SIMULATING SELECTIVE HARVEST AND IMPACT ON AGE STRUCTURE AND HARVEST EFFICIENCY OF MOOSE IN SWEDEN

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Abstract: I simulated selective harvest strategies of moose (*Alces alces*) using antler point restrictions and protection of cows with calves to assess the impact of these strategies on population age structure and potential harvest efficiency (proportion of allowed shooting opportunities). The post-hunt, adult bull:cow ratio was held constant throughout the simulations, but age structure of the bull cohort was allowed to vary. The simulation showed that protecting bulls with few antler points (<5) reduced the average bull age in the post-hunt population, whereas protecting bulls with more points (4 – 8) yielded a higher average age. Regardless of type, restrictions caused a measurable drop in harvest efficiency, and subsequently, substantially more hunting days to achieve the harvest quota. Only 33% and 55% of the bulls in the population were eligible for harvest under the <5 points and 4-8 points restrictions, respectively. For cows, the post-hunt, average age was unaffected when cows accompanied by calves were protected during the first 3 weeks; likewise, harvest efficiency was unaffected by harvest restrictions on cows. However, restrictions protecting reproductive cows reduced harvest efficiency of calves, making it more difficult to reach calf harvest quotas. I suggest that antler point and cow hunting restrictions be abandoned in favour of sex-differentiated harvest quotas.

ALCES VOL. 54: 15–26 (2018)

Key words: *Alces alces*, antler points, average age, harvest, hunting restrictions, moose management, selective harvest, reproduction

INTRODUCTION

In general, Sweden has a healthy moose (*Alces alces*) population with a high reproductive rate and rapid population turnover. The annual harvest is ~80,000 moose from a summer population estimated at ~300,000 animals. This high turnover rate is challenging for moose managers because of the resulting low average age in the population. Many adults are harvested before, or in the midst of their reproductive peak (e.g., Schmidt et al. 2007). Furthermore, because trophy bulls are rare, the assumed positive effects that older bulls have on breeding behavior and reproductive success are limited (Sæther et al. 2003, Broberg 2004, Malmsten et al. 2015). Although aspects such as reproductive rate and antler size can also be related to density dependence (Schmidt et al. 2007), the debate among hunters in Sweden has focused on increasing the adult age structure to improve the quality of the moose population at large.

Selective harvest has the potential to affect offspring sex ratio, timing of birth, reproduction, survival rate, age structure, and body weight (Milner et al. 2007). Selective harvest strategies have been implemented in many Swedish hunting areas to address issues associated with the high turnover rate in the moose population. Two common restrictions are protecting individual bulls based on the number of antler points (e.g., Schwartz et al. 1992), or alternatively, protecting cows based on the presence of calves (e.g., Balciauskas 2002, Doak et al. 2016). The implementation of these restrictions varies, but the typical goal is to increase the age structure within a local population; albeit, antler point restrictions have been used to proportionally reduce bull harvests (Timmerman 1987, Schwartz et al. 1992) and cow:calf combinations to reduce the population (Doak et al. 2016).

Moose hunting in Sweden, to a high degree, is a decentralized bottom-up management system. Hunting rights are tied to property ownership and about 80% of forest and agricultural land is owned by private individuals or private companies (Swedish Statistical Yearbook of Sweden 2014). Hunters and landowners collaborate in moose management units (MMU) to develop an operative management plan which is presented before the regional authority. Although MMUs vary in size, 10,000 ha is typical in southern Sweden (Wennberg DiGasper 2008). Management plans are formally accepted by the county administrative board and it is uncommon for the authority to intervene directly in practicalities such as recommended hunting strategy.

Kalmar county, located in southeast Sweden, has a land area of ~1 million ha of which 80% is spruce- (*Picea abies*) and pine-dominated (*Pinus sylvestris*) hemiboreal forest. A hunting strategy developed within this county ~15 years ago focused on the desire to simultaneously increase the productivity of cows and the proportion of bulls within the population. At the time, bulls represented ~30% of the adult population. A central theme in this strategy was to increase the average age of adults by targeting calves while saving cows (particularly reproductive cows), and also protecting younger bulls through antler point restrictions (Fagerlund and Andersson 2007). It was anticipated that this strategy would result in a post-hunt population consisting principally of reproductive cows, a lower calf:adult ratio, and a higher proportion of older bulls. Local variations of this strategy are employed, but the most common is the "Kalmar Model" named after the county of its origin (Fagerlund and Andersson 2007). Although regional authories usually avoid interference with practical hunting, the moose management plan in Kalmar County explicitly advises to adhere to management principles derived from the Kalmar Model (Regional County 2015).

The theoretical basis for the Kalmar model has been partially described earlier. For example, a simulation study concluded that a calf-biased harvest would increase yield, the average age in the post-harvest population, the adult male:cow ratio, and the average age of bulls (Sylvén 1995). Schwartz et al. (1992) demonstrated that antler size restrictions can target a specific population age structure and sex ratio, and also influence population characteristics. Balciauskas (2002) found a positive response in productivity using simulations that protected cows accompanied by twin calves.

The objective of my study was to simulate selective harvest to assess the demographic effect on a moose population while keeping the desired moose density (1 animal/km^2) and post-hunt, bull:cow ratio (2:3) constant. The aim was to determine if these restrictions produce the desired effect on age structure relative to its influence on hunting efficiency (i.e., allowed shooting opportunities).

METHODS

Model structure

A dynamic population model with an integrated decision-support system for analysis of managing a moose population was developed and written in Delphi, a Pascal oriented development environment (Helge, www.simthinc.com). The core of Helge is a matrix/array population model equivalent in structure to other mathematical models developed for moose (e.g., Solberg et al. 1999, Nilsen et al. 2005). Male and female age-cohorts (i.e., age-classes from 0 to 19 years) are modelled separately, but the model is not spatially explicit and does not account for individual characteristics (Kalén 2004). However, harvest is modelled by using probability functions to draw a representative individual from the population matrix.

Prior to each simulation run, the model was initialized to obtain a demographic structure that is representative of the parameter values. During initialization, the model adjusts the harvest level iteratively to meet a steady-state target population density of 1 moose/km^2. A steady-state equilibrium is possible as the initialization does not include stochastic events.

Density dependence (d) is included in Helge as a multiplier (ranging from 0-1) with a function including winter population (p), carrying capacity (c), and a constant (k) that determine the shape of the curve (Equation 1). The multiplier affects fecundity and natural mortality. In density dependence models, the constant k can vary among species to more accurately reflect the population growth traits of a species.

$$d = 1 - \left(\frac{p}{c}\right)^k \qquad (1)$$

In all simulation runs, the population was held approximately at half the carrying capacity. The constant k was set to 2 to accommodate for stronger effects of density dependence at population densities closer to carrying capacity (Fowler 1981). In Helge, reproduction and calf mortality rates are more responsive to density dependence than mortality of adults (e.g., Musante et al. 2010). However, because carrying capacity and population density were held constant during all simulations, the impacts of density dependence could not directly influence the simulation results.

Fecundity and natural mortality

The simulated population in Helge is updated 3 times a year. The first update occurs during spring to account for births and winter mortality. The total number of new-born calves entering the population is a function of age-specific fecundity (F) and number of cows (n) within each age class (Equation 2).

$$Calves = \sum_{age=1}^{19} F_{age} n_{age} \qquad (2)$$

The second update captures summer mortality and occurs in the autumn just prior to the hunting season. The age-dependent relationship of fecundity and natural mortality was initially based on data from Sylvén (1995; Fig. 1).

Hunting

The third population update occurs sequentially after each individual harvest throughout the hunting season, starting in autumn and continuing until the harvest quota is reached or the number of harvest opportunities is exhausted (see beyond). The number of individuals remaining after the

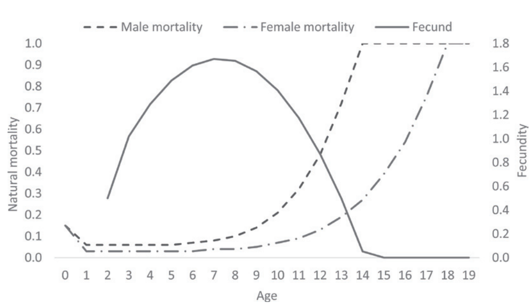

Fig. 1. The relationships between age and average fecundity and natural mortality; these relationships were used in the simulations.

hunt constitutes the post-hunt winter population. Hunting is treated as compensatory mortality as winter mortality is calculated on the post-hunt population. In general, < 20% of the total mortality was related to natural causes in the simulations, which is a reasonable assumption for Sweden, although mortality varies geographically due to factors such as predators and traffic volume (Swedish Hunters Association, unpublished data).

Simulating a hunting event

The modelled hunting process starts by a random draw of one moose in the adult population (Fig. 2). The probability of drawing a bull is assumed as equal to the proportion of bulls in the adult population: p (bull) = bulls/adults. Consequently, the probability of drawing an adult cow was the inverse; p (cow) = 1-p (bulls). Age is determined thereafter by a probability function based on the relative proportion of the sex in each age class: p (age) = n/N, where n is the number of individuals for the specific sex in each age class and N is the total number of individuals for that sex.

Antler points

Statistics collected by hunters on 3,347 bulls harvested between 2014 and 2016 in southern Sweden were used to parameterise a Hoerl model (Hoerl 1954) to obtain an estimate of the average number of antler points

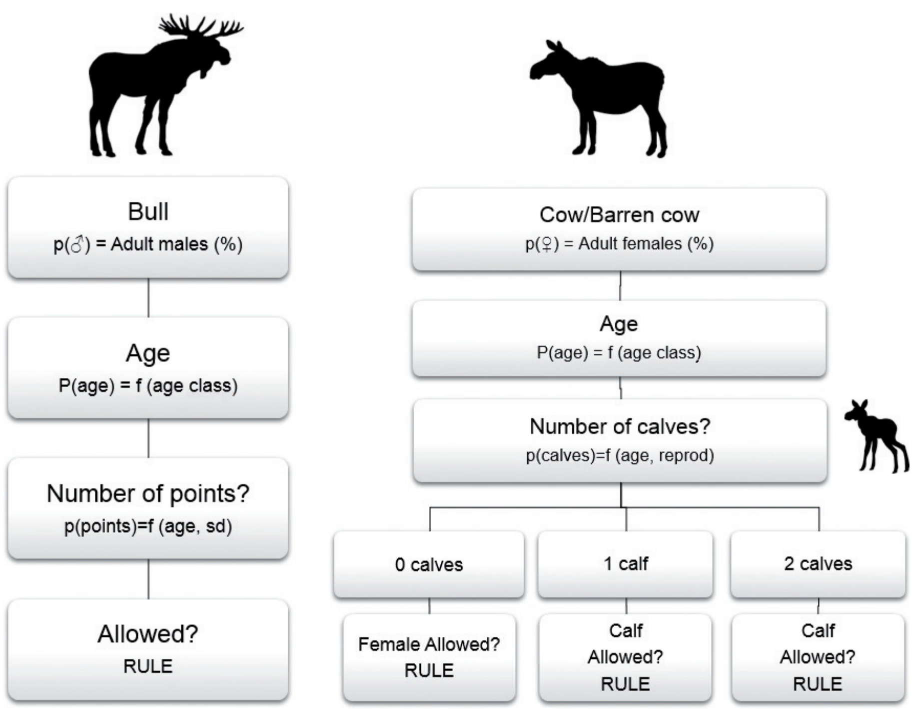

Fig. 2. A hunting event was initiated by randomly drawing an adult individual from the population. A sequence of probability functions was used to determine the action of the present shooting opportunity: p (♂) = proportion of males in the adult population; p (♀) = 1 - p(♂). Age was determined by a probability function that is related to the relative distribution of individuals in each age class. The number of antler points was derived from a normal distribution function determined by a mean and standard deviation that was age dependent. A cow belonged to one of three categories depending on the number of calves with her.

($\bar{x}$) at a given age (Equation 3). The shape of this curve, with a plateau in prime age between 6-12 years, was similar to that reported by Bowyer et al. (2001) for Alaskan moose. The constants a, b, and c were set to 1.85, 0.844, and 1.44, respectively.

$$\bar{x} = ab^{age} * age^{c} \quad (3)$$

A regression coefficient (intercept through zero) of 0.43 was used to estimate the standard error (se) of the mean in each age class. For a given hunting event that included a bull, the number of antler points was calculated using a Gaussian distribution function where mean and standard error for a specific age class is used (Equation 4, Fig. 3).

$$Antler\ \ points = Norm\left(\bar{x}_{age},\ se_{age}\right) \quad (4)$$

Harvest of cows and calves

In all simulations cows were never harvested before calves. This restriction reflects an informal hunting ethic among hunters in Sweden based on the belief that orphaning increases overwinter mortality (Markgren 1975, Sweanor and Sandgren 1989). Therefore, if a cow is derived when drawn from the adult population with the probability function, the algorithm determines the probability whether she was alone or accompanied by 1 or 2 calves. The probability for a given cow having 0, 1, or 2 calves is determined with a distribution function in combination with age dependent fecundity (F_{age}) (Equation 5).

$$\begin{bmatrix} p(0) = \max\left(0,\ 1-0.5F_{age}\right)^{k} \\ p(1) = 1-\min\left(1, p(0)+p(2)\right) \\ p(2) = \min\left((1,\ 0.5p(0)\right)^{k} \end{bmatrix} \quad (5)$$

The constant k was set to 1.65 (Kalén, unpublished data) and the possibility of having 3 calves was omitted due to the rarity of that event and to simplify the model. The simulation model also omits the possibility that a calf could exist unaccompanied by a cow, which is also a rare event in Sweden according to hunter statistics (Kalén, unpublished data).

As the hunting season proceeds in the simulated environment, calves are harvested and the number of single-calf cows (S) and twin-calf cows (T) declines. A twin-calf cow switches to a single-calf cow if one of her calves is harvested, and to a barren cow if the last calf is harvested (S = S + 1; T = T − 1). Therefore, a cow accompanied by 2 calves has 2 "life insurance policies" prior to its risk of being harvested.

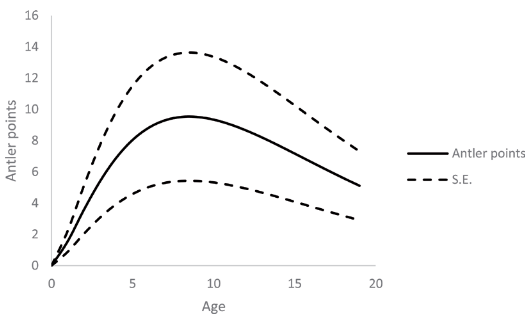

Fig. 3. Antler points were simulated as a function of age and parameterised from harvest statistics in southern Sweden (n = 3347).

Harvest efficiency

A moose from a specific sex and age class was harvested only if permitted according to the restriction rules. Thus, if the probability function produced a moose that could not be legally harvested, the algorithm continued to select another adult moose. Each hunting event, legal or not, represented a shooting opportunity, but only those moose that met the restrictions resulted in an actual harvest. Harvest efficiency was defined as the proportion of allowed shooting opportunities (Equation 6).

$$Harvest\ \ Efficiency = \frac{harvest}{shooting\ \ opportunities} \quad (6)$$

As the focus of this study was to distinguish between permitted and unpermitted shooting opportunities, I did not account for other circumstances that may interfere with (delay) harvesting an individual. An increased scrutiny period and other possible stochastic events or hunt conditions (e.g., effect of weather on behaviour, deciduous concealment cover, or hunter access) were treated independently of the model restrictions. While necessary to simplify the model, this likely forced the model to underestimate the impacts of restrictions on hunting efficiency.

Post-hunt analysis

Four parameters were of interest when analysing the effect of selective harvest: 1) average age of the winter population, 2) average age of harvested animals, 3) hunting efficiency, and 4) the proportion of the harvest quota met during the first week of hunting. Data associated with parameters 1) and 2) were used to address the success of harvest restrictions in meeting population objectives, whereas parameters 3) and 4) were used to evaluate the influence of harvest restrictions on hunting success and efficiency.

The proportion of the total harvest felled within the first week of the hunting season was calculated by estimating the temporal distribution of the harvest. Hunting statistics show that harvest rate declines continuously during the hunting season towards reaching an asymptote. Hunting day (D) was estimated by a function that saturates to an asymptote (Equation 7):

$$\mathrm{D} = \frac{kHS}{1+k-H} \quad (7)$$

where H is the proportion of maximum shooting opportunities used at a given hunting event, S is the length of the hunting season in days, and k is a constant; S and k were set at 140 and 0.3. A learning mechanism that allowed for adjusting the maximum shooting opportunities available was incorporated into the model to simulate a more realistic adaptation among hunters to varying harvest rates. Hunting restrictions (i.e., lower efficiency) led to an increase in the maximum number of shooting opportunities available within the next season. This function made it possible to determine the harvest reached within the first week of hunting, as well as an estimate of the number of hunting days needed to complete the hunt.

Simulation restriction regimes

Three hunting strategies were simulated for bulls: 1) no antler restrictions on bulls, 2) protecting bulls with <5 antler points, and 3) protecting bulls with 4-8 antler points. Adult cows accompanied by one or more calves were not allowed to be harvested in all simulation scenarios. Three hunting strategies were also simulated for females: 1) no additional restrictions on adult cow harvest, 2) singleton calves were protected from harvest during the first 3 weeks of hunting, and 3) twin calves were protected from harvest during the first 3 weeks of hunting.

Throughout the simulations, the population density was held constant at 1 moose/km^2, the adult post-hunt sex ratio at 2:3 (male:female), and the harvest calf:adult ratio at 1:1. The simulations were run for 15 years to allow the population to stabilize under a particular strategy. The length of the hunting season was set at 20 weeks beginning in October.

RESULTS

In this simulation, protecting bulls with <5 points caused a decrease in the average age of bulls in the post-hunt population from

Table 1. The outcome of three hunting strategies on relevant parameters as the population reaches a new equilibrium (i.e., steady state) as simulated in the decision support system.

Hunting strategy	Average age in the harvest (years)	Average age in the remaining population (years)	Allowed shooting opportunities (%)	Proportion of target reached after week 1 (%)
BULL				
No restrictions	3.1	2.7	100	63
Save young males (<5 points)	3.5	1.9	33	24
Save older males (4-8 points)	2.9	3.1	55	35
COW				
No restrictions	4.4	5.0	55	63
Single calf	4.4	5.1	46	55
Twin calf	4.0	5.0	54	57
CALVES				
No restrictions	-	-	100	24
Single calf	-	-	75	13
Twin calf	-	-	72	10

2.7 years without restrictions to 1.9 years under harvest restrictions (Table 1). The average age of harvested bulls under harvest restrictions increased from 3.1 to 3.5 years old. When bulls with 4-8 points were protected, the average age in the remaining post-hunt population increased from 2.7 to 3.1 years, whereas the average age in harvest declined from 3.1 to 2.9 years (Table 1). The demographic age structure of bulls in the post-hunt population was skewed towards younger individuals in the <5 point restriction, whereas in the 4-8 point restriction it was similar to the no restriction scenario (Fig. 4).

Point restrictions had a measurable influence on hunting efficiency, dropping it from 100% (without restrictions) to 33% and 55% in the <5 point and 4-8 point restrictions, respectively (Table 1). The proportion of the bull quota harvested during the first week was 63% without restrictions, declining to 24% and 35% in the <5 point and 4-8 point restrictions, respectively (Table 1). The total number of hunting days needed to meet the harvest quota for bulls was 14 days without restrictions, and increased to 109 and 33 days with <5 point and 4-8 point restrictions, respectively (Fig. 5). An additional qualitative effect was that population density was increasingly unstable as restrictions were applied, and frequent harvest adjustment was necessary to maintain the desired density (1 moose/km^2).

Protecting singletons or twin calves during the first 3 weeks had no impact on the average age of post-hunt cows. The average age of cows in the harvest was slightly lower when twin calves were restricted from harvest during the first 3 weeks (Table 1). The informal rule of shooting calves before the cow had a substantial impact on harvest efficiency of cows, allowing 55% of the shooting opportunities (Table 1). The impact on harvest efficiency declined to 46% when singletons where protected during the first 3 weeks; efficiency was unaffected when twin calves

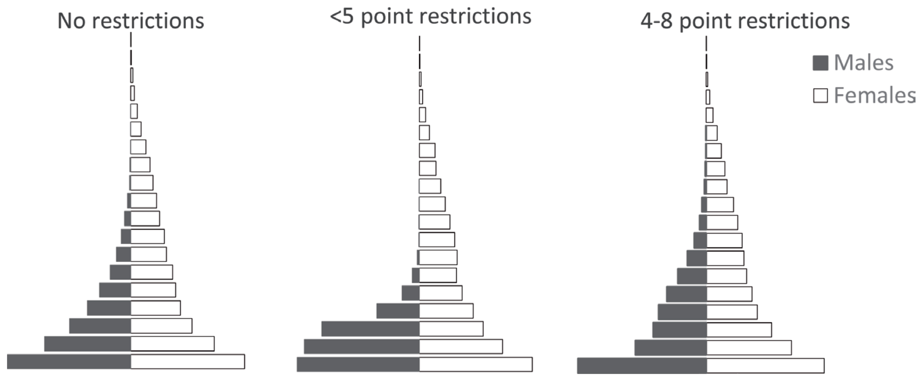

Fig. 4. The post-hunt age structure of the population illustrates the long-term effect of the different hunting strategies on the bull population.

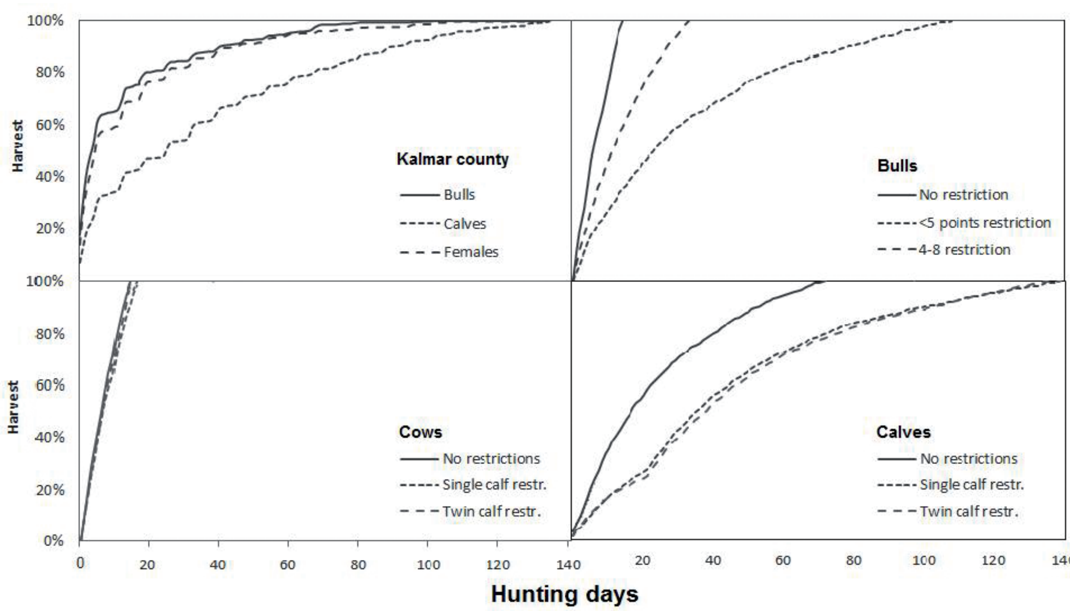

Fig. 5. The selective harvest strategy used had an impact on harvest efficiency manifested by the time required to complete the hunt. Three hunting strategies were simulated; no restriction on antlers points, <5 point restriction, and 4-8 point restriction. For cows, three time-limited strategies were simulated: no restriction, restrict single calves, and restrict twin calves. After three weeks the restrictions were lifted. As a reference, real data are shown for the hunt in Kalmar County (2014–2015) when 2672 moose were harvested.

where likewise protected (Table 1). The number of hunting days used to reach the harvest quota for cows was, in principal, unaffected by restrictions on calves (Fig. 5). Instead, the reduction in harvest efficiency was manifested in the harvest of calves, dropping from 100% to 66-68% as an effect of calf protection. Therefore, the number of days doubled to fill the harvest quota of calves (Fig. 5).

DISCUSSION

Effective management systems require that managers understand and foresee how given harvest strategies influence both moose population dynamics and hunter behaviour. I developed a population model to simulate various hunting restrictions to assess how they may affect the structure and dynamics of a moose population and harvest efficiency. As with any simulation, it should be recognized that not all influential characteristics of moose and hunter behavior can be entirely controlled or predicted. Nevertheless, this approach was useful to compare the relative success and efficacy of specific harvest strategies, and in this case, to identify an unintentional outcome counterintuitive to the goal of increasing the post-hunt, average age in the population.

In Sweden, a common argument to adopt restrictions aimed at protecting bulls with fewer antler points is that these individuals will mature and secure the future availability of older bulls. My results, however, indicate that protecting small bulls is likely to reduce the post-hunt, average age of bulls. The decline from 2.7 to 1.9 years was related to an increased harvest of larger bulls needed to meet the target on the diversity and adult sex ratio. Conversely, the simulation indicated that protecting mid-range bulls with a 4-8 point antler restriction increased the post-hunt, average age of bulls from 2.7 to 3.1 years.

The average age and its magnitude of change is dependent on many population characteristics. Hence, interpreting these results requires comparison of the magnitude of change between the different restrictions tested, and recognizing the direction in change of the average age.

Although the post-hunt, bull:cow ratio was held constant in the simulations, it should be recognized that point restrictions can also be used to control bull:cow harvest ratios without sex-differentiated licencing (Schwartz et al. 1992).

In a dynamic environment, selective harvest of moose using antler point restrictions may result in a directed selection of bulls (Huntermark et al. 1998, Harris et al. 2002, Child et al. 2010). This is of particular interest with a restriction of <5 points since individuals with lower quality (i.e., smaller antlers) have an increased chance of survival.

A critical finding of this study was the impact that antler point restrictions had on hunting efficiency manifested by the drop in allowed shooting opportunities from 100% to 33% and 55% in the <5 points and 4-8 points strategies, respectively. Protecting bulls with fewer antler points reinforced a low average age of bulls in the population, and made it less likely to encounter bulls legal for harvest. Protecting mid-range bulls with 4-8 points had less impact on efficiency and contributed to the goal of increasing the post-hunt, average age. A secondary effect of reduced efficiency (prolonged hunting season and lower harvest) is that more moose remain on the winter range which increases the risk of browsing damage and vehicular or train collisions (Gundersen et al. 1998, Neumann et al. 2012).

It is reasonable to believe that restriction rules have additional influence on hunter behaviour and efficiency. Presumably, hunters need to consider specific restrictions during the hunt, necessarily evaluating individual animals which likely increases the probability of missed shooting opportunities. Because the simulation could not account for this behaviour, the reduction in efficiency should be considered a conservative estimate.

Where point restrictions are implemented, the proportion of bulls in the total harvest will likely decline because both formal and informal regulations influence harvest selection patterns (Schwartz et al. 1992, Deikert et al. 2016). In areas where restrictions do not specify sex, one would expect that the post-hunt bull:cow ratio would be affected by point restrictions, as occurred in Kalmar County where it increased from 0.4 to 0.6 between 2003 and 2007. This should also increase average age and antler size in bulls.

A sex-differentiated harvest could also be used as a direct and efficient way to increase the proportion of adult bulls in the post-hunt population. For example, when simulating a population with a post-hunt, adult bull:cow ratio of 0.43 (i.e., 30% of the adult population are bulls), the expected harvest of mature bulls (between 6-12 years old) was ~3%; whereas, mature bulls stabilize at 13% of the harvest when this ratio is increased to 0.67 (i.e., 40% adult bulls, Kalén unpublished data). The use of sex-differentiated harvest quotas has increased in local MMUs since new regulations were adopted by Swedish Environmental Protection Agency in 2012.

Restriction strategies aiming for an increase in average age of post-hunt cows is designed to protect cows that manifest their reproduction. Presumably, cows followed by 2 calves were likely to be older and more reproductive than those with a single calf, which in turn are likely to be older and more reproductive than a cow without calves. Therefore, protecting calves following a cow increased the survival rate of that cow, provided it was never harvested before her calves. Balciauskas (2002) simulated the protection of cows accompanied with twins during the entire hunting season and found a positive effect on reproduction. My simulation that protected cows and calves for 3 weeks, regardless of specific strategy, indicated negligible influence on harvest efficiency or the post-hunt, average age of cows. A possible explanation for this difference is that the relative influence of the informal rule of never shooting a cow before her calves reduced the intended effect. For example, harvest efficiency of calves declined substantially which exacerbated the difficulty in achieving the calf harvest quota, usually set to a calf:adult ratio of 1:1. Harvest statistics collected in Kalmar County illustrate that reaching the harvest quota of calves is more time consuming than for adults (Fig. 5).

In 2012, Sweden adopted a new moose management system highlighting the need of ecosystem-based management to better balance the benefits of the moose population with unwanted and negative effects of forest damage, moose-vehicular collisions, and reduced biological diversity (Prop 2009/10:239, Sandström et al. 2013). While hunting restrictions analysed in this study primarily aim to improve quality aspects of the moose population, underestimated drawbacks are also important to consider. Lower harvest efficiency will increase the time and difficulty to achieve harvest quotas, which in turn, lead to higher risk of browsing damages and vehicular collisions. An effective, ecosystem-based management system will benefit from a balanced and transparent approach that specifically identifies the varied influences of selective harvest restrictions in moose management.

ACKNOWLEDGEMENTS

J. Malmsten, E. Bergman, P. Pekins, and 3 anonymous reviewers provided valuable comments on the draft.

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