

IN UTERO PREGNANCY RATE, TWINNING RATE AND FETUS PRODUCTION FOR AGE-GROUPS OF COW MOOSE IN SOUTH-CENTRAL ALASKA

Ronald D. Modafferi

Alaska Department of Fish and Game, 1800 Glenn Highway, Suite 4, Palmer, AK 99645

ABSTRACT: The relationship of reproductive parameters (i.e., pregnancy rate, twinning rate and fetus production) to 5 age-groups (calf = C, yearling = Y, teen = T, prime = P and senior = S) of cow moose (*Alces alces*) were investigated. Age-class and *in utero* fetus counts from 895 cow moose killed in 14 area-specific antlerless/cow-moose hunts (year/area (Y/A) samples) during November-February, 1964 to 1974, in south-central Alaska were analyzed. Measures of central tendency and dispersion were used to characterize the reproductive parameters in each age-group classification. There was evidence of age-group effects on pregnancy rate ($P = 0.0000$). None of the C moose examined carried a fetus(es). Age-groups ordered by pregnancy rate were $Y < T < S < P$. The difference in pregnancy rate between P and S age-groups was not statistically significant ($P = 0.1019$). Y/A effects on pregnancy status were insignificant ($P = 0.8414$). There was evidence of age-group effects ($P = 0.0001$) and Y/A effects ($P = 0.0001$) on occurrence of twinning. None of the Y age-group moose examined carried twin fetuses. Age-groups ordered by twinning rate were $T < S < P$. The difference in twinning rate between T and P age-groups was statistically significant ($P = 0.05$). Age-groups ordered by fetus production (fetuses/100 cows) were $Y < T < S < P$. Based on the reproductive parameters studied, cow moose attain their maximum productivity after 3-years-of-age. Findings emphasize the importance of considering cow moose reproductive maturity in measuring productivity, interpreting information on productivity, modeling moose population dynamics and implementing selective harvests of cow moose.

ALCES VOL. 28 (1992) pp. 223-234

Simulation models are becoming important tools in everyday management of moose (Page 1987). Population models highlight parameters that are basic and important in understanding moose population dynamics (Karns 1987). Productivity parameters are important, basic components in models of moose population dynamics and in management of moose populations (Simkin 1974, Verme 1974, Moen and Ausenda 1987). Quantitative information on some moose productivity parameters is scarce (Karns 1987, Crichton 1988). Refinements in knowledge about parameters of moose productivity will improve the quality of moose population models and lead to better moose management decisions. In this study, I was not particularly concerned with Y/A effects on cow moose productivity. Rather, the purpose of my study was to: (1) consolidate and analyze archived information on productivity parameters for

cow moose in south-central Alaska, (2) explore relationships between productivity parameters and age-class based age-groups and (3) provide moose managers, who are most familiar with net productivity in fall in the form of ratios of calves to adult cows, with baseline information on moose gross productivity.

STUDY AREA

Moose hunts took place in south-central Alaska (Fig. 1). The area included Alaska Game Management Unit (GMU) 7 and Game Management Subunits (GMS) 14A, 14B, 14C, 15A, 15B and 15C. Management Units 7, 15A, 15B and 15C were located on the Kenai Peninsula (Kenai). GMSs 14A and 14B were located in the Matanuska and Susitna River valleys (Mat-Su). The Ft. Richardson hunt area (Ft. Rich) was located in GMS 14C near Anchorage. The Kenai, Mat-Su and Ft. Rich

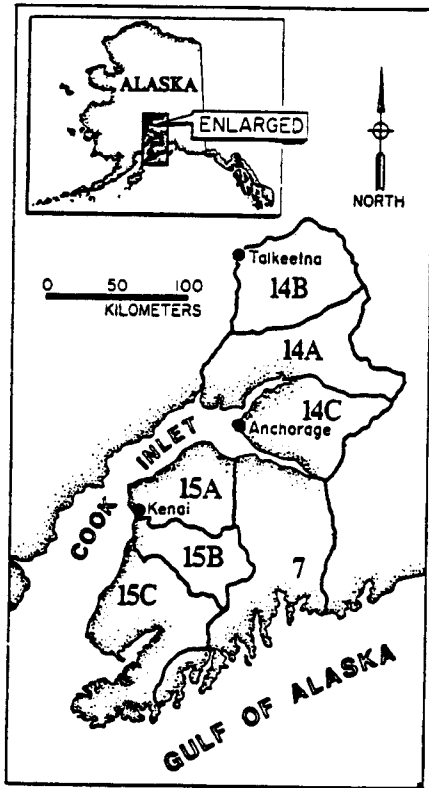


Fig. 1. Location of study area in south-central Alaska, showing the towns Talkeetna, Anchorage, and Kenai and Game Management Units/Subunits (7, 14A, 14B, 14C, 15A, 15B and 15C) where samples of hunter-killed cow moose were collected.

areas are mainly bordered by water and some high elevation mountains or glaciers and interconnect by narrow strips of moose habitat. Climate differs considerably between the 3 areas. The Mat-Su area mainly has a continental climate characterized by relatively warm summers and long cold snow-rich winters. Climate in the Kenai area is moderated by nearby large bodies of water. Compared to the Mat-Su area climate, the Kenai area has cooler summers and less severe winters. Climate in the Ft. Rich area is more similar to climate in the Mat-Su area than climate in the Kenai area.

METHODS

Data Collection

In Alaska, moose hunters may be required to collect biological data from animals they kill. Stipulations in certain antlerless/cow-moose hunts during 1964-74, required that hunters collect jaws with incisor teeth and gather data on the number of *in utero* fetuses in female moose they killed. Hunters and/or biologists macroscopically examined reproductive tracts in killed female moose to count the number of *in utero* fetuses. Fetus count data were used to determine pregnancy rate, twinning rate and fetus production. Jaws and incisor teeth collected from killed moose were submitted to the Alaska Department of Fish and Game (ADF&G) for age-class determination (Sergeant and Pimlott 1959).

Archived (ADF&G files) information on pregnancy rate, twinning rate, fetus production and age-class of 895 female moose killed in 14 area-specific antlerless/cow-moose hunts held in late November-February during 1964-74 were analyzed.

Data Analysis

Y/A Samples and Age-Groups

Moose data from 14 Y/A-specific antlerless/cow-moose hunts were merged into 11 Y/A samples based on hunt year and/or hunt/area-location (GMU or GMS) (Table 1). Sample data were assigned to 5 age-class based age-groups; C = age-class 0, Y = age-class 1, T = age-classes 2 and 3, P = age-classes 4-11 and S = age-classes 12 and greater. Such age-group classifications and age-group names were introduced by Bubenik *et al.* (1975) and Bubenik (1981) as social-class names to describe maturation status of moose. In addition to rationale stated by Bubenik *et al.* (1975) for age-class break points between age-group classifications T, P and S, I used age-class 3 as the break point between age-groups T and P because female moose in Alaska attain maximum body size at about 4 years (Schwartz *et al.* 1987:305). Age-class

Table 1. Number of specimens (n), hunt area (GMU/S), hunt month and year (Date) and year *in utero* fetus(es) were conceived for 11 year/area (Y/A) samples of cow moose killed by hunters in south-central Alaska, 1964-74.

Y/A sample	n	GMU/S	Date	Year fetus(es) conceived
A	52	7	Nov 1964	1964
B	91	15C north	Nov 1964	1964
		15C south	Nov 1964	1964
C	59	15	Nov 1965	1965
D	139	15B	Feb 1970	1969
		15C	Jan 1970	1969
E	101	15A	Dec 1970	1970
F	140	14A	Jan-Feb 1970	1969
		14B	Jan-Feb 1970	1969
G	46	14C	Nov 1965	1965
H	36	14C	Feb 1969	1968
I	36	14C	Jan 1973	1972
J	46	14C	Feb 1974	1973
K	159	14A	Nov-Dec 1965	1965

11 was used as the break point between age-groups P and S because antler size measurements suggest senescence begins at about this age in male moose in Alaska (Gasaway 1975).

Managers are most familiar with moose productivity parameters in the form of data as % cows with calves, % cows with twins, and ratios of calves/100 cows collected in fall when calf survival/recruitment is appraised. Some managers exclude yearling cows from calculations of cow productivity or calf recruitment. To allow managers to relate such data on net productivity to the parameters of gross productivity in my study, fetus production (productivity rate) was determined for each Y/A sample after the data in each sample were pooled by age-group into classifications consisting of the Y-S and the T-S age-groups.

Statistical Methods

Importance of the variable age-group, in explaining the productivity parameters, preg-

nancy rate and twinning rate, in 11 Y/A samples of cow moose was determined with logit loglinear models (Agresti 1984). To study pregnancy rate, the logit ($\ln(\text{pregnant}/\text{non-pregnant})$) was formed for each combination of Y/A by age-group. Pregnant or non-pregnant status of cow moose specimens = presence or absence of *in utero* fetus(es), respectively. The C moose age-group was excluded from pregnancy rate analyses because none of the calves examined carried a fetus(es). The most parsimonious model explaining the data was selected by a backward elimination process (Agresti 1990). Model parameter estimates, coefficients and their SEs and CIs (95%) were compared for evidence of age-group effects. The test statistic used to indicate significance in pregnancy status by age-group was non-overlap of 95% CIs. Positive logit values were associated with pregnancy rates >50% while negative logit values were associated with pregnancy rates <50%. The

estimated proportion of pregnant cow moose in each age-group (p) was determined by $p = \exp(\alpha + \tau_j) / (1 + \exp(\alpha + \tau_j))$. A 1-sided test of proportions (D'Agostino *et al.* 1988) was used to test for a significant decline in pregnancy rate as cow moose moved from the P to the S age-group.

To study the relationship between twinning rate and age-group, the logit ($\ln(2\text{-fetus pregnancies}/1\text{-fetus pregnancies})$) was formed for each Y/A by age-group, and the analysis was performed as described above. Two- or 1-fetus pregnancy status of cow moose specimens = a 2-fetus or 1-fetus *in utero* pregnancy, respectively. The Y moose age-group was excluded from twinning rate analyses because none of the yearlings examined carried 2 fetuses. Estimated proportion of cow moose pregnant with 2 fetuses for each age-group within each Y/A (p) was determined by $p = \exp(\alpha + \beta_i + \tau_j) / (1 + \exp(\alpha + \beta_i + \tau_j))$. Model parameter estimates, coefficients and their SEs and CIs (95%) were used to examine the association of age-group and twinning rate with Y/A effects held at their mean values.

In utero fetus production, in the form of fetuses/100 cow ratios, was determined in each Y/A by age-group and Y-S and T-S classification. Fetuses/100 cow ratios, used to evaluate productivity rates in moose age-group classifications, were calculated as the number of fetuses *in utero* in cow moose examined divided by the number of cow moose examined.

Statistics measuring central tendency and dispersion were used to characterize productivity parameters in each age-group classification.

RESULTS

Pregnancy Rates

The most parsimonious model fitting the data was: $\ln(\text{pregnant}/\text{non-pregnant}) = \alpha + \tau_j$. There was a significant age-group effect on pregnancy status ($G^2 = 261.6445$, 3 df, $P =$

0.0000). However, examination of the standardized residuals plus parameter estimates from a model containing a Y/A effect (β_i) indicated that the pregnancy rates in Y/A J (GMS 14C 1974) were significantly lower ($P = 0.0009$) than in the other Y/A samples. Since my intent was not to focus on Y/A effects on pregnancy rate, and 3 other samples, from different years, came from this same area, the Y/A J data were dropped and the data re-analyzed. The effect of an overall Y/A effect went from marginally significant ($G^2 = 16.1139$, 10 df, $P = 0.0964$) to very insignificant ($G^2 = 4.9183$, 4 df, $P = 0.8414$). The model did not change and there was a significant age-group effect ($G^2 = 256.8175$, 3

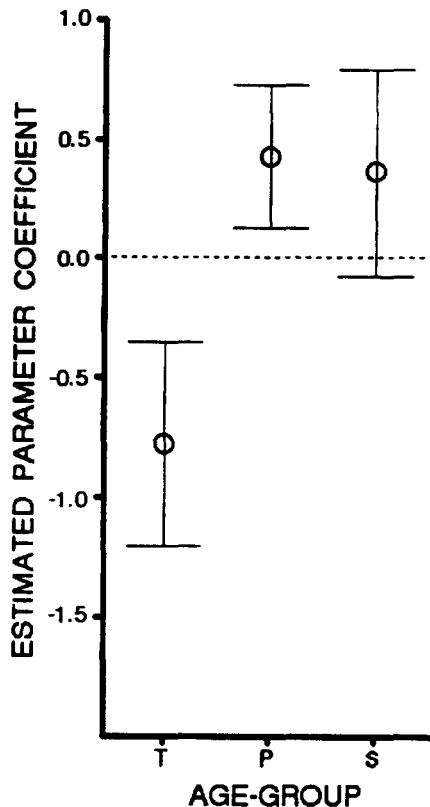


Fig. 2. Model estimated parameter coefficients (circles) and coefficient $\pm 95\%$ CIs (vertical lines) from the model, $\text{logit} = \alpha + \tau_j$, consisting of the $\text{logit} = (\ln(\text{pregnant}/\text{non-pregnant}))$, α = mean logit (α_j) and age-group effects (τ_j , $n=4$). Mean logit, $\alpha = 1.4926$.

df, $P = 0.0000$) on pregnancy status. Examination of the age-group parameter coefficient estimates and their 95% CIs (Fig. 2) indicates that the majority of cows were pregnant ($a > 0$) and that age-groups ordered by pregnancy rate were $Y < T < S < P$. The Y age-group had a lower pregnancy rate than the other age-groups ($P = 0.05$). The P age-group had a higher pregnancy rate than the Y and T age-groups ($P = 0.05$). The S age-group pregnancy rate was more variable and could not be distinguished from pregnancy rates in the T and P age-groups. Point estimates of pregnancy rates (Table 2) indicate that difference in pregnancy rate of moose progressing through the age-group classifications decreased greatly in magnitude comparing the transition from the Y to T age-group (ca. a 70% + change) to the transition from the T to P age-group (ca. a 8-9% + change). Pregnancy rate change in the transition from the P to S age-group was of much smaller magnitude (ca. a 3-5% - change) than transitions from the Y to T age-group and from the T to P age-group. There was insufficient evidence of a decline in pregnancy rate in the transition from the P to the S age-group

($t = -1.2311$, $P = 0.1019$, power = 0.3386).

Twinning Rates

The best fitting parsimonious model, $\text{logit} = \alpha + \beta_i + \tau_j$, indicated that twinning rate was a function of Y/A effects ($G^2 = 37.3708$, 10 df, $P = 0.0001$) and age-group effects ($G^2 = 18.8888$, 2 df, $P = 0.0001$). Examination of the age-group parameter coefficient estimates and their 95% CIs (Fig. 3) indicates that the majority of cow moose had 1 calf ($\alpha < 0$) and that age-groups ordered by twinning rate were $T < S < P$. The T age-group had a lower twinning rate than other age-groups ($P = 0.05$). Twinning rate in the S age-group was more variable and could not be distinguished from twinning rate in the P age-group. Y/A D had a lower twinning rate than average ($\beta_d = -0.7805$) and Y/A C and Y/A H had higher twinning rates than average ($\beta_c = 0.7730$, $\beta_h = 1.5757$). Point estimates of twinning rate by age-group (Table 3) indicate that difference in twinning rate of moose progressing through age-group classifications decreased greatly in magnitude comparing the transition from the T to P age-group (ca. a 10-16% + change) to

Table 2. Point estimates, range and median values of pregnancy rate (% pregnant) by age-group for 11 year/area (Y/A) samples of hunter-killed cow moose examined for *in utero* fetuses in south-central Alaska, 1964-74.

Age group	Y/A samples pooled by age-group		Model p^a	Y/A samples		
				Range		Median
	n	%	%	n^b	%	%
Y	92	17.4	17.4	9	10.5-50.0	16.7
T	169	86.4	87.7	11	50.0-100.0	87.5
P	489	95.1	95.3	11	86.4-100.0	95.7
S	93	90.3	92.1	6	50.0-100.0	91.3

^a $P = \exp(\alpha + \tau_j) / (1 + \exp(\alpha + \tau_j))$ based on the logit ($\ln(\text{pregnant}/\text{non-pregnant})$) and the model, $\text{logit} = \alpha + \tau_j$, consisting of a mean logit (α) and age-group effects (τ_j , $n = 4$).

^b $N = \text{Y/A samples with } >3 \text{ moose.}$

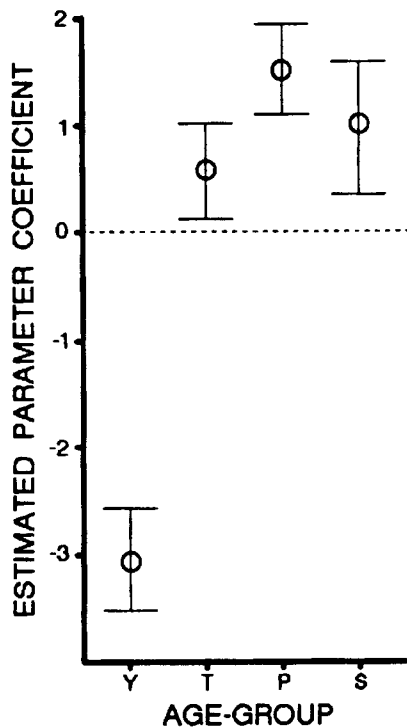


Fig. 3. Model estimated parameter coefficients (circles) and coefficient $\pm 95\%$ CIs (vertical lines) from the model, $\text{logit} = \alpha + \beta_i + \tau_j$, consisting of the logit ($\ln(2\text{-fetus pregnancies}/1\text{-fetus pregnancies})$), a mean logit (α), year/area effects (β_i , $n = 11$), and age-group effects (τ_j , $n = 3$). Mean logit, $\alpha = -1.4362$.

the transition from P to S (ca. a 1-7% - change). The between-age-group relationship of twinning rate with age-group, $T < S < P$, was similar among descriptive statistics.

One 6-year-old moose in the Y/A H sample was gravid with 3 fetuses.

Fetus Production

Descriptive statistics of fetus production by age-group (Table 4) indicate that fetus production rates of $< 18/100$ cows were associated with the Y age-group, that fetus production rates in the T, P and S age-groups were $\geq 95.0/100$ cows and that age-groups ordered by fetus production were $Y < T < S < P$. As a consequence of the fetus production

by age-group relationship (i.e., $Y < T < S < P$), age-group aggregations ordered by fetus production were $Y-S < T-S$. Point estimates of fetus production by age-group indicate that difference in fetus production of moose progressing through age-group classifications decreased greatly in magnitude comparing the transition from the Y to T age-group (ca. a 78/100 cows + change) to the transition from the T to P age-group (ca. a 21/100 cows + change). Fetus production change in the transition from the P to S age-group was of much smaller magnitude (ca. a 8-10/100 cows - change) than in the transitions from the Y to T age-group and from the T to P age-group. Fetus production range values showed that fetus production varied greatly between Y/A samples in each age-group classification. Within age-group relationship between fetus production in the Y/A sample with highest fetus production and fetus production in the Y/A sample with lowest fetus production indicates that the magnitude of age-group by Y/A variation in fetus production was less in the P age-group (1.5) than that in the other age-groups (2.1-4.8). Referring to fetus production in the Y-S and T-S age-group aggregations, in both classifications, fetus production rate was lowest in the 1973 GMS 14C sample (Y/A J) and highest in the 1968 GMS 14C sample (Y/A H).

DISCUSSION

My observations that productivity of cow moose is related to age-group agree with findings of many others (Edwards and Ritcey 1958, Pimlott 1959, Rausch 1959, Simkin 1965, Houston 1968, Markgren 1969 and 1973, Blood 1973, Schladweiler and Stevens 1973, Eriksson and Sylvén 1979, Sæther and Haagenrud 1983, Boer 1987, Crichton 1988). Most studies showed productivity differences between calf, yearling and adult age-class categories. Few studies demonstrated age-class differences in productivity in moose age-classes > 1 (Markgren 1969, Eriksson and

Table 3. Point estimates, range and median values of twinning rate (% 2-fetus pregnancies) by age-group for 11 year/area (Y/A) samples of hunter-killed moose examined for *in utero* fetuses in south-central Alaska, 1964-74.

Age group	Y/A samples pooled by age-group		Y/A samples				
			Mean of model p's ^a		n ^b	Range	Median
	n	%	n	%		%	
T	146	10.0	11	11.5	11	0.0-30.0	11.1
P	465	24.3	11	28.2	11	14.7-71.4	21.1
S	84	19.0	11	26.9	5	8.3-35.3	14.3

^aP = $\exp(\alpha + \beta_i + \tau_j) / (1 + \exp(\alpha + \beta_i + \tau_j))$ based on the logit ($\ln(2\text{-fetus pregnancies}/1\text{-fetus pregnancies})$) and model, $\text{logit} = \alpha + \beta_i + \tau_j$, consisting of a mean logit (α), Y/A effects (β_i , $n = 11$) and age-group effects (τ_j , $n = 3$).

^bN = samples with >3 pregnant moose.

Sylvén 1979, Sæther and Haagenrud 1983). No studies grouped cow moose into 5 age-class based age-groups and provided evidence that productivity parameters varied in relation with age-group.

Van Ballenberghe (1979) pointed out potential problems in assessing moose population welfare and productivity with calf pro-

duction and survival indices derived from postpartum aerial survey data. His concern was focused on shortcomings of survey techniques, but he also recognized a need to refine the base (denominator) used in expressing productivity ratios. He cautioned that the inclusion of variable sized cohorts of yearlings and non-breeding 2-year-olds in ratio

Table 4. Point estimates, range and median values of fetus production (fetuses/100 cows (F/100 C)) by age-group for cow moose in 11 year/area (Y/A) samples of hunter-killed moose examined for *in utero* fetuses in south-central Alaska, 1964-74.

Age group	Y/A samples pooled by age-group		Y/A samples		
			n ^a	Range	Median
	n	F/100 C		F/100 C	F/100 C
Y	92	17.4	9	10.5-50.0	16.7
T	169	95.9	11	57.1-118.2	95.0
P	489	118.2	11	104.5-160.0	114.5
S	93	107.5	6	50.0-127.8	107.1
Y-S	843	101.5	11	88.6-129.0	101.1
T-S	751	111.9	11	88.6-140.7	111.5

^aN = samples with >3 moose.

bases could result in deceptively low productivity indices. He noted that a "more restrictive ratio" (p.16), based on adult cows, which accounts for juveniles yields a more useful index of productivity. My results indicated that productivity differences were discernable in 5 age-class based age-groups of cow moose; cow moose in age-classes 0-3 are juvenile (sub-adult) and cow moose in age-classes 4 and greater (age-groups P and S) have attained maximum productivity and should be used as the base or denominator in ratios of productivity in cow moose in south-central Alaska. My observation that cow moose attained maximum productivity later than 3-years-of-age, agrees with findings from moose populations in Sweden (Sylvén *et al.* 1980), Norway (Sæther and Haagenrud 1983, Saether 1987) and USSR (Danilov 1987).

Pimlott (1959) and Van Ballenberghe (1979) pointed out methodological problems in measuring productivity and in interpreting productivity information collected postpartum. My findings indicated that similar problems may confound productivity data collected *in utero*. The use of percentage expressions of productivity parameters, is inappropriate if the expression fails to account for changes in components of population structure (e.g. age-group) that affect the composition of denominators in ratios. For example, relatively low productivity parameter values based on cow moose age-classes >0 could result from: (1) relatively low productivity in a population with a female age structure skewed toward the highly productive older age-class age-groups (e.g. the P and S age-groups); or (2) relatively high productivity in a population with a female age structure skewed toward lowly productive younger age-class age-groups (e.g. the Y and T age-groups).

In many jurisdictions, complex systems of selective harvest have replaced simple general open hunting seasons as tools for management of moose populations (Lykke 1974, Smith *et al.* 1979, Demarchi *et al.* 1983,

Timmermann and Gollat 1986, Haagenrud *et al.* 1987, Sylvén *et al.* 1987, Child and Aitken 1989). Selective harvest strategies focus hunting effort and harvest on productive mature bull and prime cow or non-productive young bull and calf components of moose populations, depending on whether management goals are to decrease or increase the population and/or to manage the population for recreation or meat production. Gaps in knowledge about productivity led to the "old, barren-cow" concept (Pimlott 1959, Rausch 1959, Markgren 1969); the belief by some hunters that barren cow moose were old in age or that old cow moose tended to be barren. Such beliefs and hunter ethics led to differing degrees of protection of 2-calf cows, 1-calf cows and calfless cows (Markgren 1969). Consequently, in some instances, moose managers proposed and justified cow-moose hunts to remove old, barren, non-productive females from populations. I found evidence that cow moose in age-classes >11 (the S age-group), were less productive than cow in age-classes 4-11 (the P age-group). However, the difference in pregnancy rate between S and P moose age-groups was not statistically significant. Yet, more importantly than establishing statistical significance is determining whether such small differences in productivity of P and S moose age-groups are biologically significant to moose managers. Such a query would have to be addressed case by case though a population modeling process. Nevertheless, if managers decide to selectively remove S age-group cow moose from a population and "calflessness" is used as an identifying criteria, my study showed that many moose in the Y and T age-groups would be erroneously selected for removal.

Prior moose studies have shown that twinning rate is related to age-class, year, nutrition, weather, climate and region (Edwards and Ritcey 1958, Pimlott 1959, Simkin 1965, Markgren 1969 and 1973, Blood 1973, Schladweiler and Stevens 1973). In my

study, there was evidence that twinning rate was affected by age-group effects and Y/A effects. Evidence of Y/A effects on twinning rate contrasts with the lack of evidence of Y/A effects on pregnancy rate. However, these contrasting findings are not necessarily contradictory, as twinning rate may be more sensitive than pregnancy rate to changes or differences in the environment of cow moose. Edwards and Ritcey (1958) analyzed white-tailed deer (*Odocoileus virginianus*) and moose data that indicated multiple pregnancy was a more sensitive indicator of nutritional status than rate of pregnancy. Franzmann and Schwartz (1985) analyzed data containing Y/A differences in twinning rate and provided evidence that twinning rate was an indicator of the relationship of a moose population to quality of its habitat.

The influence of winter weather on productivity is documented in many studies of cervids (Cheatum and Servinghaus 1950, Ransom 1967, Markgren 1969, Verme 1974, Mech *et al.* 1987, Sæther 1987). In my study, lowest and highest Y/A fetus production values were noted in years that were preceded by winters that were rated greatly different in severity. Lowest fetus production (e.g., 88.6/100 cows) was noted in 1973 (Y/A J); a year that was preceded by a series of warm shallow snow winters (1970-72) that were rated (Bishop and Rausch 1974:570, Coady 1974:427) as severe for moose throughout Alaska. Whereas, highest fetus production (e.g., 129.0-140.7/100 cows) was noted in 1968 (Y/A H), a year that was preceded by a series of warm shallow-snow winters that were rated (Bishop and Rausch 1974) as average or < average in severity for moose.

Moose managers strive to maximize the number of moose available for recreation and meat production (Rausch *et al.* 1974, Sylvén *et al.* 1987). In south-central Alaska, managers manipulate vegetation in habitats to increase abundance and distribution of moose (Oldemeyer and Regelin 1987). My results

imply that managers could increase productivity of moose populations by managing for more P age-group females. Furthermore, difference between estimates of gross productivity in my study (e.g., Y/A range = 89-129 fetuses/100 cows) and estimates (Bishop and Rausch 1974) of net productivity in fall in comparable years and areas (e.g., Y/A range = 15-53 calves/100 cows) implies that managers could realize large improvements in net productivity of moose populations in south-central Alaska by managing to reduce the mortality of moose <6 months-of-age. To compare *in utero* productivity data obtained from hunter-killed moose with productivity data obtained from fall aerial surveys, I made the assumption that the age structure of hunter-killed cow moose was not different from that of the moose populations surveyed in fall. This assumption is not unreasonable, excluding calves, which hunters may avoid killing because of their smaller size. Recent studies on the extent of predation on moose calves in the Kenai area (Franzmann *et al.* 1980, Franzmann and Schwartz 1986) lend support to my contention that the majority of moose calves produced are dead before fall. Furthermore, I believe that data on gross productivity, as that provided in my study, are essential for moose managers to fully appreciate the magnitude and importance of calf mortality in moose population dynamics.

In my study, the between-Y/A variation in pregnancy rate and twinning rate was lower among cows in the P age-group than among cows in the other age-groups. These data imply that P age-group cow moose produced fetuses at a relatively consistent rate while exposed to different environmental conditions in the form of Y/A effects. Furthermore, I believe that only when environmental conditions are more favorable than average do the productivity rates of cow moose in other age-groups, particularly in the S age-group, approach the productivity rate of cows in the P age-group. Studies on cervids (Verme 1974)

indicate that given marginal nutrition during pregnancy, the physically superior animals in a population are most likely to drop viable offspring and rear them successfully. Based on the productivity parameters I studied, cow moose in age-classes 4-11, the P age-group, are superior in comparison to female moose in the other age-groups.

Knowledge and data on demographics and structure of populations are critical to understanding population dynamics (Bubenik 1975). Bubenik (1975) emphasized that the terms juvenile and adult were grossly inadequate to describe the array of classes (e.g. physical, physiological and behavioral) of animals in a population. To more precisely describe the maturation status of individuals in a population Bubenik (1975) used the terms: infant, pre-teen, teen, prime and senior. My results indicate that such classifications are relevant and necessary in studies of cow moose reproduction.

ACKNOWLEDGEMENTS

I wish to recognize the many biologists, protection officers, military personnel and hunters who participated collecting the data I analyzed. I acknowledge ADF&G biologists and technical staff who processed moose specimens for age determinations. A special thanks to E. B. Becker, ADF&G, for advice and counseling on statistics and statistical analyses and for performing the statistical analyses and tests used in this paper. I thank my supervisor, K. B. Schneider, ADF&G, for providing comments on this manuscript and for permitting me to pursue this study. Comments by M. L. Wilton and several anonymous reviewers were graciously accepted; their comments greatly improved the quality of this paper. Sincerest thanks to C. C. Schwartz, ADF&G, for his critique of an early version of this manuscript and suggestions for its improvement. I thank R. A. Hite, H. J. Griese and M. W. Masteller, area staff at ADF&G, Palmer, for shielding me from dis-

turbances during preparation of this paper. D. C. McAllister, ADF and G, drafted Fig. 1. This study is a contribution of Fed. Aid Wildl. Restor., Proj. W-23.

REFERENCES

- AGRESTI, A. 1984. Analysis of ordinal categorical data. John Wiley and Sons. New York, N.Y. 287pp.
- . 1990. Categorical data analysis. John Wiley and Sons. New York, N.Y. 558pp.
- BISHOP, R. H., and R. A. RAUSCH. 1974. Moose population fluctuations in Alaska, 1950-1972. *Naturaliste can.* 101:559-593.
- BLOOD, D. A. 1973. Variation in reproduction and productivity of an enclosed herd of moose (*Alces alces*). XIth Internat. Congr. Game Biol. Stockholm, pp. 59-66.
- BOER, A. 1987. Reproductive productivity of moose in New Brunswick. *Alces* 23:49-60.
- BUBENIK, A. B. 1981. Moose research and social biological management. *Alces* 17:78-94.
- , H. R. TIMMERMANN, and B. SAUNDERS. 1975. Simulation of population structure and size in moose on behalf of age-structure of harvested animals. Proc. N. Am. Moose Conf. Workshop 11:391-463.
- CHEATUM, E. L., and C. W. SEVERINGHAUS. 1950. Variations in fertility of white-tailed deer related to range conditions. *Trans. N. Amer. Wildl. Conf.* 15:170-189.
- CHILD, K. N., and D. A. AITKEN. 1989. Selective harvests, hunters, and moose in central British Columbia. *Alces* 25:81-97.
- COADY, J. W. 1974. Influence of snow on behavior of moose. *Naturaliste can.* 101:417-436.
- CRICHTON, V. 1988. *In utero* productivity of moose in Manitoba. *Alces* 24:143-

- 149.
- D'AGOSTINO, R. B., W. CHASE, and A. BELANGER. 1988. The appropriateness of some common procedures for testing the equality of two independent binomial proportions. *The Amer. Statistician* 42:198-202.
- DANILOV, P. I. 1987. Population dynamics of moose in USSR (literature survey, 1970-1983). *Swedish Wildl. Res., Suppl.* 1:503-523.
- DEMARCHI, R. A., A. J. WOLTERSON, and W. J. WARKENTIN. 1983. Restoration of moose sex ratios and age class structures via antler restrictions and limited entry antlerless seasons in the east Kootney sub-region of B.C. *Alces* 19:204-221.
- EDWARDS, R. Y., and R. W. RITCEY. 1958. Reproduction in a moose population. *J. Wildl. Manage.* 22:261-268.
- ERIKSSON, J.-Å., and S. SYLVÉN. 1979. Results of simulation studies for optimum meat production from the Swedish moose population. *Alces* 15:32-53.
- FRANZMANN, A. W., C. C. SCHWARTZ, and R. O. PETERSON. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. *J. Wildl. Manage.* 44:764-768.
- _____, and _____. 1985. Moose Twinning Rates: A possible population condition assessment. *J. Wildl. Manage.* 49:394-396.
- _____, and _____. 1986. Black bear predation on moose calves in highly productive versus marginal moose habitats on the Kenai Peninsula, Alaska. *Alces* 22:139-154.
- GASAWAY, W. C. 1975. Moose antlers: How fast do they grow? Alaska Dept. of Fish and Game, Brochure, 6pp.
- HAAGENRUD, H., K. MOROW, K. NYGRÉN, and F. STÅLFELT. 1987. Management of moose in Nordic countries. *Swedish Wildl. Res., Suppl.* 1:635-642.
- HOUSTON, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. *Grand Teton Nat. Hist. Assoc. Tech. Bull.* 1. 110pp.
- KARNS, P. 1987. Moose population dynamics in North America. *Swedish Wildl. Res., Suppl.* 1:423-429.
- LYKKE, J. 1974. Moose management in Norway and Sweden. *Naturaliste can.* 101:723-735.
- MARKGREN, G. 1969. Reproduction of moose in Sweden. *Viltrevy* 6:127-299.
- _____. 1973. Factors affecting the reproduction of moose (*Alces alces*) in tree different Swedish areas. XIth Internat. Congr. Game Biol. Stockholm, pp. 67-70.
- MECH, L. D., R. E. McROBERTS, R. O. PETERSON, and R. E. PAGE. 1987. Relationship of deer and moose populations to previous winters' snow. *J. Anim. Ecol.* 56:615-627.
- MOEN, A. N., and F. AUSENDA. 1987. Sensitive population parameters in modeling long-lived species as moose. *Alces* 23:33-47.
- OLDEMEYER, J. L., and W. L. REGELIN. 1987. Forest succession, habitat management, and moose on the Kenai National Wildlife Refuge. *Swedish Wildl. Res., Suppl.* 1:163-179.
- PAGE, R. 1987. Integration of population dynamics for moose management-A review and synthesis of modelling approaches in North America. *Swedish Wildl. Res., Suppl.* 1:491-501.
- PIMLOTT, D. H. 1959. Reproduction and productivity of Newfoundland moose. *J. Wildl. Manage.* 23:381-401.
- RANSOM, A. B. 1967. Reproductive biology of white-tailed deer in Manitoba. *J. Wildl. Manage.* 31:114-123.
- RAUSCH, R. A. 1959. Some aspects of population dynamics of the railbelt moose populations Alaska. M.S. Thesis. Univ. Alaska, Fairbanks. 81pp.

- _____, R. J. SOMERVILLE, AND R. H. BISHOP. 1974. Moose management in Alaska. *Naturaliste can.* 101:705-721.
- SÆTHER, B-E. 1987. Patterns and processes in the population dynamics of the Scandinavian moose (*Alces alces*): Some suggestions. *Swedish Wildl. Res., Suppl.* 1:525-537.
- _____, and H. HAAGENRUD. 1983. Life history of the moose (*Alces alces*): Fecundity rates in relation to age and carcass weight. *J. Mamm.* 64:226-232.
- SCHLADWEILER, P., and D. R. STEVENS. 1973. Reproduction of Shiras moose in Montana. *J. Wildl. Manage.* 37:535-544.
- SCHWARTZ, C. C., W. L. REGELIN, and A. W. FRANZMANN. 1987. Seasonal weight dynamics of moose. *Swedish Wildl. Res., Suppl.* 1:301-310.
- SERGEANT, D. E., and D. H. PIMLOTT. 1959. Age determination in moose from sectioned incisor teeth. *J. Wildl. Manage.* 23:315-321.
- SIMKIN, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. *J. Wildl. Manage.* 29:740-750.
- _____. 1974. Reproduction and productivity of moose. *Naturaliste can.* 101:517-526.
- SMITH, C. A., J. B. FARO, and N. C. STEEN. 1979. An evaluation of trophy moose management on the Alaska Peninsula. *Proc. N. Am. Moose Conf. Workshop* 15:280-302.
- SYLVÉN, S. A., W. L. HAWLEY, and M. WILHELMSON. 1980. Study of reproductive organs of female moose in Sweden. *Proc. N. Am. Moose Conf. Workshop* 16: 124-136.
- _____, G. CEDERLUND, and H. HAAGENRUD. 1987. Theoretical consideration on regulated harvest of a moose population - a simulation study. *Swedish Wildl. Res., Suppl.* 1:643-656.
- TIMMERMANN, H. R., and R. GOLLAT. 1986. Selective moose harvest in north central Ontario - A progress report. *Proc. N. Am. Moose Conf. Workshop* 22:395-417.
- VAN BALLEMBERGE, V. 1979. Productivity estimates of moose populations: A review and re-evaluation. *Proc. N. Am. Moose Conf. Workshop* 15:1-18.
- VERME, L. J. 1974. Problems in appraising reproduction in cervidae. *Proc. N. Am. Moose Conf. Workshop* 10:22-36.

ERRATUM: In utero pregnancy rate, twinning rate and fetus production for age groups of cow moose in south-central Alaska.

Ronald D. Modafferi

Alces 28:223-234.

Figures 2 (:226) and 3 (:228) were reversed and should be as follows:

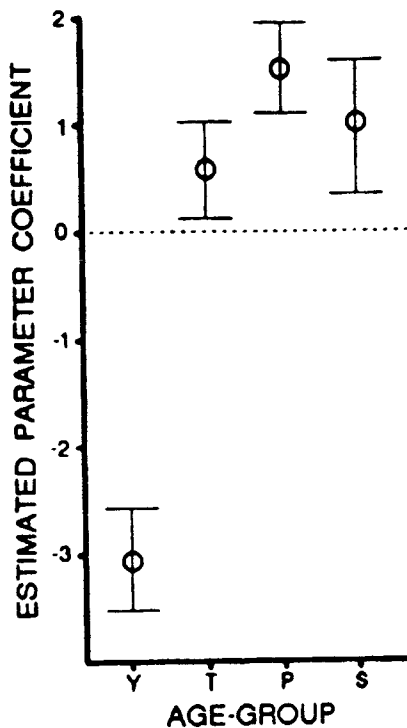


Fig. 2. Model estimated parameter coefficients (circles) and coefficient $\pm 95\%$ CIs (vertical lines) from the model, $\text{logit} = \alpha + \tau_j$, consisting of the logit $= (\ln(\text{pregnant}/\text{non-pregnant}))$, α = mean logit (α) and age-group effects (τ_j , $n=4$). Mean logit, $\alpha = 1.4926$.

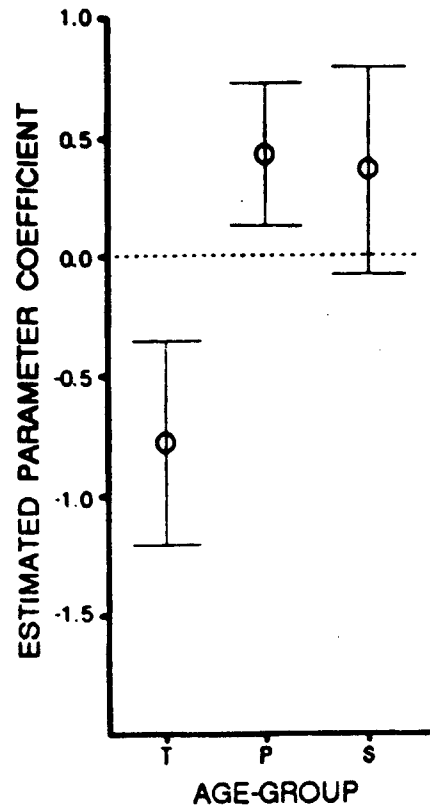


Fig. 3. Model estimated parameter coefficients (circles) and coefficient $\pm 95\%$ CIs (vertical lines) from the model, $\text{logit} = \alpha + \beta_j + \tau_j$, consisting of the logit $(\ln(2\text{-fetus pregnancies}/1\text{-fetus pregnancies}))$, α = mean logit (α), year/area effects (β_j , $n = 11$), and age-group effects (τ_j , $n = 3$). Mean logit, $\alpha = -1.4362$.