POPULATION AND GENETIC EFFECTS OF SELECTIVE HARVEST STRATEGIES IN MOOSE: A MODELING APPROACH

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ABSTRACT: We evaluated the changes in population structure and frequencies of hypothetical alleles controlling antler growth of a simulated population of moose (*Alces alces*) subjected to a variety of harvest strategies based upon antler morphology. Legal bulls in the different selective harvest strategies were characterized by having at least one spike or forked antler (spike/fork), bulls having an antler spread of ≥91 cm, or ≥127 cm, and bulls with either a spike/fork antler or a spread of ≥127 cm. In those strategies in which legal bulls were defined by spreads of a certain size, existence of at least one brow palm with three or more tines was considered as an alternative harvest criterion. A strategy allowing harvest of bulls with either a spike or fork antler or having antler spreads of ≥127 cm, but which ignored brow tines also was simulated, as was a strategy allowing hunters to harvest any bull, regardless of antler form. We assumed that antler growth is controlled by a polygenic two-allele (favorable/unfavorable) system and that brow palm formation is controlled by a two-allele monogenic locus and is independent of antler size. The strategies were evaluated based upon their ability to maximize the harvest, post-hunt bull:100 cow ratios, and frequency of favorable antler alleles. All harvest strategies, with the exception of any-bull hunting, yielded post-hunt bull:100 cow ratios of >20, but the population regulated by the 91-cm legal threshold was characterized by extremely low ratios of large-antlered (≥127-cm spread) bulls:100 cows. Harvesting any bull produced the highest annual harvest, followed in decreasing order by the strategy with the 91-cm threshold, the strategies with the 127-cm threshold, and the spike/fork strategy. Spike/fork hunting apparently increases the frequency of favorable antler alleles, but this is seemingly offset by harvesting bulls having antler spreads above a legal threshold, particularly the 91-cm threshold. Those strategies enabling harvest of bulls based on brow tines caused significant declines in favorable brow alleles. Frequency of alleles favoring antler growth is seemingly affected by hunting based on brow tine architecture, and frequency of alleles favoring growth of brow tines is similarly affected if hunting is based on antler spread even though loci controlling these traits are not linked. Of the strategies simulated, the one by which legal bulls are defined as those having either spike/fork antlers or antlers with a spread ≥127 cm best met the three management objectives although frequency of alleles favoring growth of brow tines declined. We propose that a strategy utilizing an open season on spike/fork bulls in combination with a limited-participation any-bull season is a suitable alternative to harvest strategies based upon antler spread and brow tines alone.

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In 1987, a selective harvest strategy was implemented for moose hunting on the Kenai Peninsula, Alaska. This strategy (designated hereafter as SF/50) defined legal bulls as those having a spike/fork (SF) antler or those with an antler spread of at least 127 cm (≥50 inches). To assist hunters in identification of large-antlered bulls in the field, hunters had the option of taking a bull with at least 3 brow tines on one brow palm in lieu of estimating the spread. The SF/50 strategy was implemented to provide greater numbers of bulls in the post-hunt population while maintaining reasonable harvest levels. A detailed description of this strategy as well as the response of hunters and of moose population parameters to the first five years of this program were documented by Schwartz *et al.* (1992).

An additional objective of SF/50 was to focus hunting pressure on yearling bulls with

"inferior" antler structure (spikes and forks). Bulls with antlers larger than forks as yearlings were not subject to hunting mortality until they achieved a spread of 127 cm or had at least 3 brow tines on one brow palm. This protection allowed animals with "superior" antlers to reach maturity and provided them an opportunity to breed. The degree to which this objective was met was not evaluated, nor was the effectiveness of harvest strategies using different definitions of legal bulls in meeting these population and genetic objectives.

The impact of selective harvest on the genetic composition of a population is dependent in part on the degree to which the genotype contributes to the phenotype (heritability). Arguments for either nutrition or genetics as the primary factors governing antler growth are common (*see* Goss 1983). The limited data available indicate that the form of the antler and its potential size are genetically controlled. Harmel (1983) reported that of the male offspring produced by a male white-tailed deer (*Odocoileus virginianus*) with superior antlers, only 5% exhibited spikes as yearlings, whereas 44% of the sons of a male with inferior antlers had spikes. As all of the deer in this study were maintained on high-quality feed, it suggests that the size of antlers is partly heritable. Harmel *et al.* (1988) further reported estimates of heritability to be 0.5 and 0.75 for certain antler characteristics.

Thelen (1991) described changes in harvest levels and in frequencies of alleles controlling antler growth in simulated populations of elk (*Cervus elaphus*) subjected to different harvest strategies. When harvesting elk by a minimum antler-point criterion the frequency of alleles favoring production of points always decreased, whereas when harvesting only spike-antlered elk the frequencies increased. He noted also that maximizing total harvest and trophy harvest were inconsistent with maintaining the frequency of favorable antler alleles, and concluded that combining selection criteria offered the best compromise between genetic gains and harvest levels. We evaluated a number of harvest strategies used for moose management in Alaska to determine their effect on harvest, frequency of alleles favoring antler growth, and post-hunt bull:cow ratios.

METHODS

A stochastic population model similar to that developed by Thelen (1991) was used to simulate populations subjected to different harvest strategies. The model took populations through annual cycles of birth of calves, summer mortality of calves, harvest, breeding, and winter mortality of adults and calves. All adult mortality was assumed to occur in winter. Each animal in the population was characterized by age, sex, and antler genotype and phenotype.

The initial population was created using estimates of age structure from a population from the northern Kenai Peninsula, Alaska (Schwartz *et al.* 1992). Survival rates of females were based upon those reported for the northern Kenai Peninsula by Bangs *et al.* (1989) but were adjusted slightly to produce a stable population. Summer and winter survival rates of calves were 0.55 and 0.40, respectively. Annual survival rates of females older than calves were 0.88, 0.95, 0.90, 0.85, 0.80, 0.70, 0.60, 0.45, 0.25, and 0.0 for yearlings, 2-5, 6-10, 11-12, 13-14, 15-16, 17, 18, 19, and 20 year olds, respectively. Male survival rates were based upon those of females but were reduced by an exponential decay function in which a bull's antler-size-dependent survival (ASDS) decreases as it ages and its antler size increases. In the function,

$ASDS = 1 - [(SCORE - SOD)/60]^2$,

SCORE is a numerical value (explained later) determined by a bull's genotype and the environment unique to that bull, and SOD is an age-dependent value that reflects a score at

which survival begins to drop. SOD values for calves and yearlings were 40, and for bulls aged 2-7 were 20, 16, 12, 8, 6 and 4, respectively. For bulls 8 years old or older the value of SOD was 2. We assumed that mortality would increase as a function of antler size because the energy required to produce and carry large antlers, as well as that required to achieve and maintain dominance during rut would place large-antlered bulls in a greater energy deficit during winter compared with smaller-antlered bulls. With these assumptions, the initial ratios of all bulls and large bulls:100 cows were 80 and 34, respectively for a population with no harvest mortality.

Based upon data from the Kenai Peninsula moose population (Alaska Dept. of Fish and Game, unpubl. data) we assigned a harvest rate equal to 50% of all legal bulls. We did not assume a relationship between the age of the bull and its ability to avoid hunters, unlike the elk model developed by Thelen (1991).

Reproductive rates (calves/cow) were 0.0 for calves, 0.22 for yearlings, 1.27 for ages 2-15, 0.14 for ages 16-19, and 0.0 for age 20 (Schwartz and Hundertmark 1993). To produce these rates in the model we assumed that 12% of yearlings would produce single calves, 5% would produce twins, and 83% would produce no offspring. Respective values for other age classes were 63%, 32%, and 5% for ages 2-15, and 8%, 3%, and 89% for ages 16-19. The sex ratio of offspring at birth was 1:1 (Schwartz and Hundertmark 1993).

Antler growth was assumed to be an age-dependent polygenic trait. In the model, 5 pairs of genes and environmental influences were assumed to contribute to an antler growth score (SCORE). For each locus, there were two possible alleles: favorable and unfavorable, which contributed 4 and 0 points to the genotype score, respectively. Thus, the genotype score for antler growth varied from 0-40 (allele score x two alleles/locus x five loci). The model tracked the frequency of favorable antler alleles (Q_A) and favorable brow alleles (Q_B). Environmental scores were generated randomly from a distribution with the same mean and variance as the genotype scores and one was permanently assigned at birth to each male. A combination of an individual's genotype and environmental scores created its antler phenotype score which determined age-specific antler size. The degree to which the genotype and environmental scores contributed to the phenotype score was determined by the chosen level of heritability (the proportion of phenotype explained by genotype). We assumed a heritability of 0.5 (equal contribution of the two factors), but we also ran the simulation using heritability values of 0.25 and 0.75 to determine the effect of other heritabilities on our results.

Slower rates of antler growth in yearlings were manifested in spike/fork antlers. Antlers of this size were assumed to be present only in yearlings, and accounted for 60% of antlers in this age class (Schwartz *et al.* 1992). Other yearlings and bulls older than yearlings have palmated antlers that were characterized by a spread measurement. Age-dependent antler spreads (Table 1) were assigned to the initial population based upon data from hunter check stations on the Kenai Peninsula. Maximum spreads occurred in animals 8-12 years old (Gasaway *et al.* 1987). The number of brow points is assumed to be under monogenic control, but is also influenced by an animal's age and unpredictable environmental factors. In our initial population, 27% of bulls 2 years or older had 3 or more brow points on at least one brow palm. Of the 2-year-olds, 16% of those homozygous for the favorable allele, and 2% of the heterozygotes, had 3 brow points on one side (the limit of 3 is a simplification having no outcome on the results). Among moose 3 and older, 60% of homozygous favorable and 24% of heterozygotes had 3 brow tines. All homozygous unfavorable bulls had a maximum of 2 brow tines on one side.

Table 1. Percentage of bulls in four age classes characterized by antler size in the initial population.

Age (yrs)	Spike/ fork	<36 inches	≥36 and <50 inches	≥50 inches
1	60	25	15	
2-3		25	60	15
4-5			60	40
≥6			5	95

For our analysis we evaluated 7 different harvest strategies. One strategy specified no harvest, another the harvest of any antlered bull (any-bull strategy), and the other 5 were selective harvests based on antler type. These last 5 included: a spike/fork strategy (hereafter designated SF), in which only bulls with a spike or forked antler were legal; SF/50, which was described previously; a strategy in which any bull with an antler spread of ≥91 cm (36 inches) or with at least 3 tines on one brow palm was legal (referred to as the "36-inch" strategy); a strategy in which any bull with an antler spread ≥127 cm (50-inches) or with at least 3 tines on one brow palm was legal (50-inch strategy); another 127-cm strategy (SF/50/NB) that is identical to SF/50 except that the brow tine criterion was eliminated. All of these strategies, with the exception of SF and SF/50/NB, are or were used for moose management in Alaska.

As our model is stochastic, we ran ten simulations of each strategy, from which we generated estimates of means and variances of population parameters and allele frequencies. Each simulation lasted 50 years. Estimates of population composition and allele frequencies from the initial population (year 0) were compared with those from year 50. Harvest data represent means from years 20-50 of the simulations.

RESULTS AND DISCUSSION

Population Composition

Changes in sex and age composition of the population were apparent among the seven strategies after 50 years of simulation (Table 2). The number of bulls older than calves present in the that year's pre-hunt population was highest with no harvest and lowest under the strategy allowing the harvest of any bull. Among the strategies providing selective harvest, the 36-inch and SF/50 strategies yielded the least number of bulls prior to the hunt and the SF strategy provided the greatest number of large-antlered bulls. Despite having among the lowest number of bulls and the lowest number of large bulls, the 36-inch strategy resulted in the highest total harvest among all strategies, while the SF strategy was characterized by the lowest harvest.

Numbers of medium-sized bulls (> spike/fork but with spreads <127 cm) and large bulls (spread ≥127 cm) in the final pre-hunt populations varied greatly (Table 2). The number of medium bulls was highest under the 50-inch and no harvest strategies and lowest under the any-bull and SF strategies. However, all selective harvest strategies tended to conserve more medium bulls than did the any-bull strategy, and the 50-inch strategy maintained more bulls in this category than when no harvesting occurred. Large bulls were most abundant under the no harvest and SF strategies, and were least abundant under

Table 2. Mean (SD) numbers of bull moose in three size/age classes prior to harvest in the final year of the simulations (year 50), mean (SD) annual harvest during years 20-50, and post-hunt bull:100 cow ratios in the final year.

	Number in final population prior to harvest			Annual harvest (years 20-50)			Bull:100 cow ratios after final harvest	
Harvest strategy	Yearling	Medium[a]	Large[b]	Spike/fork	Medium[c]	Large	All bulls: 100 cows	Large bulls: 100 cows
No harvest	462 (30.2)	1494 (50.1)	1418 (42.9)	0 (0)	0 (0)	0 (0)	79.4	33.4
Any bull	603 (24.9)	420 (18.2)	61 (9.3)	124 (2.9)	368 (8.1)	31 (4.4)	10.5	0.6
SF	504 (30.0)	1000 (24.8)	1354 (31.3)	106 (2.6)	0 (0)	0 (0)	60.4	29.7
SF/50	539 (30.4)	1051 (35.3)	388 (14.3)	134 (4.9)	60 (2.0)	185 (2.7)	32.6	4.1
36-inch	557 (22.8)	1381 (48.6)	55 (7.8)	0 (0)	375 (6.7)	31 (1.0)	32.4	0.5
50-inch	520 (27.0)	1694 (52.0)	438 (20.5)	0 (0)	85 (3.3)	208 (6.7)	51.0	5.0
SF/50/NB	529 (23.5)	1118 (27.3)	420 (24.3)	140 (3.4)	0 (0)	210 (2.8)	36.1	4.4

[a] Bulls older than yearlings that had antler spreads <127 cm.
[b] Bulls older than yearlings that had antler spreads ≥127 cm.
[c] Includes yearlings with palmated antlers.

the any-bull and 36-inch strategies.

The bull:100 cow ratio (Table 2) in year 50 of the no harvest strategy was similar to that of the initial population. This strategy also was characterized by the greatest ratio of large bulls:100 cows. Of the selective harvest strategies, the spike/fork strategy yielded the highest bull:100 cow ratios while the 36-inch strategy had the lowest. The large bull:100 cow ratios were extremely high under the no harvest and SF strategies, were intermediate under SF/50, 50-inch, and SF/50/NB strategies, and were very low under the any-bull and 36-inch strategies.

Genetic Parameters

All of the strategies effected a change in Q_A, the frequency of alleles favorable for spread (Table 3). The slight but significant difference in frequency for the no harvest strategy (1.1% decline over 50 years) may have resulted from genetic drift. The two strategies causing the greatest declines were the 36-inch and 50-inch strategies (-27.8 and -16.1%, respectively), while the any-bull and SF strategies caused the greatest increases (10.7 and 13.2%, respectively).

When any bull can be harvested legally, the proportion of older bulls in the population decreases. Consequently, a greater incidence of mating by young bulls likely occurs, particularly those bulls with larger antler mass. Young bulls generally have smaller antlers than their older counterparts and therefore they do not exhibit much of the decrease in survival related to large antler sizes. Conversely, the reduction in survival for older bulls is higher, particularly those with the largest antlers, and the decrease is cumulative over time. Therefore, Q_A tends to be higher in young bulls. Harvesting only spike/fork bulls does not change appreciably the population

Table 3. Mean (SD) frequencies of alleles favoring growth of antlers (Q_A) and brow tines (Q_B) in the initial (year 0) and final (year 50) populations. Q_B was 0.5000 in the initial population. Ten simulations were run for each harvest strategy.

Harvest strategy	Initial Q_A	Final Q_A	Final Q_B
No harvest	$0.4958^{a}(0.0022)$	$0.4904^{Aa}(0.0033)$	$0.5065^{Ba}(0.0113)$
Any bull	$0.4967^{a}(0.0017)$	$0.5500^{Ab}(0.0053)$	$0.5002^{Ba}(0.0104)$
SF	$0.4953^{a}(0.0008)$	$0.5611^{Ac}(0.0039)$	$0.4946^{Ba}(0.0128)$
SF/50	$0.4959^{a}(0.0020)$	$0.4995^{Bd}(0.0074)$	$0.2932^{Ab}(0.0156)$
36-inch	$0.4955^{a}(0.0012)$	$0.3576^{Ae}(0.0056)$	$0.3878^{Ac}(0.0160)$
50-inch	$0.4959^{a}(0.0013)$	$0.4160^{Af}(0.0078)$	$0.2502^{Ad}(0.0076)$
SF/50/NB	$0.4963^{a}(0.0017)$	$0.4697^{Ag}(0.0024)$	$0.5100^{Ba}(0.0169)$

[A] Mean final frequency of alleles differs ($P > 0.01$, paired t-test) from initial frequencies.
[B] Mean final frequency of favorable alleles does not differ ($P > 0.01$, paired t-test) from initial frequencies.
[a,b,c,d,e,f,g] Means within the same column having the same superscript are not significantly different ($P > 0.01$, ANOVA and Tukey pairwise comparisons).

composition but does increase Q_A due to the elimination of small-antlered yearling bulls and conservation of large-antlered yearlings. The presence of these genetically superior large-antlered yearlings should increase the proportion of favorable alleles in the breeding population.

Changes in Q_B, the frequency of the favorable brow allele, were related directly to the presence or absence of a 3-brow-tine criterion in the harvest strategy. Those strategies governed by this harvest criterion (SF/50, 36-inch, and 50-inch strategies) were characterized by 41.4, 22.4, and 50.0% declines in allele frequency over 50 years, respectively. Differences among these declines were significant (Table 3).

It is apparent from these simulation results that different antler-spread criteria had different effects on Q_B. The 50-inch strategy caused the greatest declines in Q_B, followed by the SF/50 and 36-inch strategies. Directing harvest toward animals with greater spreads causes greater declines in these alleles, whereas the spike/fork criterion has an ameliorating effect. Conversely, comparison of the SF/50 and SF/50/NB strategies (Table 3) indicates that inclusion of the brow tine option in a strategy results in less of a decline in Q_A.

The inclusion of the brow-tine option lessens the decline in Q_A for 2 reasons. First, harvesting animals based on the presence of 3 brow tines tends to increase Q_A in general because harvest is focused on older animals, resulting in an age effect similar to that discussed for the any-bull strategy. Second, animals with inferior antler spreads are more likely to be harvested under brow tine regulations than are their superior-antlered counter-

parts. By the time a bull reaches the minimum legal spread, the hunter tends to select him on that basis; therefore, there is no direct selection against favorable brow alleles after this point. Bulls with relatively low potential for antler growth would spend more years in the medium class than would bulls with greater growth potential, and therefore would have a higher probability of being harvested based on the presence of legal brow tines. The SF/50/NB strategy shows more of a decrease in Q_A compared with the SF/50 strategy because the brow tine option gives hunters more seasons to take a particular inferior bull with 3 brow tines as compared to a superior bull, as the superior bull reaches the legal spread at an earlier age. Thus, by including the brow tine option, we are increasing selection for favorable antler alleles. By this same principle, the SF/50 strategy results in less of a decrease in Q_B compared to the 50-inch strategy. The addition of the SF option to a strategy increases Q_A (Table 3), which causes bulls to reach the legal spread at an earlier age than without this option. Thus, fewer animals would be harvested based upon hunter selection for brow tines, which in turn would cause less of a decline in brow alleles.

Obviously, hunter behavior influences the degree to which this interaction is expressed. Bulls with antler spreads slightly greater than the minimum threshold often are harvested based upon the presence of three brow tines. To account for this we altered the 50-inch strategy by reducing hunting mortality by fifty percent for bulls having less than 3 tines on the brow palm but had spreads from 50-55 inches (127-140 cm). This had the effect of increasing Q_A from 0.4160 to 0.4251, decreasing Q_B from 0.2502 to 0.2409, and decreasing harvest from 293 to 266 bulls.

The degree to which each selective harvest strategy meets the three objectives can be evaluated with a three-dimensional plot (Fig. 1). The strategies that best meet all three objectives were those having a minimum legal spread of 50 inches (the SF/50, 50-inch, and SF/50/NB strategies). These strategies varied little in terms of post-hunt bull:cow ratios and therefore can be evaluated on harvest potential and Q_A. In this respect, the SF/50 strategy is apparently the best harvest option. The disadvantage of this strategy is that it significantly reduces Q_B, which could be corrected by eliminating the brow tine option altogether or by increasing the legal threshold from three to four tines on one brow palm. The choice between these options depends upon the predominant antler growth form in the area being managed. Eliminating this option on the Kenai Peninsula undoubtedly would cause hunter dissatisfaction because many hunters rely on brow tines to identify legal bulls. Also, in this population very few bulls develop four or more tines.

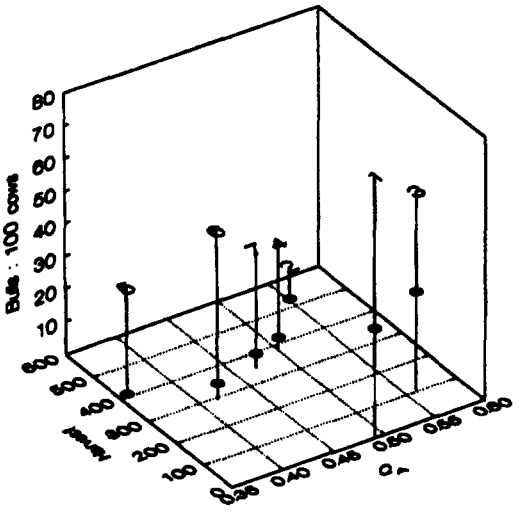

Fig. 1. Comparison of mean annual harvest in years 30-50 of the simulations, post-hunt ratios of bulls:100 cows, and the frequency of favorable antler alleles (Q_A) in year 50 for each of seven selective harvest strategies (1 = no harvest, 2 = any bull, 3 = SF, 4 = SF/50, 5 = 36 inch, 6 = 50 inch, and 7 = SF/50/NB). Total elevation of spikes indicates the estimate of all bulls:100 cows, and the filled circles indicate the estimate of large bulls:100 cows for each strategy. Ten simulations were conducted for each strategy.

Table 4. Mean final allele frequencies (Q_A and Q_B) and harvest levels for model runs using heritabilities of 0.25 and 0.75.

	Heritability = 0.25					Heritability = 0.75				
			Harvest					Harvest		
Harvest strategy	Q_A	Q_B	Yearling	Medium	Large	Q_A	Q_B	Yearling	Medium	Large
None	0.4981	0.5020	0	0	0	0.4934	0.5057	0	0	0
Any bull	0.5239	0.5203	141	358	23	0.5721	0.4901	105	384	31
SF	0.5290	0.5011	119	0	0	0.5771	0.5063	90	0	0
SF/50	0.5079	0.2907	131	61	179	0.5218	0.2871	123	61	186
36-inch	0.4456	0.4306	0	387	36	0.3476	0.3874	0	375	25
50-inch	0.4674	0.2685	0	84	214	0.4098	0.2518	0	91	194
SF/50/NB	0.4953	0.4976	133	0	215	0.4887	0.4999	137	0	210

Analysis of the influence of heritability indicates that higher values tended to cause more rapid genetic changes and associated population changes (Table 4). For instance, those strategies that increased Q_A (any bull, SF, and SF/50) under a heritability of 0.5 were characterized by lesser spike/fork and equal or greater harvest of medium- and large-antlered bulls when using a heritability of 0.75. Despite these differences, the relative differences between the harvest strategies were the same regardless of heritability.

MANAGEMENT IMPLICATIONS

The post-hunting bull:100 cow ratio is a parameter of great interest to moose managers because of its potential ramifications on reproduction. In Alaska, the generally accepted minimum ratio is 20 bulls:100 cows. All of the strategies, with the exception of traditional any-bull harvest, easily achieved this benchmark. However, the ratio of large-antlered bulls:100 cows varied considerably. The 36-inch strategy had approximately three times as many bulls:100 cows than did the any-bull strategy, yet these two strategies had similar low ratios of large bulls:100 cows. Similarly, the SF/50 strategy showed an eight-fold difference in large bulls when compared to the 36-inch strategy despite a similar bull:100 cow ratio. In our simulations, the SF strategy was the only scenario that resulted in a population of large bulls similar to that of the no harvest strategy, but SF resulted in no trophy harvest. Of the other strategies, those specifying a legal spread of ≥127 cm (SF/50, 50 inch, and SF/50/NB) yielded what we believe to be adequate post-hunt numbers of large-antlered bulls and thereby provided the highest trophy harvest. Any-bull and 36-inch strategies were characterized by low trophy harvests as well as low numbers of large-antlered bulls for viewing. Under these two strategies the paucity of large bulls prior to the hunting season, combined with a greater harvest would result in many instances of yearling bulls acquiring mates. Such a circumstance could lead to second and third estrus breeding (Rausch 1965, Rausch *et al.* 1974) which could lead to lower over-winter survival of calves. Aside from reproduction concerns, the presence of large bulls in the population can be an important management consideration in areas where interest in wildlife viewing and/or trophy hunting is high.

Populations characterized by low hunter participation or low harvest rates will respond differently than described. In his analysis of the effects of selective harvest on elk, Thelen (1991) determined that changes in allele frequencies were related directly to magnitude of harvest rates. Thus, under lower harvest rates the genetic changes we described would be less pronounced, and higher harvests would produce the opposite effect.

Until heritability of moose antler characteristics is determined, the selection of an appropriate harvest strategy should be based upon its relationship to management objectives, rather than to absolute numbers per se. It is apparent in this analysis that a spike/fork regulation criterion favors greater antler development in the population whereas minimum spread regulations inhibits expression of antler development. Combinations of these two selection criteria were intermediate in their effects. Defining legal bulls by brow tine characteristics is seemingly deleterious to superior brow formation, and management strategies that include such a regulation should be evaluated in order to determine if such a change is acceptable.

Schwartz *et al.* (1992) proposed an alternative to the SF/50 strategy, which consisted of a SF season with unlimited hunter participation followed by an any-bull season in which hunter participation is limited by availability of permits. The number of permits issued would be dependent upon the number of bulls that could be harvested but still maintain an acceptable post-season bull:100 cow ratio. Although we did not evaluate such a

strategy, from the information presented here we conclude that this harvest strategy is desirable from a management standpoint. The primary disadvantage of the SF strategy is the limited harvest it provides, whereas the disadvantage of an any-bull strategy is the low post-hunt bull:100 cow ratio it generates. Both strategies are very desirable from a genetics standpoint however. By combining these two strategies, the disadvantages of both could be minimized without limiting their advantages. Also, this combination would eliminate any need to selectively harvest bulls based on brow tine architecture.

Fulfillment of harvest demand, reproduction, and viewing are all important management considerations that are dependent upon the number of bulls in a population. Balancing these conflicting objectives in populations subjected to high hunting mortality can best be accomplished by selective harvesting. Managers must be aware, however, of the genetic ramifications of the selective criteria upon which their harvest strategies are based. Although the genetic mechanism discussed here is hypothetical, the appropriate harvest strategy can be selected only after population objectives are quantified and the genetic consequences are evaluated.

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