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Authors: Doak, Patricia, Carroll, Cameron J., and Kielland, Knut

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Harvest of female moose at high density: modelling the impacts of harvest on population size and biomass yield

Patricia Doak, Cameron J. Carroll and Knut Kielland

P. Doak (pdoak@alaska.edu), C. J. Carroll and K. Kielland, Inst. of Arctic Biology, Univ. of Alaska Fairbanks, Fairbanks, AK 99775, USA, and: Dept of Biology and Wildlife, Univ. of Alaska Fairbanks, Fairbanks, AK 99775, USA. Present address for CJC: Alaska Dept of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA

Management of harvested moose *Alces alces* populations at or above ecological carry capacity risks habitat degradation, nutritional limitation, and increased population vulnerability during severe winters. Selective female harvests have the potential to curb population growth while providing hunting opportunities. Using a female-only, stage-structured population model parameterized from an Interior Alaska moose population, we examined numbers of harvested individuals and biomass yield associated with reducing a population from 14 500 to 10 000 individuals over 3, 5 and 8 years. We compared harvest of cow–calf pairs versus unaccompanied females. The higher potential for adult female survival compared with calf survival to impact population growth rate resulted in higher yields from cow–calf harvests. Achieving the population objective required the mean annual harvest of 889, 626 and 477 cow–calf pairs or 1161, 805 and 605 unaccompanied females, for the three harvest durations, respectively. Over a five-year period, cow–calf harvests yielded approximately 56% more individuals and 17% greater biomass, an estimated difference of 130 metric tonnes. The two harvest scenarios resulted in similar stage distributions and population growth rates following the termination of harvest. While the cow–calf harvests can provide higher yields, they also require substantially higher hunter effort to achieve population objectives. The harvest of unaccompanied females will result in greater population reduction per individual harvested and will therefore be the preferable strategy when hunter effort is limited. In addition, the large harvest numbers necessary to achieve the modelled management goal, suggest that some moose populations may escape the range where they can be easily be controlled through female harvest, especially when harvest is limited by hunter interest or access.

Harvested populations are often managed to provide for higher annual yields. However, maintaining populations near ecological carrying capacity can result in reductions in individual condition and population performance (McCullough 1979). For example, a management strategy that focuses on elevated yield for an interior Alaska moose *Alces alces* population has resulted in the population nearing nutritional limitation due to over-browsing and reduced habitat quality (Boertje et al. 2007, Seaton et al. 2011) and has likely made the population more vulnerable to declines during severe winters (Boertje et al. 2009). These issues are well known from other ungulate populations experiencing reduced predation pressure (Côté et al. 2004, Milner et al. 2006). A number of studies have suggested that when released from predation, moose populations do not attain a stable equilibrium with the environment but are apt to become overabundant causing long-lasting habitat degradation (Côté et al. 2004, Simard et al. 2013, Gingras et al. 2014) and resulting in population fluctuations (Sæther et al. 1996, Sæther 1997, Gingras et al. 2014). Managing for high population abundance also carries risks because it may not be possible to use harvest to reduce populations in a timely manner (Brown et al. 2000, Simard et al. 2013). The necessary harvests may be unattainable due to limited hunter demand, resistance to specific harvest strategies, and difficulty of access (Brown et al. 2000, Young et al. 2006).

Selective harvests are often used as tools to obtain management objectives (Timmerman and Buss 1998). When population growth of cervids must be curtailed or reversed, harvest of adult females has the greatest potential to bring about these goals (Gaillard et al. 1998). In contrast, while reducing current population size, male harvests are less likely to change population growth rates unless the number of reproductive males is reduced below that needed to ensure breeding success of females (Milner et al. 2007). Due to low juvenile survival rates and the resulting low reproductive value, calf harvest is also unlikely to result in major reductions in population growth (Milner et al. 2011), and, in some cases, may even lead to increased rates of population growth (Solberg et al. 1999).

Whereas harvest of adult females has the potential to curtail population growth, its effective implementation faces

specific challenges. Female harvests are well accepted in some cultures, but in many cases the public, including hunters, are resistant to harvesting females (Brown et al. 2000, Milner et al. 2006, Van Deelen et al. 2010, Young and Boertje 2011), thereby reducing participation in antlerless harvests and their effectiveness as management tools.

Harvesting females can also result in the orphaning of calves. A number of studies have linked increases in overwinter calf mortality to orphaning but the magnitude of these impacts varies greatly across years and study populations (Markgren 1975, Jolicoeur and Crête 1988, Mytton and Keith 1981, Berger 2012). Markgren (1975) also hypothesized that poor body condition in surviving calves may negatively impact lifetime fitness. The mortality of orphaned calves represents a loss of a potential subsistence resource. Furthermore, if surviving calves have reduced fitness, this could result in decreased population growth rates. Both Sweden and Norway have promoted the harvest of calves prior to accompanying cows as a way to reduce orphaning (Sweanor and Sandegren 1989, Olaussen and Skonhoft 2011). However, hunters in many regions (including interior Alaska) and cultures are resistant to harvesting calves and the successful implementation of calf harvests is likely to require long term investments in public education (Young and Boertje 2004, Milner et al. 2011).

In addition to lack of acceptance of particular harvest strategies, the management of ungulate populations through harvest is often handicapped by lack of adequate hunter demand and limited access to portions of the population (Brown et al. 2000). Limited access is a major limitation in large and remote management areas (McLaren et al. 2004, Milner et al. 2006) such as those for many Alaskan moose populations (Boertje et al. 2007).

Population models are an important tool in wildlife management and can be used to explore different harvest strategies to most effectively achieve management objectives (Sæther et al. 2001, 2009, Nilsen et al. 2005, Xu and Boyce 2010). Here we use a stage-structured population model parameterized for the female segment of an Interior Alaska moose population to examine the potential for using female harvest strategies to mitigate nutritional stress and susceptibility to stochastic stressors by decreasing population growth rate and intraspecific competition. In particular, we compare two strategies: harvest of cows that are unaccompanied by calves versus harvest of cow–calf pairs. Both strategies are designed to avoid orphaning of calves, thereby avoiding potential losses through overwinter mortality of calves or long term reduction in the fitness of surviving calves. We originally hypothesized that cow–calf harvests would be desirable by yielding more biomass while still stemming over-population.

Methods

Model structure and parameterization

We constructed a deterministic, female-only, post-reproductive, stage-structured population model (Caswell 2001) to examine harvest strategies for reducing high-density moose populations. Based on similarities in survival and reproduction among ages, we defined five primary demographic stages (Table 1). Model parameters were taken from an Interior Alaska moose population on a low nutritional plane (Boertje et al. 2007). We used 12 years (1996–2007) of age-specific parturition, fecundity, and survival rates from a subpopulation of moose occupying the Tanana Flats and adjacent foothills of the Alaska Range just south of Fairbanks in central Interior Alaska (Alaska Dept of Fish and Game, ADF&G, Game Management Unit, GMU, 20A; Boertje et al. 2009). These age-specific rates were weighted by within-stage stable age distributions to calculate annual stage-specific survival and recruitment rates (Table 2).

Our interest in female harvest strategies led to elaborations of the basic population model. In order to consider harvest strategies targeting cows with or without calves, we subdivided the population into 11 stages (Table 1, Fig. 1), allowing the model to track cows with twins, singletons or without a calf. Next, to model female harvest, we needed to consider stage-specific population sizes at multiple times during the annual cycle: recruitment, pre-harvest (immediately prior to harvest), and post-harvest. To do this, we used three transition matrices describing: 1) survival for the 3.5-month period from parturition to pre-harvest resulting in transitions 'within' the primary age-based stages; 2) harvest survival; and 3) survival for the remainder of the year to birth of the next calf cohort, resulting in transitions 'among' the primary age-based stages (Fig. 1; for details see Supplementary material Appendix 1).

We considered the impacts of three additional factors on our population models: density-dependence in reproductive rates, environmental stochasticity, and the occurrence of reproductive pauses. None of these additions altered our qualitative results and conclusions about the relative benefits of different harvest strategies. Therefore we present the analyses of the density-independent, deterministic model without reproductive pauses here and include details of the other analyses in the Supplementary material Appendix 1.

Table 1. Primary demographic stages for female moose and the 11 stages used in population models. Note that only female calves are considered in the calf stages, but male and female calves are considered when categorizing whether a calf has a twin and whether a cow is accompanied by a calf.

Primary stages	Model stages	Description	Age (years)
Calf			
	CS	singleton calf	0–1
	CT	calf with twin	
Yearling	Y	yearling	1–2
Young adult			2–4
	YAC	young adult with calf	
	YAN	young adult without calf	
Prime adult			5–11
	PAT	prime adult with twins	
	PAC	prime adult with calf	
	PAN	prime adult without calf	
Old adult			12+
	OAT	old adult with twins	
	OAC	old adult with calf	
	OAN	old adult without calf	

Table 2. Stage-specific vital rates used in the moose population model. Annual survival (S_x), parturition (P_x) and twinning (w_x) rates.

	Vital rate[1]		
Stage	S_x	P_x	w_x
Calf	0.50	0.00	0.00
Yearling	0.85	0.00	0.00
Young adult	0.98	0.34	0.00
Prime adult	0.94	0.77	0.10
Old adult	0.71	0.71	0.13

[1]Average annual survival and reproductive data from a moose population occupying the central Tanana Flats near Fairbanks, Alaska (Boertje et al. 2009, Boertje unpubl).

Sensitivity analyses

Elasticity values were calculated to determine the sensitivity of population growth rates to proportional changes in stage-specific survival, parturition, and twinning rates. Elasticity was calculated as the proportional change in the finite rate of increase divided by the proportional change in a vital rate based on a 1% change in vital rate (Morris and Doak 2002).

Harvest srategies

We used the model to consider harvest strategies for reducing the size of a moose population. Given a fixed initial population size and population objective, first we examined the necessary harvest numbers to meet this objective over varying time periods. Then we compared the effects of harvest of unaccompanied females (cows ≥ 1 year that are not accompanied by a calf) to harvest of cow–calf pairs (CN and CC harvest scenarios, respectively).

We began with a total moose population of 14 500, of which approximately 10 000 were females (estimates for Fall 2010 survey of ADF&G management unit 20A encompassing 13 044 km^2 of moose habitat in a total area of 17 000 km^2; Young 2012). The population objective established in 1998 was 10 000–12 000 total moose (Young 2010), corresponding to 6897–8276 females. We focused our analyses on the lower population objective because this would result in multiple years within the target range. Survival and reproductive rates were assumed to be constant across years. We also assumed that survival and fecundity were the same for all individuals within each primary stage. For instance, prime adults with twins, singletons, or no calf all had the same survival, parturition and twinning rates.

Because most hunters cannot readily distinguish between adult female age-classes of moose and likely do not distinguish between yearlings and adults, we assumed that these stages were harvested in proportion to their availability. Harvest of unaccompanied females was distributed across yearling and adult stages (Y, YAN, PAN, OAN; as defined in Table 1). Given the low twinning rate in the modelled population, whether or not cows with twins were included in the cow–calf harvest model had almost no impact on model outcomes (Supplementary material Appendix 1). Therefore, in the analysis presented here we assumed that cows with twins were not harvested and harvest of cow–calf pairs was proportionally distributed across the three adult stages (YAC, PAC, OAC; Table 1). For the cow–calf pair harvest strategy we assumed a 50% chance of harvesting a female versus a male calf based on sex parity in the calf cohort (Harris et al. 2008, Boertje et al. 2009).

Given fixed starting and ending population sizes, we used optimization to determine the yearly harvest rates necessary to give a fixed rate of decline over 3, 5 or 8 years. We then compared the harvest scenarios and durations in terms of stage-specific numbers and proportions of individuals harvested, population trajectories following the harvest period and biomass yield.

We compared the biomass harvested in unaccompanied cow versus cow–calf harvests over a 5 year harvest period. We used mean carcass weights (after removal of the internal organs, head, lower legs and hide) for calves (81 kg), yearlings (139 kg), and adult females (200 kg). Calf and cow weights are from interior British Columbia (Aitken et al. 2012) and are in close agreement with 0.5 mean total body weight as measured for AK moose (Franzmann et al. 1978, Schwartz et al. 1994); yearling weight is calculated as 0.5 total body weight (Peterson 1974).

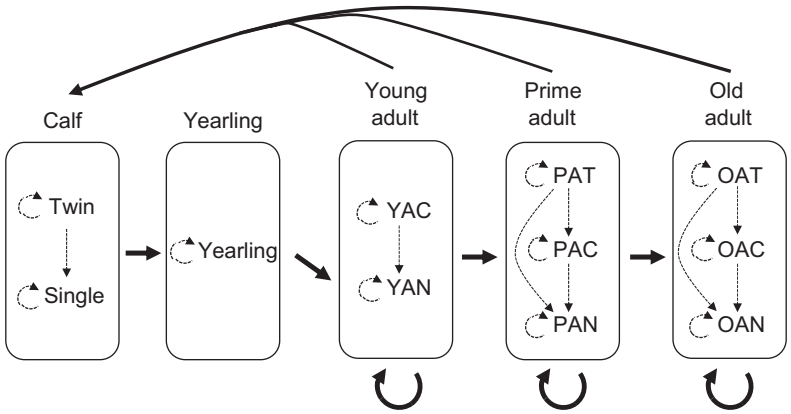

Figure 1. Moose life-cycle diagram with model transitions. Dotted arrows within boxes indicate within-stage transitions occurring from parturition to pre-harvest (three months). Arrows outside of boxes indicate transitions from post-harvest to birth of the next calf cohort. Adult stages are divided into cows with twins, a single calf, or no accompanying calf (e.g. PAT, PAC and PAN, respectively).

Results

Sensitivity analyses

Based on our model using vital rates estimated from an Interior Alaska moose population, changes in survival of young adults and prime adults have the most potential to influence population growth rate (Fig. 2). Rates of parturition and twinning as well as survival of old adults had relatively little impact on population growth rate in our model (Fig. 2).

Harvest strategies

Without harvest the modeled population had an annual growth rate of 1.04 (similar to that reported by Boertje et al. 2009 for 1996–2004, prior to liberal antlerless harvests). In order to reduce the total population to 10 000 individuals over 3, 5 or 8 years, the annual finite rate of growth needed to be reduced to 0.8835, 0.9284 and 0.9546, respectively. This corresponded to a reduction of the female segment of the population from 10 000 to approximately 6700 (Fig. 3). Once released from harvest all populations took approximately 5 years to exceed the upper population objective and approximately 10 years to surpass the original population size (Fig. 3). Due to the lengthened draw down of the population, the longer harvest period resulted in a longer interval when the population was within the objective range.

The stable stage distribution (SSD) for the model was 21:10:23:34:11 for calf, yearling, young adult, prime adult, and old adult, respectively. Our harvest scenarios resulted in stage distributions varying from the SSD by ≤ 2% in any stage. At the end of the harvest period, harvest of unaccompanied females resulted in a stage distribution of 21:12:21:33:13, while cow–calf harvest resulted in 22:9:25:34:11.

Meeting the lower population objective in 3 years required an average annual harvest of 1161 unaccompanied females or 889 cow–calf pairs (Fig. 4), corresponding to harvests of 28 and 15% of unaccompanied yearlings and adult females or 31 and 14% of calves and adult females. The 5 year harvest required taking 805 unaccompanied females or 626 cow–calf pairs, while the 8 year harvest required 605 unaccompanied females or 477 cow–calf pairs (Fig. 4). The proportion of the calf population harvested was 23 and 20% for the 5 and 8 year harvests, respectively.

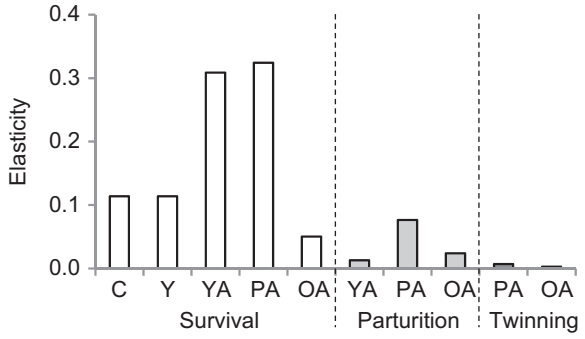

Figure 2. Modelled elasticity of moose population growth rate (λ) to small changes in vital rates. Abbreviations: C-calf, Y-yearling, YA-young adult (2–4 years), PA-prime adult (5–11 years), OA-old adult (> 11 years).

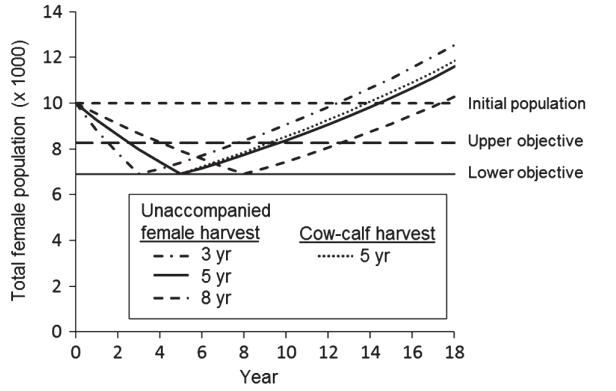

Figure 3. Projected total female moose population for unaccompanied cow (CN) harvests over 3, 5 and 8 years and 5 year cow–calf (CC) harvest. Horizontal lines indicate the initial population size and the upper and lower population objectives.

The 5-year cow–calf harvest resulted in decreased annual calf survival from 50 to 38%. Approximately 29% of all calves born in the spring died prior to harvest. In the cow–calf harvest, 16% were harvested, and another 16% died prior to the next recruitment period. In contrast, in a no harvest scenario, 21% of calves died during the post-harvest season (Fig. 5). If harvest is random with respect to calf condition, approximately 4.8 of the 16% harvested would likely have died during their first winter. This portion of the harvest could be compensatory but the remainder is almost certainly additive.

Cow–calf harvests would yield more biomass than would unaccompanied cow harvests. In the 5 year harvest period, cow–calf harvested biomass exceeded that of the

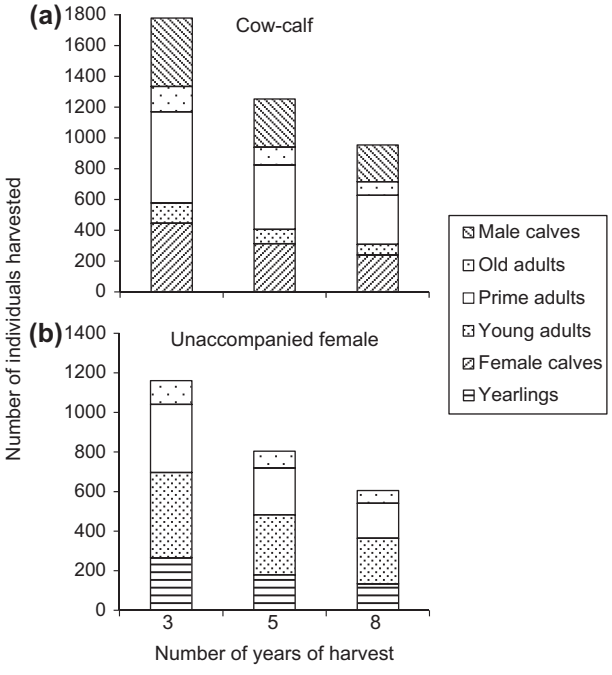

Figure 4. Mean moose harvest numbers per primary stage for cow–calf (a) and unaccompanied female (b) harvest scenarios. All models consider the necessary female harvest needed to reduce a total population of 14 500 to 10 000 at a fixed rate of decline over 3, 5 or 8 years. Note that y-axes differ in scale.

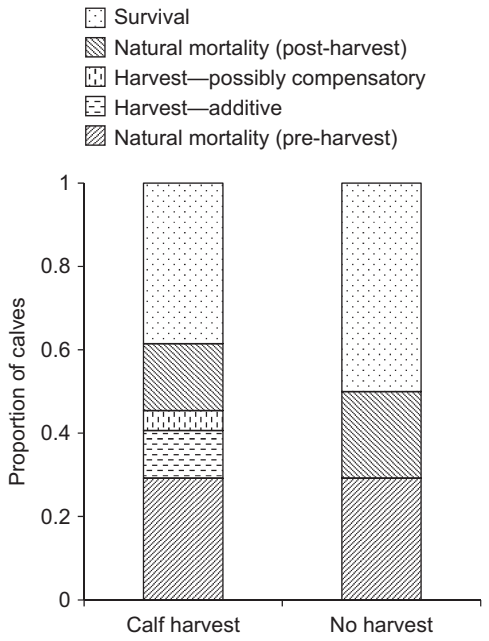

Figure 5. Comparison of annual moose calf mortality and survival rates between the cow–calf harvest scenario and a no calf harvest. For the cow–calf harvest, annual calf survival rate is the result of completely additive harvest. The 'possibly compensatory' portion of the harvest accounts for the proportion of harvested calves that would likely have died over the winter if not harvested. Harvest above this is labelled as additive.

unaccompanied cow strategy by 8% in year 1 and 19–21% in following years, which represents a difference of 14.8 to 31.6 metric tonnes biomass per year (Fig. 6).

Discussion

In deer, adult female survival is the vital rate that generally has the greatest potential to alter population growth rates (Heppell et al. 2000), suggesting that harvest of female deer might provide a useful management tool for controlling

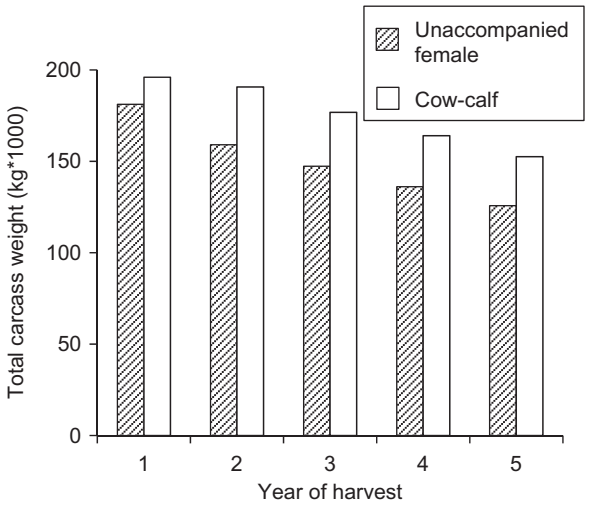

Figure 6. Estimated total biomass yield for the unaccompanied female and cow–calf strategies over the five year harvest period.

population growth or decreasing populations that have exceeded the nutritional limits of their habitat. However, whether female harvests will be successful in attaining these goals and which female harvest strategies are best suited to a particular situation will vary. Female harvests may provide opportunities to achieve population reduction while also maximizing harvestable yield. Yet, when harvest numbers required for population reduction exceed hunter interest, managers may instead need to focus harvest on individuals that will have the greatest impact on population growth. Additionally, when populations have grown well above their nutritional carrying capacity, realistic levels of female harvest may be inadequate to return populations to target levels (Brown et al. 2000, Simard et al. 2013) and habitats may be slow to recover from the impacts of over-browsing (Côté et al. 2004, Simard et al. 2013, Gingras et al. 2014).

Moose are relatively long-lived with high adult female survival and relatively low calf survival. In addition, for a large ungulate, moose have high reproductive capacity and plasticity in offspring number (Gaillard 2007), which may allow populations to rapidly compensate for juvenile harvest through increased recruitment (Solberg et al. 1999, Milner et al. 2011). Calf harvest is likely to be partially compensatory (McCullough 1979, Bartmann et al. 1992, Singer et al. 1997). However, hunting is likely to be less compensatory than mortality incurred through other predators. For instance, wolves typically select calves in poor condition (i.e. with a low probability of overwinter survival) whereas hunters do not display similar selectivity (Sand et al. 2012). Given moose life history traits, changes in survival of adult females has greater potential to influence population growth rates than do changes in calf survival (Gaillard et al. 1998). This means that when trying to maximize harvest yield, more focus should be placed on harvesting calves. On the other hand, when trying to maximize population reduction per animal harvested (i.e. minimal harvest), the focus should be on adult females. In accordance, our models predict that the 5-year cow–calf harvest would yield 17% greater biomass but require harvesting 56% more individuals to achieve the same population reduction as a harvest of unaccompanied females. The two harvest strategies we examined differed little in their impacts on the stage distribution of the population and therefore would have little impact on the capacity of the population to rebound when harvest pressure was reduced.

While we did not consider the impacts of a general cow harvest (with or without accompanying calf/calves), we can extrapolate that when compared to our unaccompanied cow harvest, this strategy would require the harvest of slightly fewer individuals for the same population decline. This is because some proportion of the orphaned calves would likely die over their first winter. However, given the lower sensitivity of population growth to calf survival, this would not lead to major differences in harvest numbers between a general and an unaccompanied cow harvest. The general cow harvest would also incur the loss of yield from the orphaned calves and might result in long-term impacts of low fitness individuals entering the adult population.

Whereas cow harvests have the most potential to curb population growth and calf harvests can increase yield while having relatively little impact on population growth, hunters are often resistant to both strategies (Young and Boertje

2004, Nilsen and Solberg 2006, Young et al. 2006, Sæther et al. 2009, Milner et al. 2011). When successfully implemented, calf harvest can contribute to the maintenance of a productive population that supports high annual harvest (Nilsen and Solberg 2006), and in some regions calf and cow–calf harvests have been successfully integrated into the hunting culture (Sweanor and Sandegren 1989, Milner et al. 2011, Olaussen and Skonhoft 2011). On the other hand, when moose populations have exceeded nutritional carrying capacity, it may be difficult to curb population growth and restore over-browsed habitats even through adult female harvest. Our demographic model suggests that the annual harvest numbers of unaccompanied females necessary to achieve the targeted population reduction (1161, 805 and 605 for 3, 5 and 8 year harvest periods, respectively; Fig. 4b), were well above actual female harvest numbers for the modelled population (ADF&G unit 20A). Actual harvest numbers exceeded 600 females (excluding harvested calves) in only 1, and 400 females in an additional 3 of the 10 years of liberal antlerless harvest (Young 2004, 2006, 2008, 2010, 2012). Limited access to remote portions of a population (McLaren et al. 2004, Young et al. 2006, Gingras et al. 2014) and the different potential impacts of hunter versus predator pressure on habitat-use patterns (Beschta and Ripple 2009, Simard et al. 2013) may decrease the effectiveness of population management through selective harvests.

Individual variation in vital rates beyond those captured by modelled stage structure will influence the dynamics of real populations (Pfister and Stevens 2003, Plard et al. 2015, Vindenes and Langangen 2015). Of particular relevance to our analyses is individual heterogeneity among cows in reproductive potential. For instance, if cows with and without calves in a given year represent distinct groups of high and low reproductive value individuals, this could alter the relative impacts of the two harvest strategies. Both genetics and persistent environmental effects may influence individual variation in reproductive potential of cow moose (moose: Solberg et al. 2004, Testa 2004; other ungulates: Stopher et al. 2008, Hamel et al. 2009, Plard et al. 2015). However, it seems unlikely that in the modelled population, the two harvest scenarios target groups with strikingly different long-term reproductive potential. The unaccompanied cow population is not comprised of only individuals with low reproductive potential, rather it includes pre-reproductive individuals (yearlings and some young adults), individuals that reproduced but lost their calf/calves, and individuals taking reproductive pauses. Similarly, cows with calves may undergo reproductive pauses in other years and therefore do not represent a distinct group of high reproductive potential individuals. Thus, the high transition rates of individuals between the two harvested groups reduces the likelihood that these strategies will strongly target individuals of differing quality.

Our results comparing cow–calf and unaccompanied female harvest strategies appear robust to exclusion of empirically-based variations in reproductive rates (density-dependent twinning, reproductive pauses) and inter-annual stochasticity in vital rates. It is not surprising that these reproductive parameters had little impact on model results given their low impact on population growth rates. Given the large size of the modeled population, we did not consider impacts of demographic stochasticity, but for smaller populations considering both demographic and environmental stochasticity could be important when setting harvest numbers. In general, stochasticity will necessitate more conservative management strategies to reduce the probability of major population declines. However, this stochasticity is unlikely to alter the relative benefits of the two harvest strategies. Finally, while we only considered females in our models, management strategies must consider the impact of concurrent male harvests on overall population number, sex ratios, and age distributions.

Given that moose populations seldom attain stable equilibriums without the top–down effects of predators (Sæther 1997, Côté et al. 2004, Simard et al. 2013, Gingras et al. 2014), reduction or removal of natural predator populations can present major management challenges. The use of harvest for effective top–down control requires that hunter effort be distributed across the entire population (McLaren et al. 2004). This is particularly challenging for North American moose, which often occupy remote regions that effectively prevent access to the majority of hunters. For instance, Young et al. (2006) estimate that $<5\%$ of ADF&G GMU 20A is accessible by roads. A few hunters and trappers may effectively reduce remote predator populations, but it will take many more hunters (constrained by individual harvest limits and access) to exert the control on moose populations that is eliminated through predator harvest. Lack of adequate top–down control may lead to overpopulation, habitat degradation, poor body condition, and increased population vulnerability to stochastic stressors, such as deep-snow winters.

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Supplementary material (available online as Appendix wlb-00163 at <www.wildlifebiology.org/appendix/wlb-00163>).
Appendix 1.

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