RELATIONSHIP BETWEEN IN UTERO PRODUCTIVITY OF MOOSE AND POPULATION SEX RATIOS: AN EXPLORATORY ANALYSIS

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ABSTRACT: We investigated the in utero productivity of moose (*Alces alces*) in the central interior of British Columbia from 1981 to 1990. Variations in the ovulation, fertilization, fetal and in-utero twinning rates were correlated to adult sex ratios. Significant correlations between the fetal rates and bull:cow ratios as well as between the twinning rates and bull:cow ratios are presented. Implications of these relationships on moose management and harvest strategies are discussed.

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In utero productivity of moose has been studied across its circumpolar ranges (Aitken and Child 1991, Blood 1974, Boer 1987, Edwards and Ritcey 1958, Faro and Franzmann 1978, Glushov 1987, Markgren 1969, Pimlott 1959, Saether and Haagenrud 1983, Schladweiler and Stevens 1973, Sylven et al 1980, Thomson 1991). Productivity is usually described by corpora lutea counts, pregnancy rate, fetal and twinning rates for both the population and specific age-classes of cow moose. Generally, all studies report that productivity changes with age and maximal in utero productivity is expressed by mature cows $\geq$ 5 years of age (Aitken and Child 1991, Crichton 1988, Edwards and Ritcey 1958, Simkin 1965).

Bubenik (1971, 1987) suggests that potential productivity of cows is realized when social structure is managed to maintain a breeding sex ratio at or near parity (100:100) and that 50% of the male segment should be of the mature social classes ($\geq$5 yrs). Crête et al (1981) recommended that a minimum 40:60 (67:100) bull:cow ratio would likely maintain a stable level of productivity and sustain a huntable population. Timmerman (1992) concurred and suggested that a 50:100 bull:cow ratio is likely the minimum threshold necessary to maintain a productive moose population.

In this paper, we present an exploratory analysis of the relationship between measures of in-utero productivity and bull:cow ratios in the central interior of British Columbia.

METHODS

Hunters were selected by lottery to participate in a late season (late November to early December) for antlerless moose. The purpose of these hunts was to permit monitoring of female reproductive performance and herd productivity (Child and Aitken 1989). Reproductive tracts were examined from cows harvested in Management Units (MU) 7-10, 7-12 and 7-15 from 1981 to 1990 while from 1986 to 1990 additional collections were required in MU 7-07, 7-16 and 7-24 (Fig. 1). Successful hunters were required to submit the complete reproductive tract (Appendix 1) and an incisor tooth from all cow moose harvested. Age of cows was determined from inspection of cementum annulations (Sergeant and Pimlott 1959). All cows 1.5 years of age were included in the analyses.

Ovaries and fetal tissues were formalized (10%) for 30 days. Only those samples with both ovaries intact were considered in these analyses. Ovaries were sectioned sagitally by razor blade (1-2mm sections) and visually examined for corpora lutea (CL).

Potential productivity was described by the ovulation rate. We assumed all CLs to be primary, and therefore indicative of ovulation

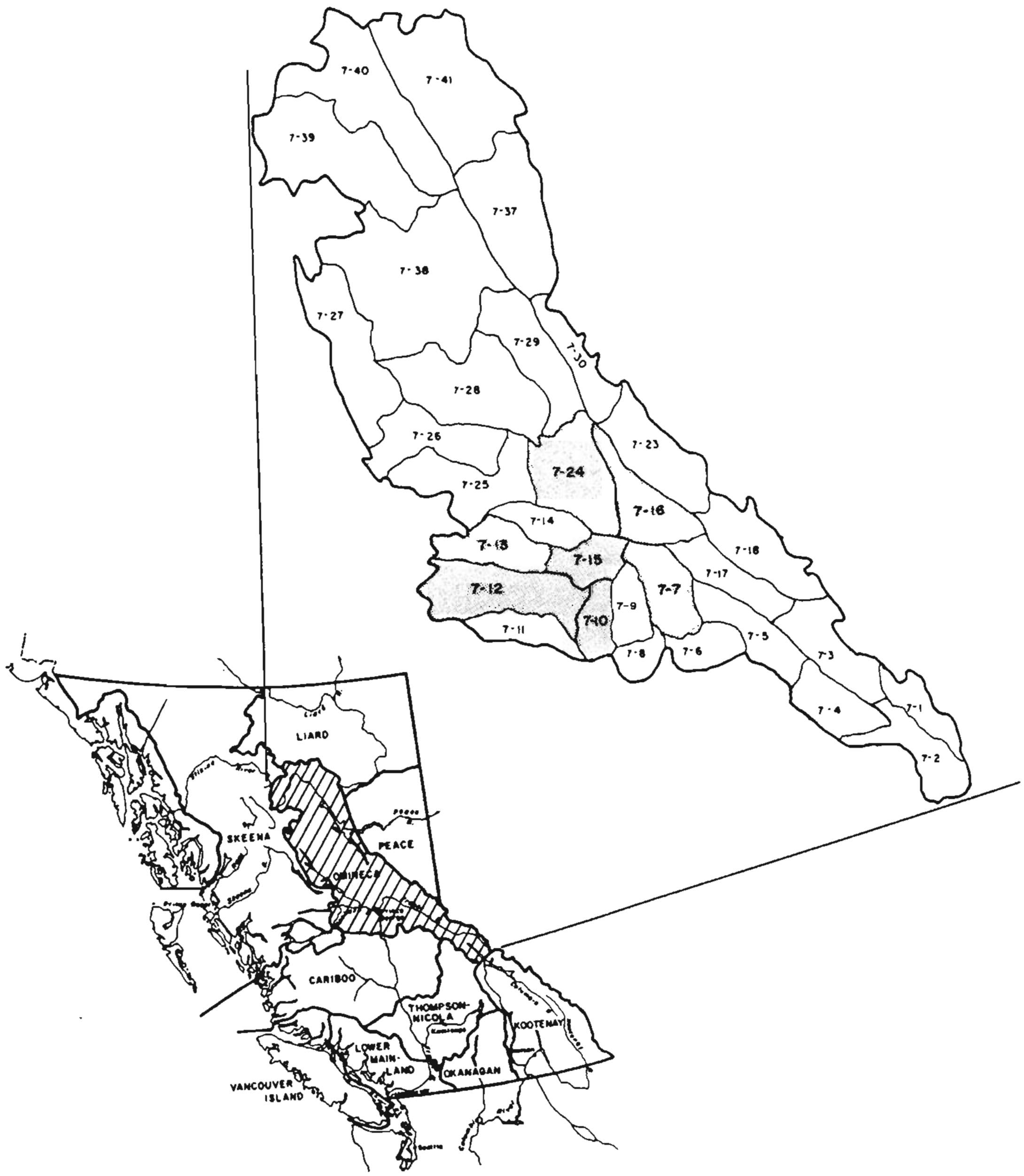


Fig. 1. Management units in which aerial inventories and reproductive tract collections were conducted from 1981-1990.

and potential progeny production. Potential twinning (multiple CLs) and non-ovulation rates were expressed as the percentage of cows with 2 or more CLs and 0 CL respectively.

Pregnancy was determined by presence of one or more foeti. The pregnancy rate was expressed as the proportion of adult cows pregnant. In-utero productivity was expressed by the fetal rate (number of foeti:100 cows). The twinning rate was determined by the proportion of cows with 2 foeti in-utero. The barren rate was recorded as the proportion of cows with 0 foeti in-utero. The fertilization rate (Simkin 1965) was calculated by the ratio of fetal rate to ovulation rate.

Gestational "age" of all foeti and embryos was interpolated from forehead-rump and crown-rump measurements from a composite growth curve (in prep) of known-aged elk (Morrison *et al.* 1959), white-tailed deer (Cheatum and Morton 1946) and mule deer embryos and foeti (Hudson and Browman 1959). The date of conception for cow moose was calculated by backdating from date of kill (Cheatum and Morton 1946, Morrison et al. 1959). The mean date of conception in each management unit was calculated after converting the conception dates to Julian dates.

Each of the productivity indices were calculated for the adult (≥1.5 years) population as well as for immature (1.5 - 4.5 years) and mature (≥5.5 years) cows in each management unit (MU) over the period of collections.

Helicopter surveys were conducted with varying frequency (Appendix 2) in six management units (MU) from 1981 to 1990 (Fig. 1). The surveys were conducted during the first two weeks of December to determine the social structure of the bull segment, the status of the population by adult (≥1.5 yrs) sex ratios and cow:calf ratios. Numbers of immature and mature bulls were determined by antler architecture (Child and Barry 1991, Oswald 1982).

We compiled all available aerial survey information. For those instances when bulls were not classified by antler architecture we used the proportions of immature and mature bulls in all other years combined for that management unit to determine the number of bulls in each class. Numbers of immature and mature cows in the aerial inventory were determined by extrapolation from the proportions of each class in the aged harvest from 1981 to 1990.

Bull:100 cow ratios (BC 1 to 9, Table 1) were determined from the adjusted inventories (Appendix 2). The significance of relationships between the productivity indices and various bull:100 cow ratios were determined by correlation analysis (P=0.05). BC 1, 4, 7 were tested against productivity indices for all cows, whereas BC 2, 5, 8 were tested against productivity indices for immature cows and BC 3, 6, 9 were tested against productivity indices for mature cows.

RESULTS

Population (All cows):

No significant correlations were found between the ovulation and fertilization rates, mean dates of conception and the total bull:100 cow ratios, immature bull:100 cow ratios, and the mature bull:100 cow ratios. However, 5 of 27 correlations tested between the in-utero productivity indices and population structures were significant (Table 2). Specifically, the pregnancy rate was positively correlated to the immature bull:100 cow ratio (BC 4); the fetal rate was positively correlated to both the total bull:100 cow ratio (BC 1) and the immature bull:100 cow ratio (BC 4). Variations in

Table 1. Combinations of observed numbers of bulls and cows used to derive the various bull:cow ratios.

	Adult Cows	Immature Cows	Mature Cows
Adult Bulls	BC 1[1]	BC 2	BC 3
Immature Bulls	BC 4	BC 5	BC 6
Mature Bulls	BC 7	BC 8	BC 9

[1] Bull:cow ratio

population ratio from 38 bull:100 cows to 66 bulls:100 cows were significantly correlated with fetal rates varying from 84 foeti:100 cows to 109 foeti:100 cows (Fig. 2a). Also, variations in sex ratio from 21 immature bulls:100 cows to 33 immature bulls:100 cows were strongly correlated with variations in fetal rate from 84 foeti:100 cows to 109 foeti:100 cows (Fig. 2b).

Additionally, the twinning rate was positively correlated to both the immature bull:100 cow ratio (BC 4) and to the mature bull:100 cow ratio (BC 7). Twinning rates between 7.4% and 22.7% were positively correlated

Table 2. Correlation coefficients between productivity indices for all cows and various bull:cow ratios.

Productivity index		Bull:cow ratio (as in Table 1)		
		BC 1	BC 4	BC 7
Ovulation rate	r=	0.0818	-0.0296	0.4690
	n=	6	5	5
	P=	0.878	0.962	0.426
Potential twinning rate	r=	-0.0251	-0.2097	0.2781
	n=	6	5	5
	P=	0.962	0.735	0.651
Non-ovulating rate	r=	-0.5264	-0.6954	-0.6265
	n=	6	5	5
	P=	0.283	0.192	0.258
Pregnancy rate	r=	0.7740	0.8826	0.6925
	n=	6	5	5
	P=	0.071	0.047*	0.255
Fetal rate	r=	0.8398	0.9843	0.8215
	n=	6	5	5
	P=	0.036*	0.002*	0.088
Twinning rate	r=	0.8054	0.9066	0.8921
	n=	6	5	5
	P=	0.053	0.034*	0.042*
Barren rate	r=	-0.7103	-0.8786	-0.6025
	n=	6	5	5
	P=	0.114	0.050	0.282
Fertilization rate	r=	0.4277	0.6470	0.1883
	n=	6	5	5
	P=	0.398	0.238	0.762
Mean date of conception	r=	-0.2475	-0.7534	-0.4028
	n=	6	5	5
	P=	0.636	0.141	0.501

* denotes significance at P=0.05

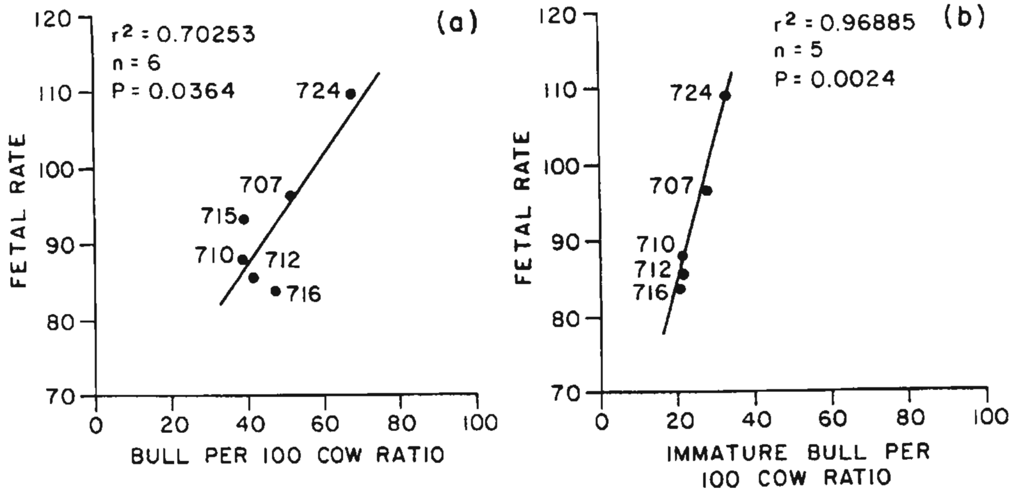


Fig. 2. Correlations of population in utero fetal rate with bull:100 cow ratios.

with both immature bull:100 cow ratios ranging from 21.5:100 to 33:100 (Fig. 3a) and with mature bull:100 cow ratios ranging between 17.8:100 to 33.5:100 (Fig. 3b).

Immature Cows:

The only significant correlation detected for immature cows was that between the mean date of conception and the mature bull:100 immature cow ratios (BC 8) (Table 3). In this case, variations in mature bull:100 immature cow ratios ranging between 34:100 and 53:100 were negatively correlated with a 3 day variation in mean date of conception from October 6 to October 3.

Mature Cows:

Significant correlations were detected between the fetal and twinning rates of mature cows and the total bull:100 mature cow ratios, the immature bull:100 mature cow ratios, and the mature bull:100 mature cow ratios (Table 4). Fetal rates between 97:100 mature cows and 133:100 mature cows were significantly correlated with bull:100 mature cow ratios that varied from 80 bulls:100 mature cows to 180 bulls:100 mature cows (Fig. 4a). These fetal rates were also significantly correlated

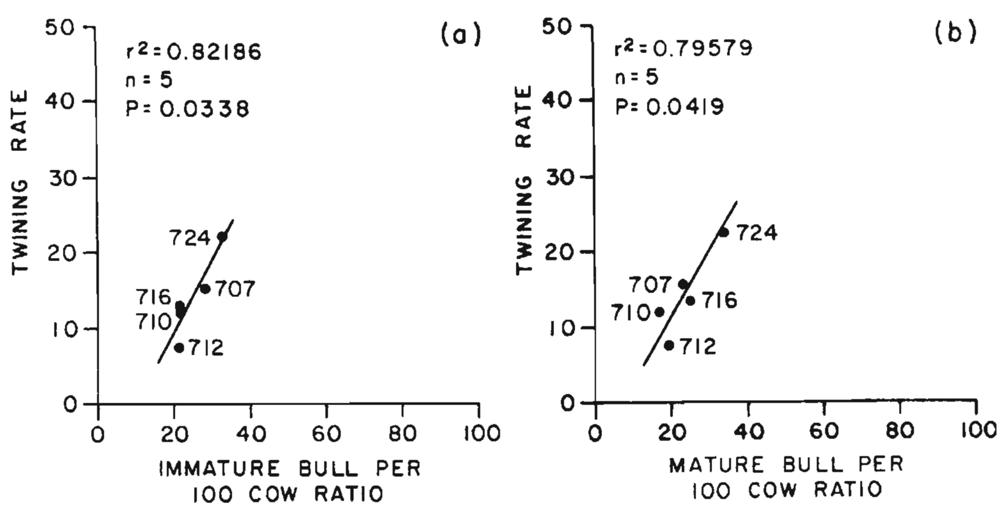


Fig. 3. Correlations of population in utero twinning rate with bull:100 cow ratios.

Table 3. Correlation coefficients between productivity indices for immature cows and various bull:cow ratios.

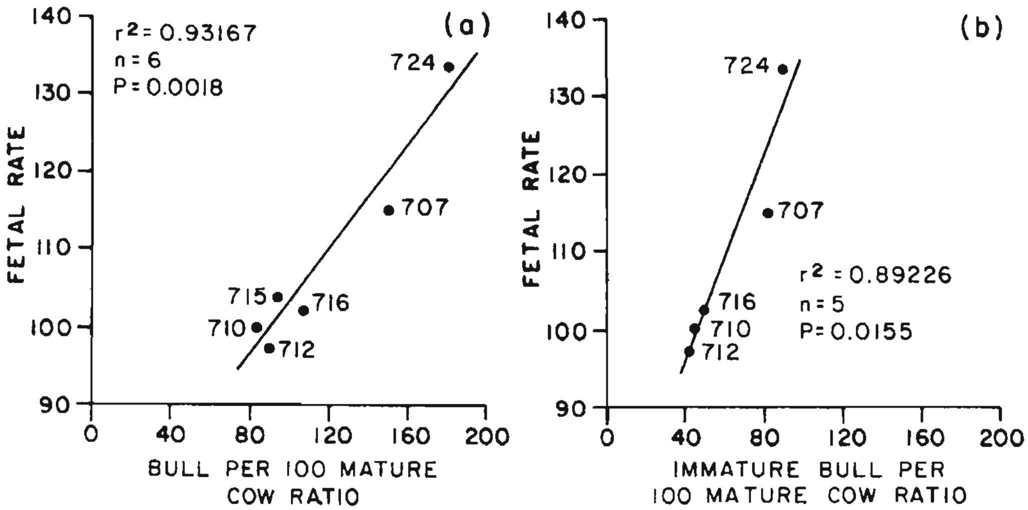
Productivity index		Bull:cow ratio (as in Table 1) BC 2	BC 5	BC 8
Ovulation rate	r=	0.4519	0.4981	0.7888
	n=	6	5	5
	P=	0.368	0.393	0.113
Potential twinning rate	r=	-0.0953	-0.1889	0.5496
	n=	6	5	5
	P=	0.857	0.761	0.337
Non-ovulating rate	r=	-0.6890	-0.7134	-0.5187
	n=	6	5	5
	P=	0.130	0.176	0.371
Pregnancy rate	r=	0.4161	0.6532	0.1930
	n=	6	5	5
	P=	0.412	0.232	0.756
Fetal rate	r=	0.3818	0.7752	0.3816
	n=	6	5	5
	P=	0.455	0.124	0.526
Twinning rate	r=	0.0288	0.6949	0.7559
	n=	6	5	5
	P=	0.957	0.193	0.139
Barren rate	r=	-0.4109	-0.6558	-0.1964
	n=	6	5	5
	P=	0.410	0.229	0.752
Fertilization rate	r=	-0.0719	0.2860	-0.4138
	n=	6	5	5
	P=	0.892	0.641	0.489
Mean date of conception	r=	-0.4935	-0.3713	-0.8940
	n=	6	5	5
	P=	0.320	0.538	0.041*

* denotes significance at P=0.05

with immature bull:100 mature cow ratios ranging from 44 immature bulls:100 mature cows to 89 immature bulls:100 mature cows (Fig. 4b) and with mature bull:100 mature cow ratios (Fig. 4c) ranging from 37 mature bulls:100 mature cows to 91 mature bulls:100 mature cows.

Similarly, twinning rates ranging from 11.5% to 38.1% were significantly correlated with these bull:100 mature cow ratios (Fig. 5a,b,c).

No significant correlations were detected



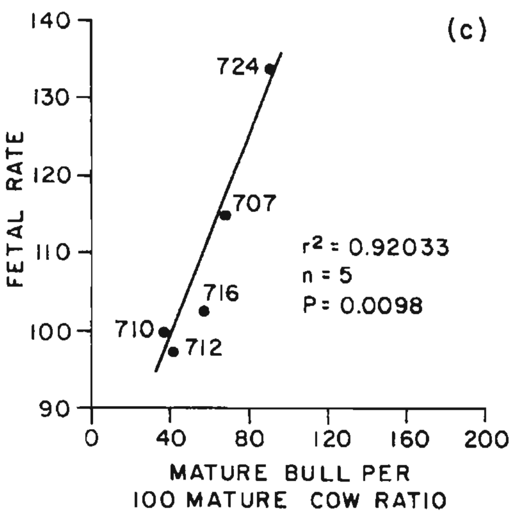


Fig. 4. Correlations of in utero fetal rates for mature cows with bull:100 cow ratios.

between the ovulation rates, pregnancy rates, fertilization rates or mean dates of conception for mature cows and various bull:100 mature cows ratios (Table 4).

DISCUSSION

Traditionally, productivity in moose has been described by the pregnancy rate and cow:calf ratios. Boer (1992) demonstrated relatively constant pregnancy rates across North America. Similarly, Thomson (1992) showed constant pregnancy rates throughout British Columbia but he did not find a correlation between pregnancy rates and bull:100 cow ratios. We only detected one positive correlation of nine tested between pregnancy rate and the various bull:100 cow ratios. These observations suggest that pregnancy rate is a questionable productivity index. Also, Boer (1992) cautioned that the proportion of calves observed in aerial surveys may not be a reliable measure of productivity since yearlings and adult cows are not easily separated and post-partum survival of calves is unknown. Thomson (1992) did not find a correlation between calf:100 cow ratios and bull:100 cow ratios in British Columbia. But, managers continue to use both pregnancy rates and cow:calf ratios as indicators of productivity and suggest that population sex ratios remain favourable despite the fact that no relationship has been established between these variables and the population sex ratio (Timmerman 1992, VanBallenberghe 1979).

Adult twinning rate may be a better index of productivity since it and yearling pregnancy rate are the variable components of fecundity (Boer 1992). Twinning has been suggested to be an indicator of nutritional status of the cow (Franzmann and Schwartz 1985). Nutrition may not be impacting productivity since densities are relatively low (0.2 moose/km² in MUs 712 and 724; 0.6

Table 4. Correlation coefficients between productivity indices for mature cows and various bull:cow ratios.

Productivity index		Bull:cow ratio (as in Table 1) BC 3	BC 6	BC 9
Ovulation rate	r=	0.0818	-0.0296	0.4690
Ovulation rate	r=	0.6829	0.6870	0.8213
	n=	6	5	5
	P=	0.135	0.200	0.088
Potential twinning rate	r=	0.5714	0.4850	0.6487
	n=	6	5	5
	P=	0.236	0.408	0.236
Non-ovulating rate	r=	0.1053	-0.2318	0.1178
	n=	6	5	5
	P=	0.843	0.708	0.850
Pregnancy rate	r=	0.4942	0.4494	0.5573
	n=	6	5	5
	P=	0.319	0.448	0.329
Fetal rate	r=	0.9652	0.9446	095936
	n=	6	5	5
	P=	0.002*	0.016*	0.010*
Twinning rate	r=	0.9706	0.9722	0.9343
	n=	6	5	5
	P=	0.001*	0.006*	0.020*
Barren rate	r=	-0.4942	-0.4494	-0.5573
	n=	6	5	5
	P=	0.319	0.448	0.329
Fertilization rate	r=	0.7250	0.7349	0.6426
	n=	6	5	5
	P=	0.103	0.157	0.242
Mean date of conception	r=	-0.0679	-0.3165	0.0437
	n=	6	5	5
	P=	0.898	0.604	0.944

* denotes significance at *P*=0.05

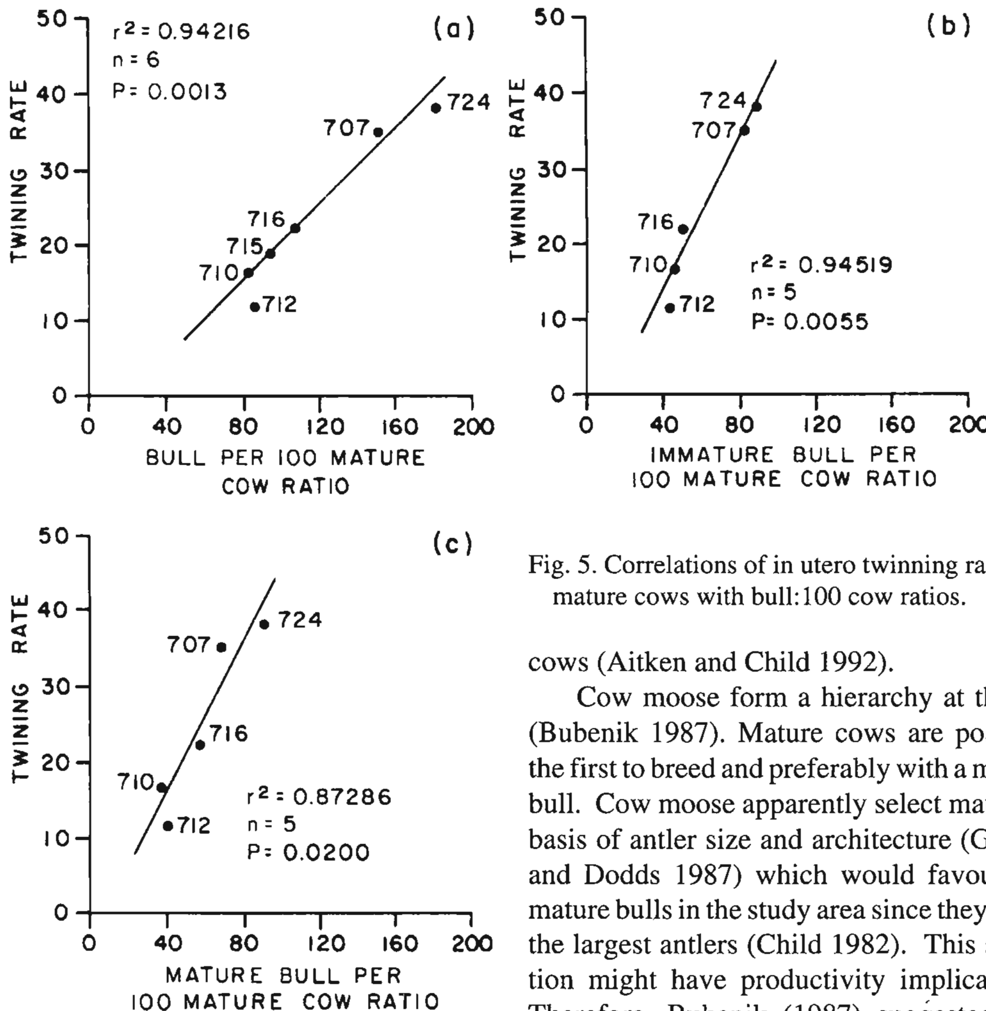


Fig. 5. Correlations of in utero twinning rates for mature cows with bull:100 cow ratios.

moose/km^2 in MUs 707, 710 and 716), food resources appear adequate and body condition (kidney fat index) is moderate to high (S. Barry, pers. comm.). Twinning has also been related to the age of the cow (Crichton 1988, Simkin 1965). Since age distributions are similar across the MUs, differences in the twinning rates are likely related to factors other than age of the cow.

The expression of potential productivity may be a function of the sex ratio since in utero fetal and twinning rates are correlated with the bull:100 cow ratio. More specifically, the observed differences in productivity may be due to realization of the full reproductive potential (twinning rate) of the mature cows (Aitken and Child 1992).

Cow moose form a hierarchy at the rut (Bubenik 1987). Mature cows are possibly the first to breed and preferably with a mature bull. Cow moose apparently select mates on basis of antler size and architecture (Gilbert and Dodds 1987) which would favour the mature bulls in the study area since they carry the largest antlers (Child 1982). This selection might have productivity implications. Therefore, Bubenik (1987) suggested that equal proportions of both mature and immature bulls are necessary for achieving potential productivity, because: (1) an adequate number of mature bulls will be available as mates, (2) mature bulls exhibit fully developed courtship behaviour and (3) mature bulls are the better breeders because of larger volumes of semen and viable sperm (Bubenik and Timmerman 1982). Miquelle (1991) demonstrated that mature bulls are not only important as mates but they may enhance the breeding effectiveness of immature bulls through contact with the sex pheromones of the mature bull (Bubenik 1987). Our analyses suggest that fetal rates and twinning rates of the mature cows are correlated with either the immature bull:100 mature cow ratios or with the mature bull:100 cow ratios. We were unable to distinguish between the relative importance of either maturity class of bulls on productivity.

A sex ratio at or near parity has been suggested to be necessary to realize full reproductive participation of cows (Boer 1992, Bubenik 1977, 1985, 1987, Crête *et al* 1981, Page 1992, Timmerman 1992). We also submit that harvest strategies should address the need to maintain high bull:100 cow ratios (≥60 bulls:100 cows). We concur with Bubenik (1972, 1977) and Timmerman (1992) who advocate that hunting strategies for moose should protect the "primes" of the population and direct harvest to the senile and juvenile segments. A light harvest of mature bulls and cows with a more liberal harvest of younger-aged individuals might be a reasonable harvest practice to maintain high bull:100 cow ratios in a managed population. This strategy should result in a population that is characterized by a balanced social structure with a sex ratio near parity (Page 1992) and high calf production (Timmerman 1992).

RECOMMENDATIONS

The observations we present in this exploratory analysis suggest some relationships that are important to moose management and warrant further investigation. We would recommend that:

1. Similar relationships be investigated in a larger sample of management units over a wider geographic distribution;
2. Manipulative experiments be conducted to verify the effect of altering bull:cow ratios on in utero productivity;
3. Studies be conducted to determine the relative importance of different proportions of mature and immature bulls to in utero productivity; and
4. Populations be managed to maximize productivity, or achieve other management objectives, by manipulation of sex ratios.

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Appendix 1. Summary of reproductive collections from 1981-1990.

Management unit	Years of collection	Number of reproductive tracts		
		Total	Mature cows	Immature cows
707	6[1]	52	20	32
710	10	100	60	40
712	10	202	122	80
715	10	90	53	37
716	5	82	41	41
724	5	44	21	23

[1]includes 1 cow harvested in 1981.

Appendix 2. Summary of inventory observations from 1981-1990.

MU1 unit	Years counted	Inventory counts					
			Bulls			Cows	
		Tot[2]	Mat[3]	Imm[4]	Tot[2]	Mat[3]	Imm[4]
707	9	583	318	265	1139	750	389
710	7	358	196	162	911	469	442
712	9	312[5]	141	130	755	386	369
715	4	51[5]	-	-	132	78	54
716	9	697[5]	300	343	1503	852	651
724	5	149[5]	65	42	224	141	83

[1] - Management Unit
[2] - Total
[3] - Mature
[4] - Immature
[5] - Totals ≠ Mature + Immature since maturity classes were not identified in all years.