GROWTH OF MOOSE CALVES CONCEIVED DURING THE FIRST VERSUS SECOND ESTRUS

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ABSTRACT: It has been hypothesized that a low bull:cow ratio can result in delayed or late breeding in some female moose (*Alces alces*). A consequence of late breeding is late born calves. It also has been speculated that late born calves grow faster and eventually attain a size similar to early born calves. We tested this accelerated growth hypothesis by breeding cow moose during their first or second estrus, and tracking the growth rates of their calves. We conducted the experiment over a 4 year period using 10 mature cow moose that produced 33 calves in 22 litters. Birth mass of calves conceived during the first and second estrus did not differ ($P = 0.613$) but mass of single calves was greater ($P = 0.006$) than twins regardless of date conceived. Body mass gained from birth through autumn (Oct) of calves born to cows bred during their first estrus was significantly ($P = 0.0019$) greater than calves conceived during the second estrus. However, by spring (May), mass gain was not signifcantly different (P=0.1368)between the two groups. We reject the hypothesis that second estrous calves exhibit accelerated growth during their first summer of life. Body mass of second estrous calves, however, increased at a faster rate than that of first estrous calves during winter (P=0.0094), indicating the potential for accelerated growth at least while on a high nutritional plane. By autumn as yearlings, mass of second estrous born calves was not significantly different ($P = 0.125$) than mass of first estrous calves, suggesting compensatory growth for second estrous calves during their second summer. There was no relationship ($P = 0.1424$) between April body mass of short yearlings and their gain in body mass over summer. We concluded that second estrous calves do not gain more mass by fall and consequently enter winter at a lower body mass. As a consequence, they are more likely to be susceptible to winter mortality, especially in deep snow years. Management implications are discussed.

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Throughout North America where moose are abundant, there is generally a controlled harvest. In many areas, hunting is directed at the males (Timmermann 1987), which can result in skewed bull:cow ratios in the population. In Alaska, for example, post-hunting season bull:cow ratios as low as 5-10 bulls/ 100 cows have been reported (Spencer and Chatelain 1953, Rausch *et al.* 1974, Schwartz *et al.* 1992). With few bulls in the population, it has been hypothesized that the remaining adult males can not breed all of the females (Rausch et al. 1974) or that some females may not breed or conceive during their first estrus (Rausch 1965).

Speculation about the increased frequency of second estrous breeding was supported by plots of fetal size and age (Edwards and Ritcey 1958, Schwartz and Hundertmark 1993), observations of small calves weeks after the peak in calving (Bailey and Bangs 1980), and a lengthened breeding season (Rausch 1965). The consequences of late breeding may include late-born calves, a shorter gestation period in the cow, or possibly faster growth in late born calves.

At the Moose Research Center, a research facility of the Alaska Department of Fish and Game, we designed a series of studies to evaluate the effects of late breeding by comparing gestation length, birth timing, and calf growth and development between moose conceived during the first and second estrus.

Schwartz and Hundertmark (1993) confirmed that gestation length in moose averages 231 days and does not differ between cows bred their first or second estrus. The length of the estrous cycle averages 24.4 days and does not lengthen with subsequent cycles. Consequently, calves conceived to second estrous bred cows are born, on average, 22-28 days later than calves conceived during the first estrus. Here, we test the hypothesis regarding faster growth rate of late born calves.

According to Price and White (1985) growth in biological terms is difficult to define, but in simple terms can be considered as an increase in size. It is not accurate to assume that mass is an infallible measure of size, though it is the best measure for most purposes. Growth may be positive, static, or negative. Some wildlife species possess the ability to improve their rates of growth in response to physiological deprivation and ultimately achieve body mass similar to undeprived individuals. It is important to differentiate increased positive growth following a period of negative growth from increased continuous growth. The former is best referred to as compensatory or catch-up growth (Williams *et al.* 1974, Robbins 1983), and here we define the latter as accelerated growth. In either case animals exhibiting compensatory or accelerated growth must increase deposition of protein relative to fat, reduce maintenance requirements, improve the efficiency of forage utilization, or have a greater intake of food over a particular time period (Ryan 1990).

To attain a similar body mass of first estrous calves by autumn, late born calves must exhibit accelerated growth. If not, then second estrous calves must exhibit compensatory growth during the second or subsequent summer(s) to attain a similar body size of first estrous calves by autumn. If there is no compensatory growth, there would be no change in growth rate (Ryan 1993*a*, *b*).

METHODS

Studies were conducted at the Moose Research Center, located on the Kenai Peninsula, in southcentral Alaska. Breeding stock was obtained from wild moose on the Kenai Peninsula, interior Alaska (Fairbanks area), or Matanuska Valley north of Anchorage. All were of the subspecies *A. a. gigas*. Cows were either hand-reared and trained to accept handling (Regelin *et al.* 1979) or offspring of tame cows. Calves for this study were raised by these cows, habituated to confinement, and trained to accept handling for mass determination.

We maintained our moose on a pelleted ration (Schwartz *et al.* 1985) in a 4 ha enclosure from pre-rut (Sep) until post-calving (Jun). At 1-2 weeks post parturition, cows and their calves were released into one of 3 2.4-km^2 enclosures where they foraged on natural vegetation. Vegetation within the enclosure was typical northern coniferous forest (LeResche *et al.* 1974). A detailed description of the habitat was presented by Schwartz and Franzmann (1991).

During the winters of 1986-89, we treated about 3.5 km^2 of the regrowth within the enclosures using a mechanical tree crusher. This method of habitat rehabilitation created large areas of high quality natural forage (Oldemeyer and Regelin 1987). Major moose foods were paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and willow (*Salix* spp.). Lowbush cranberry (*Vaccinium vidis-idaea*) also was utilized as a food source (LeResche and Davis 1973). Moose in our study represented animals on an above average plane of nutrition. Each fall prior to the rut, all cows and calves were again returned to the small enclosure and maintained on the pelleted ration throughout the winter.

From 1987-91, we conducted studies of first and second estrous breeding. Prior to the rut in 1986, 2 adult bull moose were vasectomized on 5 and 11 September following the procedures outlined by Franzmann and Schwartz (1987). To determine the day of breeding, we observed captive moose daily during daylight hours beginning in early-

September and continuing until all cows were bred. Estrus was defined as time during which a female would stand for mounting. Estrus was confirmed by observing mounting by a bull, or indirectly by physical appearances of the female's rump hairs, which were ruffled, parted, bent, and generally showed signs of mounting. Rump hair of a non-estrous female was orderly. On many mornings there was a layer of frost on the rump hairs of non-estrous females. Frost was absent on females mounted during the night. Some cows were maintained with an intact bull from pre-rut until they were bred. A second group of cows was maintained with a vasectomized bull from pre-rut until 2 weeks after their first observed estrus. These cows then were bred by the intact bull during their second estrus, and length of the estrous cycle determined. Cows were alternated between treatments over 4-years. Two yearling females were bred by a bull during their third estrus, and these data are included for comparison. We lost some individuals and added others, but over the 4 year period we used 10 different females.

We calculated length of gestation for all females observed breeding. During the calving season (late May-early Jun), each female was observed daily for signs of birth. Cows frequently paced enclosure fences within 24 hours of parturition. We observed birth in many cases, and when we did not, we estimated it to within 6 hours. Day length during the calving season was 18-19 hours. Gestation was calculated as the time from conception (day of breeding) to parturition.

We determined mass of moose on a walk-on cattle scale accurate to a kg (Schwartz *et al.* 1987). Mass of neonates was determined <24 hours after birth using a sling and a spring scale that was accurate to 0.5 kg. We weighed calves in the autumn just after weaning (Oct), after rut (Nov), and after winter (May). Yearling were weighed in the fall prior to rut (late-Sep to early-Oct) and after winter (May). Some calves were used in other studies, hence not all individuals were monitored as yearlings. Most animals were weighed on more than one day each month (n = 1-6); we averaged daily measurements within each month for analysis. Mass gain was calculated as the body mass minus birth mass.

STATISTICAL TESTS

An alpha of 0.05 was used for all tests. Gestation length, birth date, and birth mass were analyzed using analysis of variance (Steel and Torrie 1980) with estrous cycle (1, 2, and 3), litter size (1, 2), sex (M, F), and year (1987, 1988, 1989, 1990) as main effects.

We compared gain in body mass the first year with a repeated measures analysis of variance (Winer *et al.* 1991) testing for differences among estrous cycle (1,2), sex (M,F), litter size (raised as single or twin), month (Oct, Nov, and May), and their interactions, as explanatory variables. The variance was partitioned into between- and within-moose variation. Between-moose effects (estrus, sex, litter size, and interactions) were tested with a univariate analysis and between-moose variation as the mean square error (MSE) (Little *et al.* 1991). Normality and homogeneity of variances were tested using Wilks' W statistic (Little *et al.* 1991) and a Spearman rank correlation between predicted mass gain and the absolute value of the residuals (Carrol and Ruppert 1988), respectively. We tested within-moose effects (month and month interactions with between-moose main effects) with a multivariate analysis of variance, thereby eliminating the sphericity assumption about correlation structure of mass gain within-moose (LaTour and Miniard, 1983; Little *et al.* 1991). In order to preform contrasts, the sphericity assumption was tested using a chi-square statistic; if this assumption was violated, the degrees of freedom of the F-statistic were adjusted with a Greenhouse-Geiser epsilon to obtain a non-biased *p*-values (Fleiss 1986).

Yearling data were analyzed with a repeated measures analysis of variance (Winer *et al.* 1991). Because there were only 2 months, the sphericity test was not needed (Little *et al.* 1991). We used a univariate model, and all non-significant ($P < 0.05$) interaction terms from the first repeated measure analysis were omitted. The analysis was then rerun testing for differences between main effects (estrus, sex, litter size, and month).

The relationship between spring body mass of short yearlings and their mass gain over summer through 1.4 years of age was tested with least squares linear regression (Draper and Smith 1966).

RESULTS

There were 22 litters with a total of 33 calves born during the study to 10 different females. Of the 22 litters, 12, 8, and 2 were from first, second, or third estrous bred cows, respectively. Breeding date did not differ among years (ANOVA, $F = 0.426$, 3, 21 df, $P = 0.738$) of study, so data were pooled for presentation here. We did detect a significant (ANOVA, $F = 113.29$, 2, 19 df, $P = 0.0001$) difference among the dates of breeding for cows bred their first, second, or, third overt estrus (Table 1).

Length of the gestation period ranged from 216-240 days (X= 229.7, SD = 5.6, n = 21), and did not differ among years (ANOVA, $F = 1.40$, 3 df, $P = 0.276$) or between litters of 1 or 2 calves ($t = 0.682$, $P = 0.504$). The length of gestation for cows bred their third estrus was significantly shorter (ANOVA, $F = 7.23$, 2 df, $P = 0.005$) than cows bred their first of second estrus (Table 1). The number of days between the first and second and second and third overt estrus was 22 and 27 days, respectively.

We did not detect a significant difference (ANOVA, $F = 0.503$, 3, 13 df, $P = 0.262$) among years of study in the mean dates of birth, so data were pooled. The mean birth dates of calves born to cows bred their first, second, or third estrus were significantly dif-

Table 1. Breeding dates, gestation length, birth dates, and birth mass of calves born to cow moose bred during their first, second, or third overt estrus.

	Overt estrus			
Criteria	1	2	3	*P*
Breeding date	5 Oct^A	27 Oct^B	23 Nov^C	0.0001
SD (days)	4.52	5.64	1.41	
n	12	8	2	
Gestation	231.4^A	230.1^A	218.5^B	0.005
SD	3.6	5.4	3.5	
n	11	8	2	
Birthday	26 May^A	15 Jun^B	3 Jul^C	0.0001
SD (days)	3.80	4.88	4.24	
n	12	8	1	
Birth mass (kg)				
single^D	15.7^A	16.4^A	15.4^A	
n	3	2	1	
twin^D	14.3^A	13.7^A		
n	8	10		

^{ABC}Any two means within a row followed by different superscripts are significantly different.

^{D}Single calves weighed significantly more than calves born in twin litters ($t = 3.013$, $P = 0.0064$).

ferent (ANOVA, $F = 95.49$, 2, 19 df, $P = 0.0001$). Calves conceived to cows bred during their first estrus were born (26 May) about 20 days earlier than calves born (15 Jun) to second estrous bred cows; likewise, calves conceived to cows bred in their second estrus were born about 18 days earlier than calves born (3 Jul) to cows bred their third estrus (Table 1).

We were unable to obtain the birth mass for two of three calves born to cows bred during their third estrus, so statistically we compared only estrous one and two. We also excluded one male calf born in a twin litter that only weighed 6.0 kg at birth. There was no difference between the birth mass of calves born to cows bred their first (14.6 kg) and second (14.2 kg) overt estrus ($t = 0.71$, 22 df, $P = 0.613$) or between male (14.4) and female calves (14.5)($t = 0.191$, 22 df, $P = 0.850$). Mass of single calves was significantly more (15.9 kg) than mass of calves born in twin litters (13.9 kg) ($t = 3.013$, 22 df, $P = 0.006$) (Table 1) regardless of conception date.

We were able to obtain repeated measurements of body mass for 24 calves from birth to one year of age. Of these, 12 (8 singles, 4 twins) and 12 (3 singles, 9 twins) were from first and second estrous bred cows, respectively. The model fit suggested that all of the interactions were non-significant except for month by estrus ($F = 3.74$; df = 2,15; $P = 0.0482$), and month by twin ($F = 7.03$; df = 2,15; $P = 0.0070$). There was no evidence that either the normality ($W = 0.9832$, $P = 0.7650$) nor the homogeneity of variance (Spearman $r = 0.0930$, df = 70, $P = 0.4373$) assumptions were violated. There was no evidence that males gained more mass than females ($P = 0.2019$) as calves.

Analysis of the month by estrus and month by twin interactions was preformed using contrasts with the degrees of freedom adjusted via a Greenhouse-Geiser epsilon (0.6523) because there was evidence that the sphericity assumption was violated ($X^2 = 11.42$, df = 2, $P = 0.003$). The month by estrus contrast indicated mass gain in first estrous calves was significantly more than second estrous calves (Fig. 1) in October ($F = 15.4$; df = 0.6523, 27.3966; $P = 0.0019$) but not May ($F = 2.4$; df = 0.6523, 27.3966; $P = 0.1287$)(Table 2). The interaction was significant because second estrous calves gained significantly more mass (69 kg) between October and May ($F = 9.95$; df = 0.6523, 27.3966; $P = 0.003$) than first estrous calves (60 kg). Because of limited degrees of freedom, we could not make similar comparisons to November mass.

Analysis of the month by twin contrast indicated that single calves (20.6 kg) gained significantly more mass from October to May than twin calves (8.6 kg)($F = 11.80$; df = 0.6523, 27.3966; $P = 0.0013$) (Fig. 2). Because of limited degrees of freedom, we could not make similar comparisons to November mass.

We were able to obtain repeated measurements of body mass for 15 yearlings. Of these, 8 (6 singles, 2 twins) and 7 (1 singles, 6 twins) were from first and second estrous bred cows, respectively. The initial model fit sug-

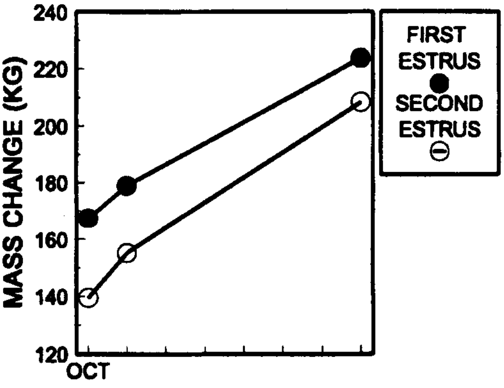

Fig. 1. Change in body mass of calf moose from birth through May. Calves were conceived to cows bred during their first or second overt estrus. There was a significant month by estrous interaction ($P = 0.0482$) because second estrus calves gained more mass from October through May than first estrous calves.

Table 2. Monthly body mass (kg) for moose born to cows bred their first, second, or third overt estrus. Standard deviation in parentheses.

Age Class	Month	Body Mass Overt estrus (kg) 1	2	3	Overt estrus (No. calves) 1	2	3
Calf	Oct	169.7(15)A[1]	139.5(15)B	103(9)	12	12	3
	Nov	182.4(19)	155.1(19)		12	12	
	May	229.4(18)A	208.5(21)A		12	12	
Yearling	Oct	332.1(29)A	322.4(22)A		8	7	
	May	369.99(54)A	354.5(22)A		8	7	

[1] Any two means within a line without the same letter are significantly different ($P < 0.05$); We only compared first and second estrous statistically, third estrous is provided only for comparisons.

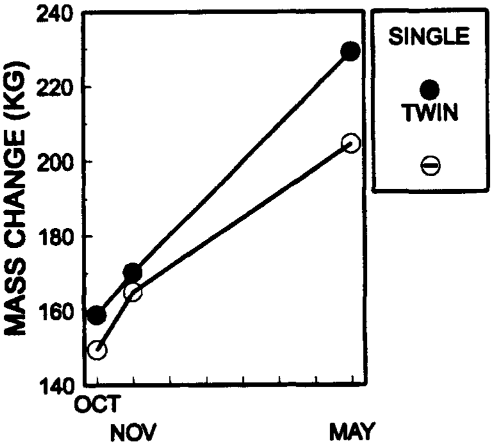

Fig. 2. Change in body mass of calf moose from birth through May. Calves were conceived to cows bred during their first or second overt estrus. There was a significant month by litter size (single vs. twin) interaction ($P = 0.007$) because single calves gained more mass from October through May than twin calves.

gested that all of the interactions were non-significant ($P < 0.05$). The reduced model met assumptions of normality (Wilks' $W = 0.9820$, $P = 0.8902$) and constant variance (Spearman $r = 0.3325$, df = 28, $P = 0.0726$) (Carrol and Ruppert 1988). Significant main effects were sex ($P = 0.0108$) and month ($P = 0.0001$). Regardless of treatment, all animals gained mass over winter (X= 35.1 kg)(month effect). The sex effect occurred because females were significantly heavier than males in both October (21.5 kg) and May (47.8 kg)(Fig. 3). There was no evidence single animals grew faster than twins ($P = 0.8559$)

We did not detect a positive relationship ($F = 2.437$; $P = 0.1424$; df = 1.14) between April body mass of short yearlings (10 or 11 month old animals) and their gain in body mass as yearlings through September (Fig. 4).

DISCUSSION

We must reject the hypothesis that moose calves born to cows bred during their second estrus experience accelerated growth during their first summer of life. Mass gained from birth to autumn (Oct) was significantly less for second estrous born calves when compared to calves born to first estrous bred cows. Our data also suggest that late born calves are capable of accelerated growth over winter if adequate nutrition in available. This was supported by the significant month by estrous interaction which indicated that second estrous calves gained more body mass between October and May (Fig. 1). In both groups, rate of growth was greater from birth to the autumn breeding season and then gradually declined

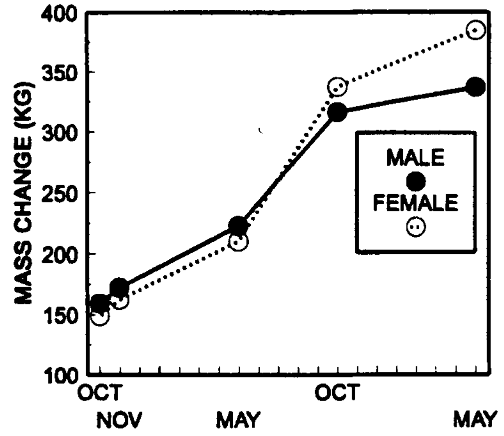

Fig. 3. Change in body mass of male and female moose from autumn as calves through May as short 2-year-olds. Calves were conceived to cows bred during their first or second overt estrus. Change in mass was significantly different ($P = 0.0108$) from October through May as yearlings.

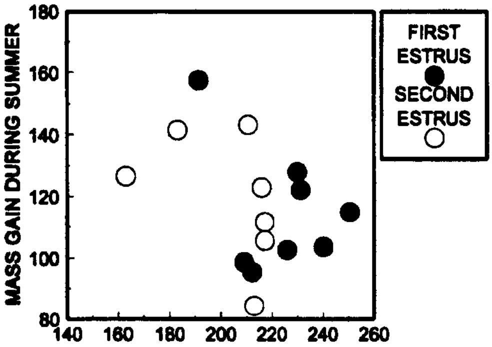

Fig. 4. The relationship between spring body mass as short yearlings (May) and mass gain during summer as yearlings for moose conceived to cows bred their first or second overt estrus. The relationship was not significant ($P = 0.142$; df = 1,14; $r = 0.397$)

over the winter. However, late born calves apparently were able to attain enough energy and protein to reach similar body mass of early born calves by spring. Growth in first estrous calves over the winter was consistent with that previously described (Schwartz *et al.* 1987), but suggested that even though first estrous calves were on a high plain of nutrition, their growth was not maximum.

The ability of second estrous calves to catch up to first estrous calves is dependent upon growth potential between the two groups. Growth rates during summer were similar between the two groups and likely approached maximum, preventing any catch-up in the second estrous treatment. In the wild, moose calves do not gain mass during winter (Franzmann *et al.* 1978). However, with adequate nutrition calves have the potential to gain mass over the winter (Schwartz et al. 1987). This growth in first estrous calves is apparently below maximum providing late born calves an opportunity to catch up by maintaining a growth rate approaching maximum.

By fall as yearlings, there was no difference ($P = 0.1257$) between first and second estrous calves in mass gained, suggesting compensatory growth during summer. Cows as yearlings gained more body mass than bulls because males lost more mass due to the rigors of the rut and the associated anorexia (Schwartz *et al.* 1987, Miquelle *et al.*. 1992) during autumn, plus growth and development of the conceptus in females. All yearlings in this study bred and were pregnant.

Both red deer and wapiti (*Cervus elaphus*) have a well-developed capacity for compensatory growth on summer pasture following winter nutritional restriction (Suttie *et al.* 1983, Suttie *et al.* 1984, Adam and Moir 1985, Hudson *et al.* 1985, Watkins *et al.* 1991). Mass gain from the flush of spring growth in mid-April until the rut in September is inversely related to body mass at the end of winter. Compensatory gain in wapiti on spring pastures is related primarily to higher forage intake relative to maintenance requirements (Watkins *et al.* 1991). Additional research addressing compensatory growth in moose is warranted.

The estrous cycle ranged from 22-28 days and did not change with time. Cow moose tended to cycle at approximately 24 day intervals and there was little variation revealing rather discrete heat periods (Fig. 5). Variation among individuals resulted in a few cows entering their second heat close to the time other cows were experiencing their first heat although the two did not overlap.

Based on the data presented here and our previous studies (Schwartz and Hundertmark 1993) we can conclude that the consequences of delayed breeding in cow moose result in late born calves. These calves develop during a normal gestation period and are born at the same body mass as early born calves, but approximately 1 estrous cycle later. Late born calves grow and develop at the same rate as early born calves and consequently weigh less by autumn. Although we did not stress our calves nutritionally during winter, we believe that these smaller late born calves are more prone to winter mortality. This would be especially true during severe winters with deep snow.

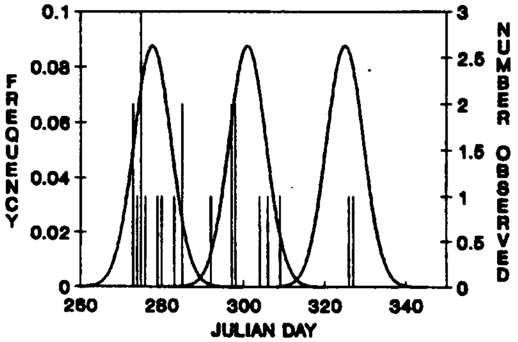

Fig. 5. Estrous cycle in moose cows showing the frequency of breeding date (Julian day) by cycle in this study. Julian day 274, 305, and 335 represent the first days of October, November, and December, respectively.

Our data do not allow for extrapolation beyond age 1.4, but information presented by Mech *et al.* (1987) suggests that calf moose born in inferior cohorts tend to remain inferior throughout their lives, especially when dealing with wolf (*Canus lupus*) predation.

MANAGEMENT IMPLICATIONS

Management of moose herds that includes hunting must ensure adequate bull:cow ratios during the rut to minimize the length of the breeding season. Moose are polyestrous so cows that do not conceive during their first heat will recycle. Late conceived calves are at a distinct disadvantage when compared to calves conceived during the normal breeding season. Late born calves do not employ the advantage of accelerated growth to achieve ideal body size before winter and are likely more vulnerable to overwinter mortality from starvation and deep snow. This difference probably results in increased vulnerability to predation. Finally, selective harvest systems that target small antlered bulls (Schwartz *et al.* 1992) increase the likelihood that these individuals are removed from the population through harvest yet insures that the larger bulls survive. This type of management strategy promotes positive herd health via selective removal of small bodied bulls while retaining a high bull:cow ratio to ensure timely breeding.

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REFERENCES

ADAM, C. L. and C. E. MOIR. 1985. Effect of winter nutrition on young farmed red deer on their subsequent growth at pasture. Anim. Prod. 40:135-142.

BAILEY, T. N., and E. E. BANGS. 1980. Moose calving areas and use on the Kenai National Moose Range, Alaska. Proc. N. Am. Moose Conf. Workshop 16:289-313.

CAROLL, R. J., and D. RUPPERT. 1988. Transformation and weighting in regression. Chapman and Hall. New York, N.Y. 249pp.

DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. John Wiley and Sons, Inc. New York, N.Y. 405pp.

EDWARDS, R. Y., and R. W. RITCEY. 1958. Reproduction in a moose population. J. Wildl. Manage. 22:261-268.

FLEISS, J. L. 1986. The design and analysis of clinical experiments. John Wiley and Sons. New York, N.Y. 432pp.

FRANZMANN, A. W., and C. C. SCHWARTZ. 1987. Anesthesia of moose for vasectomy using carfentanil/xylazine and reversal with naloxone/yohimbine. Alces 23:221-226.

———, R. E. LeRESCHE, R. A. RAUSCH and J. L. OLDEMEYER. 1978. Alaskan moose measurements and weights and measurement-weight relationships. Can. J. Zool. 56:298-306.

HUDSON, R. J., W. G. WATKINS, and R. W. PAULS. 1985. Seasonal bioenergetics of wapiti in western Canada. Pages 447-452, *in* K. R. Drew and P. F. Fennessy eds. Biology of deer production. R. Soc. N.Z. bull. No. 22.

LeRESCHE, R. E., R. H. BISHOP, and J. W. COADY. 1974. Distribution and habitats of moose in Alaska. Naturaliste can. 101:143-178.

———, and J. L. DAVIS. 1973. Importance of nonbrowse foods to moose on the Kenai Peninsula, Alaska. J. Wildl. Manage. 37:279-287.

LaTOUR, S. A., and P. W. MINIARD. 1983. The misuse of repeated measures analysis in marketing research. J. of Marketing Research 20:45-57.

LITTLE, R. C., R. J. FREUND, and P. C. SPECTOR. 1991. SAS system for models. 3rd ed. SAS Institute, Cary, NC. 329pp.

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.

MIQUELLE, D. G., J. M. PEEK, and V. VAN BALLENBERGHE. 1992. Sexual segregation in Alaskan moose. Wildl. Monogr. 122, 57pp.

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.

PRICE, M. A., and R. G. WHITE. 1985. Growth and development. Pages 183-214, *in* R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton, FL.

RAUSCH, R. A. 1965. Moose Report 5 and 6, Proj. W-6-R-5 and W-6-R-6. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Annu. Rep., Proj. W-6-R-5 and W-6-R-6. 115pp.

———, R. J. Somerville, and R. H. Bishop. 1974. Moose management in Alaska. Naturaliste can. 101:705-721.

REGELIN, W. L., C. C. SCHWARTZ, and A. W. FRANZMANN. 1979. Raising, training and maintaining moose (*Alces alces*) for nutritional studies. Proc. Int. Congr. Game Biol. 14:425-429.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York. 343pp.

RYAN, W. J. 1990. Compensatory growth in cattle and sheep. Nutr. Abst. Rev. 60:653-64.

———. 1993. Compensatory growth in sheep and cattle. I. Growth pattern and feed intake. Aust. J. Agric. Res. 44:1609-1621.

______. 1993. Compensatory growth in sheep and cattle. II. Changes in body composition and tissue weight. Aust. J. Agric. Res. 44:1623-1633.

SCHWARTZ, C. C., and K. J. HUNDERTMARK. 1993. Reproductive characteristics of Alaskan moose. J. Wildl. Manage. 57:454-468.

______ and A. W. FRANZMANN. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl. Monogr. 113. 58pp.

______, W. L. REGELIN, and A. W. FRANZMANN. 1985. Suitability of a formulated ration for moose. J. Wildl. Manage. 49:137-141.

______, ______, and ______. 1987. Seasonal weight dynamics of moose. Swedish Wildl. Res. Suppl. 1:301-310.

______, ______, and T. SPRAKER. 1992. An evaluation of selective bull moose harvest on the Kenai Peninsula, Alaska. Alces 28:1-13.

SPENCER, D. L., and E. F. CHATELAIN. 1953. Progress in the management of the moose of south central Alaska. Trans. North Am. Wildl. Conf. 18:539-552.

STEEL, R. G. D., and J. H. TORRIE. 1980. Principles and procedures of statistics, a biometrical approach. R. R. Donnelley & Son, Inc. 633pp.

SUTTIE, J. M., E. D. GOODALL, K. PENNIE, and R. N. B. KAY. 1983. Winter food restriction and summer compensation in red deer stags (*Cervus elaphus*). Br. J. Nutr. 50:737-747.

SUTTIE, J. M., G. WENHAM, and R. N. B. KAY. 1984. Influence of winter feed restriction and summer compensation on skeletal development in red deer stags (*Cervus elaphus*). Res. Vet. Sci. 36:183-186.

TIMMERMANN, H. R. 1987. Moose harvest strategies in North America. Swedish Wildl. Res. Suppl. 1:565-580.

WATKINS, W. G., R. J. HUDSON and P. L. J. FARGEY. 1991. Compensatory growth of wapiti (*Cervus elaphus*) on aspen parkland ranges. Can. J. Zool. 69:1682-1'687.

WILLIAMS, J. P. G., J. M. TANNER, and P. C. R. HUGHES. 1974. Catch-up growth in male rats after growth retardation during the suckling period. Pediatr. Res. 8:149-

WINER, B. J., D. R. BROWN, and K. M. MICHELS. 1991. Statistical principles in experimental design. 3rd ed. McGraw-Hill Inc. New York, N.Y. 1057pp.