# REPRODUCTIVE BIOLOGY OF NORTH AMERICAN MOOSE

**Charles C. Schwartz**

Alaska Department of Fish and Game, Moose Research Center, 34828 Kalifornsky Beach Road, Soldotna, AK 99669

ABSTRACT: An understanding of the reproductive biology of moose (*Alces alces*) facilitates wise management. Moose are polyestrous cervids with relatively high ovulation rates in adult females. Puberty varies among populations, but no calves are sexually mature. In populations on good range or below carrying capacity, yearling ovulation and pregnancy occurs. The estrous cycle averages 24 days and ranges from 22-28 days. If not bred, moose have up to 6 recurrent estrous cycles. The period of heat when a female will accept the male is short, lasting from 1-36 hours. Gestation length ranges from 216-240 days with a mean of 231 days. Gestation length is not different for single vs. twin litters, or primiparous and pluriparous females. Pregnancy rates in adult moose are remarkably constant averaging about 84%. Twinning rates vary with range quality and may be a good indicator of carrying capacity. Bull moose reach puberty as yearlings. Antler growth is initiated in response to increasing day-length and other endogenous rhythms. High levels of testosterone activate Leydig cells which begin spermatogenesis. By fall, bull moose are ready for the breeding season with hardened antlers and fully developed sperm. Breeding season is relatively short, with >85% of all pregnancies occurring in <10 days. Peak rut occurs in late-September and early-October. Rutting season is relatively constant across North America. Out of season births are rare, but have been reported as late as August. Declining levels of testosterone following the rut are responsible for antler drop in bulls, which occurs from early-December through March. Large bulls tend to shed their antlers earlier than young bulls.

ALCES VOL. 28 (1992) pp. 165-173

Management of any wildlife species can be facilitated by knowledge of its reproductive potential. Peterson (1955:55) stated that "the preservation of the species is dependent on the interaction of its biotic potential and environmental resistance, the resultant rate of reproduction becomes of vital importance in the general life history and ecology of moose." Hence a clear understanding of the biological potential and environmental factors acting upon moose reproduction are requisite to sound moose management.

Our early knowledge of moose reproduction (Peterson 1955) was derived from field observations made by naturalist during all seasons. Based on these data Peterson (1955) concluded that moose have a very low reproductive rate for cervidae. Based on more recent information, we now know this not to be the case (Simkin 1974, Sadleir 1982, Boer 1992).

The temperate climate of North America subjects moose to severe nutritional deficiencies during winter and a period of lush vegetative growth during the growing season. Like the other cervid species of North America, moose are seasonal breeders, with breeding timed in the fall to provide optimum conditions for rearing of young (Lent 1974).

Breeding strategies vary geographically with the open tundra moose forming harems (Lent 1974) and the taiga moose breeding in pairs (Knorre 1959). Bubenik (1987) describes the former as an advanced strategy where the male monopolizes many females and the later as the more pristine form where the female monopolizes the male.

This review describes our current state of knowledge about moose reproduction. It does not detail reproductive behavior nor strategies for management. Emphasis was placed on empirical rather than anecdotal observation where possible.

**The Female Cycle**

The annual cycle of reproduction begins in the fall with the breeding season, continues through spring with the gestation period, and is followed by calf rearing and weaning about the time the cycle renews (Fig. 1). The cycle repeats itself for virtually all mature females each year. The cycle can be interrupted, usually during the period of calf rearing as a result of neonatal mortality, but can be interrupted at any phase.

Females that are sexually mature first begin to cycle in late summer (Fig. 2). Under stimulation of follicle stimulating hormone and luteinizing hormone released from the anterior lobe of the pituitary, the ovary produces increasing quantities of estrogens and progesterone (Stewart *et al* 1985, Monfort *et al* 1993), which cause increased development of the uterus, vagina, and oviducts. Primary sex cells in the ovary develop and form the mature ovum (*Proestrus period*). As the ovarian follicle increases in size, it exerts pressure on the surface of the ovary. Eventually the ovary wall thins and ruptures. The follicular fluids and ovum are expelled into the Fallopian tube, completing ovulation. In moose ovulation is closely associated with heat (*Estrus period*) at which time mating occurs. Ovulation is closely associated with estrus because of the absorption into the blood stream of large amounts of estrogens just prior to ovulation.

The *Metestrus period* is the post-ovulatory phase during which the corpus luteum is formed and changes in the vaginal and uterine wall occur to accept the embryo. Progesterone secreted by the corpus luteum prevents further development of follicles and hence the occurrence of further estrous periods. The progesterone produced by corpus luteum is necessary for proper implantation in the uterus, for nourishment of the developing embryo, and for development of the mammary glands. If pregnancy occurs, the corpus luteum remains intact for all or most of the gestation period. Progesterone levels remain high (Stewart *et al* 1985). If pregnancy does not occur, the corpus luteum regresses. Regression of the corpus luteum is followed by development of a new ovarian follicle and the cycle repeats.

Some ruminants (Robinson 1959) and probably moose (Edwards and Ritcey 1958, Simkin 1974, Bäckström 1952) have a silent heat period. This first ovulation is not normally accompanied by overt estrus or breeding. Its ecological significance is not understood.

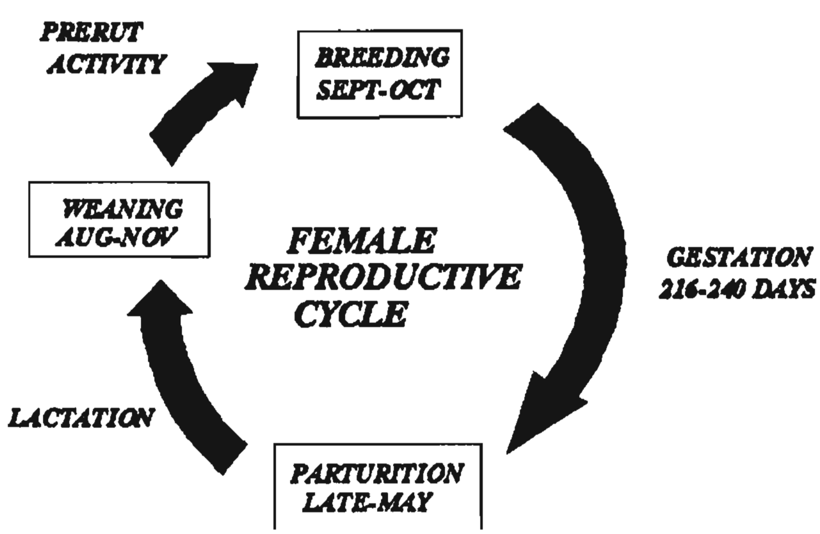


Fig. 1. The reproductive cycle of the female moose. See text for details.

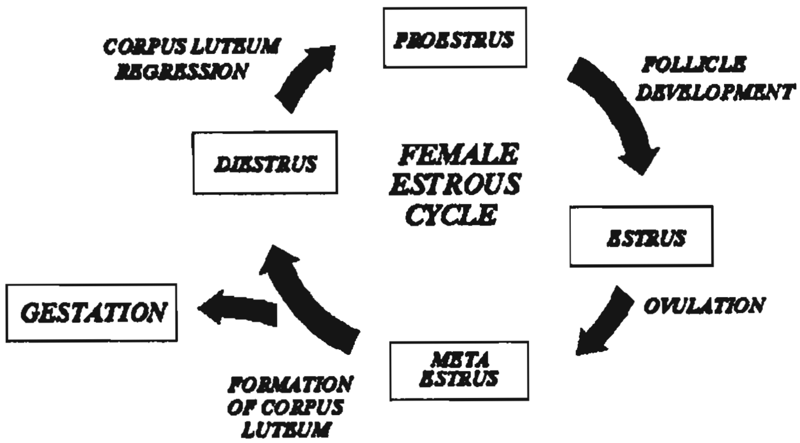


Fig. 2. The estrous cycle of the female moose. See text for details.

## Estrus and Ovulation

The majority of cervid species (Sadleir 1982) including moose are polyestrus (Edwards and Ritcey 1958, Pimlott 1959, Markgren 1969). Based on work by Soviet scientists, and backdating embryos to conception date, estimates of the duration of the estrous cycle were reported to last only 20-22 days by Lent (1974) and as long as 30 days by Edwards and Ritcey (1958), respectively. Recent studies by Schwartz and Hundertmark (1993) where the length of the cycle was measured in captive moose showed that the modal period of estrus was 24-25 days ($\bar{x}$ = 24.4, range 22-28, $n$ = 38)(Fig. 3). The length of the estrous cycle was significantly shorter for primiparous ($\bar{x}$ = 23.7 days) than pluriparous females ($\bar{x}$ = 24.5 days). A shorter cycle in primiparous females was documented in domestic cattle (Hansel 1959).

If not bred, moose may experience as many as 6 recurrent estrous cycles (7 heats) during a breeding season extending into late-March (Schwartz and Hundertmark 1993). Unlike black-tailed deer (*Odocoileus hemionus*) (Wong and Parker 1988), white-tailed deer (*O. virginianus*) (Know *et al.* 1988), and red deer (*Cervus elaphus*) (Guinness *et al.* 1971) the length of the estrus cycle does not lengthen with each additional cycle. The ecological significance of such a change in estrous cycle length is unknown.

Estrus or heat is defined as the period of time when the cow will stand and allow the bull to mount. Lent (1974) summarized the literature and concluded that the heat period in moose lasts a day or two. By observing captive moose in heat, Schwartz and Hundertmark (1993) documented that the heat period of moose showed marked variation between individuals lasting for as little as one hour to as long as 36 hours. They estimated that most heats lasted for 15-26 hours. Because their moose were not observed during the night, exact lengths for some individuals were not quantified.

## Gestation

There is some confusion in the literature regarding the mean length of gestation of moose. Markgren (1969), in Sweden, calculated a gestation length of 234 days based on the difference between time from mean date of breeding and birthing. Peterson (1955:99) stated that "the gestation period is generally conceded to be approximately eight months, 240-246 days." The gestation of 2 yearling moose in Saskatchewan was measured as 216 days by Stewart *et al.* (1987). Schwartz and Hundertmark (1993) working with captive moose in Alaska, measured gestation length in 23 cows over a 5 year period. Actual breeding and parturition dates were observed. Mean gestation for all females was 231 days,

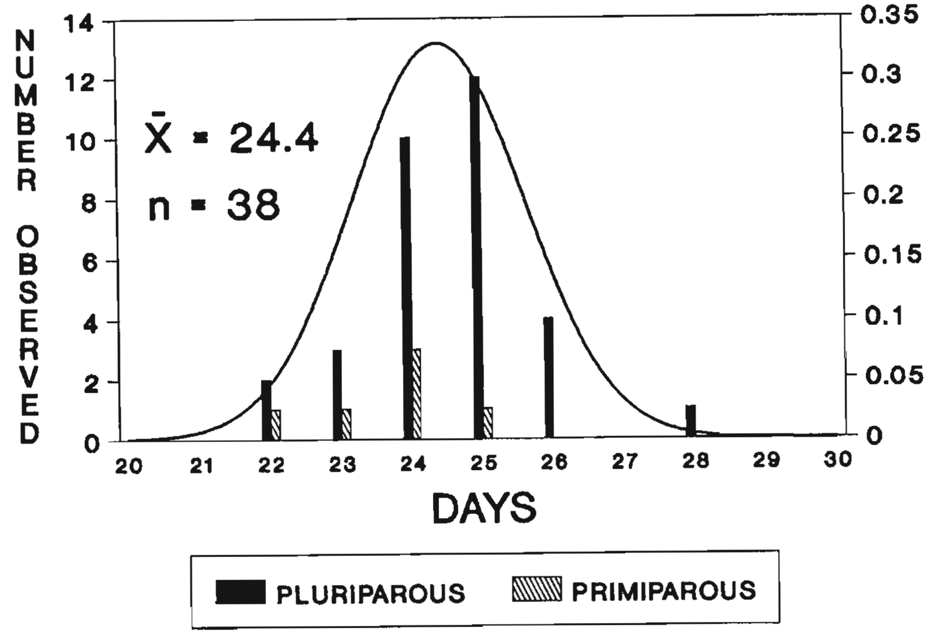


Fig. 3. Length of the estrous cycle in moose. The cycle was different for primiparous (23.7) and pluriparous (24.5) females. Original data from Schwartz and Hundertmark (1993).

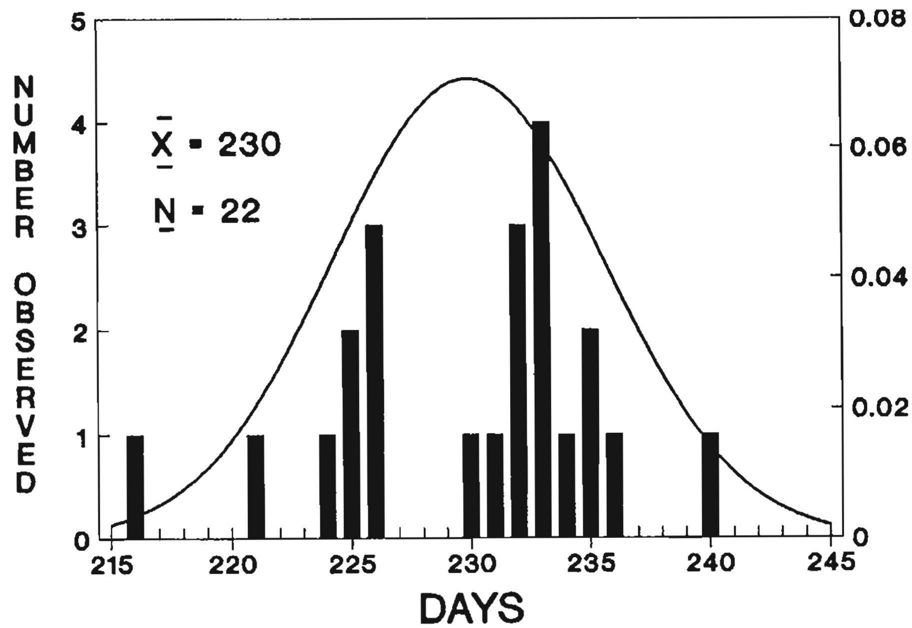


Fig. 4. Length of gestation in moose. Original data from Schwartz and Hundertmark (1993).

with a range from 216 to 240 (Fig. 4). The modal gestation period was 233 days, with 87% of all observations occurring between 225-236 days. There was no difference ($P <$ 0.05) in length of gestation between primiparous and pluriparous females, between litters of one or two calves, between cows bred their first or second estrous, or among years of study.

**Age at First Breeding**

Puberty is the period during which reproductive organs first become functional. In moose, this generally occurs when the cow is around 16 months of age, but it can be delayed until they are 28 months of age. Unlike white-tailed deer (Ramsey *et al.* 1979) moose do not reach puberty in their first year of life (i.e., as calves). There is great variation found throughout North America, since puberty is influenced by climatic conditions, level of nutrition, heredity, and other factors.

Ovulation has been detected in moose by examining ovaries from a sample of cows collected during and after peak breeding season. Corpora lutea can be identified macroscopically, and indicate recent ovulation.

Moose ovulate for the first time at ages 16-28 months. I am unaware of a single study where ovulation has been documented in a calf moose. The age at first ovulation varies considerably between populations and years. This was reviewed by Schladweiler and Stevens (1973) and Simkin (1974), and more recently by Gasaway *et al.* (1992) and Boer (1992). In Norway, it has been shown that the proportion of yearling moose which ovulate increases after they have reached a carcass weight of about 150 kg (Saether and Haagenrud 1983, 1985).

Although yearling ovulation rates are a good indication of population condition, not all ovulations result in pregnancy. Yearling pregnancy rates vary from 0 to >50% depending upon area (Edwards and Ritcey 1958, Pimlott 1959, Simkin 1965, Markgren 1969). Summarizing published literature, Boer (1992) found that fecundity rates for yearling moose were 64.5, 41.1, and 17.7 calves/100 yearling females in populations below, near, and above carrying capacity.

Age at first reproduction is generally related to sexual maturity and body size (Saether and Haagenrud 1983, 1985). Moose on a high plane of nutrition grow faster and tend to reach adult body size sooner (Schwartz *et al.* 1987). Boer (1992) found a significant relationship between yearling pregnancy rates and twinning rates in adult cows.

**Pregnancy Rates of Adults**

In his review of moose reproduction, Boer (1992) indicated that "adult pregnancy rates averaged 84.2% and were remarkably consistent". Franzmann (1981) reported a pregnancy rate of 59.4% for an Alaskan population which was known to be undernourished. Twinning rates were independent of pregnancy rates. Average fecundity rates for moose populations below, near and above carrying capacity were 124.1, 106.1, and 88.0 calves/100 adult females. Twinning rates also vary with the age structure of the female population with cows being most fecund roughly between 5 and 11 years of age (Franzmann 1981, Saether and Haagenrud 1983, Boer 1992).

Several authors (Pimlott 1959, Simkin 1965, Franzmann and Schwartz 1985) speculated that twinning rates in adults were an indication of nutritional status of the moose population. The proportion of females with twins varies considerably among populations. Gasaway *et al.* (1992) showed that in populations below carrying capacity, that twin births ranged from as high 90% to a low of 25% of all births in cows >29 months of age. Twinning rates in populations near carrying capacity ranged from around 5 to 25%, while twinning was <5% in populations above carrying capacity.

**The Male Cycle**

The annual cycle for the male (Fig. 5) begins in spring with initiation of antler growth, continuing through the summer when the antlers fully develop. With increasing production of testosterone, antlers ossify and velvet is shed. At about the same time, there is an enlargement of the testicles, and spermatogonia begin the production of sperm. By early fall, bulls are prepared for the rutting

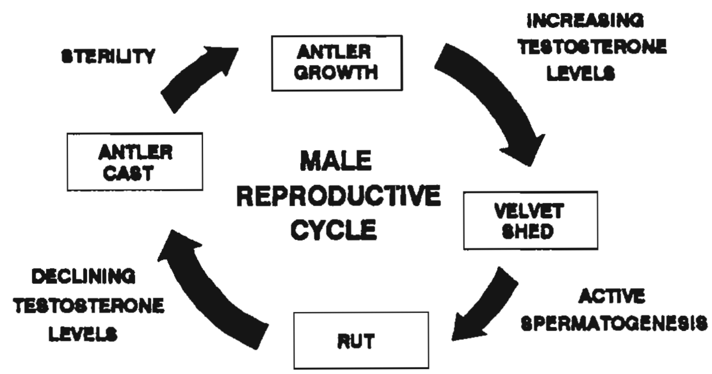


Fig. 5. The reproductive cycle of the bull moose. See text for details.

season. After the rut, there is a rapid decline in testosterone production which ultimately is responsible for the casting of antlers. Large bulls tend to shed their antlers earlier than young bulls. Antler casting is followed by a period of sexual inactivity until early spring when the cycle renews (Fig. 6).

Puberty in bull moose occurs the autumn following their first birthday. Although yearling bulls have not attained mature body weight (Schwartz et al. 1987), spermatogenesis has been reported (Houston 1968, Bubenik and Timmermann 1983). Yearling bulls may be excluded from actively breeding by more mature dominant males (Lent 1974, Knowles 1984, Bubenik 1987), but in their absence are capable of impregnating females (Schwartz *et al.* 1982).

Although testicular weight of calves increases rapidly in the fall no spermatogenesis occurs (Bubenik and Timmermann 1983). Increased activity is associated with development of the cells of Leydig also known as interstitial cells which produce testosterone (Frandson 1965). Testosterone is required for the formation of the pedicle in the calf (Bubenik and Timmermann 1983, Goss 1983). Pedicle development is requisite to antler development in subsequent years.

Testosterone levels measured in two captive 3.5 year-old bulls were low in July (0.4 ng/ml), peaked in September (1.25-4 ng/ml) and declined rapidly following the rut (<0.3 ng/ml) (Hundertmark *et al.* 1989). Levels were lower than expected when compared to peak concentrations found in roe deer (*Capreolus capreolus*) which reach 7 ng/ml at peak rut (Sempere and Boissin 1983). Lower values in moose might have been associated with sampling as neither bull moose was associated with cows during the rut.

**Male Pheromones**

The role of the bull moose in courtship and breeding from an ethological perspective is fairly well documented (Lent, 1974, Bubenik 1987). The role of the bull as a primer of rut synchrony is not clearly understood. Chemical compounds play a major role in ungulate reproduction (Müller-Schwartze 1991), and can serve as signaling compounds (Bubenik *et al.* 1979) and possibly as primers (Schwartz *et al.* 1990, Miquelle 1991).

A recent study by Schwartz *et al.* (1990) isolated primary sex pheromones from the saliva of bull moose. These compounds belong to a special group of steroids which have no hormonal activity but are released in the saliva prior to mating. In red deer and swine they are responsible for synchronizing and promoting male and female courtship behavior. Although the concentrations were low, Schwartz *et al.* (1990) speculated that these compounds may play a role to synchronize the rut, and could possibly be responsible for inducing estrus in the female. Their findings suggested that the bull moose must be viewed as an active participant in the rutting

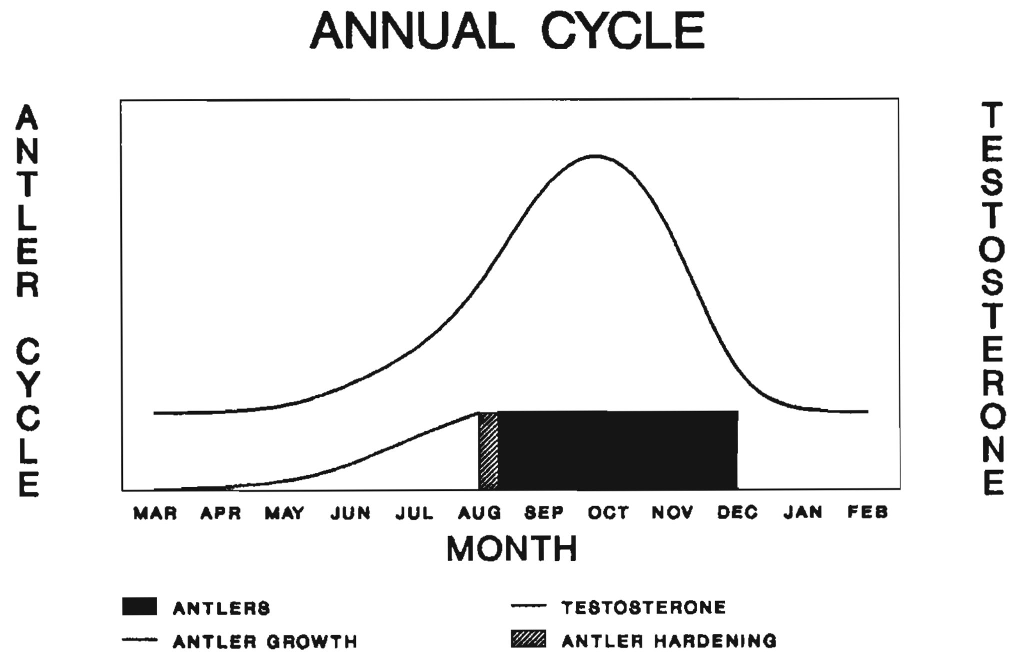


Fig. 6. The antler and testosterone cycle of the bull moose.

sequence and not simply viewed as a sperm donor. More recent information presented by Miquelle (1991) supports this hypothesis.

**Breeding Season**

The length of the breeding season is relatively short for most moose. Based on back-dating embryos, Edwards and Ritcey (1958) concluded that 89% of all females conceived within a 10 day period in their second estrus which occurred during the peak of the rut. Five percent became pregnant during the first estrus prior to peak rut, 3.5 and 2.5% became pregnant in the 3 or 4th estrus. In a similar study Schwartz *et al.* (1993) estimated that 83, 16, and 1 percent of the embryos examined were conceived during the 1st, 2nd, and 3rd estrus, respectively. They did not detect any calves conceived prior to the peak of the rut as discussed by Edwards and Ritcey (1958).

Out of season breeding is relatively rare, with only a few reported cases (Coady 1974, Markgren 1969, Maehulum 1981). We have witnessed one cow give birth to a calf in mid-August. This cow was not with a bull during the normal breeding season. She was put with a bull in mid-December, and probably bred her next estrus.

## REFERENCES

BÄCKSTRÖM, A. K. 1952. Avslutade studier över älgbrunsten. Svenska Jägare-förbundets Tidskrift 90:70-71.

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

BUBENIK, A. B. 1987. Behavior of moose (*Alces alces* spp) of North America. Swedish Wildl Res. Suppl 1:333-366.

______, and H. R. TIMMERMANN. 1982. Spermatogenesis in the taiga-moose of North Central Ontario. Alces 18:54-93.

______, M. DOMBALAGIAN, J. W. WHEELER, and O. WILLIAMS. 1979. The role of the tarsal glands in the olfactory communication of the Ontario moose-a preliminary report. Proc. N. Am. Moose Conf. Workshop. 15:119-147.

COADY, J. W. 1974. Late pregnancy of a moose in Alaska. J. Wildl. Manage. 38:571-572.

EDWARDS, R. Y., and R. W. RITCEY.

1958. Reproduction in a moose population. J. Wildl. Manage. 22:261-268.

FRANDSON, R. D. 1965. Anatomy and physiology of farm animals. Lea and Febiger, Philadelphia, PA. 501pp.

FRANZMANN, A. W. 1981. *Alces alces*.—Mamm. Spec. 154:1-7.

———, and C. C. SCHWARTZ. 1985. Moose twinning rates: a possible population condition assessment. J. Wildl. Manage. 49:394-396.

GASAWAY, W. C., R. D. BOERTJE, D. V. GRANDGARD, K. 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.

GOSS, R. J. 1983. Deer antlers: regeneration, function, and evolution. Academic Press, New York, N.Y. 316pp.

GUINESS, 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.

HUNDERTMARK, K. J., C. C. SCHWARTZ, and D. C. JOHNSON. 1989. Evaluation and testing of techniques for moose management. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Rest. Proj. Rept. W-23-2. 30pp.

HOUSTON, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. Grand Teton' Nat. Hist Assoc. Tech. Bull. No. 1 110pp.

KNORRE, E. P. 1959. Ekologiya losya. Trudy Pechoro-Ilychskohgo Gos. Zapov. 7:5-122.

KNOWLES, W. C. 1984. An ethological analysis of the use of antlers as social organs by rutting bull moose (*Alces alces gigas* Miller). M. S. Thesis, University of Alaska, Fairbanks. 93pp.

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

LENT, P. C. 1974. A review of rutting behavior in moose. Naturaliste can. 101:307-323.

MAEHLUM, J. 1981. Elgkalv in Januar. Fauna 34:131.

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

MIQUELLE, D. G. 1991. Are moose mice? The function of scent urination in moose. The Am. Natural. 138:460-477.

MONFORT, S. L, C. C. SCHWARTZ, and S. K. WASSER. 1993. Monitoring reproduction in moose using urinary and fecal steroid metabolites. J. Wildl. Manage. 57:(in press).

MÜLLER-SCHWARTZE, D. 1991. The chemical ecology of ungulates. Appl. Anim. Behav. Sci. 29:389-402.

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

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

RAMSEY, P. R., J. C. AVISE, M. H. SMITH, and D. F. URBSTON. 1979. Biochemical variation and genetic heterogeneity in South Carolina deer populations. J. Wildl. Manage. 43:136-142.

ROBINSON, T. J. 1959. The estrous cycle of the ewe and doe. Pages 291-334, *in* H. H. Cole and P. T. Cupps, eds. Reproduction in Domestic Animals. Academic Press, New York, N.Y.

SADLEIR, R. M. F. S. 1982. Reproduction of female cervids. Pages 123-144, *in* C. M. Wemmer, ed. Biology and Management of the cervidae. Research symposia of the National Zoological Park Smithsonian Institute, Washington D. C.

SAETHER, B. E., and H. HAAGENRUD. 1983. Life history of the moose (*Alces*

*alces*): fecundity rates in relation to age and carcass weight. J. Mamm. 64:226-232.

_______, and _______. 1985. Life history of the moose *Alces alces*: relationship between growth and reproduction. Holarctic ecology 8:100-106.

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

SCHWARTZ, C. C., and K. J. HUNDERTMARK. (1993). Reproduction in Alaskan Moose. J. Wildl. Manage. 57(in press)

_______, _______, and T. H. 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. 1982. Male moose successfully breed as yearlings. J. Mamm. 63:34-335.

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

_______, A. B. BUBENIK, and R. CLAUS. 1990. Are sex-pheromones involved in moose breeding behavior. Alces 26:104-107.

SEMPERE, A. J., and J. BOISSIN. 1983. Neuroendocrine and endocrine control of the antler cycle in roe deer. Pages 109-122, *in* R. D. Brown, ed. Antler development in cervidae. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX.

SIMKIN, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. J. Wildl. Manage. 29:740-750.

_______. 1974. Reproduction and productivity of moose. Naturaliste can. 101:517-525.

STEWART, R. R., L. COMISHEN STEWART, and J. C. HAIGH. 1985. Levels of some reproductive hormones in relation to pregnancy in moose: a preliminary report. Alces 21:393-402.

_______, _______, and _______. 1987. Gestation periods in two yearling captive moose, *Alces alces*, in Saskatchewan. Can. Field Nat. 101:103-104.

WONG, B., and K. L. PARKER. 1988. Estrus in black-tailed deer. J. Mamm. 69:168-171.