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Appendix 1

Transition matrices

As described in the manuscript, we used an 11×11 population projection matrix to model the effects of female harvest strategies on moose populations. The need to consider stage-specific population sizes at multiple times during the annual cycle resulted in decomposing the matrices to describe: 1) survival for the 3-month period from recruitment to pre-harvest

$$\mathbf{M}_{\text{PRE}} = \begin{bmatrix}
 S_{CS}^E & S_{CT}^E * (1 - S_{CT}^E) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & (S_{CT}^E)^2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & S_Y^E & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_{YA}^E * S_C^E & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_{YA}^E * (1 - S_C^E) & S_{YA}^E & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & S_{PA}^E * (S_C^E)^2 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 2 * S_{PA}^E * S_C^E * (1 - S_C^E) & S_{PA}^E * S_C^E & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & S_{PA}^E * (1 - S_C^E)^2 & S_{PA}^E * (1 - S_C^E) & S_{PA}^E & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{OA}^E * (S_C^E)^2 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 * S_{OA}^E * S_C^E * (1 - S_C^E) & S_{OA}^E * S_C^E & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{OA}^E * (1 - S_C^E)^2 & S_{OA}^E * (1 - S_C^E) & S_{OA}^E
 \end{bmatrix} \quad (\text{A1})$$

2) harvest survival for the cow-calf and unaccompanied cow harvests

$$M_{CCHRV} = \begin{bmatrix} S^{CCH} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S^{CCH} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S^{CCH} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S^{CCH} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad (A2)$$

and

$$M_{CNHRV} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S^{CNH} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S^{CNH} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S^{CNH} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S^{CNH} \end{bmatrix} \quad (A3)$$

respectively, and 3) survival for the remainder of the year

$$\mathbf{M}_{\text{POST}} = \begin{bmatrix}
0 & 0 & 0 & F_{YA_CS} & F_{YA_CS} & F_{PA_CS} & F_{PA_CS} & F_{PA_CS} & F_{PA_CS} & F_{OA_CS} & F_{OA_CS} & F_{OA_CS} \\
0 & 0 & 0 & F_{YA_CT} & F_{YA_CT} & F_{PA_CT} & F_{PA_CT} & F_{PA_CT} & F_{PA_CT} & F_{OA_CT} & F_{OA_CT} & F_{OA_CT} \\
G_C & G_C & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & S_{YA}^L * P_{YA} & S_{YA}^L * P_{YA} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & G_Y & S_{YA}^L * (1 - P_{YA}) & S_{YA}^L * (1 - P_{YA}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & G_{YA} * P_{PA} * w_{PA} & G_{YA} * P_{PA} * w_{PA} & S_{PA}^L * P_{PA} * w_{PA} & S_{PA}^L * P_{PA} * w_{PA} & S_{PA}^L * P_{PA} * w_{PA} & S_{PA}^L * P_{PA} * w_{PA} & 0 & 0 & 0 \\
0 & 0 & 0 & G_{YA} * P_{PA} * (1 - w_{PA}) & G_{YA} * P_{PA} * (1 - w_{PA}) & S_{PA}^L * P_{PA} * (1 - w_{PA}) & S_{PA}^L * P_{PA} * (1 - w_{PA}) & S_{PA}^L * P_{PA} * (1 - w_{PA}) & S_{PA}^L * P_{PA} * (1 - w_{PA}) & 0 & 0 & 0 \\
0 & 0 & 0 & G_{YA} * (1 - P_{PA}) & G_{YA} * (1 - P_{PA}) & S_{PA}^L * (1 - P_{PA}) & S_{PA}^L * (1 - P_{PA}) & S_{PA}^L * (1 - P_{PA}) & S_{PA}^L * (1 - P_{PA}) & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & G_{PA} * P_{OA} * w_{OA} & G_{PA} * P_{OA} * w_{OA} & G_{PA} * P_{OA} * w_{OA} & G_{PA} * P_{OA} * w_{OA} & S_{OA}^L * P_{OA} * w_{OA} & S_{OA}^L * P_{OA} * w_{OA} & S_{OA}^L * P_{OA} * w_{OA} \\
0 & 0 & 0 & 0 & 0 & G_{PA} * P_{OA} * (1 - w_{OA}) & G_{PA} * P_{OA} * (1 - w_{OA}) & G_{PA} * P_{OA} * (1 - w_{OA}) & G_{PA} * P_{OA} * (1 - w_{OA}) & S_{OA}^L * P_{OA} * (1 - w_{OA}) & S_{OA}^L * P_{OA} * (1 - w_{OA}) & S_{OA}^L * P_{OA} * (1 - w_{OA}) \\
0 & 0 & 0 & 0 & 0 & G_{PA} * (1 - P_{OA}) & G_{PA} * (1 - P_{OA}) & G_{PA} * (1 - P_{OA}) & G_{PA} * (1 - P_{OA}) & S_{OA}^L * (1 - P_{OA}) & S_{OA}^L * (1 - P_{OA}) & S_{OA}^L * (1 - P_{OA})
\end{bmatrix} \quad (\text{A4})$$

Stage-specific parameters used in the female-only, post-reproductive matrices are defined in Table A1 and values are given in Table A2.

During periods of female harvest population projections are as follows using the appropriate harvest matrix (M_{CCHRV} or M_{CNHRV}):

$$N_{t+1} = M_{\text{POST}} \times M_{\text{HRV}} \times M_{\text{PRE}} \times N_t \quad (\text{A5})$$

When female harvests are not occurring, the population projection is:

$$N_{t+1} = M_{\text{POST}} \times M_{\text{PRE}} \times N_t \quad (\text{A6})$$

Table A1. Definition of demographic parameters. For stages lasting more than one year, we partitioned survival within the stage and survival with growth to the next stage (Caswell 2001).

Parameter	Definition
S_x^E	early survival within stage x , recruitment to pre-harvest (3.5 months).
S_x^L	late survival within stage x , post-harvest to following recruitment (8.5 months)
G_x	late survival with growth to stage $x+1$
P_x	probability of parturition for ind in stage x
w_x	probability of twinning for ind in stage x
$F_{x_CS}^1$	production of single calf: $0.5 \times \{ [S_x^L \times P_x \times (1 - w_x)] + [G_x \times P_{x+1} \times (1 - w_{x+1})] \}$
$F_{x_CT}^1$	Production of twin calves: $0.5 \times [(S_x^L \times P_x \times w_x) + (G_x \times P_{x+1} \times w_{x+1})] \times 2$

¹assumes sex ratio parity of calves (Schwartz and Hundertmark 1993, Harris et al. 2008, Boertje et al. 2009)

Table A2. Parameter values.

Stage	S_x^E	S_x^L	G_x	F_{x_CS}	F_{x_CT}
Calf singleton (CS) ¹	0.709	0	0.705	0	0
Calf with twin (CT) ¹	0.703	0	0.711	0	0
Yearling (Y)	0.954	0	0.891	0	0
Young adult (YA)	0.994	0.662	0.324	0.225	0.025
Prime adult (PA)	0.982	0.838	0.119	0.327	0.076
Old adult (OA)	0.905	0.785	0	0.242	0.072

¹ Early calf survival is adjusted for cow survival. We assumed that early season calves would not survive if their dam died. We weighted adult cow survival by the SSD for cows with singletons or cows with twins, and used the resulting mean early season cow survival probabilities in our calculations of calf survival. This results in slightly different survival probabilities for singletons and calves with twins. Late season survival and transition to the yearling stage is then calculated as annual survival divided by early season survival.

Density-dependence of reproductive rates

Methods

We used data collected over a 50 year period (1960–2010; $n = 27$ years with estimates of both population density and twinning rate; ADF&G, Moose Management Reports and unpubl. data), where the density ranged from 0.09 to 0.75 moose km^{-2} , to examine density-dependent effects on parturition and twinning rates. We used linear regressions to independently examine the relationships between the natural log of parturition or twinning and female population size at times t , $t - 1$ and $t - 2$. Regressions did not include the effects of multiple years because of non-independence of population size across consecutive years. We found no evidence for density-dependence in parturition rates ($p > 0.10$), but twinning rates significantly declined with population size with time lags of 1 ($F_{1,23} = 7.69$, $p = 0.01$; Fig. A1) and 2 years ($F_{1,23} = 6.25$, $p = 0.02$).

We then incorporated the impact of density-dependent twinning into our harvest models. The population sizes of most relevance in our simulations are 7000 to 10 000 females, corresponding to twinning rates of 11 and 8%, respectively (Fig. A1). The twinning data were not stratified by cow age, however the majority of adult females will be prime age individuals due to the longer duration of this stage and mortality losses prior to reaching old age. Therefore, we used the regression as an estimate of prime adult twinning rate and added 3% to this for old adult twinning rate because this was the difference between prime and old adult twinning in the baseline data set (Table 2 in Doak et al. main text).

Results

Inclusion of this density dependence had very little impact on modelled outcomes. Without harvest, for a population of 7000, the density-dependent model would result in the annual production of 19 additional calves and a finite rate of increase of 1.0450 as compared to 1.0431 for the density-independent model; for a population of 10 000, the density-dependent model would result in the annual production of 26 fewer calves and a finite rate of increase of 1.0406 as compared to 1.0430 for the density-independent model. When we compare the harvest numbers necessary to meet the population objectives over five years, they are almost indistinguishable for the density-dependent and density-independent models (Fig. A2). Thus inclusion of observed levels of density-dependence in reproductive parameters had very little quantitative and no qualitative impact on our results and conclusions.

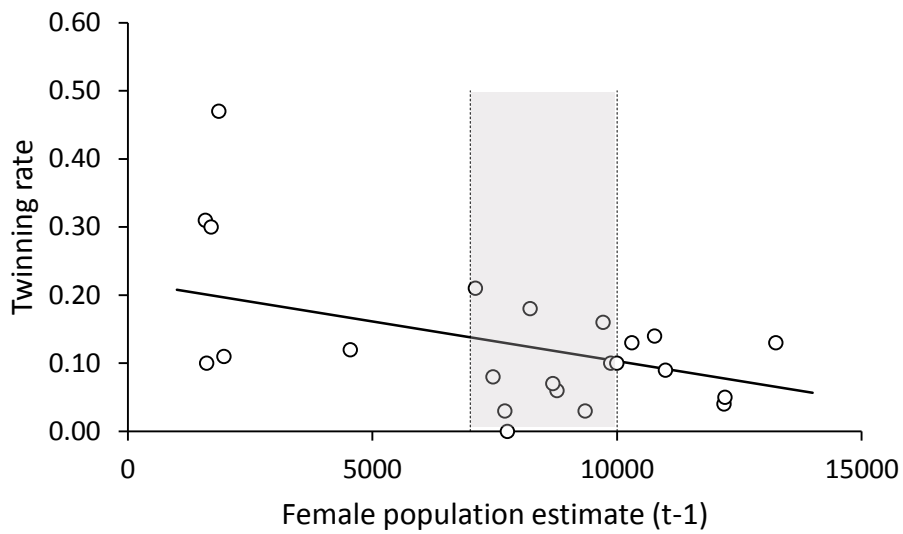


Figure A1. Relationship between twinning rate and female moose population size ($t - 1$) in Alaska GMU 20A during the period 1960–2010. Best fit line from a linear regression of \ln twinning rate on population size in the previous year. The shaded area indicates the range of population sizes considered in our models.

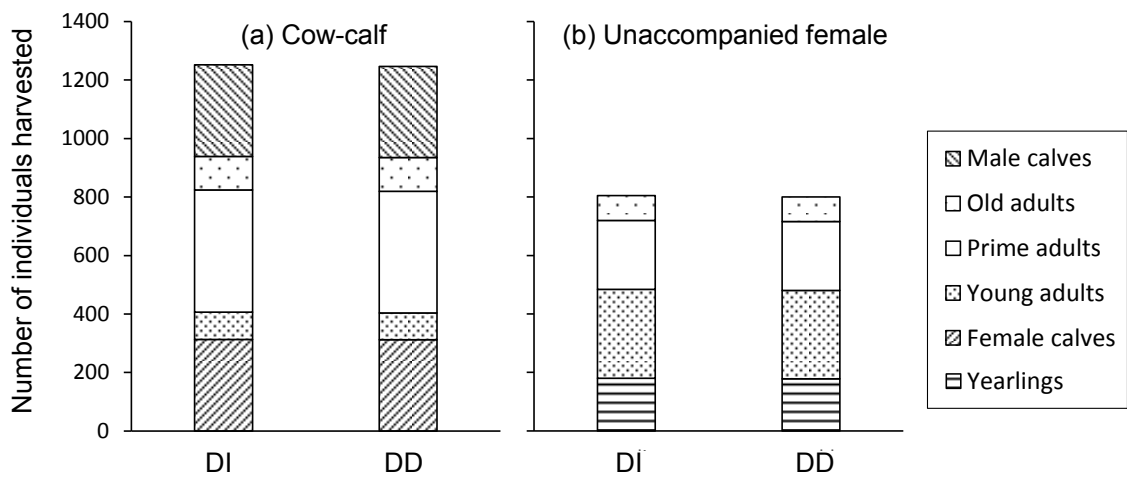


Figure A2. Comparison of mean harvest numbers over a five year harvest interval in deterministic models with either density-independent (DI) or density-dependent (DD) twinning rates.

Inter-annual stochasticity in vital rates

Stochasticity in vital rates can have important impacts on population dynamics. The modeled population and the real population on which it is based are large, which will eliminate any significant effects of demographic stochasticity. Therefore we considered models including inter-annual stochasticity in stage-specific vital rates but did not include individual variation in vital rates, and used these models to compare the five year unaccompanied cow versus cow-calf harvest strategies.

Model development

All the vital rates included in our models are binary; therefore we modelled them as beta-distributed random variables. We did not have access to estimates of inter-annual variance in survival rates for the population in Alaska GMU 20A, therefore we used mean coefficient of variation (CV) from Gaillard et al. (2000) for cervids to estimate variance based on the mean vital rates in our population (Table A3). Gaillard et al. (2000) conclude that CVs are quite similar across species of cervids. Gaillard et al. (2000) does not report a separate CV for young adult survival, therefore we applied the CV for adult survival to both YA and PA stages. This may over-estimate stochastic effects given the very high rate of YA survival and its likely low level of variability.

We estimated stage-specific inter-annual variance in parturition and twinning rates from radio-collared cows in GMU 20A over the years 1996 to 2007 (R. Boertje unpubl.). We used Kendall's (1998) method to estimate mean parturition and twinning rates while accounting for sampling variance and unequal sample sizes of these binary rates (Morris and Doak 2002) (Table A3).

It is likely that annual survival and reproductive rates are correlated, but we did not have access to data allowing correlation estimates. Therefore we considered both simulations with low (0.2) and high (0.8) correlations across all vital rates.

Harvest quotas cannot be instantaneously adjusted to account for stochasticity in vital rates. Therefore we applied the yearly harvest numbers calculated from the deterministic models. However, we assumed that managers would likely be able to detect a marked drop in population size and respond to this by canceling the harvest. Therefore modelled harvest were cancelled when the female population fell below 6000 individuals.

We ran 5000 simulations of both the unaccompanied female and cow-calf harvest models.

Results

Addition of inter-annual stochasticity of vital rates did not alter any of the major conclusions from our deterministic models. In stochastic models the numbers of harvested individuals and biomass yield were slightly decreased due to cancelled harvests when the population fell below 6000 females (Tables A4). This led to 4–5% and 7–8% reductions of both harvested individuals and biomass yield in the stochastic models with low and high correlations among vital rates, respectively (Table A5). While environmental stochasticity decreases the predictive power of population models (Fig. A3) and may warrant more conservative harvest quotas, it does not impact our general conclusions about the relative benefits of these two harvest strategies.

Table A3. Variance estimates for vital rates used in stochastic models.

Vital rate	Estimated variance around the mean
Survival	
calf	0.0400
yearling	0.0065
young adult	0.0081
prime adult	0.0081
old adult	0.0099
Parturition	
young adult	0.0288
prime adult	0.0062
old adult	0.0020
Twinning rate	
prime adult	0.0014
old adult	0.0156

Table A4. Proportion of 5000 simulations where the female moose population fell below 6000 triggering the cancelation of harvest during a five-year cow-calf (CC) or unaccompanied cow (CN) harvest with either low (0.2) or high (0.8) correlation among annual vital rates.

		<u>Proportion of simulations when harvest was discontinued</u>				
Harvest strategy	Correlation	Year 1	Year 2	Year 3	Year 4	Year 5
CC	0.2	0	0.00	0.02	0.06	0.14
CC	0.8	0	0.02	0.06	0.11	0.20
CN	0.2	0	0.00	0.02	0.07	0.17
CN	0.8	0	0.02	0.06	0.14	0.22

Table A5. Comparison of total harvest numbers and biomass yield for five-year cow-calf (CC) and unaccompanied female (CN) harvest strategies.

Harvest strategy	Model (corr)	Total individuals*	Total biomass (kg)
CC	Deter.	6262	879,767
CC	Stoch (0.2)	6005	843,766
CC	Stoch (0.8)	5807	815,871
CN	Deter.	4023	749,553
CN	Stoch (0.2)	3833	714,331
CN	Stoch (0.8)	3707	690,888

*includes male calves for CC harvests

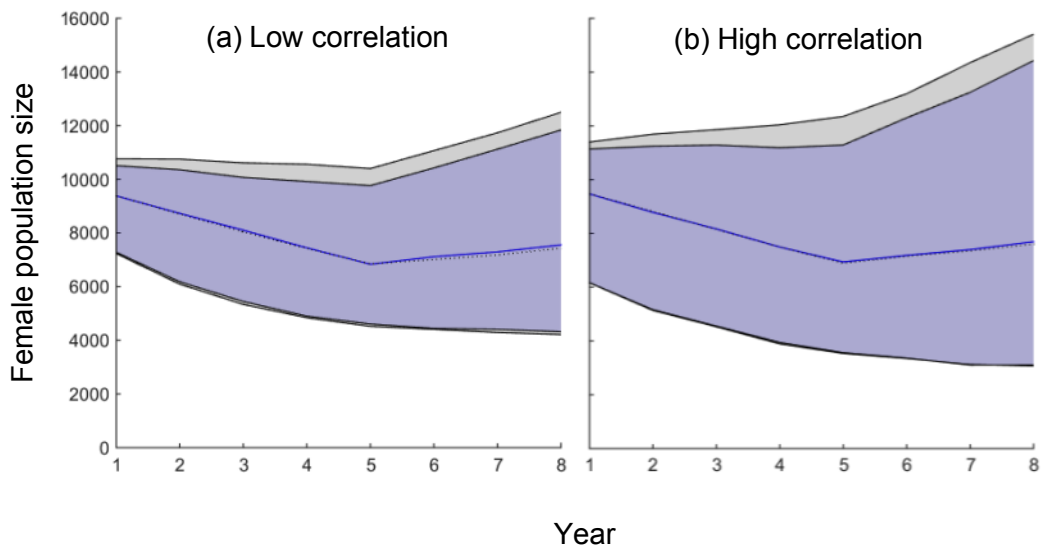


Figure A3. Stochastic projections of female moose population size during and after a five-year harvest period. Median population size and the boundaries containing 95% of the simulated population sizes are indicated for the cow-calf (blue line and area) and the unaccompanied female (dotted black line and gray area) harvest strategies. Results are shown for models with low (0.2) and high (0.8) correlations in vital rates.

Reproductive pauses

Working in southcentral Alaska, Testa (2004) found that reproductive rates of female moose were lower for cows that were accompanied by a calf during the preceding fall. Given our comparison of harvesting cows with and without calves, it seemed relevant to consider whether incorporating these differences in reproductive rates would alter our conclusions about the relative benefits of the two harvest strategies.

Methods

Testa (2004) found a significant impact of being accompanied by a calf during the previous fall on both parturition and twinning rates. We used the estimated impacts from his research to adjust reproductive rates of females with or without fall calves. This was easy to incorporate into our model because we already had defined stages that distinguished cows with or without calves and estimations of stage-specific numbers during the fall. We then compared five-year harvests of cow-calf pairs versus unaccompanied females.

Results

While the incorporation of reproductive pauses led to strikingly different parturition and twinning rates for cows with and without a fall calf (Table A6), impacts on model outcomes were negligible. The inclusion of reproductive pauses results in slightly higher harvest numbers of cow-calf pairs and slightly lower numbers of unaccompanied females needed to achieve the desired population decline (Table A7). This result is not surprising given the low elasticity of reproductive rates.

Table A6. Estimated stage-specific reproductive rates for cow moose from our original model and for the model incorporating differential reproduction of cows with and without calves during the previous fall.

Stage	Parturition rates			Twinning rates		
	Original	With fall calf	Without fall calf	Original	With fall calf	Without fall calf
Young adult	0.34	0.11	0.39	0	0	0
Prime adult	0.77	0.62	0.90	0.1	0.02	0.17
Old adult	0.71	0.56	0.87	0.13	0.03	0.23

Table A7. Mean number of female moose harvested per year to achieve the desired population reduction over a 5 year harvest period.

Harvest Strategy	Mean individuals harvested per year (\pm SE)	
	Original	Reproductive pause
Cow-calf	1252 (51)	1293 (60)
Unaccompanied cow	805 (45)	788 (40)

Harvest of cows with singletons and twins

The models presented in Doak et al. assume that the cow-calf harvest only impacts cows with singletons. To determine the influence of this assumption on model outcomes, here we compare results from 5 year cow-calf harvests either with only harvest of cows with singletons or with harvest of any cow accompanied by a calf or calves.

Methods

Cows with singletons and twins were harvested relative to their frequency in the population. We assumed that all calves with a cow were also harvested. Given an assumption of sex ratio parity of calves, this resulted in an average of 0.5 female calf harvested when the cow was accompanied by a singleton and an average of 1.0 female calf harvested when the cow was accompanied by twins. While it is likely that harvest rates of cows with singleton and twin calves would differ based on the size of the hunting party and the demands of simultaneously processing 2 versus 3 carcasses, the assumption of equal harvest pressure on all cows with calves provides a good comparison to our original model with no harvest of cows with twins, and places boundaries around the likely real case of lower but not zero harvest rates of cows with twins.

Results

Given the low twinning rate in the modelled population, including harvest of cows with singletons and cows with twins resulted in an average of only 6% of harvested cows having twins. This resulted in a slight shift in harvest intensity from YA (that do not twin in the modelled population) to PA and OA cows; but the low rates of twinning rendered this shift minor (Fig. A4). With the inclusion of cows with twins, the average annual harvest of adult females dropped from 626 to 616 and that for female calves increased from 313 to 326. The average annual biomass yield increased by less than a tenth of one percent, from 175.95 to 176.06 metric tonnes. At the end of the 5 year harvest period, the modelled populations including harvest with and without cows with twins contained 7242 and 7233 females respectively, and the population stage structures were the same. Thus the inclusion of cows with twin calves in the harvest had very little impact on modelled outcomes.

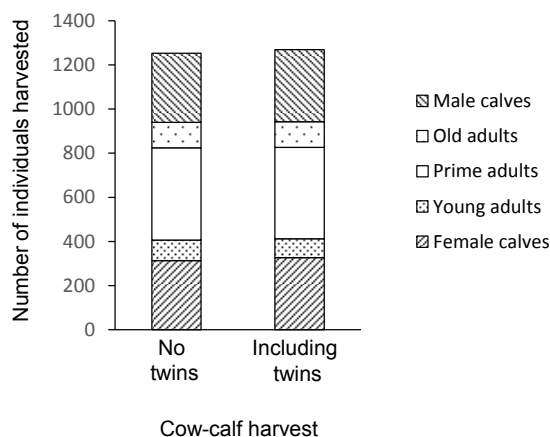


Figure A4. Comparison of mean harvest numbers over a five year harvest interval in deterministic models of cow-calf harvest that either excluded or included the harvest of cows with twin calves.

References

- Boertje, R. D. et al. 2009. Managing for elevated yield of moose in Interior Alaska. – J. Wildl. Manage. 73: 314–327.
- Gaillard, J. M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – Annu. Rev. Ecol. Syst. 31: 367–393.
- Harris, N. C. et al. 2008. Inferences about ungulate population dynamics derived from age ratios. – J. Wildl. Manage. 72: 1143–1151.
- Kendall, B. E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. – Ecol. Appl. 8: 184–193.
- Morris, W. F. and Doak, D. F. 2002. Quantitative conservation biology: theory and practice of population viability analysis. – Sinauer.
- Schwartz, C. C. and Hundertmark, K. J. 1993. Reproductive characteristics of Alaskan moose. – J. Wildl. Manage. 57: 454–468.
- Testa, J. W. 2004. Population dynamics and life history tradeoffs of moose (*Alces alces*) in south-central Alaska. – Ecology 85: 1439–1452.