital rates ensures sustainable harvests except when harvests are exceptionally high. Concavity in the yield function resulted in yields that were reduced as a consequence of stochastic fluctuations in the environment (Engen et al., 1997; Saether et al., 2001; Xu et al., 2005).

For monitoring based on aerial survey, we assumed that population estimates would achieve the target precision of $\pm 20\%$, and that population estimates would be done at the current frequency of once every 10 years. Based on this monitoring scheme, we found that persistent populations could be maintained so long as bull harvests did not exceed 6% of total population size, or 43% of the available antlered moose. Population size was reduced as harvest rate increased (Fig. 3(a)), and the minimum number of antlered bulls in the WMU declined as harvests increased

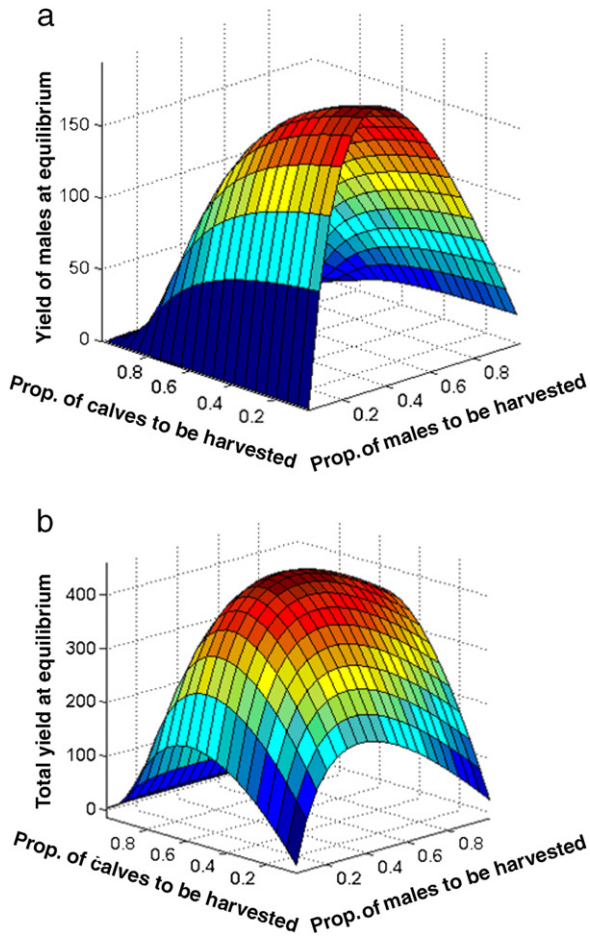


Fig. 2. Yield of the number of males (a) and total yield of harvested moose (b) at equilibrium as a function of proportion of calves and males to be harvested. Moose harvest yield was calculated using the structured deterministic model at Eqs. (1)–(3). We did not include any harvest of cow moose; note population resilience is highly sensitive to the harvest of cows (Eq. (6)).
Source: From Xu and Boyce, 2010.

(Fig. 3(b)). The coefficient of variation in N increases up to a harvest rate of about 5% and then becomes highly unpredictable (Fig. 3(c)), increasing the risk that bull numbers will be depleted. Because population estimates and herd composition were obtained every 10 years, harvest intensity can be set as a proportion of estimated population size (Fig. 3(d)).

In contrast, only crude estimates of abundance are available when setting harvest quotas based on hunter success or KPUE. We designed a rule for issuance of hunting licenses based on change in hunter success during the previous 2 years (Fig. 4). Expected hunter success was estimated based on the previous 18 years of harvest data. Observed change in hunter success was used to calculate the proportion change in hunting licenses to be sold. Harvest was simulated by multiplying the projected number of licenses to be sold times expected hunter success with additive error ($SE = 10.6$) based on a linear mixed model of hunter success versus population density with WMU as a random effect. Using this mixed models approach to the analysis of 99 WMUs in Alberta from 1993–2010 we determined that hunter success was a better predictor of density than was KPUE ($\Delta AIC = 89.2$). We did not use both hunter success and the number of days hunted to kill a moose in the same predictive model because collinearity resulted in an unstable model (see Fig. 5).

Implementing the proportional hunter success rule for determining the quota of hunting licenses, we observed that harvests oscillated likely due to the time-delay associated with calculating the

Table 1

Comparison of alternative harvest strategy rules, averaged over 95-year projections. Aerial survey monitoring was performed every 10 years. Licenses is the harvest quota, harvest rate is the proportion of the total population killed, \bar{N} is mean total population size, Min(bull) is the minimum number of bull moose during a 95-year projection, and is the mean annual harvest of antlered moose. The Δ -hunter-success rule adjusts the license quota to match exactly the change in hunter success from 2 years previously to last year. Constant quota is where 400 licenses are sold annually to approximate maximum sustained yield according to Xu and Boyce (2010).

Aerial survey monitoring						
Quota						
Licenses	Harvest rate	\bar{N}	CV(N)	Min(bull)	\bar{Kill}	CV(Kill)
10	0.00	2744	10.1%	550	13	0.0%
67	0.01	2715	10.2%	486	29	4.16%
208	0.03	2637	10.6%	311	90	16.58%
330	0.05	2540	10.6%	122	143	33.76%
379	0.065	2495	10.2%	95	164	43.07%
Δ -hunter-success rule						
Licenses	Bulls killed	\bar{N}	CV(N)	Min(bull)	\bar{Kill}	CV(kill)
173	13.3%	2639	10.9%	328	76	33.8%
Constant quota						
400	49.9%	2403	11.7%	65	177	24.1%

change, Δ , in hunter success from one year to the next (Fig. 6(a&d)). Indeed, such time-delay models are well known to generate oscillations and probably account for periodic fluctuations in the harvested population of elk (*Cervus elaphus*) at the National Elk Refuge in Wyoming (Sauer and Boyce, 1979). However, because this “seat of your pants” monitoring cannot provide information on herd composition and only crude indices of abundance, fine tuning of the harvests is not possible. Consequently, yields were lower and harvesting was sustainable (Table 1).

This Δ -hunter-success rule is contingent on current conditions, and clearly this rule produced lower than optimal moose harvest levels. So we increased harvests at 10% per year for the first 10 years of implementation after which we adopted the Δ -hunter-success rule. This increased the yield and obtained sustainable yields (Fig. 6(b)).

Finally we implemented the constant quota system setting the harvest based on the deterministic optimum identified by Xu and Boyce (2010) harvesting approximately 50% of the antlered bulls. This method produced the highest yields, lowest coefficient of variation in N and kill (Fig. 6(c)). Also, the oscillations in harvest caused by the Δ rule had disappeared (Fig. 6(f)). For the level of variance that we simulated in the system we did not observe overharvest, but hunter success and KPUE are readily monitored to identify potential excessive kills should they occur.

4. Discussion

Density dependence in the vital rates of moose populations affords population resilience so that sustainable yields can be had over a broad range of harvest rates (Boyce et al., 1999; Xu and Boyce, 2010). However, if harvests are excessive, populations and subsequent hunter success could decline precipitously. Without predation moose populations can sustain heavy harvest rates of 35%–44% (Bowyer et al., 1999). But given uncertainties in Alberta moose populations associated with aboriginal harvest of moose (Lynch, 2006) and predation by wolves and bears (Ballard et al., 1991; Gasaway et al., 1992), overharvest is a genuine threat. If harvests are monitored only every 10 years the population could be nearly extirpated before a decline was detected whereas annual monitoring of hunter success and KPUE can identify WMUs where overharvest might be occurring, followed by more detailed

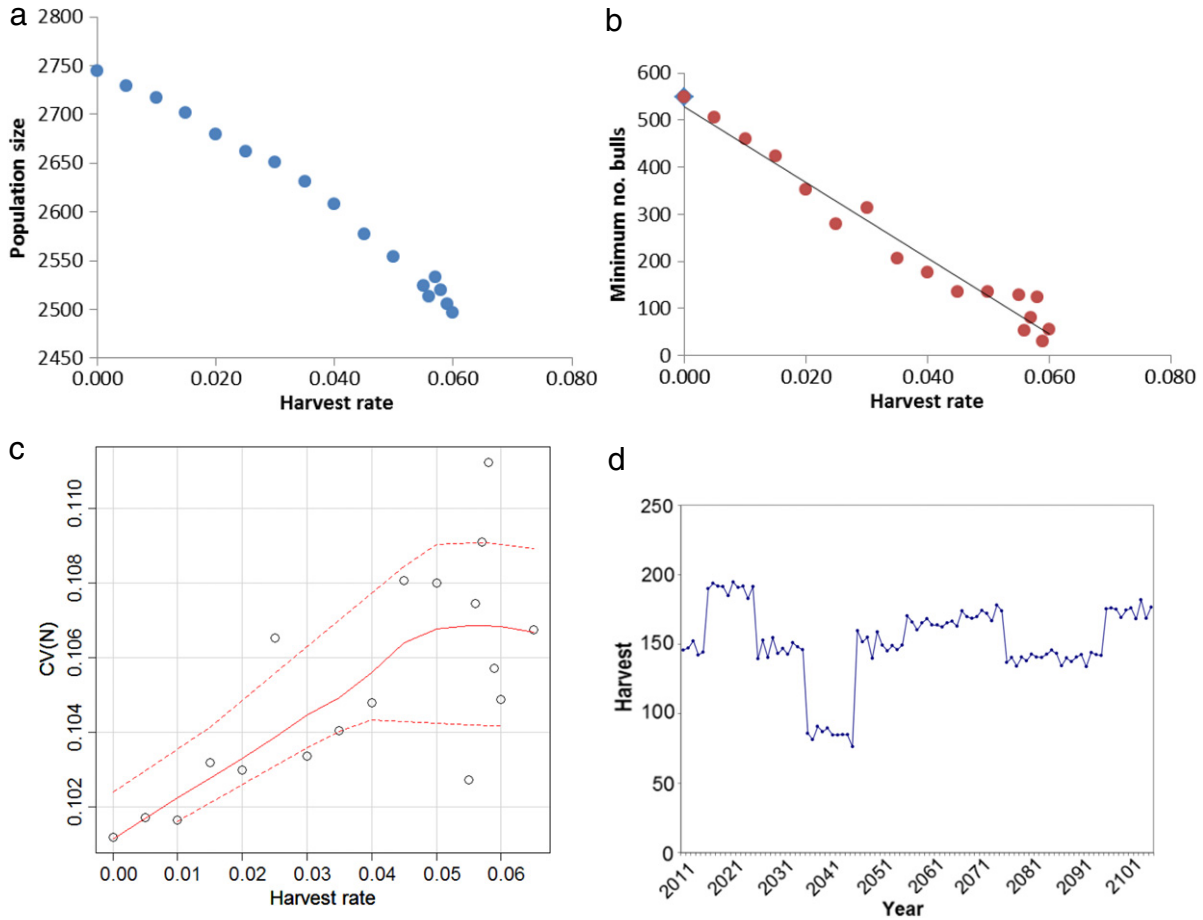


Fig. 3. Mean population size (a), minimum number of bulls (b), and the coefficient of variation in population size (c) as a function of harvest rate of antlered bull moose in Alberta's WMU 544 projected over 95 years with harvests, as shown in (d), based on aerial surveys conducted once every 10 yrs.

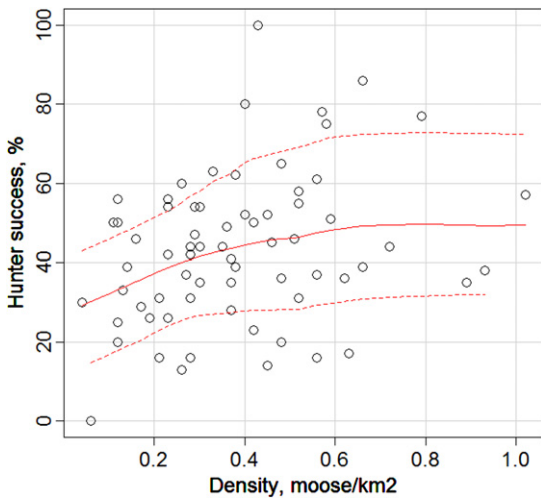


Fig. 4. Percent hunter success, y , as a function of the number of moose $\cdot \text{km}^{-2}$ in Alberta 1993–2010. Of the modeled variance in y , approximately 1/3 is attributable to a random effect associated with Wildlife Management Unit, WMU ($SE = 4.674$), and 2/3 to moose population density ($SE = 10.608$) based on a random-effects mixed model (R ver. 2.13.1, lme4).

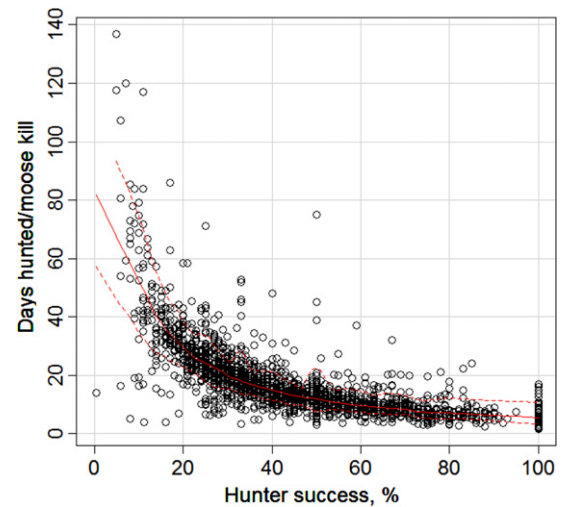


Fig. 5. Nonlinear relationship between the number of days hunted for each moose killed and probability of hunter success based on moose harvest data from 99 boreal, foothills, and montane region WMUs in Alberta 1993–2010.

investigation with aerial survey and herd classification. However, there is a trade-off because attempting adaptive management based on imprecise harvest data achieves only about 70% of the yields that could be sustained even with aerial surveys every

10 years. Using MSE facilitates easy evaluation of alternative rules for quota setting.

In most of Alberta harvests are restricted to antlered bulls only because aboriginal harvests and wolf predation are not monitored. But even with bulls-only restrictions, harvests can be excessive

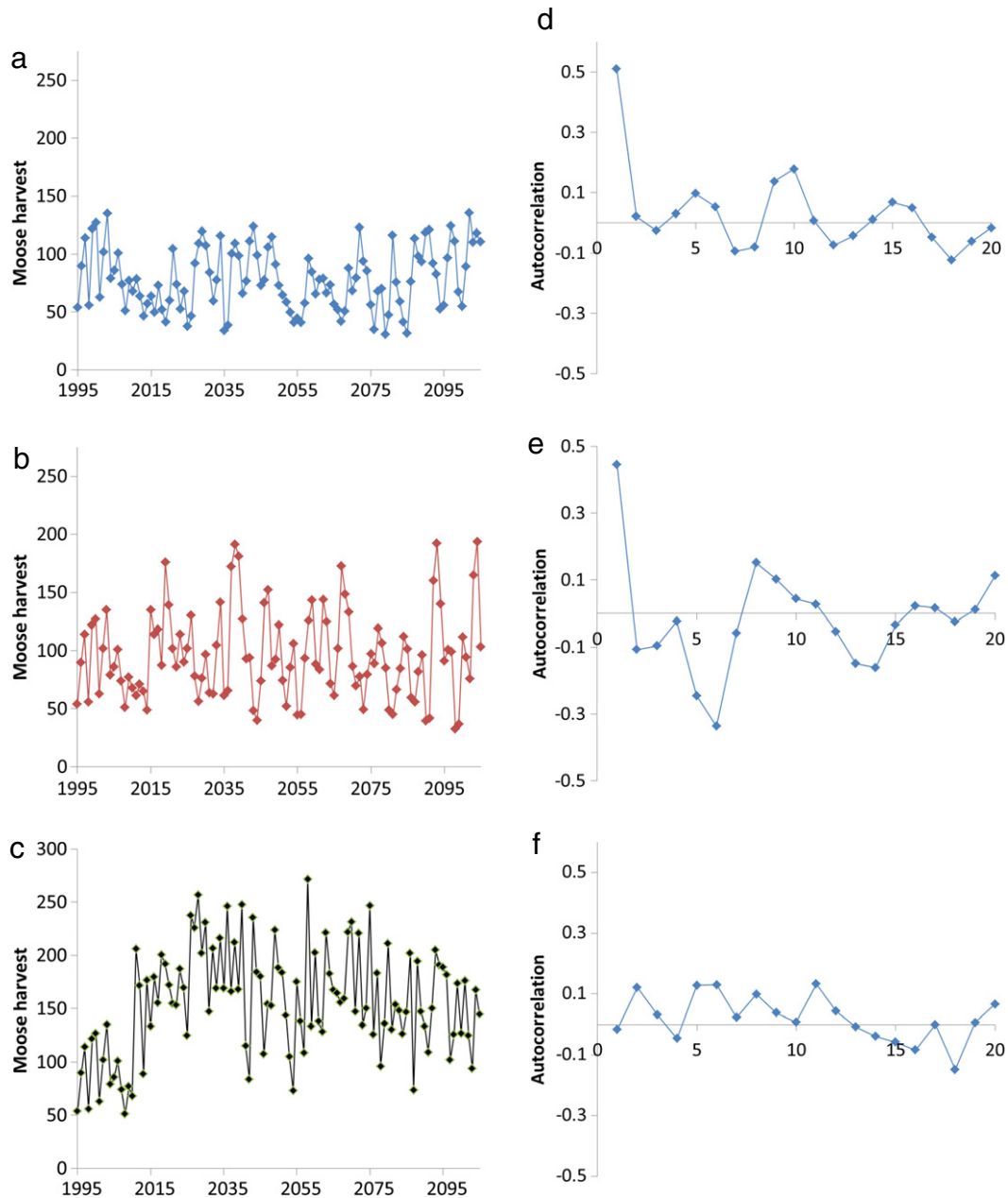


Fig. 6. Observed harvests of moose in WMU 544 for 1995–2010, and projected to 2105 based on a simulation using a Δ -hunter-success rule for issuing hunting licenses (a). Note autocorrelated oscillations (d) relative to the dynamics based on 10-year interval aerial survey monitoring in Fig. 3(d). Harvests of moose under the same rule set as at (a) except that the licenses issued were increased by 10% per year for the first 10 years (b), giving a higher baseline with a target of approximately 30% less than MSY to prevent overharvest in a stochastic environment (see Boyce, 2000). This still yields fewer animals harvested than can be obtained based on aerial survey monitoring, but the reduction in yield is <30% of that obtained with aerial surveys. Fixed harvest policy issuing 400 licenses each year without attempting adaptive adjustments in response to fluctuations in hunter success is at (c). The target harvest rate was identified from the deterministic model illustrated in Fig. 2 with about 50% of bulls being harvested each year. This strategy of issuing a fixed number of licenses actually performs well, and yields less variation in yields but less temporal autocorrelation (f) than either of the two previous rules.

because highly skewed sex ratios can result in some females going unbred (Rausch et al., 1974) or possibly missing an estrus resulting in late-born calves with a low probability of over-winter survival (Keech et al., 2000). Evidence for sex ratio effects on mating success appear mixed (Myserud et al., 2002; Solberg et al., 2002), but maintaining mature bulls in the herd has been associated with increased twinning and recruitment, especially in taiga habitats (Aitken and Child, 1993). Therefore, excessive harvests of bulls under infrequent aerial survey monitoring can risk rapid population declines. This occurs because errors in abundance estimates can result in overharvest that is then maintained for 10 years until another survey is scheduled.

Benefits from hunting come with the sale of moose hunting licenses totaling over \$960 000 and the value of moose harvests for meat. Body mass of adult male moose in Alberta averages 450 kg and 418 kg for adult females (Stelfox, 1993). Slaughter body weight is approximately 55% of live weight (Olausson and Skonhott, 2011). Although it is illegal to sell moose meat in North America, it is highly prized by hunters and the value of \$13.80 kg⁻¹ from Norway seems appropriate (Olausson and Skonhott, 2011). Based on the harvest of 8486 moose taken in Alberta during the 2010 hunting season, we calculated the total value of meat from harvested moose of approximately \$29.3 million. In addition to hunting for meat, approximately 5%–10% of the moose harvest is appropriated

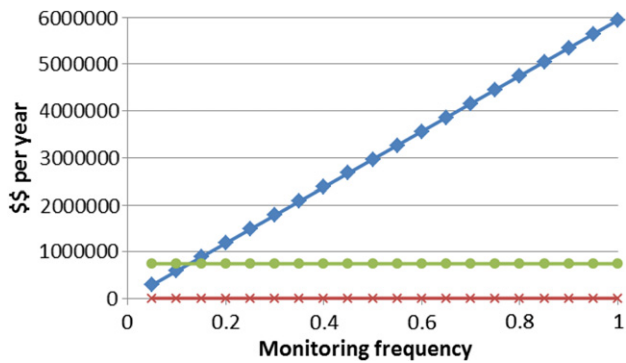


Fig. 7. Costs for aerial monitoring (◆) increase linearly with frequency, whereas annual costs of harvest monitoring barely register at \$9628 yr⁻¹ (×). Annual license revenue presuming approximately constant sales of moose hunting licenses (●) at \$749 330 could support aerial survey monitoring only once every 8 years even if all license revenues were allocated to aerial surveys.

for guided non-resident hunters who mostly target trophy bulls attracting revenues for guides and outfitters and a non-resident hunting license fee of \$135.31 compared with \$36.85 for resident hunters. We have ignored other economic and social benefits that could be included, e.g., expenditures by hunters, multiplier effects, non-consumptive values, or non-use (preservation) values (Adamowicz et al., 1991).

The cost of moose-vehicle collisions on rural highways in Alberta during 2007–2009 is approximately $\$64.4/3 = \21.5 million \cdot yr⁻¹ according to the Alberta Department of Transportation (M. Imran, unpublished data). We assume that the risk of a moose-vehicle collision is proportional to the abundance of moose (*sensu* (Olausson and Skonhoft, 2011)). In Scandinavia moose damage forest regeneration and plantings by browsing (Hörnberg, 2001), although this is not a significant issue on Crown lands in Alberta (Elston Dzus, Alberta Pacific Forest Industries, pers. comm.). Nevertheless, moose can cause significant damage to hybrid poplar plantations and sometimes damage fences or crops. For these reasons maintaining intermediate populations of moose that are sufficient to sustain hunter harvest while minimizing adverse impacts is desirable.

Benefit-cost calculations for moose hunting in Alberta are driven largely by benefits from the value of meat and license revenues minus costs resulting from moose-vehicle collisions and monitoring. Given 2010 harvests and recent vehicle collisions, the benefits are approximately (\$29.3 million meat + \$749 330 licenses =) \$30 049 330 minus estimated costs of (\$21.5 million vehicle collisions + \$600 000 aerial survey + \$9628 harvest monitoring =) \$22 109 628 yielding a net benefit of \$7 939 702 (see Fig. 7). These calculations do not include the economic value of outfitters and guides who manage moose hunting for an average of 750 non-resident hunters generating approximately \$3.5 million \cdot yr⁻¹ for trophy moose hunts.

Supplemental sources of information beyond the harvest and KPUE estimates might improve decision making. Additional indices of abundance have been used for moose populations including hunter observations of moose (Solberg and Saether, 1999), pellet-group counts (Ronnegard et al., 2008; Månsson et al., 2011), and frequency of road kills (Hicks, 1993; Rolandsen et al., 2011).

Based on simple economics alone one might argue that the societal value of moose is sufficient to justify a tenfold increase in monitoring costs to perform aerial surveys for each WMU annually. With these data Alberta Fish and Wildlife could do a more precise job of managing moose harvests to minimize vehicular collisions and to maximize yields for hunters. Alternatively, one might argue that by engaging less-costly monitoring alternatives the net benefits from moose harvesting would be better invested in other

conservation actions such as habitat acquisition programs with greater rewards for biodiversity while concomitantly ensuring the long-term sustainability of moose populations in Alberta.

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References

- Adamowicz, W.L., Asafu-Adjaye, J., Boxall, P.C., Phillips, W.E., 1991. Components of the economic value of wildlife: an Alberta case study. *Can. Field-Nat.* 105, 423–429.
- Aitken, D.A., Child, K.N., 1993. Relationships between in utero productivity of moose and population sex ratios: an exploratory analysis. *Alces* 28, 175–187.
- Ballard, W.B., Whitman, J.S., Reed, D.J., 1991. Population-dynamics of moose in south-central Alaska. *Wildl. Monogr.* 114, 1–49.
- Baxter, P.W.J., McCarthy, M.A., Possingham, H.P., Menkhorst, P.W., McLean, N., 2006. Accounting for management costs in sensitivity analyses of matrix population models. *Conserv. Biol.* 20, 893–905.
- Bonenfant, C., Gaillard, J.M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L.E., Blanchard, P., Pettorelli, N., Owen-Smith, N., Du Toit, J., Duncan, P., 2009. Empirical evidence of density-dependence in populations of large herbivores. *Adv. Ecol. Res.* 41, 313–357.
- Bowyer, R.T., Nicholson, M.C., Molvar, E.M., Faro, J.B., 1999. Moose on Kalgin Island: are density-dependent processes related to harvest? *Alces* 35, 73–89.
- Boyce, M.S., 2000. Whaling models for conservation. In: Ferson, S., Burgman, M. (Eds.), *Quantitative Methods for Conservation Biology*. Springer-Verlag, New York, pp. 109–126.
- Boyce, M.S., Haridas, C.V., Lee, C., 2006. NCEAS working group on stochastic demography. *Demography in an increasingly variable world. Trends Ecol. Evol.* 21, 141–148.
- Boyce, M.S., Sinclair, A.R.E., White, G.C., 1999. Seasonal compensation of predation and harvesting. *Oikos* 87, 419–426.
- Brown, G.S., 2011. Patterns and causes of demographic variation in a harvested moose population: evidence for the effects of climate and density-dependent drivers. *J. Anim. Ecol.* 80, 1288–1298.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*, second ed. Sinauer Associates, Sunderland, Mass., USA.
- Caswell, H., 2008. Perturbation analysis of nonlinear matrix population models. *Demogr. Res.* 18, 59–115.
- Caswell, H., Takada, T., 2004. Elasticity analysis of density-dependent matrix population models: the invasion exponent and its substitutes. *Theor. Popul. Biol.* 65, 401–411.
- Clutton-Brock, T., Coulson, T.N., Milner-Gulland, E.J., Thomson, D., Armstrong, H.M., 2002. Sex differences in emigration and mortality affect optimal management of deer populations. *Nature (London)* 415, 633–637.
- Crête, M., Dussault, C., 1987. Using hunting statistics to estimate density, cow-calf ratio and harvest rate of moose in Quebec. *Alces* 23, 227–242.
- Crête, M., Taylor, R.J., Jordan, P.A., 1981. Optimization of moose harvest in southwestern Quebec. *J. Wildl. Manage.* 45, 598–611.
- Crichton, V., 1993. Hunter effort and observations—the potential for monitoring trends of moose populations: a review. *Alces* 29, 181–186.
- de Kroon, H., Plaisier, A., van Groenendael, J., Caswell, H., 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67, 1427–1431.
- Eberhardt, L.L., 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83, 2841–2854.
- Engen, S., Lande, R., Saether, B.-E., 1997. Harvesting strategies for fluctuating populations based on uncertain population estimates. *J. Theoret. Biol.* 186, 201–212.
- Fryxell, J.M., Mercer, W.E., Gellately, R., 1988. Population dynamics of Newfoundland moose using cohort analysis. *J. Wildl. Manage.* 52, 14–21.
- Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O., Larsen, D.G., 1992. The role of predation in limiting moose at low-densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr.* 120, 1–59.
- Gasaway, W.C., Dubois, S.D., Reed, D.J., Harbo, S.J., 1986. Estimating moose population parameters from aerial surveys. *Biol. Pap. Univ. Alaska* 22, 1–108.
- Hatter, I.W., 2001. An assessment of catch per unit effort to estimate rate of change in deer and moose populations. *Alces* 37, 71–77.

- Hauser, C.E., Pople, A.R., Possingham, H., 2006. Should managed populations be monitored every year? *Appl. Ecol.* 16, 807–819.
- Hicks, A.C., 1993. Using road-kills as an index to moose population change. *Alces* 29, 243–247.
- Hörnberg, S., 2001. Change in population density of moose (*Alces alces*) and damage to forests in Sweden. *For. Ecol. Manag.* 149, 141–151.
- Huijser, M.P., Duffield, J.W., Clevenger, A.P., Ament, R.J., McGowen, P.T., 2009. Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada; a decision support tool. *Ecol. Soc.* 14 (2), 15. [online] URL: <http://www.ecologyandsociety.org/vol14/iss2/art15/>.
- Keech, M.A., Bowyer, R.T., VerHoef, J.M., Boertje, R.D., Dale, B.W., Stephenson, T.R., 2000. Life-history consequences of maternal condition in Alaskan moose. *J. Wildl. Manage.* 64, 450–462.
- Latham, A.D.M., Latham, M.C., McCutchen, N.A., Boutin, S., 2011. Invading white-tailed deer change wolf-caribou dynamics in Northeastern Alberta. *J. Wildl. Manage.* 75, 204–212.
- Lefkovich, L.P., 1965. The study of population growth in organisms grouped by stage. *Biometrics* 21, 1–18.
- Lynch, G.M., 2006. Does first nation's hunting impact moose productivity in Alberta? *Alces* 41, 25–32.
- Lynch, G.M., Shumaker, G.E., 1995. GPS and GIS assisted moose surveys. *Alces* 31, 145–151.
- Månsson, J., Hauser, C.E., Andrén, H., Possingham, H.P., 2011. Survey method choice for wildlife management: the case of moose *Alces alces* in Sweden. *Wildl. Biol.* 17, 176–190.
- Mattsson, L., 1990. Moose management and the economic value of hunting: towards bioeconomic analysis. *Scand. J. For. Res.* 5, 575–581.
- McDonald-Madden, E., Baxter, P.W.J., Fuller, R.A., Martin, T.G., Game, E.T., Montambault, J., Possingham, H.P., 2010. Monitoring does not always count. *Trends Ecol. Evol.* 25, 547–550.
- Milner-Gulland, E.J., 2010. Integrating fisheries approaches and household utility models for improved resource management. *Proc. Natl. Acad. Sci. USA* 108, 1741–1746.
- Mysterud, A., Coulson, T., Stenseth, N.C., 2002. The role of males in the dynamics of ungulate populations. *J. Anim. Ecol.* 71, 907–915.
- Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. *Trends Ecol. Evol.* 21, 668–673.
- Nielson, R.M., McDonald, L.L., Kovach, S.D., 2006. Aerial line transect survey protocols and data analysis methods to monitor moose (*Alces alces*) abundance as applied on the Innoko National Wildlife Refuge, Alaska. http://www.west-inc.com/reports/moose_survey.pdf.
- Olaussen, J.O., Skonhøft, A., 2011. A cost-benefit analysis of moose harvesting in Scandinavia. A stage structured modelling approach. *Resour. Energy Econ.* 33, 589–611.
- Pople, A.R., 2008. Frequency and precision of aerial surveys for kangaroo management. *Wildl. Res.* 35, 340–348.
- Pople, A.R., Evans, M., Farroway, L., Gilroy, J., Grigg, G.C., Lundie-Jenkins, G., Payne, N., 2009. Using harvest statistics to monitor temporal variation in kangaroo density and harvest rate. In: Coulson, G., Eldridge, M. (Eds.), *Macropods. The Biology of Kangaroos, Wallabies and Rat-Kangaroos*. CSIRO Publishing, Melbourne, pp. 371–397.
- Possingham, H.P., Wintle, B.A., Fuller, R.A., Joseph, L.N., 2012. The conservation return on investment from ecological monitoring. In: Lindenmayer, D.B., Gibbons, P. (Eds.), *Biodiversity Monitoring in Australia*. CSIRO Publishing, Melbourne, pp. 49–61.
- Rausch, R.L., Sommerville, R.J., Bishop, R.H., 1974. Moose management in Alaska. *Nat. Can. (Que.)* 101, 705–721.
- Rolandson, C.M., Solberg, E.J., Herfindal, I., Van Moorter, B., Sæther, B.-E., 2011. Large-scale spatiotemporal variation in road mortality of moose—is it all about population density? *Ecosphere* 2, Art. 113 <http://dx.doi.org/10.1890/ES11-00169.1>.
- Ronnegard, L., Sand, H., Andrén, H., Månsson, J., Pehrson, A., 2008. Evaluation of four methods used to estimate population density of moose *Alces alces*. *Wildl. Biol.* 14, 358–371.
- Rout, T.M., Hauser, C.E., Possingham, H.P., 2009. Optimal adaptive management for the translocation of a threatened species. *Appl. Ecol.* 19, 515–526.
- Sæther, B.-E., Engen, S., Solberg, E.J., 2001. Optimal harvest of age-structured populations of moose *Alces alces* in a fluctuating environment. *Wildl. Biol.* 7, 171–179.
- Sauer, J.R., Boyce, M.S., 1979. Time series analysis of the National Elk Refuge census. In: Boyce M.S. and Hayden-Wing L.D. (Eds.), *North American Elk: Ecology, Behavior and Management*, University of Wyoming, Laramie, pp. 9–12.
- Schmidt, J.I., VerHoef, J.M., Maier, J.A.K., Bowyer, R.T., 2005. Catch per unit effort for moose: a new approach using Weibull regression. *J. Wildl. Manage.* 69, 1112–1124.
- Solberg, E.J., Loison, A., Ringsby, T.H., Sæther, B.-E., Heim, M., 2002. Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*. *Wildl. Biol.* 8, 117–128.
- Solberg, E.J., Sæther, B.-E., 1999. Hunter observations of moose *Alces alces* as a management tool. *Wildl. Biol.* 5, 107–117.
- Stelfox, J.B., 1993. *Hoofed Mammals of Alberta*. Lone Pine Publ., Edmonton, Alberta.
- Varley, N., Boyce, M.S., 2006. Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. *Ecol. Modell.* 193, 315–339.
- Webb, N.F., Hebblewhite, M., Merrill, E.H., 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. *J. Wildl. Manage.* 72, 798–807.
- Williams, B.K., 2011. Adaptive management of natural resources—framework and issues. *J. Environ. Manag.* 92, 1346–1353.
- Xu, C., Boyce, M.S., 2010. Optimal harvesting of moose in Alberta. *Alces* 46, 15–35.
- Xu, C., Boyce, M.S., Daley, D.J., 2005. Harvesting in seasonal environments. *J. Math. Biol.* 50, 663–682.