REPRODUCTION IN A MOOSE POPULATION[1]

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Moose (Alces alces) in Wells Gray Park, British Columbia, have been under study by the authors since 1955. Part of this study has included the examination of uteri and their contents. The purpose of this part of the program was to obtain information on reproduction in this moose population. Some results of this work are presented in this paper.

Early in our study it was apparent that counts of calves at heel in summer and fall were providing unreliable information, despite considerable physical effort and expenditure of time to gather these data. Many cows without calves were seen. Questions invariably arose as to whether these cows were barren, had lost their young, or simply were active while their calves lay in a nearby thicket. A meaningful picture of the ability of these moose to reproduce might best be based, therefore, on assessment of initial reproduction - the number of females carrying young. Even this approach is, of course, rather gross. A detailed study would include the production of ova and sperms, fertilization, and mortality of embryos. Some data have accumulated on these subjects, but lack of sufficient study material and of facilities for such detailed studies made intensive investigation at this level impossible.

Hunting is encouraged in this park as a legitimate, intensive, desirable form of recreation, to be fostered if adequate research and management ensures the perpetuity of game species concerned, and if hunting does not conflict with greater numbers of people using the park for other purposes. Hunting season has been variable in length, but most have begun in September and closed in middle or late December. Any-moose seasons are the rule and have made possible for us to gather data on a scale otherwise impossible. A total of 218 uteri have been collected through the years from 1952 to 1956, inclusive, most of them by guides, some by hunters, and a few from moose taken in winter for autopsy. Our samples for study were not randomly selected from the population of moose in Wells Gray Park; hence the conclusions drawn in this paper apply only to data we have been able to collect.

The present study examines variations in the occurrence of pregnancy and of twins and the periodicity of oestrus as we encountered them in the population.

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METHODS

Hunters and guides were requested to leave uteri at park headquarters, which visitors must pass in order to leave the park. Plastic bags were provided to facilitate carrying fresh uteri. Few hunters co-operated. Guides provided most of the material. Even after verbal instructions, it was found that hunters had difficulty identifying the uterus in *situ.* On several occasions, sincere effort resulted in collecting bladder, while other hunters reported that, despite a search, the uterus was not found.

An attempt was also made to collect varies, but one or both were frequently missed by our collectors. Resulting material was so incomplete that there is no consideration of ovarian data in this paper.

Uteri were preserved in Formalin and examined later in the laboratory. Uterine contents were usually examined only grossly. Magnification was seldom used. Very small embryos were undoubtedly missed, and in some cases early pregnancy may not have been recognized as such. When membranes were found within the uterus but no embryo was found, the cow concerned was recorded as pregnant. Lengths of embryos were measured, small one crown-rump, large ones forehead-rump. In some cases, lower jaws and uteri were collected from the same cow. These jaws, useful for aging, were numbered and saved for reference.

INCIDENCE OF PREGNANCY AND TWINNING

All 218 uteri were collected in the period from September to May, inclusive. Hunters and guides brought in many uteri unaccompanied by lower jaws, so that in many cases the ages of animals concerned are not known. The data thus contained an unknown number of uteri from yearling females, an age class quite unproductive in Wells Gray Park. As a result, our uncorrected data apply to all females exclusive of calves, and include an unproductive year class.

One hundred and twenty-nine, or 59%, of the 218 uteri were pregnant. Seven of these 218 uteri were collected in September, a month in which recognizable pregnancy is not expected, as explained below. Thus, of the remaining 211 uteri, 61 percent were pregnant.

A rough calculation can be made to exclude yearlings from these data. In three years (1954-56), a total of 403 lower jaws were collected from moose killed by hunters. These can be aged more or less accurately, while the jaws of yearlings among them can be segregated with complete accuracy. Yearlings constitute 20 percent of this sample. If this percentage of the 211 uteri was from yearlings, further calculation gives the pregnancy rate of females past yearling age as 76 percent. This figure is low, however, for to it must be added pregnancies undetected in our examinations, and cows might have become pregnant in subsequent oestri.

In the process of exclusion one group from the data, questions arise whether this figure, 76 percent, applies to all other age groups. Table 1 gives data from those cows for which obtained both uteri and lower jaws. Each age class past yearling in our sample had a pregnancy rate that differed but slightly from the 76 percent, the probability that these differences were due to chance being 0.90. This suggests that pregnancy rates are fairly constant throughout all age classes except yearlings. Note, however, that the sample used here is small and that we are unable to age moose accurately, using lower jaws, once they have passed th two-year age class. Beyond that age we have defined tentative age groups, based on tooth wear, which can only be verified when jaws of known age come to hand as a result of our program of tagging moose (Ritcey and Edwards, 1956).

Table 1 – DATA ON PREGNANCY AND TWINS FOR 95 UTERI FROM COWS FOR WHICH LOWER JAWS WERE ALSO AVAILABLE

		Pregnant		Uteri with Twins	
Age of Cow	No. Uteri	No.	Percent	No.	Percent
1 +	15	0	0	0	0
2 +	11	7	64	2	29
3-4	12	11	92	2	18
4-5	22	16	73	5	31
5-7	25	20	80	3	15
7-9	9	7	80	3	43
9+	1	0	0	0	0

We have no record of a pregnant yearling. The yearling age class is easily identified in autumn by its teeth. Hunters and guides in this area have, through the years, been able to accumulate a considerable body of data fully supporting the fact that yearling females can be disregarded as a productive age class. There is no exception in our records. Female moose in Wells Gray Park breed first as two year olds in their autumn.

In 129 pregnancies, 28 cases or 22 percent involved twins. Statistical test of the incidence of twins relative to age of cows suggests that there is no significant difference among the productive age classes (chi-square: P=80 percent).

ANNUAL AND MONTHLY VARIATIONS

When data from the hunters' sample are examined by year (Table 2) and, with the addition of autopsy data, by months (Table 3), some differences appear.

Throughout the study period, uteri averaged 56 percent pregnant. Annual percentages of uteri pregnant showed some variation. The number of pregnancies observed in these annual data, when compared to the numbers expected if 56 percent of uteri were pregnant, had differences with a considerable probability of being due to chance (chi-square = 7.28, P= 10 percent).

Table 2 – Annual Percentage of Females (Yearlings Included) Pregnant and Occurance of Twins, in Samples from Hunter Kill

Year	No. Uteri	No. Pregnant	Percent Pregnant	No. Set Twins	Percent Pregnancies with Twins
1952	43	25	58	8	32
1953	42	20	48	0	0
1984	20	4	20	0	0
1955	37	22	59	4	13
1956	54	38	70	7	18
Total	196	109	__	19	__
Means			56	__	10

When examined by months, pregnancy rate became progressively higher with the onset of winter (Table 3). In this table fewer uteri appear in the hunters' sample (October to December inclusive) than in Table 2 because eight uteri were not labeled with the month of collection. In addition, uteri obtained in September are omitted from Table 3. Chi-square test of monthly differences in pregnancy rate suggests that they are significant (P = 1 percent). But further analysis indicates that this significance is due entirely to the relatively low number of pregnancies recorded for October. If a test is made of these same data exclusively of those in October, the probability increases 20 percent. These differences, then, are probably not significant. The low incidence of pregnancy recorded for October may be real, or it may be a result of our missing very small embryo in our examination of uteri.

The 22 uteri collected in winter from animals taken for autopsy are of special interest. Twenty were pregnant. The other females two were yearlings. Thus, adult females were 100 percent pregnant. These animals were taken by a biologist in the four winters from 1952-53 to 1955-56, and the numbers involved were respectively, 6,6,8,6, and 2. There is some possibility here of data being selective for pregnant animals. It is probably slight, however, for in each case the aim during hunting was simply to autopsy the first adult female encountered. The two yearlings were taken in error.

Annual data on the frequency of twins in specimens examined exhibit roughly similar trends to those of pregnancy rate (Table 2). Ten percent of all pregnancies involve twins. The number of twins observed annually when compared with the numbers expected each year if one assumes that in each year 10 percent of pregnancies had twins, exhibited differences with a 6 percent probability of occurring by chance (chi-square = 8.87, P = 6 percent.

The number of twins observed by months were compared with the numbers expected if 10 percent of pregnancies involved twins in each month. The differences were considerable, with little probability that they occurred by chance (chi-square, P = 2 percent).

TABLE 3.—PREGNANCY RATE OF COW MOOSE AND OCCURRENCE OF TWINS, BASED ON UTERINE EXAMINATION

Month	No. Uteri	No. Pregnant	No. Set Twins	Percent Pregnant	Percent Pregnancies with Twins
October	40	7	0	17	0
November	87	55	6	63	11
December	54	46	13	83	29
Jan. - May	22	20	9	91	45

Reviewing data to this point, there are four series of figures, incidence of pregnancy and incidence of twinning, each considered by years and months. All appear at first consideration to exhibit noteworth variation. Statistically testing casts some doubt on whether either series concerned with pregnancy contains significant differences. Similar testing of figures on twins shows one series (by months) to be statistically significant. The other series (by year) might or might not be considered significant depending upon one's opinion of the maximum probability acceptable as statistically significant.

The figures on twinning by months, which exhibit the most significant differences, indicates progressively more twins *in utero* as autumn advances into winter. Such changes through autumn are familiar trends in some data from this population of moose. These animals are migratory (Edwards and Ritcey, 1956), with the result that in autumn progressively more moose arrive on the valley floor with the onset of winter. Any sampling of the population on the valley floor through this period is therefore dealing with an increasing population that could be changing population in some attributes. This migration is difficult to express numerically, if for no other reason than it is different every year. There are no figures on migration by months comparable with figures on embryos *in utero*, but the migration is such a marked annual event in the moose population, and the occurrence of most twins in late season is so marked, that a relationship between the two is indicated. Cows killed in early hunting season are those more or less resident a low elevations. They carry no twins, at least such is indicated by the data. As cows that have summered at higher elevations migrate to the hunted lowlands and their numbers increasingly dominate the lowland population, the records of twins increase. It would seem that some factor in the environment at higher elevations is conducive to the production of twin embryos in this species.

If the incidence of twins *in utero* increases as progressively more moose arrive in the area hunted, the same phenomenon should influence the annual record of the incidence of twins (Table 2). As has been noted, the times of autumn migration are variable. While the hunt begins every year in September before migration has begun, the number of moose subsequently available to hunters in the lowlands is quite variable from year to year. The early arrival of snow brings migrating moose into the lowlands in October. Snowless weather throughout the hunt can result in the close of the season in December before moose have reached heavily hunted areas. Migration was early in 1952, intermediate in its timing in 1953 , late in 1954, and early in both 1955 and 1956. Those three years in which migration was early are those in which twins have occurred in our samples.

It is probably safest at present to place little importance upon the variations in pregnancy rates reported here, both annual and monthly. Note, however, that years of high pregnancy rate are years of early migration; and that monthly figures, were they taken at face value, indicate an increasing pregnancy rate through autumn as if affected by migration. Perhaps these differences are biologically real, but too small to be accepted statistically when samples are small.

THE PERIOD OF SUCCESSFUL BREEDING

The sizes of embryos collected are plotted over date of collection in Fig. 1. Two noteworthy features of this figure are: (1) most points fall as if more or less of a single curve; and (2) a few points are located well away from the curve and at roughly uniform distanced from it.

Fig. 1 may be interpreted as follows. The data contain embryos from eggs fertilized in four different oestral periods. The embryos resulting are 6mm. to 12 mm. long in early October, late October and early November, or late December. Dates of successful coition are not known. If the data presented by Cheatum and Morton (1946) for white-tailed deer *(Odocoileus virginianus*) are used as a rough indication of the early growth rate of moose embryos, then 30 days are required for an embryo to grow to 9 mm. in length. Based on this assumption, the four periods of successful breeding for Wells Gray moose would be roughly, early September and early October, late October, and late November.

Of the four successive oestri, the data indicates that 5 percent of embryos were conceived in the first oestrus, 89 percent in the second, 3.5 percent in the third, and 2.5

percent in the fourth. If we assume that growth rates of embryos resulting from different oestri are more or less constant, the interval between successive oestri is about 30 days.

INSERT FIG 1.

Fig. 1. Scatter diagram showing the length of foeti and dates they were collected from moose uteri. Two types of measurements were used, the break in the two types showing about 70 mm. (see Cheatum and Morton, 1946, figures 2B and 2C) Figures with arrows indicate approximate numbers of days between foeti of similar length, but apparently in different oestri periods.

One period of oestrus, the second, produces 89 percent of embryos in our data. This manner in which date for this oestrus fall along a uniform curve suggests that most cows experienced oestrus in the same limited period of time—approximately 10 days; and that the growth of embryos in different cows is more or less constant, at lease for the first three months.

Not only is this uniformity of conception present in a given year, but it also appears to take place in successive years about the same date.

Most cow moose in this population apparently become pregnant in the same 10 day period every year. A few became pregnant in one previous or one of two subsequent periods of oestrus.

DISCUSSION

Apparently some factor, affecting the data through migration, influences the twinning rate but has little, if any, influence on the pregnancy rate. The work of Cheatum and Severinghaus (1950) on white-tail deer in New York is relevant here. They give data by region in at state in which the percentages of adult pregnant does vary from 79 to 94 percent. They also include data from which the percentages of multiple pregnancies can be calculated, provided that all multiple births are assumed to involve twins. The assumption is incorrect, for triples occur, but the calculations are probably sufficiently close to show an accurate trend. A chi-square test for difference in twinning among these regions suggests high significance, with a probability of less than one percent. Conversely, a similar test of differences in pregnancy suggests that differences are not significant (P = 70 percent). As in moose data from Wells Gray Park, differences in pregnancy are not. Cheatum and Severinghaus *(ibid*.) attribute New York's differences in deer fertility to nutrition. If this is true, rate of multiple pregnancy may be a more sensitive indicator of nutritional status than is rate of pregnancy.

Nutrition is known to affect the incidence of twins in domestic sheep. Flushing, or the feeding of extra food to ewes prior to and during the breeding season, has increased lamb crops from 18 to 40 percent (Stoddard and Smith, 1943:470). "A rising plane of nutrition, as from poor to fresh green feed tend to cause the extrusion of a number of ova, thus resulting in a greater percentage of twins" (Belschner, 1951:204). Longhurst, *et a*l (1952) state that for mule deer (*O. hemionus*) in California that "rate of ovulation seems to be strongly affected by the level of nutrition just prior and during the rut."

Perhaps, then, in this British Columbia study we are dealing with two populations of moose from a nutritional point of view. There is no data to suggest that winter range is providing this difference. Essentially, all moose winter on the same range, which is fairly uniform throughout On the other hand, high and low summer ranges differ markedly. Lower ranges are at an elevation of about 3,000 feet on the broad bottomlands of the Clearwater Valley. Many of these lands have been burned, with the result that their dominant vegetation is seral and deciduous, composed mainly of willows (*Salix spp*.), aspen (*Populus tremuloides*), and birch (*Betula papyrifera*). In the majority of these stands, coniferous regeneration tends to be open, leaving much soil exposed to the sun. While the floor of the valley is generally flat, it is rough microtopography, a result of soils being moraines from a piedmont glacier. In some areas, natural brushy meadows are frequent, while streams draining the flats and adjacent slopes tend to meander and create oxbows. Beaver (*Castor canadensis*) have invaded some areas in numbers, creating many ponds. These wet areas are usually associated with dense stands of high shrubs, mainly willows and alder (A*lnus tenuifolia*), Moose summering in the lowlands spend most days in these moist, shaded tangles, occasionally invading adjacent dry lands.

Moose at higher elevations live in different habitat. In the cooler, moister, subalpine climate, at an elevation of 4,000-6,000 feet, they inhabit variously open stands of mature alpine fir (*Abies lasiocarpa) and Engelmann spruce (Picea engelmanni).* There are long meadows through these forests, while areas with a lush ground flora in open forests are more frequent. These are areas with water seepage down the high slopes where moving water, charged with nutrients from drained area above, provides superior growing sites for many plants. Moose have worn trails near and through these seepage areas. They also appear to favor the edges of high-elevation burns and moist areas grown to alder and willow occurring on some steep slopes.

Moose living at high elevations inhabit a cooler climate with a lusher vegetation than do moose on the valley floor. At this stage of our studies, we can only speculate as to whether these factors influence the moose herd in question. Since moose are virtually absent in summer from lower parts of the park, those at 3,000 feet seem to be summering at the lower limit of suitable habitat.

The remarkable synchrony of the female herd as to oestri results in a physiological process so well timed that it is as much a process of the whole population as of individuals within the population.

This uniformity of the oestral cycle must certainly be under the control of some environmental factor, uniform from year to year as well as in unlike environments at different elevations. The only alternative is an internal "clock," independent of environment, and in step more or less throughout the herd – an unlikely possibility. As Andrewartha and Birch (1954:290) point out, light is the environmental factor controlling the breeding of a number of animals, operating through variations of day length. Decreasing the photoperiod has been shown to influence the timing of the breeding cycle in sheep (Yeates, 1949) and goats (Bissonnette, 1941), which, like moose, breed in the autumn.

There are many references in the literature to the duration of breeding seasons among Artiodactyles. Most references, however, are based on the activity of males during the rut or are influenced by extreme dates when the young may be born. In either case, the period of time involved may be much longer than is the period when most females are successfully bred. In Wells Gray Park, grunting bull moose with antlers free of velvet have been recorded as early as August 29. Field observations suggest that most bulls are actively seeking cows by mid-September. By mid-October there is less tendency for bulls to wander, although some display interest in females until late December.

The brevity of the main season of successful coition does not appear to be confined to moose. A number of authors have noted quite brief periods of successful breeding. Cheatum and Morton (*op. cit.)* show that one-third of white-tailed deer does become pregnant in a 6-day period, the date of this period being earlier in the northern part of New York State than in the south. Chattin (1948) noted that 88 percent of mule deer does in the Interstate Deer Herd were bred in a 22 day period. Lessen, *et al*. (1952) recorded that 60 percent of successfully bred does in another herd of the same species in California became pregnant in a 12 day period. Robinette and Gshwiler (1950) noted that in Utah mule deer 61 percent of the breeding dates occurred within a 13-day period, while a study of white-tailed deer in Massachusetts showed that 77 percent of adults bred with 16 days (Shaw and McLaughlin, 1951). Darling (1937) observed that the rut in Scottish red deer (*Cervus elaphus*) may last 6 or 7 weeks, but most calves were "dropped between the 15th and 25th of June" Note here a period of 10 days, and the suggestion that calving time was constant. Speaking of pronghorn antelope (*Antilocapra americana*). Einarsen (1948) said: "The kidding season in south eastern Oregon… is very short, the majority of the drop coming between May 20 and May 27….Ten to fifteen days may cover the period in which 90 percent of the kids are born."

Apparently the main period of successful breeding for a number of Artiodactyles is short. It should be remembered, in this connection, that the period of dropping young can be longer than the period of breeding, due to individual variation in the periods of gestation.

The remarkable uniformity in times of oestrus and of conception noted in this study may be especially clear-cut because data are from more or less distinct unit of population. Similar studies over larger areas might lump data from a number of such populations, and thus, possibly, fail to note the uniformity reported here.

SUMMARY

The contents of 218 uteri of moose from Wells Gray Park, British Columbia, provided material for this study. In each autumn the incidence of twins in pregnancies increases with the onset of winter. The incidence of twins in uteri collected by hunters is variable from year to year. Both of these conditions are the result of migrating moose variously affecting the data. Increases through autumn in number of twins encountered *in utero* are affected by the proportion of migratory moose in the lowland areas being hunted. The more moose present from high summer range, the higher is the incidence of twinning. Similarly, in years when hunters encounter few migratory moose, fewer twins are encountered than in years when early migration brings moose from high elevations to the hunted lowlands. About 85 percent of pregnant moose are bred in a 10-day period in late September. This period involves the same dates each year, suggesting regulation by photoperiod. A few moose are bred during an oestrus occurring before that in which most are successfully bred, and some in two subsequent oestri. The interval between oestri is about 30 days.

LITERATURE CITED

ANDREWARTHA, M. G. and L. C. BIRCH. 1954 The abundance and distribution of animals. Chicago:Univ.Chicago Chicago Press. xv + 782pp.

BELSCHNER, H. G 1951. Sheep management and diseases. Sydney, Australia: Angus and Robertson. x + 723pp.

BISSONNETTE, T. H. 1941. Experimental modification of breeding cycles in goats. Physiol .Zool., 14:379-383.

CHATTIN, J. E. 1948. Breeding season and productivity of the Interstate deer herd. Calif. Fish and Game, 34:25-31

CHEATUM, E. L. AND G. H. MORTON. 1946. Breading season of the white-tailed deer in New York. J. Wildl. Mgmt., 10:249-263.

-AND C. W. SEVERINGHAUS, 1950. Variations in fertility of the white-tailed deer related to range conditions. Trans. N. America Wildl. Conf., 15:170-189.

DARLING. F. F. 1937. A herd of red deer. London: Oxford Univ. Press. x + 215pp.

EDWARDS. R. Y. AND R. W. RITCEY. 1956. The migration of a moose herd. J. Mammal, 37:486-494

EINARSEN, A. S. 1948. The pronghorn antelope and its management. Washington; Wildl. Mgmt. Inst. xvi + 238pp.

LARSSEN. R.W., C. M. FERREL, AND H. LEACH. 1952. Food habits, productivity and condition of the Doyle mule deer herd. Calif. Fish and Game, 38:311-224.

LONGHURST, W. M., A. S. LEOPOLD, AND R . F . DASMANN. 1952. A survey of California deer herds, their ranges and management problems. Calif. Dept. Game and Fish, Game Bull. No. 6:1-136

RITCEY,. R. W. AND R. Y EDWARDS . 1956 Trapping and tagging moose on winter range. J. Wildl. Mgmt 20:324-325.

ROBINETTE, W. .L . AND J . S. GASHWILER. 1950. Breeding season, productivity, and fawning period of the mule deer in Utah . Wildl. Mgmt., 14:457-469.

SHAW, S.P. AND C.L. MCLAUGHLIN. 1951 . The management of white-tail deer in Massachusetts . Mass. Div. Fish and Game., Res. Bull. No. 13. vi + 59pp.

STODDARD. L .A. AND A. D. SMITH. 1943. Range management. New York: McGraw-Hill Book Co. vii + 547pp.

YEATES , N. T .M. 1949. The breeding season of the sheep with particular reference to its modification by artificial means using light. J. Agric. Sci., 39: 1-43.

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