REPRODUCTIVE CHARACTERISTICS OF ALASKAN MOOSE

CHARLES C. SCHWARTZ, Moose Research Center, Alaska Department of Fish and Game, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669
KRIS J. HUNDERTMARK, Moose Research Center, Alaska Department of Fish and Game, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669

Abstract: Many aspects of moose (*Alces alces*) reproduction are poorly documented. Therefore, we quantified the estrous cycle, estrous length, gestation period, fetal development, and birth mass of calves. We evaluated empirical relationships among maternal age, mass, and previous breeding parity with litter size and neonatal sex ratio. Increased attentiveness by the bull signaled estrous behavior in cows. Estrous females did not increase activity. The estrous cycle varied from 22 to 28 days ($\bar{x}$ = 24.4 days) and did not lengthen with each successive cycle. The cycle of primiparous females was shorter ($P = 0.05$) than pluriparous females. Gestation averaged 231 days (SD = 5.4 days) and did not differ ($P > 0.05$) between primiparous and pluriparous females, litters of 1 or 2 calves, among 5 years of study, or between cows bred their first or second overt estrus. Primiparous yearlings produced fewer ($P = 0.005$) calves (1.07/cow) than primiparous 2-year-old cows (1.60/cow). Calf production was related to body mass at time of breeding in primiparous ($P = 0.0015$) but not pluriparous females ($P = 0.38$). Fetal counts collected from wild moose on the Kenai Peninsula averaged 0.22, 1.27, and 0.14 for yearlings, cows aged 2–15, and ≥16, respectively. Mean corpora lutea counts for the same groups were 1, 1.5, and 2.0/female suggesting an ova loss of 0, 9.3, and 100% for the 3 age classes. Mass of single calves ($\bar{x}$ = 16.2 kg) at birth was greater ($P = 0.001$) than twin calves ($\bar{x}$ = 13.5 kg), but within single or twin litters, males did not have more mass than females. Change from conception to birth in fetal mass ($R^2 = 0.964$) and hind foot length ($R^2 = 0.997$) was best described with a von Bertalanffy equation, whereas total ($R^2 = 0.988$) and forehead-rump ($R^2 = 0.979$) lengths were linear. Using the hind foot length-age relationship, we accurately predicted 19 of 20 known second estrus births. This technique provides a simple means of estimating the incidence of delayed breeding in moose. These statistics defining chronology of the reproductive process, productivity, and fetal growth rates permit a more refined approach to modelling and management of wild moose populations. These baseline data facilitate analyses of the impacts of harvest of bulls on the reproductive performance of managed moose herds. Continued research needs to quantify the impacts of skewed bull:cow ratios on rut timing and their potential impacts on calf production and survival.

J. WILDL. MANAGE. 57(3):454–468

Management of any wildlife species can be facilitated by knowledge of its reproductive potential. Our early knowledge of moose reproduction (Peterson 1955) was derived from field observations made by naturalists during all seasons. Based on these data Peterson (1955) concluded that moose had a very low reproductive rate for a cervid. More recent information contradicts this view (Simkin 1974, Sadleir 1982, Boer 1992).

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 could 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 second estrous breeding was supported by plots of fetal size and age (Edwards and Ritcey 1958), 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 have been hypothesized to include late-born calves, a shorter gestation period in the cow, or possibly compensatory growth.

At the Moose Research Center (MRC), a research facility of the Alaska Department of Fish and Game, a project was initiated to evaluate the effects of late breeding on gestation length, and growth and development of calves conceived during the first or second estrus. When reviewing the literature for this project, it became apparent that there were numerous discrepancies in statistics describing the most basic aspects of moose reproduction.

For example, the gestation length of moose was reported as 240–246 days (Peterson 1955), 216 days (Stewart et al. 1987), and 234 days (Markgren 1969). Only Stewart et al. (1987) actually measured gestation length in 2 yearlings. Both Peterson (1955) and Markgren (1969) estimated gestation by difference between mean date of breeding and parturition. Neither presented measures of variation about their estimates.

Published literature on the estrous cycle also varied. Lent (1974), in his review of moose reproduction, concluded that there was general agreement in the literature and that the estrous cycle lasted only 20–22 days. However, Lent (1974) cited Edwards and Ritcey (1958) who concluded that the estrous cycle was 30 days long. Edwards and Ritcey (1958) calculated length of the estrous cycle from plots of fetal size. Scatter diagrams of fetal length and time of collection showed obvious outliers. The distance from these outliers to the main cluster of data points led Edwards and Ritcey (1958) to conclude the estrous cycle was 30 days.

We concluded that there was a need to quantify the most basic parameters of moose reproduction. Herein, we summarize reproductive data collected from a wild population and a captive herd of moose. We quantified the estrous cycle, estrous length, gestation length, and discuss sex ratio, litter size, and mass of calves produced by cows varying in age and condition, as well as the use of fetal development as an estimator of conception chronology.

We thank D. C. Johnson, C. C. Shuey, P. Del Vecchio, and B. Porter for assistance with breeding observations and animal care. We especially thank A. W. Franzmann for surgical vasectomy of 2 bull moose. K. B. Schneider provided valuable editorial comments. This project was a contribution of Federal Aid in Wildlife Restoration, Projects W-22-6, W-23-1, W-23-2, W-23-3, and W-23-4. We followed an animal welfare protocol approved by the Alaska Department of Fish and Game.

METHODS

Captive Moose

We studied captive moose at the MRC, located on the Kenai Peninsula in southcentral Alaska. Moose were obtained from wild stock on the Kenai Peninsula, interior Alaska (Fairbanks area), or Matanuska Valley north of Anchorage. All were of the subspecies *A. a. gigas.* Most animals were hand-reared and trained to accept handling (Regelin et al. 1979). Others were raised by tame cows and were habituated to confinement, and trained to accept handling for mass determination and human presence.

During 1979–87, we maintained our moose on a pelleted ration (Schwartz et al. 1985) in a 4-ha enclosure all year. Beginning in 1988, moose were fed the ration from pre-rut (Sep) until post-calving (Jun). At 1–2 weeks after 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 a high plane of nutrition.

We determined the mass of moose on a walk-on cattle scale accurate to the nearest kg (Schwartz et al. 1987). Mass of neonates was determined <24 hours after birth using a spring scale that was accurate to 0.5 kg.

Estrous Cycle.—Timing and extent of recurrent estrus were monitored with 5 pluriparous (>1.5 yr old) and 3 primiparous (1.5 yr old) females. 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).

We tested 2 marking devices to determine if we could detect breeding by observing ink-marks on females. The 2 devices (Chin Ball Mating Device, Westguard Industries, Eric, Colo.; Bull Point Marker, Ag-tronics, Hastings, Nebr.) were standard chinball markers designed for domestic bulls.

We observed captive moose daily during daylight hours between 9 September and 2 March 1987 to detect changes in behavior indicative of the onset of estrus. 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. We also recorded vaginal swelling and mucus flow from the vulva, to attempt detection of the day of estrus in cow moose (Hansel 1959).

From 1987–91, we conducted studies of first and second estrous breeding. 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. We lost some individuals and added others, but over the 4 year period we recorded estrous lengths for 2 primiparous and 5 pluriparous females.

Length of Gestation.—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. For cows in heat on 2 consecutive days (15%), we used the first observed breeding as day of conception.

Wild Moose

Dates of Conception, Ovulation Rates, and Calf Production.—During 1987–92, we collected the reproductive tract and lower jaw from cow moose killed by automobiles on the Kenai Peninsula. Collections began in late November when embryos were sufficiently developed to determine sex from external genitalia. We determined cow age by tooth sectioning (Sergeant and Pimlott 1959). Each fetus was removed from the uterus, and mass determined (nearest g) after excess fluids were wiped dry with paper towels. We measured total length (tip of nose to end of tail), crown-rump or forehead-rump length, and hind foot length to the nearest millimeter (Markgren 1969). Ovaries were fixed in 10% formalin, and sectioned longitudinally into 1-mm sections (Kirkpatrick 1980). The number of corpora lutea (CL) was determined macroscopically. Ovulation rate was defined as the number of CL's per female. We considered ova loss as the difference between CL counts and number of fetuses present.

Statistical Analyses

We tested for differences between 2 means (i.e., gestation length, estrous cycle length, and litter size of primiparous and pluriparous females) with a t-test. Differences among >2 means (i.e., estrous cycle lengths over time; gestation length of first, second, or third estrus bred females; years of study; calf production by age class) were tested using analysis of variance. We tested deviations from the expected sex ratio of 1:1 with a binomial test, whereas deviations from the expected distribution of sex ratios among litter classes were tested using Chi-square. The relationships between day of breeding and cow mass or age were tested using correlation analysis. All tests were completed with SPSS/PC (Norusis 1986). We fitted sigmoidal growth equations (Zullinger et al. 1984) for fetuses and neonates using non-linear least squares (Wilkinson 1990). We accepted $\alpha = 0.05$ as significant.

RESULTS

Estrous Behavior

The onset of estrus was signaled by increased attentiveness by the bull. Often the bull would stay near a cow close to estrus. It was not unusual to find the bull either following or bedded with an estrous female.

There were marked differences among cows in the intensity of their estrous behavior. Some individuals showed conspicuous behavior and were mounted 5–7 times during their heat. Other females showed no overt signs of estrus and were only mounted once. The length of heat ranged from 1 to 36 hours with most females receptive for 15–26 hours. Because we did not observe our cows during darkness, it was not always possible to determine the exact length of the receptive period. However, on numerous occasions, we observed nonreceptive cows at dawn, witnessed mating during the day, and nonreceptivity again by dusk.

Vaginal mucus was generally observed 1–2 days post-estrus ($\bar{x} = 0.8$ days, SD = 2.8, $n = 22$) but ranged from 7 days before to 6 days

Table 1. Date of initial estrus and length in days of subsequent cycles for 6 moose, from the Moose Research Center, Alaska, 1987.

Estrous cycle	Animal (age yr)							
	1 (5)	2 (5)	3 (1)	4 (1)	5 (3)	6 (8)	$\bar{x}$ date	SD days
1	11 Oct	12 Oct	13 Oct	14 Oct	1 Oct	2 Oct	9 Oct	5.8
2	25	23	24	24	24	24	24.0[a]	0.6
3	26	24	24	22	25	26	24.5	1.5
4	25	25	25	[b]	24	25	24.8	0.4
5	25	25		46[b]	28	25	25.8	1.5
6	26	23		23	25	26	24.6	1.5
7					24	25	24.5	0.7
$\bar{x}$ SD	25.4 0.5	24.0 1.0	24.3 0.6	23.0[a] 1.0	25.0 1.5	25.2 0.7	24.6	1.2

[a] Length of each estrous cycle did not differ with each subsequent cycle ($P = 0.369$).

[b] No breeding observed, but it could have been missed. Estrous length for period 5 is the number of days since period 3. Data not used in calculations of estrous cycle length.

after mating. Discharge lasted about 2 days ($\bar{x} = 2.1$, SD = 1.0, $n = 22$). Based on these observations, we concluded that we could not predict the day of estrus using mucus flow as an indicator.

The chinball markers had little utility in detecting breeding in moose. One device (Bull Point Marker) would not mark because the spring was too strong and kept the marking ball from moving. We did not attempt to immobilize the bull wearing this marker for repairs. The other device marked females, but there was no relationship between visual observations of estrus and ink marking on receptive females.

Estrous Cycle

Six of the 8 females provided usable information on length of the estrous cycle (Table 1). The number of recurrent cycles in unbred females ranged from 4 to 7 (Table 1; $\bar{x} = 6$, SD = 1.1). Estrus was first detected on 1 October, and the last on 2 March, resulting in a minimum potential breeding season of 151 days. Length of the estrous cycle ranged from 22 to 28 days ($\bar{x} = 24.4$, SD = 1.2, $n = 28$), and the time between cycles did not increase (ANOVA, $F = 1.14$; 5, 20 df; $P = 0.369$, Table 1).

Our second estrous breeding studies ($n = 10$) revealed that the length of the estrous cycle did not differ ($P < 0.05$) between females providing only 1 estimate and those with repeated estimates (i.e., multiple years). Because cycle length did not vary with cycle number or with repeated observations within individuals, we pooled all of our data. The modal length of the estrous cycle was 24–25 days ($\bar{x} = 24.4$, range = 22–28, $n = 38$) with primiparous females ($\bar{x} = 23.7$ days) having a shorter cycle ($t = 1.62$, 36 df, $P = 0.05$) than pluriparous ($\bar{x} = 24.5$ days) females (Fig. 1).

Gestation period

We did not detect a difference ($P > 0.05$) in length of gestation between primiparous and pluriparous females, between litters with 1 or 2 calves, among 5 years of the study, or between cows bred their first or second estrus, so we combined these data. The mean gestation length was 231 days (SD = 5.4 days), and ranged from 216 to 240 days ($n = 23$) (Fig. 2.). The modal gestation period was 233 days, with 87% of all observations occurring between 225 and 236 days.

Length of Breeding Season

Mean date of first overt estrus was 5 October (range = 28 Sep–12 Oct) ($n = 14$, SD = 4.2), with no difference among years ($F = 0.513$; 4, 9 df; $P = 0.73$). Females recycled if they were not bred their first estrus. The mean date of the second estrus was 27 October (range = 19 Oct–5 Nov) ($n = 9$, SD = 5.6) with no difference among years ($F = 0.633$; 3, 5 df; $P = 0.628$). Mean date of first estrus was different ($P = 0.0001$) from second estrus.

There was no correlation between cow mass ($r = -0.047$, $n = 22$, $P = 0.83$) or age ($r = 0.08$, $n = 22$, $P = 0.72$) and day of breeding. Pluriparous females did not ($t = 0.18$, $P = 0.858$) come into heat sooner than primiparous females.

Cows bred during their first estrus gave birth from 18 May through 7 June ($\bar{x} = 26$ May, $n = 36$, SD = 4.7). Parturition ranged over a 20-day period, with 67% of all births occurring within 1 week (22–28 May). Cows bred during their second estrus calved later ($F = 94.8$, 21 df, $P =$

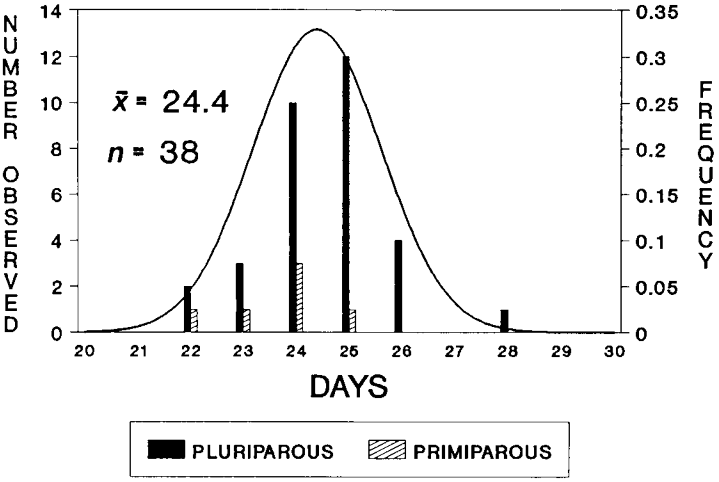

Fig. 1. Length of the estrous cycle in moose at the Moose Research Center, Alaska, 1986–91. The cycle was different (P = 0.05) for primiparous (23.7 days) and pluriparous (24.5 days) females. The solid line represents a normal distribution of the observations.

0.0001; $\bar{x}$ = 15 June, range = 8 Jun–23 Jun, SD = 4.6, n = 13) than first estrous cows.

Calf Production and Ovulation Rates

MRC cows.—During 1979–92, 18 1- to 10-year-old females (age at time of breeding) produced 58 litters. Calves were not sexually mature and did not breed. Primiparous yearlings generally produced a single calf (1.07 calves/female), whereas primiparous 2 year olds produced more (F = 4.16; 4, 54 df; P = 0.005) twin litters (1.60 calves/female) (Table 2). Body mass of primiparous females during the breeding season was greater (F = 10.0; 2, 18 df; P = 0.0015) for those producing twins (414.5 kg, range = 379–457). Mass of cows producing a female calf (349.8 kg, range = 308–376) was not different (P = 0.0015) from those producing a male calf (337.2 kg, range = 297–378). Cows with a body mass <379 kg produced a single calf, whereas cows with a body mass ≥379 kg produced twins. There was no overlap in the ranges, but our sample size for twin litters was small (n = 4). Pluriparous females produced more (F = 4.16; 4, 54 df; P = 0.005) calves per litter (1.59 calves/cow) than yearling primiparous females, but not primiparous 2 year olds (Table 2).

Autumn body mass of pluriparous females

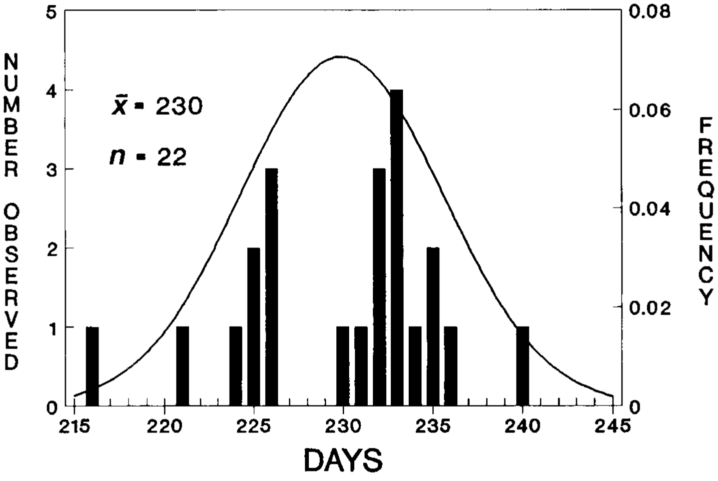

Fig. 2. Length of the gestation period in captive moose at the Moose Research Center, 1986–91. The solid line represents a normal distribution of the observations.

Table 2. Calf production by age and reproductive status for female moose at the Kenai Moose Research Center, Kenai Peninsula, Alaska, 1979–92.

Age at parturition (yr)	Status	n	Litter category Female	Male	Male/female	Female/female	Male/male	Calves/female
2	Primiparous	14	7	6	1	0	0	1.07A[a]
3	Primiparous	5	1	1	3	0	0	1.60B
3–4	Pluriparous	16	2	4	7	2	1	1.62B
5–7	Pluriparous	15	4	4	5	1	1	1.47B
8–11	Pluriparous	8	1	1	2	2	2	1.75B
3–11	Pluriparous	39	7	9	14	5	4	1.59B

[a] Within the column, means with the same letter do not differ ($P = 0.005$).

increased through age 4, was relatively constant through age 6, and began to decline by age 7 (Fig. 3). Based on these data, we divided pluriparous females into 3 age classes at time of breeding: teens (2–3 yr), primes (4–6 yr), and seniors (≥ 7 yr). Prime cows (450 kg, SD = 39) had more ($F = 4.54$; 2, 37 df; $P = 0.017$) mass than teens (418 kg, SD = 30) and seniors (412 kg, SD = 32).

There was no relationship ($F = 0.312$; 4, 34 df; $P = 0.868$) among body mass of the cow during the breeding season and litter categories (single male, single female, mixed twins, twin males, and twin females, Table 3), nor between litter size and maternal age ($F = 0.98$; 2, 37 df; $P = 0.38$). We did not detect a difference among litter categories and parity (first calf, weaned 1 calf, weaned 2 calves, or barren) of the cow the previous year ($\chi^2 = 15.10$, 12 df, $P = 0.236$).

Wild cows.—Calf production in the Kenai population averaged 1.02 calves/female ($n = 110$) and varied with cow age. Calves did not breed. Yearling cows (0.22 calves/cow, SD = 0.43, $n = 18$) and cows >15 years of age (0.14 calves/cow, SD = 0.38, $n = 7$) produced fewer ($F = 8.74$; 17, 92 df; $P = 0.0001$) calves than cows aged 2–15 (1.27 calves/cow, SD = 0.52, $n = 85$). Pregnancy rates for yearlings, cows aged 2–15, and >15 were 22, 96, and 14%, respectively.

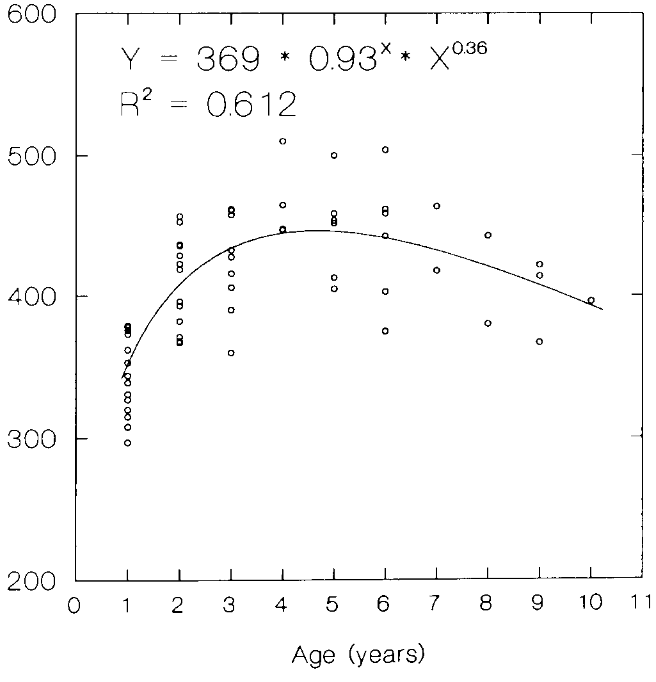

Fig. 3. Body mass at time of breeding and age of captive female moose at the Moose Research Center, Kenai Peninsula, Alaska, 1979–92.

Table 3. Calf production in pluriparous moose and cow mass (kg) during the breeding season at the Moose Research Center, Alaska, 1979–91.

Litter category	n	Cow mass[a]	Range
Single			
Male	7	428	360–504
Female	9	419	375–500
Twins			
Mixed sex	14	435	371–510
Female-female	5	421	367–461
Male-male	4	434	396–464

[a] There was no relationship among body mass of the cow and litter categories ($P = 0.38$).

Table 5. Birth mass (kg) of calves to cow moose at the Moose Research Center, Kenai Peninsula, Alaska, 1979–92.

Category	n	Mass	SD	Range
Single				
Female	16	16.1A[a]	1.8	12.3–19.0
Male	15	16.5A	2.0	12.0–20.0
Twin				
Female	30	13.3B	2.5	5.4–17.7
Male	28	14.0B	2.5	5.9–18.0

[a] Within the column, means with the same letter do not differ ($P = 0.0001$).

We obtained intact pairs of ovaries from 59 pregnant cow moose. Average ovulation rate for 2- to 15-year-old cows was 1.47 eggs/female (Table 4). Ovulation of 2 eggs was more common from a single (86%) ovary ($\chi^2 = 7.142$, $P < 0.01$) than from both ovaries (14%). Fetal counts for adult cows aged 2–15 were 1.33 fetuses/female, suggesting a 9.3% loss of ova. Ova loss in yearlings and old cows was −3.4 and 100%, respectively (Table 4). We found only 1 post-implantation mortality in 71 fetuses collected. A partially resorbed fetus (mainly skin and bones) was found in 1 horn of the uterus and a viable fetus was found in the other horn.

Calf Sex Ratio

The overall sex ratio of calves born at the MRC (1:1.05 in favor of females, $n = 86$) was not different (binomial test, $P = 0.914$) from unity. Because litter size may be a confounding factor in an analysis of sex correlates (DeGayner and Jordan 1987), we analyzed twin litters separately. Among 23 twin litters born to pluriparous females, there were 14 of mixed sex, 5 sets of twin females, and 4 sets of twin males (Table 2). These frequencies of sex-ratio categories were not different ($\chi^2 = 3.07$, 2 df, $P = 0.215$) from random expectation. Fetal sex ratio did not vary ($\chi^2 = 0.20$, 2 df, $P > 0.90$) among cow age classes.

The overall sex ratio of calves from wild Kenai cows (1:1.12 in favor of males, $n = 134$) was not different (binomial test, $P = 0.342$) from unity. Among 69 single litters, a 1:1.56 sex ratio in favor of males was not (binomial test, $P = 0.092$) different from unity. Among 33 twin litters, there were 15, 10, and 8 mixed, female, and male sets, respectively, which were not different ($\chi^2 = 0.515$, 2 df, $P = 0.773$) from random expectation.

Calf Mass

Single calves (16.2 kg, SD = 2.0, $n = 26$) had heavier ($F = 12.4$; 2, 72 df; $P = 0.0001$) masses at birth than twins (13.5 kg, SD = 2.5, $n = 50$), but within single or twin litters, mass of males did not differ (ANOVA, $F = 1.36$; 1, 72 df; $P = 0.247$) from females (Table 5). Masses of male calves (14.5 kg, SD = 2.1, $n = 18$) in mixed

Table 4. Corpora lutea and live fetus counts from cow moose during winter (Nov–May) on the Kenai Peninsula, Alaska, 1987–92.

Age class of cow (yr)	No. of corpora lutea	Litter size (no. cows)				Total no.		Fetal rate	Ovulation rate	Loss of ova (%)
		0	1	2	Total	Live fetuses	Corpora lutea			
Yearling	1	0	3	0	3	3	3	1.00	1.00	0.0[a]
2–15	1	0	27	1	28	29	28	1.04	1.00	−3.4[a]
	2	0	7	15	22	37	44	1.68	2.00	15.9
	3	0	0	1	1	2	3	2.00	3.00	33.0
Subtotal		0	34	17	51	68	75	1.33	1.47	9.3
16+	2	2	0	0	2	0	4	0.00	2.00	100.0
Total		2	37	17	56	71	82	1.27	1.46	13.4

[a] Ova loss was likely underestimated since females ovulating and losing one egg would be counted as not pregnant. A negative number resulted when only 1 corpora lutea was identified with twin fetuses.

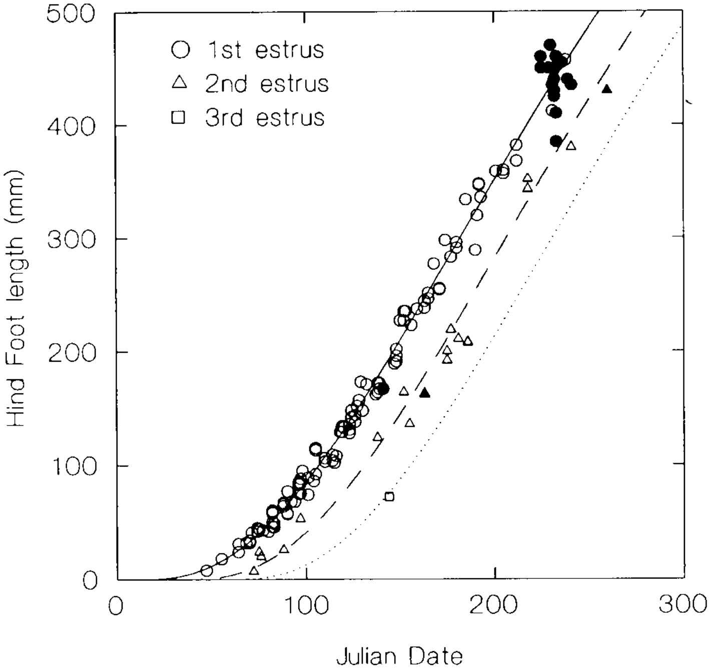

Fig. 4. Hind foot length-age relationship for fetuses collected from wild cow moose from the Kenai Peninsula, Alaska, 1987–92. Open symbols represent fetuses collected from wild cows, solid symbols represent fetuses or neonates from tame cows with known date of conception. The solid, dashed, and dotted lines represent fetuses conceived in the first, second, and third estruses, respectively.

litters were not different ($F = 2.573$; 1, 31 df; $P = 0.119$) from their female twin (13.4 kg, SD = 1.4, $n = 15$). We did not detect a difference ($F = 0.698$; 1, 22 df; $P = 0.413$) in mass of single calves born to primiparous versus pluriparous females, or between male and female calves ($F = 0.301$; 1, 22 df; $P = 0.589$); the interaction also was non-significant ($F = 0.431$; 1, 22 df; $P = 0.518$). Because of the small sample size, we did not test differences between twin litters of primiparous versus pluriparous females, but based on the above results we did not expect a difference.

Total mass of calves born in twin litters did not vary among litter categories: twin females ($\bar{x} = 26.9$ kg, SD = 5.2), twin males ($\bar{x} = 24.0$ kg, SD = 4.2), and mixed litters ($\bar{x} = 27.6$ kg, SD = 4.1), but during the course of our studies, we had 3 sets of twins born in which 1 calf was about half the mass ($\bar{x} = 5.4$ vs. 13.3 kg) of its litter mate. We also have observed twin litters in the wild where the calves were different sizes.

Fetal Development

Dates of death for 153 fetuses from road-killed cows were plotted against mass and length measurements to determine developmental patterns. Date of death was expressed as a Julian date with 5 October ($\bar{x}$ date of conception for MRC moose) being day 1. Examination of these plots indicated 3 distinct groups of measurements, which we nominally classified as fetuses conceived during the first, second, and third estrous cycles (Fig. 4). This classification yielded 135 (88.2%), 17 (11.1%), and 1 (0.7%) fetuses conceived on successive estrous cycles. We combined these data with hind foot and mass measurements of fetuses and neonates of known conception dates from MRC cows.

Temporal changes in mass and hind foot length were described by a form of the von Bertalanffy growth model (Ricker 1979) (Table 6), which was selected over a Gompertz or logistic model because it more accurately represented growth in artiodactyls (Zullinger et al. 1984). Linear models for these parameters were rejected based upon analysis of residuals (MacNeil 1983). Total length and forehead-rump length were described best with linear models. These models were fitted to data for those fetuses classified as first estrus (Fig. 5A–D). Because we detected a significant difference in

Table 6. Parameters for growth models of fetal moose conceived during the first estrus, Kenai Peninsula, Alaska, 1987–92. Mass and hind foot models include data collected from neonates at the Moose Research Center.

Measurement	Units	Equation[a]	n	A	K	I	R^2
Mass							
All	g	VB	136	499,842	0.002000	597.97	0.964
Single	g	VB	64	495,085	0.002168	562.08	0.978
Twins	g	VB	72	499,376	0.001898	622.52	0.963
Hind foot	mm	VB	124	991.37	0.006456	180.05	0.997
Total length	mm	L	85	−205.78	5.18		0.980
Forehead–rump[b]	mm	L	107	−133.55	3.54		0.979

[a] The von Bertalanffy equation (VB) was $W = A(1 - 0.333[e^{K(\mathrm{JDAY}\ I)}])^3$; where W = the dependent measurement, A = the asymptote, K = growth rate constant, JDAY = Julian day, and I = the inflection point. The linear equation (L) was $Y = A + K(\mathrm{JDAY})$, where A = intercept and K = slope.

[b] Data for embryos were crown–rump measurements.

mass between single and multiple litters at birth, we fitted separate models for singletons and twins (Fig. 5A; Table 6). We did not detect differences in hind foot lengths between MRC singletons and twins ($F = 1.512$; 1, 13 df; $P = 0.241$) or males and females ($F = 0.115$; 1, 13 df; $P = 0.740$), or their interaction ($F = 2.203$; 1, 13 df; $P = 0.162$) at birth; thus, these data were combined for regression (Fig. 5B; Table 6). We did not record total length or forehead-rump measurements for neonates at the MRC, so we pooled fetal measurements for analysis of these parameters (Figs. 5C and D; Table 6).

We fitted the hind foot model to the second and third estrous data, solving only for I_n (inflection point, where n = first, second, or third estrous fetuses). By changing I_n in the von Bertalanffy equation and holding all other variables constant, we retained the shape of the first estrous model but shifted it horizontally in time. The best fit for second estrous fetuses occurred at $I_2 = 207.8$ ($R^2 = 0.995$). This separated the second estrous equation from the first by 27.8 days ($I_2 - I_1 = 207.8 - 180.0 = 27.8$). By adding the mean length of the estrous cycle (24.4) observed in captive moose to our estimate of I_1 we predicted $I_2 = 204.4$, which was close to the lower bound of the 95% CI for I_2 (204.7–210.9) derived from regression. The estimate of I_3 (230.7) for the model fit to the single fetus we classified as third estrus was approximately 2 estrous cycles from the first model.

DISCUSSION

Estrous Behavior

Moose we observed formed a dominance hierarchy and typical assemblage of breeding moose (Bubenik 1987), and displayed normal breeding attributes (Altmann 1959, Lent 1974, Bubenik 1987). Cows during the proceptive phase of breeding showed high levels of interest in the bull and his rutting pits.

We did not witness an apparent increase in activity of females as noted for both black-tailed (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) (Cowan 1956, Rue 1978, West 1968, Wong and Parker 1988, Knox et al. 1988). Ozoga and Verme (1975) measured a 28-fold increase in pacing in confined white-tailed does prior to estrus.

We could not find a reliable indicator of overt estrus in moose. The best indication of possible female receptivity was a reduction in her personal space (intimate zone, Bubenik 1987). Anestrous females seldom allowed a bull to chin (Dodds 1958) their rump or forequarters. They tended to avoid physical contact with the bull. When courted, anestrous females generally avoided the male's approach by moving away and/or vocalizing an appeasement whine (Lent 1974). Females approaching estrus (<24 hr) tolerated the male's approach and allowed chinning and vulva licking by the bull. This activity appeared to be an incipience to mounting as suggested by Lent (1974). This reduction in personal space was overt in some females but subtle or lacking in others.

Estrous Cycle

The 22- to 28-day length of the estrous cycle in moose varied less than reported for black-tailed deer (18–30 days; Wong and Parker 1988), red deer (*Cervus elaphus*) (13–22 days; Guinness et al. 1971), and white-tailed deer (21–30 days; Knox et al. 1988). Days between estrous cycles for moose did not increase with each subsequent cycle number as reported for black-tailed deer (Wong and Parker 1988), white-tailed deer (Knox et al. 1988), fallow deer (*C. dama*) (Asher 1985), and red deer (Guinness et al. 1971).

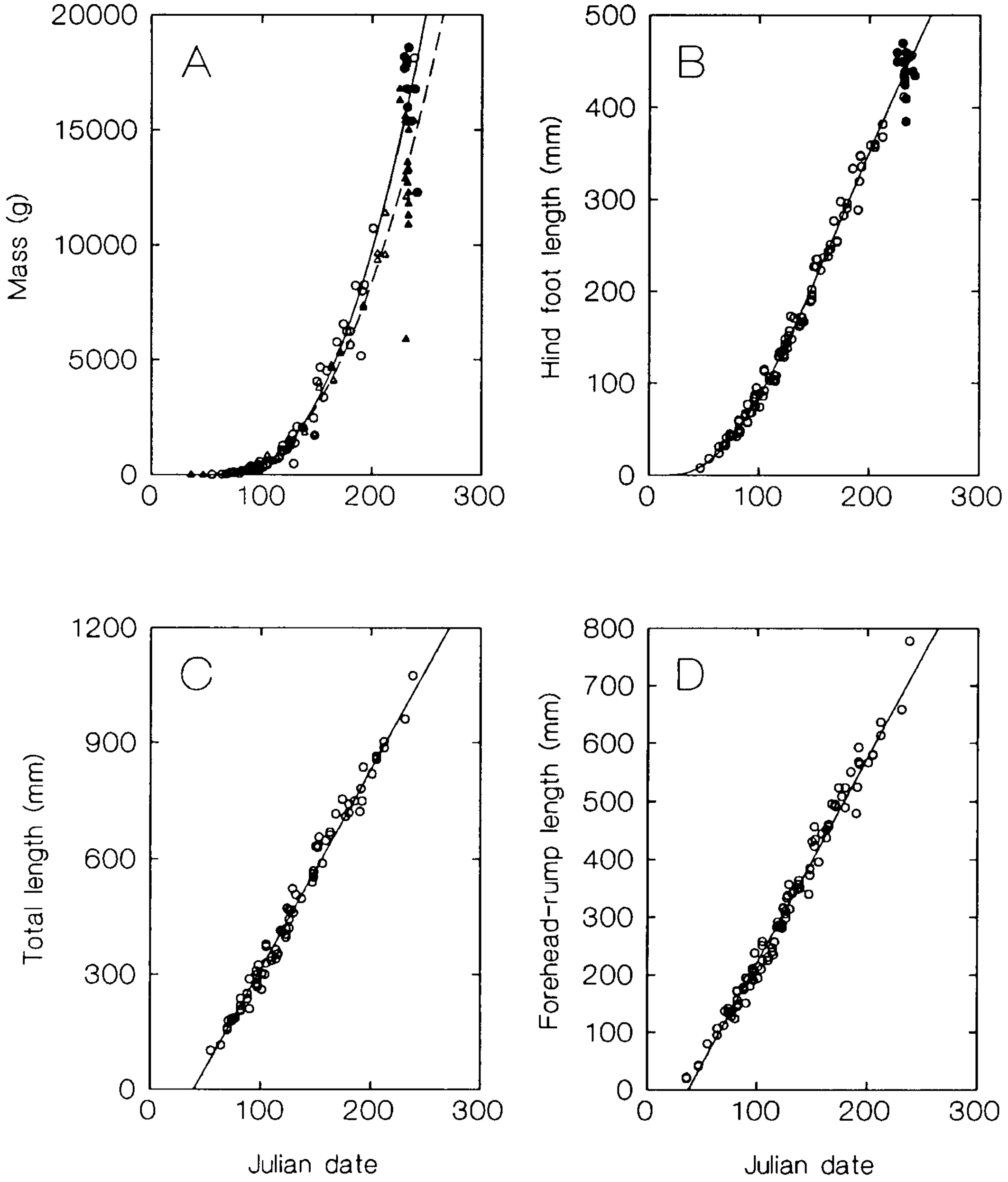

Fig. 5. Age-mass (A), hind foot (B), total length (C), and forehead-rump (D) relationships for fetuses collected from wild cow moose (open symbols) from the Kenai Peninsula, Alaska, and fetuses and neonates from tame cows (solid symbols), 1987–92. In (A) the solid line and circles represent singletons, and the dashed line and triangles indicate twins. Singletons and twins were combined for (B–D). Only fetuses/neonates known to be or nominally classified as conceived on the first estrus were included.

Variation within an individual over time and within a cycle among individuals was consistently small. A shorter cycle in primiparous females has also been documented in domestic cattle (Hansel 1959), but not white-tailed deer (Knox et al. 1988).

Gestation Period

Our observations suggest that the 216-day gestation length documented for 2 yearling moose by Stewart et al. (1987) and the 240–246 days reported by Peterson (1955) represent extreme values. Our results compare more favorably with the estimate of 234 days presented by Markgren (1969) for Swedish moose.

Although we did not test effects of nutritional plane on gestation length, we have limited data that suggest that severe undernutrition may lengthen it. While delineating winter energy requirements of adult moose, we subjected pregnant cows to varying levels of digestible energy intake (Schwartz et al. 1988). Moose received 100, 85, and 70% of ad libitum rations from late November through late April. Moose on the 100% ad libitum intake gained mass throughout winter ($\bar{x}$ = 53 g/day) and gave birth during the normal calving period ($\bar{x}$ = 25 May, SD = 1.4, $n = 2$) to healthy offspring. Cows receiving 85% of ad libitum intake lost mass throughout the winter (20 g/day) and gave birth slightly later (3 Jun, SD = 6.3, $n = 2$) to normal healthy calves. Females in the 70% ad libitum group also lost mass throughout winter (281 g/day) and gave birth significantly later ($F = 27.2$; 2, 3 df; $P = 0.012$) (21 Jun, SD = 0.7). Although the mass of these calves was not different ($P > 0.05$) from others born that year, they lacked vigor, had difficulty nursing, and died within 24 hours. These data suggest that gestation length is not fixed but closely linked to fetal development.

Length of Breeding Season

Breeding season was well defined as judged by the spread in observed breeding and births. Bulls shed their velvet and began digging rutting pits very early in September and remained interested in the cows well into November. Our data conform to the timing of rut activities presented across the range of the species (Lent 1974) and clearly demonstrate that rutting behavior begins well before and continues well after the majority of conceptions occur.

We found no relationships between date of first estrus and cow mass, suggesting that body condition did not play a major role in determining estrous timing. Lack of condition can delay conception or mean time of peak conception (Rhodes et al. 1992), but a high plane of nutrition may negate the effects. Similarly we found no relationship with cow age suggesting that dominance (older cows tended to be dominant) did not influence estrous timing. This was supported further as primiparous females came into heat during the same period as prime cows. Our data suggest that a synchronous estrus is consistent among all females regardless of condition or age.

Although we did not detect a significant difference in gestation length between cows bred during their first (232 days) and second (229 days) estrus, the difference between peak calving of cows bred their first (26 May) and second (15 Jun) estrus was only 20 days. This was 4–5 days shorter than the modal length of the estrous cycle suggesting that gestation may be shortened slightly in second estrous females. This notion was further supported by 2 females that were bred during their third estrous cycle. We witnessed the actual day of mating of 1 female and suspected it in the other based on behavior of the bull. The length of gestation in these 2 females was 218 days (SD = 3.5), which was shorter ($F = 8.62$; 2, 28 df; $P = 0.001$) than length of gestation for cows bred their first or second estrus. The mean date of parturition for these 2 cows was 3 July (SD = 4.2 days). The difference between calving dates for cows bred during their second (15 Jun) and third (3 Jul) estrus was only 18 days, again suggesting that females bred during later estrous cycles may have a slightly shorter gestation period. Our sample size was inadequate to test this possibility.

Calf Production and Ovulation Rate

Age at first reproduction and twinning rates in moose were related to climate and nutrition in other studies (Pimlott 1959; Markgren 1969, 1982; Schladweiler and Stevens 1973; Franzmann and Schwartz 1985). Gasaway et al. (1992) compared the twinning rates in several moose populations from North America. Twinning was positively related to habitat carrying capacity. The highest twinning rate of cows >29 months old in habitats below carrying capacity was reported as 90%; the lowest was 23%. Our twinning rate in pluriparous and 2-year-old primiparous females was 60%. A lack of any relationship between age or body size and twinning suggests that body condition alone does not control twinning rates in moose, at least for cows on a high plane of nutrition.

Moose reproduction was greater at the MRC compared with wild Kenai moose. Habitat and twinning rates on the Kenai Peninsula are in a state of decline (Schwartz and Franzmann 1989). The 27% twinning rate for 2- to 15-year old cows was similar to the 22–28% reported on the

Kenai in 1989 (Schwartz and Franzmann 1989). The twinning rate of 2% for all age classes of cows compares with the 2 populations (0 and 3% twinning) listed by Gasaway et al. (1992) as above carrying capacity. Moose populations on the Kenai Peninsula are currently at, or more likely above carrying capacity, and these twinning rates reflect it.

The 9.3% loss of ova we measured was close to that reported for white-tailed deer (13%) from herds across North America (Rhodes et al. 1992), and mule deer (*Odocoileus hemionus*) (Robinette et al. 1955), but is lower than the 19% loss reported for Swedish moose (Markgren 1969). Markgren cautioned that his estimate was biased by the age distribution of his sample.

Calf Sex Ratio

Sex ratio theory suggests that among polygamous mammals wherein males exhibit greater variance in reproductive success than females, maternal investment should be greater in sons than daughters (Trivers and Willard 1973). Williams (1979) extended this idea and proposed a model for optimization of sex ratios of offspring in species in which litter size is usually two, and in which males are slightly more expensive to produce than females. According to this model, as the ability to provide maternal investment increases, sex ratio and litter size go from 1 female to 1 male to twin females to mixed-sex twins to male twins. McGinley (1984) and Gosling (1986) further refined this hypothesis, but Williams (1979) found no empirical support for adaptive variation in sex ratios of offspring in outcrossed vertebrates.

Verme (1969, 1983) found from experiments with captive white-tailed deer that the nutritional status of a doe in the breeding season influenced fetal sex ratios; poor nutrition skewed conception towards males. Skogland (1986) found similar results in food-stressed wild reindeer (*Rangifer tarandus*). Kucera (1991) found that in a wild population of Rocky Mountain mule deer (*O. h. hemionus*), heavier mothers, and those with higher kidney-fat indices, tended to produce male-biased litters. He found no relationship between litter category and maternal age. DeGayner and Jordan (1987) concluded that live mass of the doe was not a reliable predictor of sex ratio in either single or twin litters, and that nutrition had no proximal effect on sex ratio of offspring. They did find that older females (age ≥4.5 yr) produced significantly more female offspring. Data from red deer (Clutton-Brock and Iason 1986), reindeer and caribou (Kojola and Eloranta 1989, Thomas et al. 1989), and bison (*Bos bison*) (Rutberg 1986) support the hypothesis of Trivers and Willard (1973). Our data support the conclusions of Williams (1979). We found no empirical evidence that maternal age, maternal mass, or prior breeding parity affected variation in litter category or sex ratios of offspring.

Changes in fetal sex ratio from 40 to 60% males reduced a moose population growth rate by 8.9% (Reuterwall 1981). Significant shifts from the expected 50:50 sex ratio of moose calves have been reported to favor both females (Larsen et al. 1989) and males (Franzmann and Schwartz 1986). There seems to be a reasonably established trend in several populations of *Odocoileus* spp. that sex ratio of embryos or neonates is female-biased with increasing maternal age (DeGayner 1982; Verme 1969, 1983), and male-biased in populations subjected to nutritional stress, poor habitat quality, or high population density (Robinette et al. 1957; Verme 1969, 1983; Pederson and Harper 1984). Our data and the review of Boer (1992) suggest that this relationship may not hold for moose. There is a possibility that the few significant shifts from parity merely represent the 5% of cases where the null hypothesis is wrongly rejected (type I error) (Clutton-Brock and Iason 1986).

Calf Mass

Sexual dimorphism at birth, with males being larger, has been documented in white-tailed deer (Verme 1989), red deer (Clutton-Brock et al. 1981), and mule deer (Kucera 1991). For both species with multiple births (mule and white-tailed deer), differences between male and female singletons were not detected. Our data suggest that for moose, sex of the fetus does not influence birth mass, but litter size does. Single calves are larger regardless of sex.

Fetal Development

We believe our classification of the estrus of conception for fetuses based on assessment of the hind foot-date of kill relationship represents an unbiased method for determination of breeding chronology in wild populations. The differences among estrous classifications were equally clear in total length and forehead-rump data, which confirmed equivocal data points. We chose hind foot length because of the slightly higher coefficient of determination, but either of the other length measurements would suffice. There is too much variation in fetal mass to accurately predict estrus of conception.

We do not think the differences we observed in hind foot length and date of collection were mainly due to variation in fetal growth among individuals conceived during the same estrous cycle. Had this been the case, we would predict a more normally distributed pattern for the data at any given time.

We correctly predicted the estrus of conception for 19 of 20 (95%) calves born at the MRC. The single anomaly was an individual from a set of twins conceived during the first estrus but having a hind foot and mass measurement of a second estrus conception (Figs. 4 and 5A and B). The mother of these twins suffered from a systemic infection during her pregnancy and experienced severe mass loss; it is unlikely she would have survived in the wild.

Edwards and Ritcey (1958) were the first to use scattergrams of forehead-rump lengths and day of collection to determine the period of successful breeding. The 2 noteworthy features of their plots were most points fell as if more or less on a single curve, and a few points were located well away from this curve and at roughly uniform distances from it. Based on these facts, they concluded it was possible to detect the estrous cycle during which a cow moose conceived. Our data support their conclusion.

The average distance of outlier points for the data of Edwards and Ritcey (1958) was 30 days compared with our 27.8 days, suggesting a longer estrous cycle than we measured at the MRC (24.4). Edwards and Ritcey (1958) did not fit a model to their data, but simply estimated the distance of each outlier from the main cluster of points on the line. Their variation was likely due to sample variation rather than a real difference in estrous cycle length for *A. a. andersoni*. By appraising our plots visually, we would have concluded that the 30-day estimate of estrous cycle length presented by Edwards and Ritcey (1958) was correct, when in fact it overestimated the cycle length by at least 5 days.

MANAGEMENT IMPLICATIONS

Management of moose populations requires understanding the basic parameters of reproduction. Our data can serve as a baseline for many of those statistics. We conclude that previous published results inaccurately estimated both the length of the estrous cycle and gestation period. We also caution managers who suspect significant shifts in calf sex ratio to continue to sample to be sure that the evidence is adequate to make such a claim before adjusting population models to reflect deviations from parity.

Our simple technique accurately predicted the incidence of delayed breeding in moose. Using this technique, managers can calculate the proportion of cow moose that breed during first and subsequent estruses. By combining these data with accurate estimates of bull : cow ratios and population social structure during the breeding season, managers can more accurately determine their effect on conception chronology. Collecting such data will ultimately lead to a better understanding of the social structure of the male population required for proper management of wild populations, especially in areas where only males are harvested.

LITERATURE CITED

ALTMANN, M. 1959. Group dynamics of Wyoming moose during the rutting season. J. Mammal. 40: 420–424.

ASHER, G. W. 1985. Oestrous cycle and breeding season of farmed fallow deer (*Dama dama*). J. Reprod. Fert. 75:521–529.

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

BOER, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces Suppl. 1:1–10.

BUBENIK, A. B. 1987. Behavior of moose (*Alces alces* spp.) of North America. Swedish Wildl. Res. Suppl. 1:333–365.

CLUTTON-BROCK, T. H., S. D. ALBON, AND F. E. GUINNESS. 1981. Parental investment in male and female offspring in polygamous mammals. Nature 289:487–489.

——, AND G. R. IASON. 1986. Sex ratio variation in mammals. Q. Rev. Biol. 61:339–374.

COWAN, I. MCT. 1956. Life and times of the coastal black-tailed deer. Pages 523–617 *in* W. P. Taylor, ed. The deer of North America. Stackpole Co., Harrisburg, Pa.

DEGAYNER, E. J. 1982. Skewed fetal sex ratios in white-tailed deer: mechanisms, correlates, and evolutionary implications. M.S. Thesis, Univ. of Minnesota, St. Paul. 49pp.

———, AND P. A. JORDAN. 1987. Skewed fetal sex ratios in white-tailed deer: evidence and evolutionary speculation. Pages 178–188, *in* C. M. Wemmer, ed. Biology and management of Cervidae. Smithsonian Inst. Press, Washington, D.C.

DODDS, D. C. 1958. Observations of pre-rutting behavior of Newfoundland moose. J. Mammal. 39:412–416.

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

FRANZMANN, A. W., AND C. C. SCHWARTZ. 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.

———, AND ———. 1987. Anesthesia of moose for vasectomy using carfentanil/xylazine and reversal with naloxone/yohimbine. Alces 23:221–226.

GASAWAY, W. C., R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLEYHOUSE, R. O. STEPHENSON, AND D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildl. Monogr. 120. 59pp.

GOSLING, L. M. 1986. Biased sex ratios in stressed animals. Am. Nat. 127:893–896.

GUINNESS, F., G. A. LINCOLN, AND R. V. SHORT. 1971. The reproductive cycle of the female red deer, *Cervus elaphus* L. J. Reprod. Fert. 27:427–438.

HANSEL, W. 1959. The estrous cycle in the cow. Pages 223–265 *in* H. H. Cole and P. T. Cupps, eds. Reproduction in domestic animals. Academic Press, New York, N.Y.

KIRKPATRICK, R. L. 1980. Physiological indices in wildlife management. Pages 99–112 *in* S. D. Schemnitz, ed. Wildlife management techniques manual. Fourth ed. Wildl. Soc., Washington, D.C.

KNOX, W. M., K. V. MILLER, AND R. L. MARCHINTON. 1988. Recurrent estrous cycles in white-tailed deer. J. Mammal. 69:384–386.

KOJOLA, I., AND E. ELORANTA. 1989. Influences of maternal body weight, age, and parity on sex ratio in semidomesticated reindeer (*Rangifer t. tarandus*). Evolution 43:1331–1336.

KUCERA, T. E. 1991. Adaptive variation in sex ratios of offspring in nutritionally stressed mule deer. J. Mammal. 72:745–749.

LARSEN, D. G., D. A. GAUTHIER, R. L. MARKEL, AND R. D. HAYES. 1989. Limiting factors on moose population growth in the southwest Yukon. Yukon Dep. Renewable Resour. Rep. 105pp.

LENT, P. C. 1974. A review of rutting behavior in moose. Nat. Can. (Que.) 101:307–323.

LERESCHE, R. E., R. H. BISHOP, AND J. W. COADY. 1974. Distribution and habitats of moose in Alaska. Nat. Can. (Que.) 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.

MACNEIL, M. D. 1983. Choice of a prediction equation and the use of the selected equation in subsequent experimentation. J. Anim. Sci. 57:1328–1336.

MARKGREN, G. 1969. Reproduction of moose in Sweden. Viltrevy 6:127–299.

———. 1982. Moose populations along a climatic gradient across Sweden. Natl. Swedish Environ. Prot. Board Rep. 1571, Stockholm. 52pp.

MCGINLEY, M. A. 1984. The adaptive values of male-biased sex ratios among stressed animals. Am. Nat. 124:597–599.

NORUSIS, J. J. 1986. SPSS/PC for the IBM PC/XT/AT. SPSS Inc., Chicago, Ill.

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.

OZOGA, J. J., AND L. J. VERME. 1975. Activity patterns of white-tailed deer during estrus. J. Wildl. Manage. 39:679–683.

PEDERSON, J. C., AND K. T. HARPER. 1984. Does summer range quality influence sex ratios among mule deer fawns in Utah? J. Range Manage. 37:64–66.

PETERSON, R. L. 1955. North American moose. Univ. of Toronto Press, Toronto. 280pp.

PIMLOTT, D. H. 1959. Reproduction and production of Newfoundland moose. J. Wildl. Manage. 23:381–401.

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. Nat. Can. (Que.) 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.

REUTERWALL, C. 1981. Temporal and spatial variability of the calf sex ratio in Scandinavian moose *Alces alces*. Oikos 37:39–45.

RHODES, O. E., JR., M. H. SMITH, AND R. K. CHESSER. 1992. Prenatal reproductive losses in white-tailed deer. Pages 390–397 *in* R. B. Brown, ed. The biology of deer. Springer-Verlag, New York, N.Y.

RICKER, W. E. 1979. Growth rates and models. Fish Physiol. 8:679–743.

ROBINETTE, W. L., J. S. GASHWILER, D. A. JONES, AND H. S. CANE. 1955. Fertility of mule deer in Utah. J. Wildl. Manage. 19:115–136.

———, ———, J. B. LOW, AND D. A. JONES. 1957. Differential mortality by sex and age among mule deer. J. Wildl. Manage. 21:1–16.

RUE, L. L., III. 1978. The deer of North America. Outdoor Life, Crown Publ. Inc., New York, N.Y. 463pp.

RUTBERG, A. T. 1986. Lactation and fetal sex ratios in American bison. Am. Nat. 127:89–94.

SADLEIR, R. M. F. S. 1982. Reproduction of female cervids. Pages 123–144 *in* C. M. Wemmer, ed. Biology and management of Cervidae. Research symp. of the Zoological Park Smithsonian Inst., Washington, D.C.

SCHLADWEILER, P., AND D. R. STEVENS. 1973. Reproduction of Shiras moose in Montana. J. Wildl. Manage. 37:535–544.

SCHWARTZ, C. C., AND A. W. FRANZMANN. 1989. Bears, wolves, moose, and forest succession, some management considerations on the Kenai Peninsula, Alaska. Alces 25:1–10.

———, AND ———. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl. Monogr. 113. 58pp.

———, M. E. Hubbert, and A. W. Franzmann. 1988. Energy requirements of adult moose for winter maintenance. J. Wildl. Manage. 52:26–33.

———, K. J. Hundertmark, and T. Spraker. 1992. An evaluation of selective bull moose harvest on the Kenai Peninsula, Alaska. Alces 28:1–13.

———, 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.

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. 1974. Reproduction and productivity of moose. Nat. Can. (Que.) 101:517–526.

Skogland, T. 1986. Sex ratio variation in relation to maternal condition and parental investment in wild reindeer *Rangifer t. tarandus*. Oikos 46: 417–419.

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.

Stewart, R. R., L. Comishen Stewart, and J. C. Haigh. 1987. Gestation periods in two yearling captive moose, *Alces alces*, in Saskatchewan. Can. Field-Nat. 101:103–104.

Thomas, D. C., S. J. Barry, and H. P. Kiliaan. 1989. Fetal sex ratios in caribou: maternal age and condition effects. J. Wildl. Manage. 53:885–890.

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

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Verme, L. J. 1969. Reproductive patterns of white-tailed deer relative to nutritional plane. J. Wildl. Manage. 33:881–887.

———. 1983. Sex ratio variation in *Odocoileus*: a critical review. J. Wildl. Manage. 47:573–582.

———. 1989. Maternal investment in white-tailed deer. J. Mammal. 70:438–442.

West, N. O. 1968. The length of the estrous cycle in the Columbia black-tailed or coast deer (*Odocoileus hemionus columbianus*). B.S. Thesis, Univ. British Columbia, Vancouver. 31pp.

Wilkinson, L. 1990. SYSTAT: the system for statistics. Systat, Inc., Evanston, Ill. 677pp.

Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. Proc. R. Soc., London, Ser. B, 205:567–580.

Wong, B., and K. L. Parker. 1988. Estrus in black-tailed deer. J. Mammal. 69:168–171.

Zullinger, E. M., R. E. Ricklefs, K. H. Redford, and G. M. Mace. 1984. Fitting sigmoidal equations to mammalian growth curves. J. Mammal. 65:607–636.

Received 20 July 1992.
Accepted 6 February 1993.
Associate Editor: Woolf.