AN ANALYSIS OF THE INFLUENCE OF MALE AGE AND SEX RATIO ON REPRODUCTION IN BRITISH COLUMBIA MOOSE (*Alces alces* L.) POPULATIONS

By

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ABSTRACT

Relations among bull age, sex ratio and reproductive parameters in British Columbia moose populations were investigated. Specifically, the effects that bull age-selective harvest regulations versus non-selective harvest regulations might have on pregnancy rate, conception timing, and recruitment were compared. Existing harvest, inventory, and reproductive data from four management subregions were analyzed. There was no evidence that reductions in the prime and senior-aged bull social classes in a population resulted in reduced pregnancy rates or later conception timing. No evidence was found that greatly skewed sex ratios in favour of cows resulted in reduced pregnancy rates. No relation was found between bull/100 cow ratios and calf/100 cows in the winter inventory.

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INTRODUCTION

Status and Management - The moose is the largest cervid in the world and is found globally throughout the subboreal and boreal forests. Three subspecies are recognized in British Columbia, *A. a. shirasi*, *A. a. andersoni* and *A. a. gigas* (Cowan and Guiget 1965). Ecologically, British Columbia is very diverse and moose are found over a wide range of habitat types and climatic regimes. Spalding (1990) provides a thorough discussion of the early colonization and historical distribution of moose in B.C.

In British Columbia, the moose is one of the most highly valued wildlife species for both consumptive and non-consumptive activities. The provincial population estimate is approximately 173,000, with the majority (135,000) in the Ministry of Environment's northern regions of Skeena and Omineca-Peace (I. Hatter pers. commun.). The Ministry of Environment's draft provincial moose statement divides the province into nine moose management areas. In four of the management areas, the population trend from 1985 to 1989 is listed as stable, in four areas it is listed as stable to declining and in one area it is listed as stable to increasing. The moose management statement discusses three options for population objectives, ranging from accepting some decline in the provincial numbers to increasing moose numbers by 20% over a 20 year period

(Hatter *et al*. 1990).

For hunters, moose in B.C. are managed for both trophies and meat, with 90% of hunters interested exclusively in meat (Hatter *et al*. 1990). Historically in North America, bull moose have been managed with open seasons and regulations in the form of bag limits and season length. In B.C., harvest management of moose has consisted of seasons for either antlered or antlerless moose or both. Varying season lengths was another common technique. In 1974, however, limited entry hunting was introduced to provide managers more control of the numbers harvested and control of the geographic distribution of the harvest. The limited entry regulation requires that hunters be drawn from a pool of applicants for the hunt. In 1981, age-selective hunting was introduced, in which specific age-classes of bulls were subjected to differing hunting pressures. The primary reason for introducing an age-selective harvest strategy for bulls was a growing concern that altered age-structures might adversely affect the productivity and health of ungulate populations through disruption of social processes. The concept of considering social aspects of ungulate populations in management strategies was introduced into North America by Bubenik (1971, 1972). Moose managers in several provinces have since implemented age-selective harvest regulations

(Stewart 1978; Macgregor and Child 1981; Euler 1983). The rationale for the age-selective harvest strategies is discussed in the remainder of this chapter.

Male Social Behaviour - Compared to other ungulate species, little is known about the behaviour of moose and much of that is anectodal. Very little quantitative analysis has been done.

Being primarily a forest dweller and a 'concentrate selective' herbivore requiring high quality forage (Hofmann 1985), moose are less social than many open terrain dwelling ungulates such as bighorn sheep (*Ovis canadensis* Shaw) (Geist 1971), and Scottish red deer (*Cervus elaphus* L.) (Geist 1963), and they are the least gregarious of the North American cervids (de Vos *et al.* 1967; Peek *et al.* 1974). Both sexes are primarily solitary during much of the year, however, bulls appear to be more gregarious than cows (Houston 1968; Peek *et al.* 1974). In a comparison of moose populations in Alaska, Montana and Minnesota, Peek *et al.* (1974) found that bull aggregations varied in size over the year and that seasonal timing of peak aggregations varied geographically. On the Kenai Peninsula, Alaska, the largest aggregations were seen in July and August before the rut. In the Montana and Minnesota populations, the largest aggregations were after the rut, from mid-October to December. In all three areas, the largest aggregations generally occurred in open habitat such as alpine tundra, willow bottoms and cutover areas. Observations on moose in Wells Gray Park, British Columbia, found small aggregations of bulls in winter, spring, and during the rut (Geist 1963). Many of these observations occurred in the open sub-alpine terrain and in burned-over brush-meadow valley bottoms. In relatively open habitat in the Jackson Hole area of Wyoming, Houston (1968) observed small aggregations of bulls but found little variation in their occurrence throughout the year.

The solitary nature of the moose may be an evolutionary adaptation to transient or small habitat patches (Houston 1968; Geist 1971). Forage supplies in riparian areas or habitat patches isolated by deep snows may be quickly decimated by large aggregations. Large patches of good habitat are often created after catastrophic events such as fire and larger groupings of moose can be found in such areas, however the use of these habitats is temporally limited by forest succession (Geist 1971). Habitat structure itself will likely affect group formation through forage distribution patterns and availability of openings. Peek *et al.* (1974) suggested that the solitary behaviour and dispersal of moose may be a predator-avoidance strategy. The large size and aggressive behaviour of the moose (Mech 1970; Geist 1971) may also reduce the need to aggregate with others as an anti-predator strategy.

During the breeding season, a bull may mate with several cows. The mating system has been referred to as a limited or conditional polygamy (Houston 1968; Markgren 1969) or serial monogamy (Bubenik 1985), because throughout much of the range of the moose, the bull spends time tending an individual breeding cow during her estrus period rather than tending several in a group.

Bulls become more aggressive with the onset of the breeding season (Lent 1974) and in open-terrain such as the tundra, they establish dominance hierarchies (Peek *et al.* 1974). Lincoln *et al.* (1985) define a dominance hierarchy as "a social order of dominance sustained by aggressive or other behavioural patterns". Clutton-Brock *et al.* (1982) stated that competition in ungulates may be most intense when the potential exists for individual males to gain exclusive access to many females for the purpose of breeding. In these situations, females are a limited resource and are very valuable for male fitness. Serious battles between bulls are rare (Markgren 1969) and generally occur only between large bulls of equal status or size. Sparring matches between young bulls of equal size tend to be less intense (Geist 1963; Peek *et al.* 1986). Young bulls with little chance of breeding would not be expected to invest much energy in fighting.

Observations indicate that the presence of higher-ranking bulls in breeding groups prevent lower-ranking bulls from participating in breeding activity, although they are almost certainly capable physiologically (Altmann 1959; Houston 1968; Bubenik 1971). Sparring matches between adult and juvenile red deer bulls have been observed late in the breeding season and probably occur because the juveniles are testing and strengthening their own abilities (Clutton-Brock *et al.* 1982). McCullough (1979) stated that for young males to move up in rank in a hierarchial system, they must continuously interact and test themselves with individuals of both lower and higher rank.

<u>Social Stress Theory</u> - Bubenik (1971) felt that the terms 'adult' and 'juvenile' were too vague for describing social classes of animals and suggested that the terms 'kids', 'pre-teens', 'teens', 'primes' and 'seniors' were more descriptive. He argued that the presence of prime (6-10 year old) bulls maintains order in a population during the rutting period by suppressing the breeding activities of younger, less experienced bulls. Hunting practices that

target prime bulls could artificially skew the population age-structure to younger bulls and also significantly alter the sex ratio in favour of cows. A surplus of cows in the population would increase the breeding opportunities for teen bulls. Bubenik argued that having a majority of younger bulls in the bull population would accelerate sexual maturation, possibly inhibiting skeletal growth. With few prime bulls in a population, the teens would lack experience in sorting out social ranks making them behave abnormally towards the primes. Also, they would not have developed the proper courting behaviour towards cows. The actions of the teens would significantly stress the prime bulls and the cows, and this in turn would negatively impact the reproductive rate. Reproduction and recruitment would be impaired because of:

a) an increase in cows being bred after their first estrus, resulting in late-born calves with reduced survival rates, and b) an overall decrease in the percentage of cows bred (Bubenik 1971, 1972; Stringham and Bubenik 1974).

Mating Systems - Behavioural studies have found the environment to be a major factor in determining mating systems, more so than phylogenetic heritage (Vehrencamp and Bradbury 1984). The lack of visibility in much of the boreal and sub-boreal forests of B.C., together with the patchiness of food resources, probably limits group formation. Low densities of moose and lack of grouping would make it difficult for a dominance hierarchy to become established in forested habitat. Peek *et al.* (1986) questioned whether dominance hierarchies would occur in forests to the south. Bubenik (1987) suggested that habitat density and climate severity cause differences between the mating systems of open-dwelling tundra moose and moose in forested habitat. Clutton-Brock *et al.* (1982) also identified habitat and climate as major factors in determining mating systems in cervids.

For a behavioural pattern to persist in a population, it must not reduce the reproductive fitness of the performer. Behaviour that reduces fitness should disappear through natural selection. Studies indicate that, in northern tundra populations at least, cow moose prefer large-antlered bulls (Knowles 1983; Bubenik 1987). If well-developed secondary sex traits (i.e., antlers, body size) increase mating success in bulls, then this behaviour of the cow would be expected, assuming it is a heritable trait. The cow should select the mate which is most likely to pass these characteristics on to their offspring, improving the mating success of the offspring and increasing the chance that her genes will continue to be passed on.

Research on captive animals has found the estrus period for cow moose to be approximately 24 hours (Schwartz 1987) and there is some evidence that the presence of a bull may play a role in initiating estrus (Bubenik 1987; Schwartz pers. commun.). It also has been suggested that calves born later because breeding in the second or third estrus will have a reduced chance of survival in their first winter because of their smaller size (Baker 1975; Crichton 1988; Child and Aitken 1989). Research on captive moose has found that late-born calves do not experience compensatory growth and go into the winter with lower body weights than calves conceived in the first estrus (Schwartz pers. commun.). Given the short estrus period and the potential importance of first estrus breeding for calf survival, it should be expected that in situations where cows may have few bulls to choose from (i.e., in low-density forest-dwelling populations or populations pioneering new habitat) cows will be less selective in their choice of mates. Courtship behaviour and secondary sexual characteristics, described by Bubenik (1987) to be significant factors in the breeding system, should be less important under these conditions. Being selective would decrease the cows chances of breeding in the first estrus and decrease her overall fitness. The degree to which a cow is selective should depend on her knowledge of the availability of bulls. This knowledge would be gained from the frequency of interactions with bulls, from vocalizing, rut pits, or visual contact, shortly before and during the rut period.

Hypothesis

Based on this review, it is my thesis that with the wide variety of habitats that moose occupy and the attraction to early seral stages encouraging them to be somewhat nomadic, the breeding behaviour of moose should be flexible enough to compensate for relatively wide variations in population density, sex ratio, and bull age structure and therefore, reproduction should not be significantly impaired. This is contrary to Bubenik's predictions described earlier.

Figure 1 illustrates the potential pathways by which density, age structure, and sex ratio may influence reproduction in a moose population. The dotted lines indicate suspected relations while the solid lines indicate relations which are more certain. Productivity was defined as the number of calves born. Recruitment in the model was defined as the number of calves surviving to approximately seven months of age (when most population inventory work is done). For the purpose of data analysis and comparison later in the paper, the number of calves per 100 cows was used as the measure of recruitment.

Density may impact reproduction in ungulates through changing nutritional levels, affecting conception timing (McCullough 1979), and pregnancy rates (Blood 1974; Boer 1987). Cow age may affect conception timing through delayed estrus of younger cows, as has been observed in red deer (Mitchell and Lincoln 1973) and in moose (Schwartz pers. commun.). Cow age has also been related to pregnancy rates (Pimlott 1959; Markgren 1969; Franzmann and Schwartz 1985) and twinning rates (Pimlott 1959; Boer 1987). Most of this relation is due to lower fecundity in yearling cows. The impact of bull age on reproduction has not been documented for moose. Several studies on elk, however, have suggested that yearling bulls are not as effective breeders as branch-antlered bulls and breeding by yearling bulls may result in later conception dates and reduced pregnancy rates (Hines and Lemos 1979; Prothero *et al.* 1979; Smith 1980). Reduced bull/cow ratios may delay conception timing (Lent 1974) and reduce pregnancy rates (Boer 1987). As previously mentioned, timing of conception has been suggested as a factor affecting calf survival and therefore may impact on recruitment. Pregnancy rates and twinning rates will be related to productivity in that they determine the maximum potential productivity. Similarly, limits to potential recruitment will be determined by productivity.

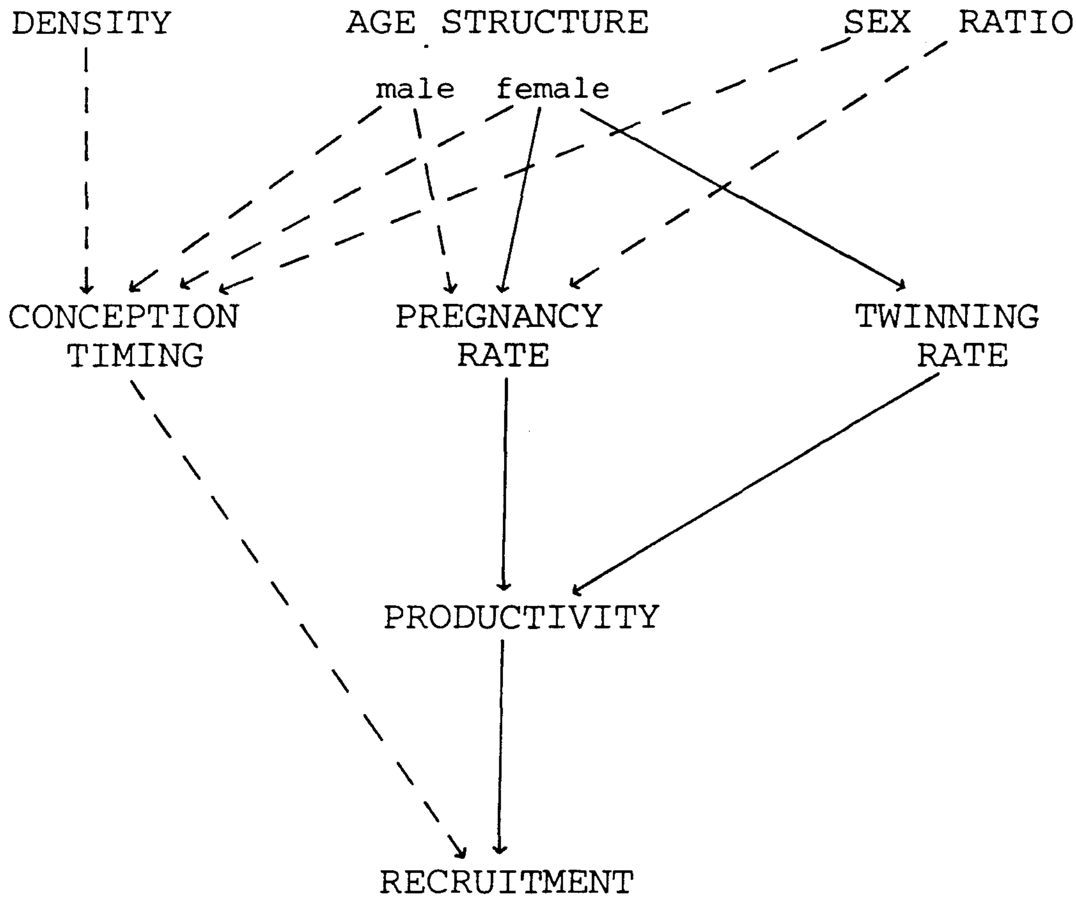


Figure 1. The proposed relationships between some demographic characteristics in a moose population.

(dotted lines indicate suspected relationships)

External mortality factors, such as predation, disease, and weather, were omitted for simplification. It should be recognized however that these factors will impact quantitatively on the model, particularly between productivity and recruitment. Also, some form of mortality is implicit in the proposed relation between conception timing and recruitment.

Bubenik's predictions of the 'social stress' theory could not be evaluated without a lengthy field study. Therefore, I identified some logical consequences of the theory that could potentially be addressed with existing harvest and inventory data. My general hypothesis can be restated in the form of several testable questions:

1. Does the reduction of prime and senior-aged bulls result in reduced pregnancy rates?

2. Does the reduction of prime and senior-aged bulls result in delayed conception dates?

3. Does skewing of the sex ratio in favour of cows result in reduced pregnancy rates?

4. Do these changes affect recruitment?

Data from several B.C. Ministry of Environment subregions were used in this study. The Omineca, Peace, Cariboo, and Thompson-Nicola subregions were chosen because of their significant moose harvests and because they have cow harvests providing reproductive tracts. There also is a difference in the harvest policies between the subregions. The Omineca implemented an age-selective bull strategy in 1981 while the other subregions have maintained non-selective bull seasons.

STUDY AREAS

The following descriptions of the subregions included in the study were adapted from the ecoregion classifications described by Demarchi *et al.* (1990).

The Thompson-Nicola subregion represents the Southern Interior Ecoprovince. This area is characterized by a warm dry climate. Vegetative cover ranges from extensive grasslands and open parkland to dense coniferous forests at higher elevations.

The Cariboo subregion represents the Central Interior Ecoprovince. Winters are cold, summers are warm,and precipitation is greater than in the Thompson-Nicola subregion. The vegetation is intermediate between the dry southern interior and the cold boreal forests. Grassland habitat in the south mixes with open coniferous forests. Extensive wetlands are also present in parts of the subregion. Denser subboreal forests in the north are primarily coniferous but deciduous stands are common.

The Omineca subregion represents the Subboreal Interior Ecoprovince. Winters are cold and arctic air outbreaks and relatively high snowfalls are common. The dominant vegetative cover is the dense coniferous forest with deciduous stands more numerous than in the south.

The Peace subregion represents the Boreal Plains Ecoprovince and is on the eastern side of the Rocky Mountains. The continental climate is relatively dry with cold winters dominated by arctic air. Extensive deciduous forests and grasslands create an aspen (*Populus tremuloides* Michx.) parkland habitat. Dense coniferous forests are also common throughout the subregion.

METHODS

Existing B.C. Wildlife Branch data were used to look for evidence of the suspected relations in the model (Figure 1) and to address the stated questions. Lack of available data on population density and on productivity, as it is defined here, precluded any analysis of relations involving these parameters. It was also felt that management actions would have little impact on cow age structure as hunters would not be selective on cow-age, therefore, no analyses were done with cow age data. As twinning rates are likely affected primarily by habitat quality and possibly by cow age (Pimlott 1959; Franzmann and Schwartz 1985), these data were not evaluated.

All data were collected by Ministry of Environment staff and made available for this study. The types of data used were: age of bulls in the harvest; age of cows in the harvest; pregnancy rate and dates of conception; and winter population composition data in the form of bull/cow/calf ratios.

Age - Teeth from harvested cows were collected along with the reproductive tracts. Cow-age data were available on the raw data sheets from each of the subregions. Bull age data were extracted from the Summary Statistics Data Base on the Ministry of Environment's VAX computer. Each year teeth from hunter-killed bull moose are voluntarily sent in by hunters for ageing. Age was determined by grinding or sectioning teeth and counting the cementum annuli in the root (Sergeant and Pimlott 1959).

Yearling bulls were excluded from the databases as graphical analysis of age distributions from the tooth return database indicated that yearlings were underrepresented. This is likely due to hunters being able to age yearlings in the field and therefore not being curious about age. Distributions of the other age classes appeared to fit that of a typical age distribution and it was therefore assumed that they were representative of the distribution of the harvest. It was also assumed that the proportion of ages in the tooth return was representative of those in the actual population. Because the age-selective bull regulations in the Omineca restricted the harvest of older bulls, the tooth return database for this subregion was biased toward younger bulls, and therefore could not be compared to other subregions. Comparisons were done using the social maturity class data from the Omineca winter inventories. Maturity classes were determined using a modified version of Oswald (1982). Based on analyses of antlers from bull harvests in the Omineca, bulls were considered to be in the prime category at age 5 1/2 (K. Child pers. commun.). In the tooth return database these animals are recorded as 5 years old.

Sex Ratio and Recruitment - Winter inventories were performed regularly by Ministry staff in the Omineca, Peace and Thompson-Nicola subregions. The timing of the inventories varied from early December to late January. The management units surveyed varied from year to year. Generally, line transect surveys were used to obtain classified count information, except in the Thompson-Nicola subregion where stratified random block inventories were done each year.

Most of the inventory information was in the form of classification at the level of bull, cow, and calf. Bull moose start to drop their antlers in early December beginning with the older animals. For this reason, it was usually not possible to classify bulls by age class. Cow moose were distinguished from antlerless bulls by the presence of a white vulval patch on the cows (Mitchell 1970) or presence of antler pedicles on the bulls. If conditions made identification difficult then an animal was recorded as an unclassified adult. Classification information was standardized for comparison by converting it to two statistics: the number of bulls per 100 cows; and the number of calves per 100 cows.

Surveys in the Omineca subregion were performed early enough to classify the bulls into maturity classes based on antler size.

Pregnancy Rate and Conception Timing - Hunters in each of the four subregions were requested to submit reproductive tracts from the limited entry cow hunts held in late November or early December. Submission of the reproductive tracts was compulsory in the Omineca, Peace, and Thompson-Nicola subregions. In the Omineca subregion, the collection of reproductive tracts began in 1977 and initial sample sizes were small. In the Thompson-Nicola subregion, collections began in 1986 and in the Peace subregion, they began in 1988. The Cariboo subregion began collecting in 1983, however, submission of reproductive tracts was not compulsory and samples were small for most years. Only data from 1985 and 1986 were used from the Cariboo.

Pregnancy was usually determined by the presence of a foetus in the uterus. In some cases where foeti were not present due to late conception, pregnancy could also be detected by the presence of embryonic threads or a blastocyst (Markgren 1969). Detailed analysis of the ovaries may also provide an indication of pregnancy (Markgren 1969), however, the Omineca was the only subregion to carry out thorough ovarian analyses. To standardize the pregnancy data, cows were only considered to be pregnant if the determination was based on examination of the uterus. In the Omineca data set, cows determined to be pregnant based on analysis of the ovaries were recorded as not pregnant.

Yearling cows were removed from the data sets because of their highly variable pregnancy rates which are likely related to nutrition (Pimlott 1959; Franzmann and Schwartz 1985). The large numbers of yearling cows could have a significant effect on the pregnancy rate of the population making it difficult to determine relationships with population sex ratio and bull age structure.

For cases of pregnancy, the conception dates could be estimated from the size of the foetus. During the first 90 days of development, foeti can be aged by measuring the crown-rump length (Markgren 1969). The Peace, Cariboo and Thompson-Nicola subregions used the foetus length/age relationship determined by Markgren (1969), for ageing. The Omineca subregion aged feoti with a modified version of the Markgren method, resulting in different ages than the other subregions for given foetal lengths. There also appeared to be some differences between the subregions using the Markgren method. For these reasons, all foetus ages were recalculated and standardized using the Markgren method. Date of conception was determined by subtracting the foetus age from the date of kill.

Statistical Tests

Differences between the percentage of primes and seniors in the Omineca bull population and the percentage of 5+ year-olds in the bull populations from the Peace, Cariboo and Thompson-Nicola subregions were tested with the Kruskal-Wallis test, a nonparametric analogue of a single classification analysis of variance test (Sokal and Rohlf 1981).

Differences in pregnancy rates between the subregions were tested for with the Kruskal-Wallis test.

Linear regression analysis (Sokal and Rohlf 1981) was used to test for relations between pregnancy rates and bull/100 cow ratios; calf/100 cow ratios and pregnancy rates; and calf/100 cow ratios and bull/100 cow ratios. Data from individual management units were used to compare pregnancy rates and calf/100 cow ratios or bull/100 cow ratios. There were few management units in each region which had both inventory data and reproductive tract samples, therefore the regions were pooled to look for relationships. Calf/100 cow ratios were compared against pregnancy rates from the previous year as this would have been when the calves were conceived. Similarly, calf/100 cow ratios were compared against bull/100 cow ratios from the previous winter as these should be the closest to the population sex ratio when the calves were conceived. Pregnancy rates were compared against bull/100 cow ratios from both the previous winter and from the winter immediately following collection of the reproductive tracts to determine which inventory provided the best relationship.

RESULTS

Does the reduction of prime and senior-aged bulls result in reduced pregnancy rates? - Figure 2 compares the proportion of prime and senior-aged bulls from the Omineca winter surveys with the proportion of bulls five years and older in the harvests of the other subregions. Yearlings were not included in the datasets. The graph indicates that the Omineca subregion has a greater proportion of prime and senior-aged bulls than the other subregions. The difference was found to be statistically significant ($p < 0.001$).

Figure 3 shows pregnancy rates, by subregion, calculated for cows two years of age and older. No significant differences were found between the subregions ($p > 0.5$).

Does the reduction of prime and senior-aged bulls result in delayed conception dates? - Figure 4 shows the mean dates of conception for each subregion. Dates were quite normally distributed in all cases with median values within one day of the means in all but one case in which the median was two days from the mean. Standard deviations were similar in all cases. Confidence limits (95%) calculated about each mean indicated

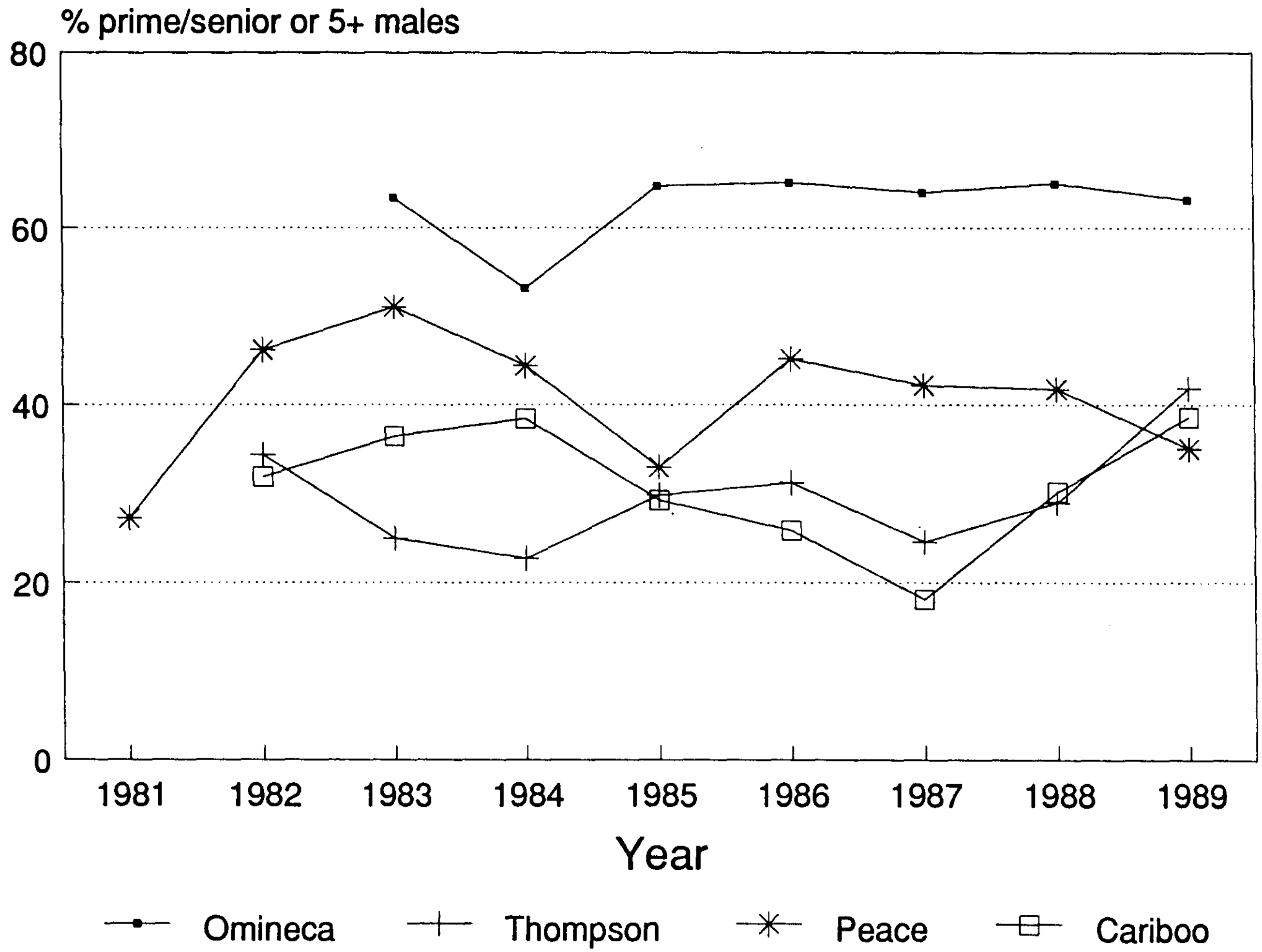


Figure 2. A comparison of the proportion of prime and senior-aged bulls using inventory data for the Omineca subregion and tooth return data for the other subregions.

	OMINECA	PEACE	THOMPSON	CARIBOO
1985	76 (n=53)			77 (n=69)
1986	80 (n=103)		80 (n=54)	83 (n=70)
1987	90 (n=83)		83 (n=86)	
1988	80 (n=86)	83 (n=193)	77 (n=60)	
1989	80 (n=86)	80 (n=159)	93 (n=96)	
1990	76 (n=80)	81 (n=149)	79 (n=65)	

Figure 3. Pregnancy rates for cows 2 years and older for four regions of British Columbia, 1985-1990.

	OMINECA	PEACE	THOMPSON	CARIBOO
1985	Oct.7 (41,5.47)			Oct.7 (57,6.36)
1986	Oct.9 (82,7.08)		Oct.7 (37,2.99)	Oct.8 (81,6.61)
1987	Oct.5 (79,5.82)		Oct.10 (67;4.31)	
1988	Oct.7 (68,6.27)	Oct.9 (166,6.08)	Oct.8 (43,4.07)	
1989	Oct.6 (72,5.92)	Oct.8 (134,6.08)	Oct.9 (83,7.08)	
1990	Oct.6 (60,4.89)	Oct.9 (119,5.78)	Oct.7 (51,4.49)	

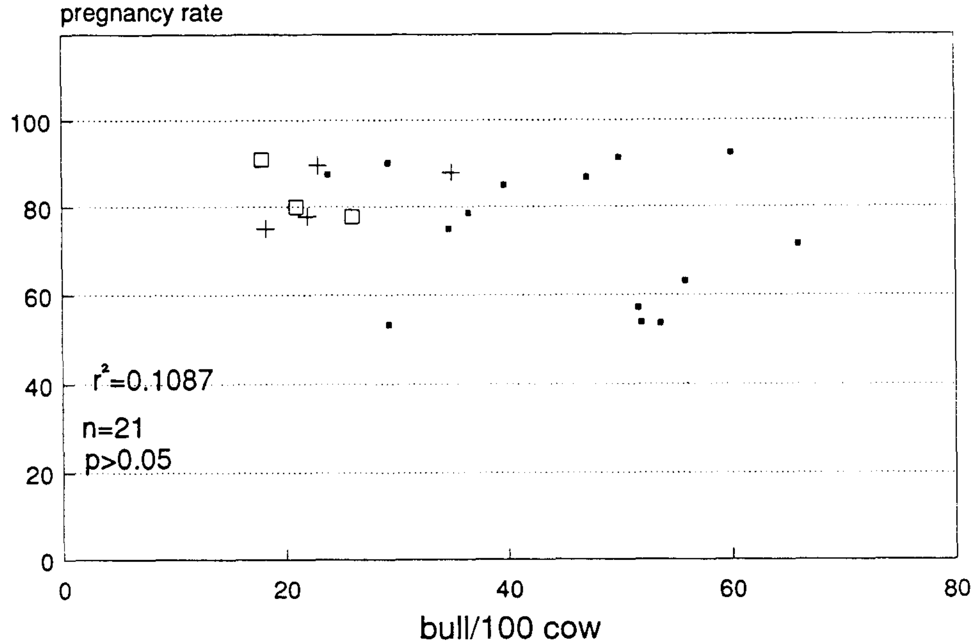
Figure 4. Mean conception dates for cows 2 years and older for four regions of British Columbia, 1985-1990.

(with sample size and standard deviation) that there were no significant differences in conception dates between subregions or between years within subregions.

Does the skewing of the sex ratio in favour of cows result in reduced pregnancy rates? - Figure 5a compares the pregnancy rates in the Omineca, Thompson-Nicola and Peace subregions with bull/cow ratios from the previous winter inventory. Over the range of bull/100 cow ratios tested, no significant relationship was found ($p > 0.05$). Figure 5b compares the pregnancy rates for the same subregions with the post-rut sex ratios. No significant relationship was found ($p > 0.25$).

Do the changes affect recruitment? - Figure 6 compares calf/100 cow ratios with the corresponding pregnancy rates from individual management units in the Omineca, Peace and Thompson-Nicola subregions. The relationship is not significant ($p > 0.05$).

a. Ratios from the previous winter.



b. Post-rut ratios.

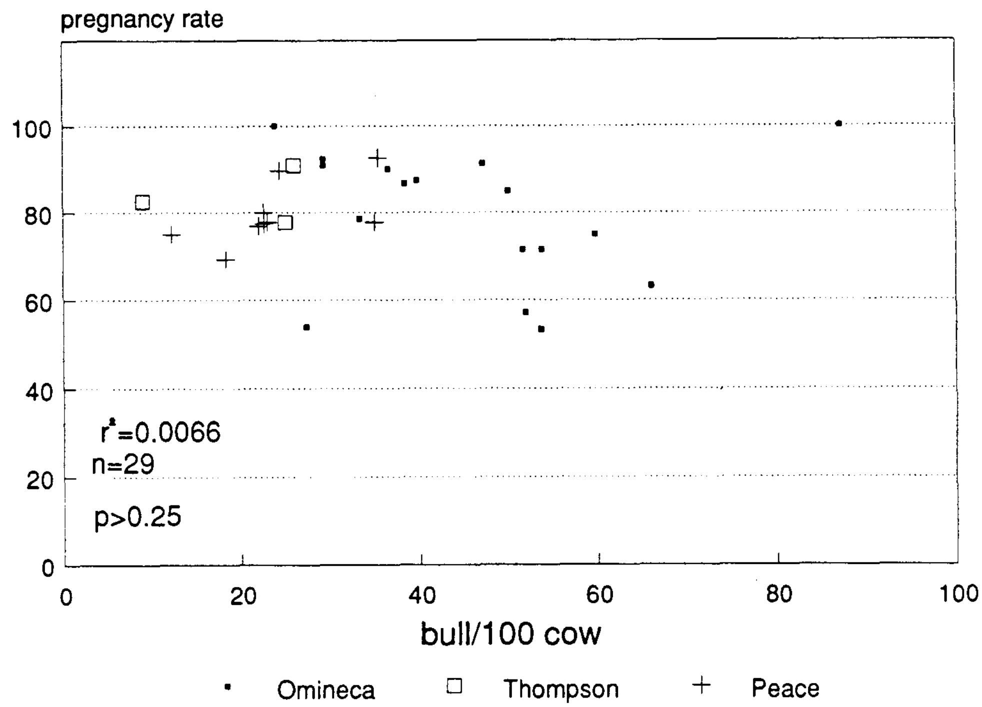


Figure 5. A comparison of pregnancy rates with ratios from the previous winter and post-rut bull/100 cow ratios.

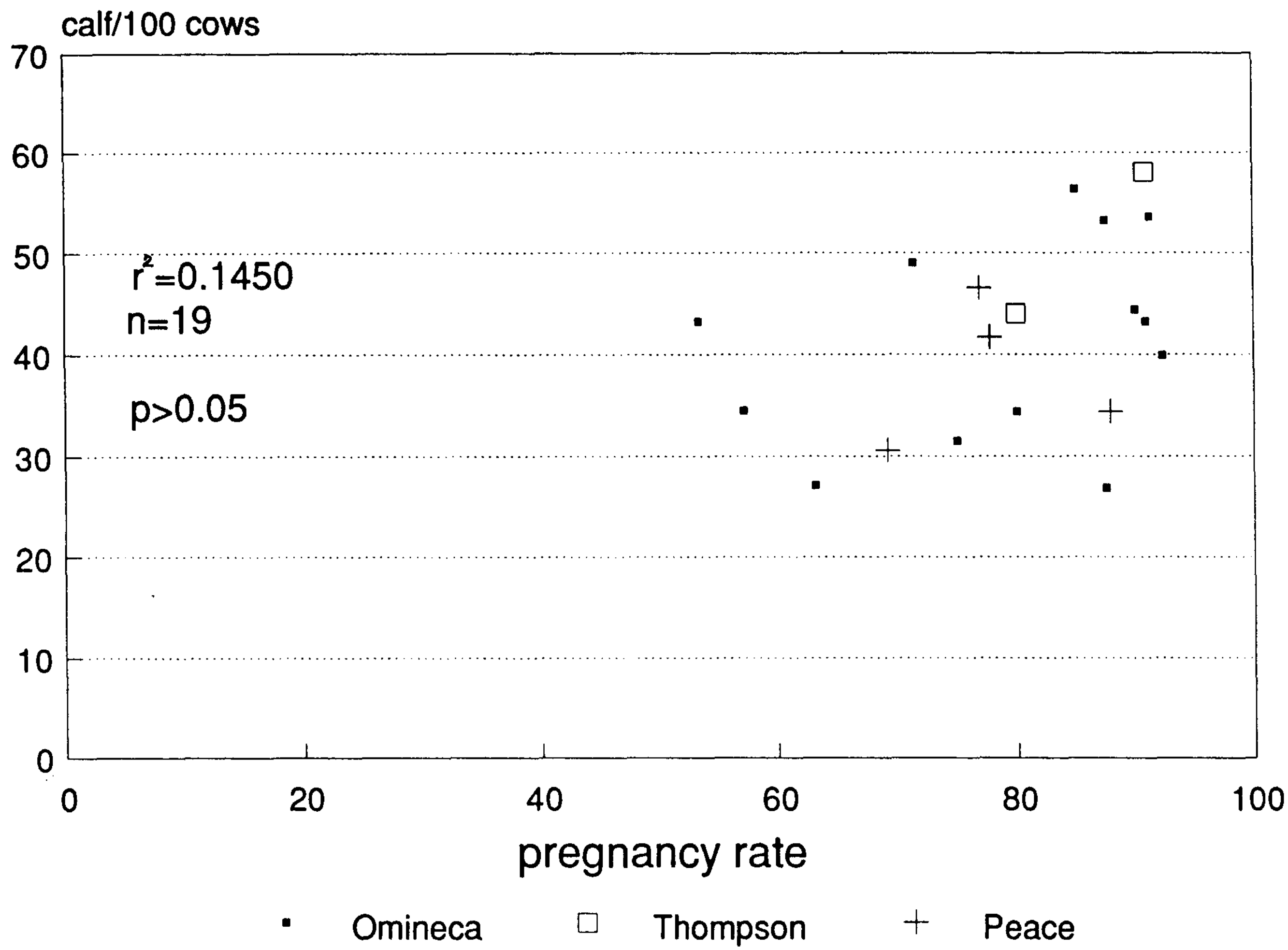


Figure 6. Calf/100 cow ratios compared to pregnancy rates in the previous year.

Figure 7 compares calf/100 cow ratios with bull/100 cow ratios from the previous year, using winter inventory data taken from 1964 to 1991 in the Thompson-Nicola subregion. The data were divided into three periods of approximately ten years each. There is a significant negative relationship ($p < 0.0005$). The graph also indicates that recruitment has been greater after 1975 than before. Bull/100 cow ratios have declined since 1975.

Figure 8 compares calf/100 cow ratios with bull/100 cow ratios from the previous winter for the Omineca subregion. The data were divided by the year when the age-selective regulations were implemented. No significant relationship was found ($p > 0.25$).

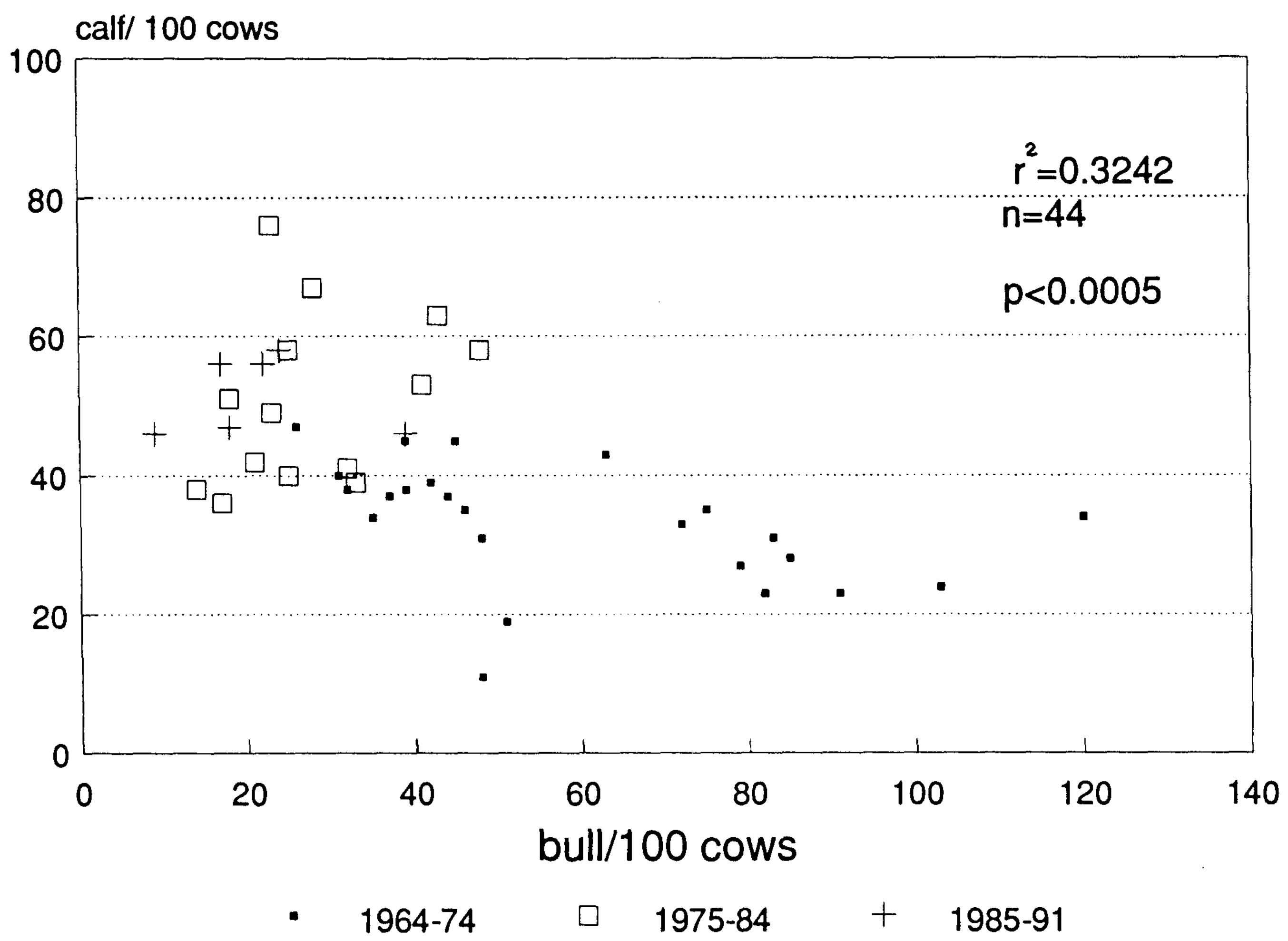


Figure 7. A comparison of calf/100 cow ratios with bull/100 cow ratios from the previous year in the Thompson-Nicola subregion, 1964-1991.

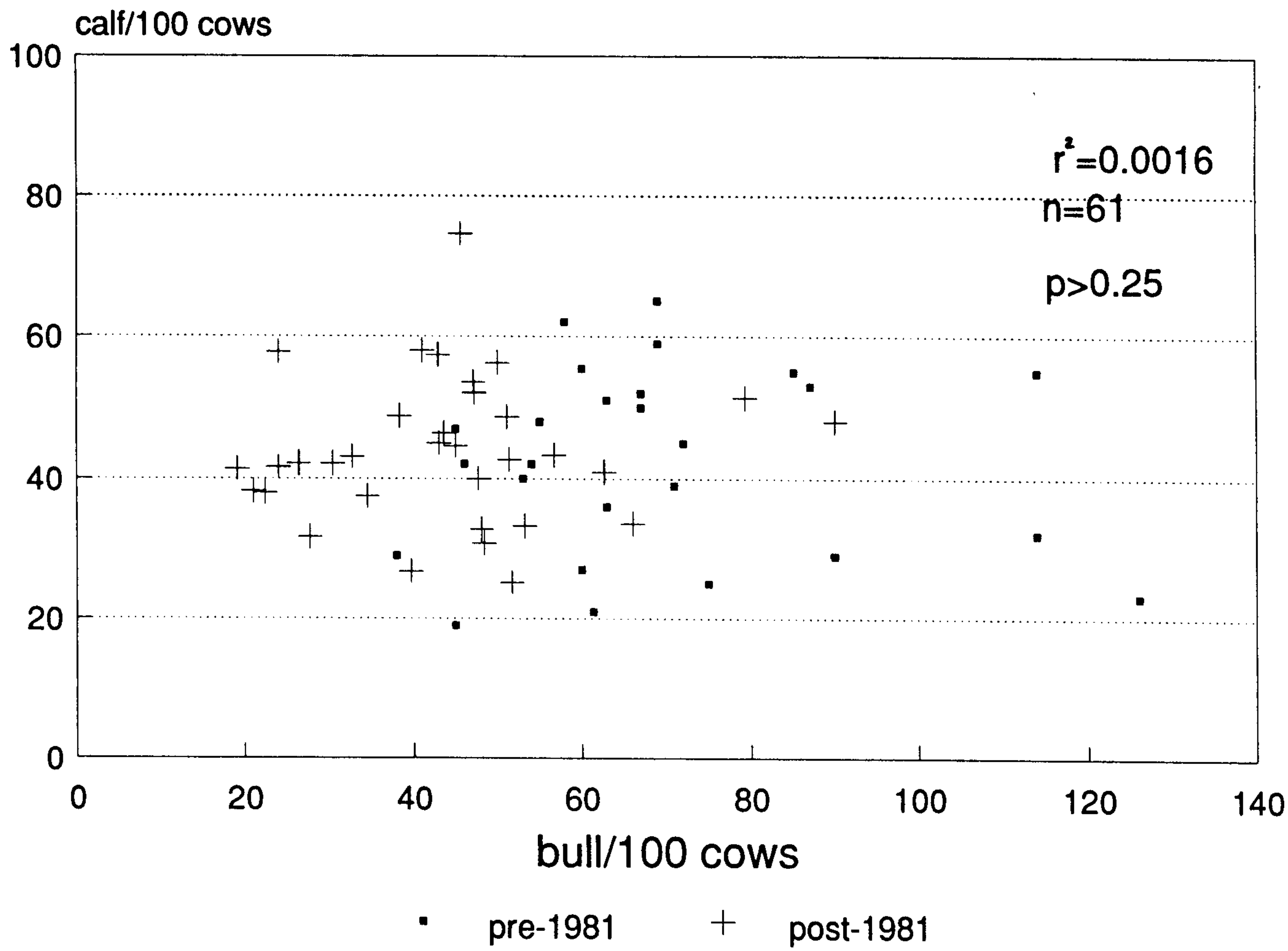


Figure 8. A comparison of calf/100 cow ratios with bull/100 cow ratios from the previous year in the Omineca subregion, 1973-1989.

DISCUSSION

Age Structure - A difference in the age structure of the bull moose population was found between the Omineca subregion and the three other subregions (Figure 2). The Omineca subregion, with the age-selective policy, had a significantly greater percentage of prime and senior-aged bulls ($p < 0.001$) based on the comparison of the inventory classification data with the tooth return data from the other subregions. There was no evidence that the lower percentage of prime and senior-aged bulls in the Peace, Cariboo and Thompson-Nicola subregions resulted in reduced pregnancy rates. No significant differences in pregnancy rates ($p > 0.5$) were found between the subregions (Figure 3).

There was also no evidence that the difference in age structure between the subregions had any affect on conception timing. Mean conception dates for all subregions and over all years sampled ranged over a 5 day period in early October (Figure 4). There was no significant difference in the mean dates based on the 95% confidence limits about the means.

The observations support the hypothesis that a reduction in the proportion of prime and senior-aged bulls in the population, over the range evaluated here, has no significant effect on reproduction. The social classes of bulls performing the majority of the breeding cannot be determined from the existing data. However, it may be reasonable to assume that in the subregions with low proportions of prime and senior-aged bulls, the younger bulls are significantly involved in the breeding activity.

Despite these findings, age structure of populations for all ungulates may be a management concern for genetic rather than reproductive reasons. Using modelling techniques and data from moose and white-tailed deer (*Odocoileus virginianus* Zimmermann), Ryman *et al.* (1981) found that different hunting regimes could greatly alter the generation interval in a population and this had severe effects on heterozygosity. Prothero *et al.* (1979) stated that the major contribution that mature males make to a population is a genetic one and they suggested that removal of the selective pressures for breeding may have longterm consequences for the fitness of the population.

Sex Ratio - No evidence was found for any relation between sex ratio and pregnancy rate or recruitment. In the cases of pregnancy rate versus bull/100 cow and calf/100 cow (Figures 5a, 5b, and 6), it is known that the relation must pass through the origin. It appears that the effect of sex ratio is only evident at very low bull/cow levels, i.e., less than 20 bulls/100 cows (Figures 5a and 5b). Only a few data points are available below this level (for the Peace and Thompson-Nicola subregions) and no reduction in pregnancy rate was obvious although sample size was small. No significant relation ($p > 0.05$) was found between pregnancy rate and recruitment (Figure 6). One likely reason for lack of a relationship would be the limited sample size that was available. Given the large size of most management units, it was only appropriate to compare pregnancy rates and calf/cow ratios from the same unit. In each subregion, there were very few management units which had a reasonable reproductive sample and a winter inventory for the appropriate years. For this reason data from the subregions were pooled and the relation illustrated in Figure 6 is based on 19 samples.

The apparent negative relation between calf/100 cow and bull/100 cow in the Thompson-Nicola subregion (Figure 7) is likely due to factors outside of the population. The apparent trend is caused by low calf/100 cow ratios in the 1964-74 period of inventory. During much of this period, inventories were performed on management areas which were larger and had different boundaries than the present management units. Areas with higher snowfall and possibly greater wolf predation levels were included in the early period but not in the later periods (D. Low and R. Ritcey pers. commun).

Sex ratios were reported to be close to 50/50 and often in favour of bulls in Newfoundland and Ontario during the late 1940's and early 1950's (Peterson 1955). Based on the literature, Bubenik (1972) stated that equal sex ratios are normal for naturally regulated moose populations. Bubenik (1987) stated that in taiga moose populations it was important to maintain a minimum 50/50 sex ratio to avoid a decrease in reproduction. Both Boer (1987) and Crete *et al.* (1981) believed that 40% bulls in the adult wintering population (67 bulls/100 cows) was the threshold below which reproduction may be reduced. I found no evidence that either of these levels are critical; pregnancy rates in B.C. moose populations with adult sex ratios much less than 40 bulls/100 cows are comparable to those reported in natural populations with higher sex ratios.

Analysis of the available data in B.C. produced no evidence that prime-aged bulls or high bull/cow ratios are necessary for maintaining relatively high pregnancy rates in moose. This analysis makes the assumptions that the age structure in the hunter sample for the Peace, Cariboo and Thompson-Nicola were representative of the actual population with the exception that yearling moose were likely underrepresented as hunters would be less likely to submit a yearling tooth for ageing.

The validity of the analysis of sex ratio and recruitment information depends upon the winter inventory data being an accurate representation of the populations. Any bias in the inventory data is likely to be greater in the bull/cow data as it is possible that one or the other sex is selecting habitat which would reduce its visibility. If groups of one sex were being missed strictly because the two sexes were not associating together, it would be expected that within and across inventories, this source of bias would be removed. Calves should remain with their mothers through the first winter and therefore, the chances that calf/cow ratios are inaccurate should be less than for bull/cow ratios. Another possible source of error in calf/cow ratios would be if there was a difference in habitat selection between cows with calves and cows without calves.

An alternative explanation to the lack of relationship between pregnancy rate (Figure 6) or bull/cow ratios (Figures 7 and 8) with recruitment is that external mortality factors were impacting calf numbers before the winter inventories were done. As most inventories were done in December or early January, it is unlikely that winter weather conditions would have had time to reduce calf numbers. Disease, predation and poor weather conditions shortly after parturition may be reducing calf numbers. Research in Alaska has found brown bear (*Ursus arctos* L.) predation to be the major mortality source for moose calves (Ballard *et al.* 1991). Wolf (*Canis lupus* L.) predation was identified as a major mortality source for moose in Quebec (Messier and Crete 1985), and the main direct mortality agent on moose calves on Isle Royale (Mech *et al.* 1987).

The possible effect of population density on reproductive parameters must be considered when interpreting these results. It was not possible to evaluate the influence of density on the variables tested due to lack of data. Density-dependent factors may have influenced the results, particularly when looking at the relation between calf/100 cow and bull/100 cow ratios (Figures 7 and 8). The majority of the high bull/cow ratios (i.e., > 50 bulls/100 cows) were observed before the 1980's and before reproductive tracts were being collected. It is possible that moose densities were higher when many of the earlier inventories were performed and this may have reduced recruitment.

MANAGEMENT RECOMMENDATIONS

1. The Wildlife Branch should continue to investigate the relations between bull age, sex ratio and reproduction to get a clearer picture of their significance in B.C. moose populations. This could be facilitated with larger samples and by ensuring that winter inventories are performed in the same management units where the reproductive samples are collected.

2. Trials should be performed to test whether inventory techniques are accurate. This could possibly be done by following transect inventories with a total block count. This should be attempted on several areas which may have different compositions of open and forested habitat.

3. Winter inventories should be performed and recorded on a management unit basis rather than a geographic area so that the information can be more easily compared with other indices such as reproductive data and hunter harvest data. This problem would be lessened if management unit boundaries were delineated along major geographical/ecological features as much as possible so that it is possible to differentiate between populations of animals. Also, georeferencing all harvest and inventory data on a computer database would greatly enhance the ability to explore relations in the data.

4. The Wildlife Branch is currently reviewing its committment to collecting and ageing tooth samples from the annual ungulate harvests. It is recommended that this program be maintained as much as possible, particularly for moose. The data set may prove valuable for future work on genetic and reproductive changes in populations. The age data also will likely be valuable and necessary for estimating moose population sizes through modelling exercises.

5. Foetus ageing techniques should be standardized across the province. The accuracy of the ageing method is less important than consistancy as the primary interest is in identifying trends or changes.

6. Reproductive data should be stored in a computer database similar to the harvest and inventory databases currently used by the Wildlife Branch.

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