MOOSE SOCIOBIOLOGY AND IMPLICATIONS FOR HARVEST

H.R. Timmermann

Ontario Ministry of Natural Resources Thunder Bay, Ontario P7C 5G6

ABSTRACT: Sociobiology is defined as the systematic study of the biological basis of all social behaviour (Wilson 1975). It focuses on animal societies, their population structure, casts, and communication, together with all of the physiology underlying their social adaptations. This review paper outlines moose (*Alces alces*) sociobiology, with an overview of behaviour, and reviews moose reproduction. Various harvest management implications based on sociobiology are discussed to focus and stimulate discussion on what type of harvest regimes are appropriate for moose.

BEHAVIOUR

Social Interactions

Geist (1963), Lent (1974), Stringham (1974), Bubenik (1987) and Miquelle (1990) have summarized current literature on moose behaviour. Bubenik (1987), however, believed that adaptive behaviour and its relationship to habitat management and appropriate hunting regulations had not been adequately documented. Moose are the least gregarious North American cervid (Hosley 1949, Altmann 1956, Denniston 1956, Geist 1963, De Vos *et al.* 1967) and are often considered solitary, or seasonally individualistic (Peterson 1955, Bubenik 1971, Knowles 1984, Lynch and Morgantini 1984). The most durable bonds are those formed between cows and their calves which can persist from birth to 28 months of age (Ballard *et al.* 1991). Usually a calf remains with its cow up to parturition. Occasionally, a yearling will rejoin its dam after calving and remain with it and the newborn calf a second year. Ballard *et al.* (1991) found that a yearling tended to stay with the cow through the second summer if her newborn calf was killed.

Late autumn and early winter aggregations of bulls and cows are the largest (Peek *et al.* 1974, Lent 1974, Ballard *et al.* 1991) but appear to be loosely knit and transitory (Coady 1982). Mean size of bull-dominated aggregates (more bulls in group than cows) reported by Mytton and Keith (1981), near Rochester, Alberta, varied from 1.0 (n=65) in early August to 2.3 (n=105) in November. Largest bull aggregations (up to 9) occurred following the rut, or breeding season (mid-October to late November). Bulls were usually solitary between December and July. Rounds (1978) observed cows without calves in fall associated with other adults up to 2 months longer than cows with calves. Houston (1974) reported group sizes of moose (*A. a. shirasi*) obtained from year round field observations in Wyoming (n=3351). Single sightings represented 58%, groups of two - 26% and groups of three or more - 16%. Groups containing both adult males and females were comparatively uncommon and involved 7% of animals observed during late spring and summer, 31% during the rutting period, and 11% during winter and early spring. Ballard *et al.* (1991) studied group dynamics of south central Alaskan moose (*A. a. gigas*) over a nine-year period. Average group size was about two moose from January through July, increasing to three in August, 4.9 in September, and 7.6 in October. After October, group size decreased to 3.2. Cows with calves did not associate with large rutting groups. Dodds (1958) reported aggregates of 3 - 10 bulls (n=83) were commonly observed up to a month prior to the rut in Newfoundland, suggesting the establishment of a dominance hierarchy in males prior to the rut, as proposed by Geist (1963). Peek *et al.* (1974,

Alces

1986) and Miquelle *et al.* (1992) reported Alaskan moose occur in larger groups than populations elsewhere, and prime bulls are able to establish dominance over younger males and acquire access to large groups of cows during the rut. Bowyer *et al.* (1991) observed a harem mating system in interior Alaska with groups of > 30 individuals. Our knowledge concerning this temporary gregariousness is incomplete and needs further study.

Vocalization and signals are used by both sexes in communication, especially during the rut (Bubenik 1987). At this time, bulls are particularly vulnerable and become active nearly 24 hours a day as hormone levels stimulate sexual activity (Pimlott 1959, Simkin 1965, Bubenik and Timmermann 1982). Young submature animals, or "teenagers," are more vulnerable to hunting in the fall than calves and mid-aged adults (Pimlott 1959, Crête *et al.* 1981, Fryxell *et al.* 1988). Altmann (1960) characterized juvenile (1.5 to 2.5 yrs old) moose of both sexes as a rejected and most erratic, non-conforming age group.

Home Range

Seasonal home range size for North American moose vary widely (Van Ballenberghe and Peek 1971, Phillips *et al.* 1973, Roussel *et al.* 1975, Addison *et al.* 1980, Gasaway *et al.* 1980, Hauge and Keith 1981, Lynch and Morgantini 1984, Garton *et al.* 1985, Courtois and Crête 1988). Migratory Alaskan moose for example, use annual ranges up to 1,703 km^2 (Ballard *et al.* 1991), while non migratory adult moose in eastern North America generally use 20 - 40 km^2 (Crête 1988). Males have larger home ranges than females, especially during the rut, and young males may move long distances (Goddard 1970). Home range size also varies seasonally: largest in autumn when moose are more mobile during the rut, followed by summer when they are also more mobile and selective for forage than in winter when they

are more sedentary and often restricted in movement by snow (Timmermann and McNicol 1988, Ballard *et al.* 1991).

Adult moose exhibit strong home range fidelity by occupying similar overlapping areas among years (Gasaway *et al.* 1980, Bailey and Franzmann 1983, Cederlund *et al.* 1987, Ballard *et al.* 1991). Some studies report moose are slow in redistributing themselves into vacant, low density, or heavily hunted areas (Goddard 1970, Lynch 1976). A depleted area adjacent to a high density area, however, may get replenished more quickly according to Ballard *et al.* (1991), and hence, resident animals may help trigger a population increase when home ranges overlap disturbed areas. Most moose have traditional movement patterns and do not randomly search for better habitat (Van Ballenberghe 1977, Gasaway *et al.* 1980, 1989, Mytton and Keith 1981, Phillips *et al.* 1973, Gasaway and Dubois 1985, Cederlund *et al.* 1987 , Ballard *et al.* 1991). The adult cow that produces and raises her offspring is sometimes responsible for determining the establishment of specific home ranges by young female moose (Markgren 1972, Cederlund *et al.* 1987). Progeny of adult cows, especially females, tend to occupy home ranges adjacent to, or overlapping, the parent cow's home range (Ballard *et al.* 1991). These 'resident' moose may have a survival advantage over displaced moose who are unfamiliar with their surroundings (Houston 1974, Bailey and Franzmann 1983). Cow moose appear to reduce predation risk on their young by spacing out to shorelines and islands at calving time, thereby using water to escape pursuit (Edwards 1983, Addison *et al.* 1985, Bergerud 1989).

Age-specific tendencies to exploit new habitat appear to vary (Gasaway *et al.* 1989). In some studies, yearling and two-year old moose, especially bulls, dispersed more frequently than older moose (Roussel *et al.* 1975, Lynch 1976, Mytton and Keith 1981, Ballard *et al.* 1991). In others, little or no differential

Alces

dispersal was found between young and older moose (Saunders and Williamson 1972, Cederlund *et al.* 1987, Gasaway *et al.* 1989). More studies are needed to determine the relationship between home range size and quality and reproductive success, as well as factors affecting home range formation and dispersal; why are some populations sedentary and others migratory; which social classes of both sexes are the first to exploit new home ranges; and why are some feeding grounds overused while others, with apparently similar attributes, avoided?

REPRODUCTION

Breeding Strategies

Moose display a phenotypic plasticity in reproduction allowing a rapid expansion into areas following vegetative disturbance and a gradual decline as forests mature (Cowan *et al.* 1950, Geist 1974). Year-round densities seldom exceed 0.5 to 1.5 moose/km² in North America, even though seasonal concentrations may occasionally reach as high as 15/km² in areas of optimum habitat (Telfer 1984). Changes in ungulate density can influence several demographic variables that may greatly affect the rate of increase (Van Ballenberghe 1983). These include; age at first reproduction, litter size, first year survival, adult survival, and sex ratios of young and adults (Caughley 1976).

Two distinct breeding strategies are recognized by Bubenik (1987). *A. a. gigas* often breed in harems or assemblages (Miquelle *et al.* 1992), while woodland or taiga moose (*A.a.* spp.) generally breed in pairs. In the open tundra of Alaska and the Yukon, bulls patrol a large mating area leaving scent marks to advertise their receptiveness (Bubenik 1987). Prime cows move into these areas prior to their estrus, join the harem (an assemblage of non-related cows), and as each comes into heat, the resident bull will breed her. The resident bull may periodically be forced to defend his harem from the challenge of other bulls. Contrasting to this behaviour is that found in forested areas where cows generally remain dispersed and separated within their respective breeding arenas (Bubenik 1987). As each woodland cow enters the attractive phase of heat, she advertises her status by calling and urinating frequently. Bulls search for these cows, often through dense bush, staying with one for several days and servicing her during a short (+ 24 hr) receptive phase.

The harem breeding strategy allows each cow to be bred by the resident bull and hence in such open tundra habitat, one bull is likely to breed and fertilize more cows within five to eight days than the woodland bull could perform throughout the entire breeding season (Bubenik 1987).

Both sexes are believed to produce phermones which are important in mutual stimulation during the breeding period (Bubenik 1984, 1985). Such triggering phermones are believed to be contained in urine and saliva, (Bubenik *et al.* 1979 , Schwartz *et al.* 1990). More research, is needed to determine the significance of these phermones in rut synchronization and induced estrus.

Rut Periodicity

Moose are seasonally polyestrus and generally the breeding season spans mid-September to mid-October, peaking during the last week of September (Dodds 1958, Edwards and Ritcey 1958, Knorre 1959, Rausch 1959, Peek 1962, Crichton 1988). The period of receptiveness for cows is short and true estrus lasts < 24 hours (Markgren 1969, Schwartz and Hundertmark 1993). The interval between heats in a recent Alaskan study averaged 25 days (range 22-28, n=23, Schwartz and Hundertmark 1993), longer than previously presented (20-22 days, see review by Lent 1974), and shorter than the 30 day period suggested by Edwards and Ritcey (1958). The peak breeding period is generally consid-

Alces

ered to occur within one estrus period, with one period earlier referred to by some as a silent heat (Edwards and Ritcey 1958, Simkin 1974), and perhaps one or more later periods accounting for only a small part of total pregnancies (Peterson 1974).

Pheromonal stimulation of both cows and bulls is beleived to play a key role in synchronizing the rut by serving as signaling compounds and possibly as a primer (Bubenik *et al.* 1979, Schwartz *et al.* 1990, Muller-Schwarze 1991). Consequently population structure and density are also important in inducing estrus and synchronizeing rut periodicity.

Mature cows are usually bred during their first overt estrus in late September or early October by a prime bull, and one or two calves are born in mid- to late May. If the cow is bred later during her second estrus (ie. late October) by a younger bull whose sexual actively peaks later (Bubenik and Timmermann 1982), then calving occurs in June, nearly a month later, and probably puts these calves at a distinct weight gain disadvantage. Ballard *et al.* (1991) reported 60% of all (*A. a. gigas*) calves were born between 29 May and 3 June in south central Alaska, 1976-86. By 10 June, 96% of births had occurred and parturition timing was similar to that reported by Hauge and Keith (1981) for *A. a. andersoni* in northeastern Alberta. Crichton (pers. comm. 1992) suggested the possibility of younger cows coming into heat later, and believes more studies are warranted.

Schwartz and Hundertmark (1992) reported mean weights of first estrus (*A.a.gigas*) calves (n=4) entering October were 15% heavier than those of second estrus calves (n=7). They speculated such lower weights (166 - 188 kg first estrus vs. 134-166 kg second estrus) could result in differential winter mortalities even though daily weight gain over summer was nearly identical for both groups. Boer (1992) suggested cows with late-born calves may not breed during the

subsequent rut because of the energetic costs associated with lactation, as reported for red deer (Cervus elaphus) by Clutton-Brock *et al.* (1982).

Pregnancy Rates

A varying proportion of young cows may potentially breed as yearlings (16-18 months) and reproduce yearly until an age 18 years. Maximum female reproductive potential is considered to be realized from 4 to 12 years of age (Markgren 1969, Franzmann 1981, Saether and Haagenrud 1983, Crichton 1988), with nutrition believed to be primarily responsible for determining yearling pregnancy rates (Schwartz *et al.* 1987). The percentage of breeding yearlings varies greatly accross North America (Table 1 and review by Boer 1992).

The impact of 'precocious' breeding in the second year of life for both sexes is poorly understood. Schwartz (1992) recently reported annual calf production averaged 1.5 calves per female per year for cows that were bred as yearlings (n=4), and 1.9 calves per cow first bred as 2-year-olds (n=3). Young, inexperienced cows that are not physically mature are believed to be less able to successfully rear their offspring, (Bubenik pers. comm. 1992).

Pregnancy rates for adult cows > 2.5 years are much higher than that of yearlings: Alaska 72 to 93% (Rausch and Bratlie 1965; Ballard et al. 1991); Wyoming 90% (Houston 1968); Ontario 87% (Simkin 1965); Montana 86% (Schladweiler and Stevens 1973); Newfoundland 81% (Pimlott 1959); British Columbia 76% (Edwards and Ritcey 1958). Boer (1992) reported mean rates for 12 published North American studies were 84.2 ± 5.7% over a broad range of geographic areas, population densities, and winter severities. Populations above, near, and below K carrying capacity were estimated to produce 0.88, 1.06, and 1.24 calves / adult cow at parturition, and 0.18, 0.41, and 0.65 calves / yearling

Alces

Table 1. Yearling moose pregnancy rates in North America

Area	% Pregnant	n	Source
British Columbia	0	15	Edwards and Ritcey (1958)
Montana	0	2	Peek (1962)
Wyoming	5 to 6	35	Houston (1968)
NW Ontario	17	12	Simkin (1965)
Alberta	29	99	Blood (1974)
Montana	32	22	Schladweiler and Stevens (1973)
New Brunswick	39	13	Boer (1987)
SC Alaska	40	5	Ballard et al. (1991)
Newfoundland	46	78	Pimlott (1959)
NC Ontario	57	7	Bergerud and Snider (1988)
Manitoba	63	8	Crichton (1988)

cow, respectively.

Recent studies in Alaska by Schwartz and Hundertmark (1993) confirmed that cow moose continue to cycle and come into estrus until successfully bred. In the wild, this probably occurs in the first or second estrus in September and October.

Gestation Length

Mean gestation length for Alaskan moose was 230.6 + 4.7 days for 14 cows in four separate years (Schwartz and Hundertmark 1993). This time period was longer than that reported by Stewart *et al.* (1987) of 216-218 days for two captive Saskatchewan yearling cows (*A. a. andersoni*) bred by a yearling bull, and shorter than 240-246 days reported by Peterson (1974) for North America. Markgren (1969) reported a mean of 234, varying from 226 to 244 days, for Swedish moose (*A.a.alces*).   Both Peterson (1974) and Markgren (1969) based their findings on mean observational times of breeding and calving.

Spermatogenesis

Spermatogenesis occurs in bulls that are physiologically capable of breeding as year-lings. Houston (1968) reported finding sper-matozoa in 12 of 13 yearlings by 21 Septem-ber in Wyoming.   Schwartz *et al.* (1982) observed breeding of yearlings in the fall of 1979 at the Moose Research Center, Soldotna, Alaska. A healthy male calf was born as a result in May 1980. In the wild, however, the opportunity of yearlings to breed may be limited by the domination of available cows by older prime bulls. 'Primes' generally domi-nate the rut and are the first in and out of sexual activity (Bubenik and Timmermann 1982). Markgren (1969) observed similar behavior in Sweden.

The amount of sperm a bull can produce and store appears to be small for such a large animal (Bubenik and Timmermann 1982; Bubenik 1985). Mature or 'prime bulls' (5-10 years of age) are capable of storing the largest amount of sperm and fertilizing the greatest number of cows in the shortest time span. Copulation in Kenai Peninsula Alaska moose generally lasts only a few seconds (Schwartz and Hundertmark 1993). Five successive copulations by one bull were observed on a single day over a period of seven hrs. 49 minutes, and four copulations over a period of

Alces

seven hrs. 39 minutes. Bubenik pers. comm. 1993 suggests many observed copulations are in fact precopulatory in nature. He believes true copulations are characterized by a longer contact and with the hind feet of the bull being off the ground. The shortest time between successful copulations observed was 32 mins. Schwartz and Hundertmark (1993) also reported rut behavioural activity changes with time. In September and October, more classic displays were associated with rutting (flehmen, vocalizing in both sexes, wallowing and thrashing). Later, in December through February, the mating intensity among two vasectomized bulls diminished with considerably less vocalizing and fewer rut pits.

Twinning Rates

In North America, moose generally produce single calves, but twins are not uncommon (Franzmann 1981). The frequency of twinning in moose has been related to weather and nutrition in several studies (Hosley 1949, De Vos 1956, Edward and Ritcey 1958, Pimlott 1959, Markgren 1969, 1982; Schladweiler and Stevens 1973, Franzmann and Schwartz 1985). Schwartz et al. 1987 reported moose on a high plane of nutrition grew faster and tended to reach adult body size sooner; while Boer (1992) reported a significant relationship between yearling pregnancy rates and twinning rates in adult cows. Observed twinning rates vary between areas, years, and between occurrence of twins in utero and post calving (Pimlott 1959; Ballard et al. 1991). Published studies often show a wide range (Table 2) and readers are cautioned in comparing rates (i.e. in utero, at birth, fall/winter).

Franzmann and Schwartz (1985) reported a 70% post-calving twinning rate (n=102) in a 13-14 year old burn on the Kenai Peninsula, Alaska. Concurrently, they found a much lower rate (22%, n=49) in a 30-31 year old burn, considered to be poorer quality habitat. Ballard et al. (1991), however, reported a

twinning rate variation of 17% to 63% over 5 years in south - central Alaska with no apparent change in vegetative quality. Skuncke (1949) reported twins to be the rule in Sweden, however great differences occur between regions. Swedish hunters reported 65% twins from the coastal region, 39% from the inland region and 17% from the foothills (Markgren 1982). These relatively high fall observations of twins may reflect the lack of predation on young calves along with high productivity (Strandgaard 1982).

The age structure of a population can influence the incidence of twinning; populations with a young age structure which contains a high proportion of yearlings will generally have a lower twinning rate than a population with an older age structure (Markgren 1969). Observations of twins in the field often vary between years, and between seasons, and may be a useful indicator of calf mortality depending upon when recorded. Addison et al. (1985) reported the occurrence of cows with twins in spring and the following winter in south-central Ontario varied from a high of 78% and 25% respectively in 1982 to a low of 16% and 4.5%, respectively, in 1984. He suggested that predation was the cause of lower rates.

The density of moose may influence the incidence of twins. Gasaway et al. (1992) reported rates as high as 25-90% of all births in cows >29 months of age in populations below carrying capacity. Twinning rates in populations near K ranged from 5-25%, while those above K were <5%.

In a moose population where subadults (1.5 - 2.5 yrs) comprise + 50% of the female cohort and predation on calves born to adults (> 3.5 yrs) is heavy (+ 50%), it is possible that only one of four cows could be left with calves at heel by September (Lynch 1991).

Adult Sex Ratio and Productivity

The potential impacts of skewed sex ratios on ungulate populations have long been

Alces

Table 2. Observed twinning rates in North American moose

Time*	Area	Percent	Range	n	Source
1-2	Isle Royale Michigan	5		87	Murie (1934)
3	Wyoming	4.5			Houston (1968)
2	Isle Royale, Michigan	10	9-10	215	Peterson (1977)
2	British Columbia	12		102	Hatter (1950)
1	Alberta	13	4-48	355	Blood (1974)
2-3	Alaska	13		1217	Spencer and Chatelain (1953)
1	Newfoundland	14		182	Pimlott (1959)
1	Montana	16		73	Schladweiler and Stevens (1973)
1-3	New Brunswick	17		385	Wright (1956)
1	Manitoba	21		47	Crichton (1988)
1	Kenai Penn., Alaska	22		49	Franzmann and Schwartz (1985)
1	British Columbia	25		61	Edwards and Ritcey (1958)
1	NW Ontario	25.3	8-50	76	Simkin (1965)
1	SE New Brunswick	26		31	Boer (1987)
1-3	Quebec	28		274	Moisan (1952)
1	SW Yukon	28		58	Larsen et al.(1989)
1	Interior Alaska	32		35	Gasway et al. (1983)
1	S Central Alaska	38	17-63	238	Ballard et al. (1991)
3	Rochester, Alberta	41	17-59	283	Rolley and Keith (1980)
1	Alaska-Yukon	52		27	Gasaway et al. (1992)
1	N Central Ontario	54		37	Bergerud et al. (1983)
1	Kenai Penn., Alaska	70		102	Franzmann and Schwartz (1985)
2	Alaska Penn., Alaska	80	0-19	15	Faro and Franzmann (1978)
1	Rochester, Alberta	88		8	Mytton and Keith (1981)

* 1. In utero and or at parturition　2. Fall　3. Winter

debated (Peterson 1977; Bailey 1978). Ballard *et al.* (1991) identified five issues: (1) concern over insufficient females being bred due to low bull densities (Peterson 1955); (2) an extended parturition period leading to late born, less viable calves (Bubenik and Timmermann 1982); (3) conception extending over two or three estrus cycles, producing calves of various sizes (Bishop and Rausch 1974); (4) sociological implications (Bubenik 1972); and (5) potential physical deterioration caused by continual breeding by younger,

small-bodied, genetically inferior bulls (Harmel 1982).

Valid population sex ratio data are difficult and costly to obtain (Simkin 1974), as well as being variable in both accuracy and precision (Crête 1987). Published studies of naturally fluctuating moose populations have reported adult (> 1.5 yr.) sex ratios near parity (De Vos 1956, Knorre 1959, Kelsall 1963, Peek 1971, Peterson 1977). Ratios reported for most studies however, have been influenced by varying degrees of human harvest

Alces

exploitation, predation, and a corresponding higher mortality among males because of human social biases against killing females.

Sylven *et al.* (1979) simulated various hunted moose herds in Sweden and reported the winter sex ratio to be the variable having the greatest impact on future population size. Bannikov (1970) found the highest calf production in the USSR in a population density range of 0.3 - 0.4 moose/km². He reported a reduction in calf production when the adult sex ratio fell below 50 bulls per 100 cows (50/ 100). Nygren (1984) concurred with Bannikov, and indicated that maximum calf production in Finland was reached with an overall density between 0.3 and 0.6 moose/ km², an adult sex ratio no lower than 70/100, and a population with a mean age between 4.5 - 7.5 years.

Crête *et al.* (1981) compared adjacent moose populations in Quebec, one lightly hunted and the other heavily hunted. Simulation runs suggested unbalanced sex ratios diminished productivity. To optimize moose harvests they recommended retaining an adult sex ratio of at least 67/100, harvesting more calves and retaining a density of about 0.2 moose/km². Cumming (1974) reported a change in sex ratio of the harvest to predomanantley females during a period of unrestricted, either sex hunting which resulted in a severe depletion of a local herd in Ontario. Van Ballenberghe (1983) reviewed the literature and indicated changes in age distribution and the sex ratio can strongly affect the rate of increase (r). Highest r values can be expected when most adults are in the 'prime' age classes where fecundity and survival are both maximal. The most productive cohorts span ages of 5 to 10 years in both sexes (Peterson 1977, Saether and Haagenrud 1983). Van Ballenberghe (1983) used simulated sex ratios of 100/100 vs. 15/100, an adult survival rate of 1.0, and fall calf:cow ratios of 0.6. These parameters produced a finite rate of increase of 1.3 and 1.53, respectively. Clearly

the higher value (1.53) is potentially possible in moose populations with an excess of females and a harem breeding strategy.

Several authors have published studies detailing unbalanced adult moose sex ratios. Mytton and Keith (1981) reported an increasing moose population on 228 km² of unhunted non-agricultural land near Rochester, Alberta. Predation was minimal. They found an adult bull/cow sex ratio of 33/100 with a mean winter density of 0.64 moose/km² in 1975-76. Hauge and Keith (1981) estimated an adult bull/cow ratio of 43/100 on 25,000 km² in north-eastern Alberta. They believed the population (0.18/km²) was either stationary or declining, with hunting and predation identified as the main causes of mortality. Lynch and Morgantini (1984) reported sex ratios in North Central Alberta between 37/100 and 53/100, and densities 0.7 - 1.6 moose/km² over eight years. Post-calving calf/cow ratios averaged 31/100 during the study. Crichton (1988) documented a declining moose population in Manitoba during the 1980's. In this area, harvest strategies had traditionally focused on fall 'bulls only' hunting seasons, followed by December limited-entry 'any moose' seasons. Adult bull/cow ratios in one Game Hunting Unit declined from 98/100 to 44/100 over a three-year period, and the late 'any moose' season was terminated to increase ratios to a minimum of 50/100 (Crichton pers. comm. 1991). Babcock *et al.* (1982) reported changes in herd recruitment for Utah moose when the adult sex ratio was manipulated by sex-discriminant harvests. They observed a mean of 45/ 100 and 74 calves/100cows in winter counts over eight years. The mean recruitment fell to 46 calves/100 cows with a mean adult sex ratio of 28/100 but increased when bull/cow ratios returned to pretreatment levels.

In 1983, Ontario initiated a selective harvest system designed to control the harvest of specific age or sex classes and increase herd productivity (Timmermann 1987). Early winter mean adult sex ratios in north central

Ontario since 1983 have varied from a mean of 48 to 76 bulls/100 cows, and densities of 0.12 to 0.46 moose/km² among five hunted Wildlife Management Units over 17 surveys (Timmermann and Whitlaw 1992, Table 3). Early winter ratios and densities in two unhunted recently-logged control areas are higher 73 to 83 bulls/100 cows and 0.82 to 2.42 moose/km². Managers are targeting 67/100 as a minimum adult bull/cow post hunt ratio in an attempt to increase the provincial population from ± 80,000 in 1983 to 160,000 by the year 2000.

Adult bull/cow ratios in Alaska are low because harvest strategies focus heavily on bulls. Cows and calves are generally protected. Bishop and Rausch (1974) reported bull/cow ratios as low as 4-9/100 in the Matawaska Valley, Alaska, during the 1960's, yet pregnancy rates remained nearly 90%. There were, however, indications that conception rates were variable, and that consider-

able size differences occurred in both unborn fetuses (Lent 1974), and in autumn calves (Ballard et al. 1991). Smaller calves, presumably, died at higher rates over winter. Ballard et al. (1991) reported annual hunter cow harvests (1963-71), contributed to a population decline of moose in Alaska's game management unit 13. From 1976 through 1986, moose populations increased and human harvests were no longer considered a limiting factor. During this period, densities ranged from 0.6 - 0.8 moose/km² with 12 - 24 bulls/100 cows. Resultant pregnancy rates were 80 - 90% with high twinning rates, tight parturition dates, and few late births. More recently, post-rut sex ratios near Homer, Alaska, approximate 4 - 5 bulls/100 cows, yet most cows successfully breed according to Schwartz (pers. comm. 1991). This is accomplished by an altitudinal migration of cows to higher scrub spruce meadow habitats during the rut. Here, as a result of the harem formation fall

Table 3. Observed adult sex ratios and calf-cow ratios as determined from rotary wing aerial surveys conducted post-hunt during Dec-Jan in North Central Ontario.

Area/WMU	Mean Bulls/ 100 Cows	Range	Nt	# of years	Year Most recent survey	Density Moose/km	Calves/100 cows*	% Calves (Ny)
Camp 236^	83	54-126	843	7	91/92	0.82	33	17.8(107)
McKenzie-Cache Lake^	73	43-101	1338	13	87/88	2.42	38	16.6 (145)
WMU 12B	66	57-79	1345	4	91/92	0.46	37	17.1 (420)
WMU 13	48	37-63	1214	4	91/92	0.36	37	21.0 (398)
WMU 15B	69	62-76	827	3	90/91	0.36	23	12.6 (425)
WMU 19	76	64-92	558	3	89/90	0.13	39	18.7 (212)
WMU 21B	58	49-68	648	3	90/91	0.17	41	20.5 (217)

* Ratio includes all cows ¯ 1.5 yrs.

^ Unhunted logged control area.

Nt - total number of observations where sex/age were ascertained.

Ny - number of observations for most recent survey.

Alces

sex ratios are generally 20 to 30 bulls/100 cows.

Calf Sex Ratio

Normally there is a slight perponderance of males in the secondary sex ratio (Markgren 1974, Ballard *et al*. 1991). Sex ratios in hunted populations, however, generally favours females due to heavier exploitation of bulls. Reuterwall (1981) found the sex ratio of male/female calves in the Swedish hunter harvest varied from 223/100 to 104/100. Haagenrud and Lordahl (1979) reported 58% males in the Norwegan calf harvest, 1971-74 (n=3735). They concluded that variations in the calf sex ratio contributes to the self-regulation of a population, and speculated that more female births would result in a more rapidly expanding population. Ballard *et al.* (1991) reported similar sex ratios in Alaska (104 male:100 female, n=155, x^2=0.8, P=0.85), except for one year when males predominated (233 males:100 females).

Moose population models are very sensitive to fetal or calf sex ratios. Van Ballenberghe (1983) simulated two populations each with identical fecundity (1.0 female calves per 2+ year old adult female), with a first year survival of 0.8, and an adult survival of 1.0. The population with a 100/100 calf sex ratio yielded a finite rate of increase of 1.58 vs. 1.43 in a population having a skewed 184/100 male/female calf sex ratio at birth. After ten years, starting with two adults in each population, 358 moose resulted from the former and 124 from the latter.

Crête (1982) reported a decline from 115/100 to 88/100 in the proportion of male calves harvested as Québec hunting seasons were advanced into the peak of the rut. Franzmann vide Verme and Ozoga (1981) found 66% of newborn calves were male in areas of Alaska where bulls were heavily hunted and he speculated this skewed sex ratio resulted from cows being bred late in estrus due to a scarcity of bulls. Crête (1982) on the other hand believed

heavy hunting mortality at rut peak could have limited most breeding to early in the rut, resulting in more female calves. Sex ratios of harvested calves however may not accurately reflect the true secondary sex ratio.

Eason (1986) suggested that although causes of sex variation in the calf cohort are poorly understood, the advantages are clear. At low densities, more female offspring maximize reproductive success as resources are often more abundant and cows are less likely to emigrate. Conversely, at higher densities and scarcer resources, the production of male calves is favoured as they are more likely to emigrate to areas with better conditions. Eason (1986) further speculated that a high proportion of male calves may indicate a high density population or one with heavy selective pressure on bulls. Conversely, a high female calf ratio may suggest a heavily hunted, low density population.

MANAGEMENT IMPLICATIONS

Policy and Objectives

Moose management strategies should be developed from a clearly defined set of policies and objectives. For example, if the objective is to manage for non-consumptive use, a trophy hunt or a 'calling rut' hunt, regulations must ensure low harvest rates of cows and light harvests of bulls ⁻2 yrs. This will ensure a longer life expectancy for bulls to reach maturity and cows to attain maximum productivity. Managing for quantity (Maximum Sustained Yield) however, requires maximum productivity, and higher harvest rates of both sexes including calves. In turn, this lowers the mean age of the population. Selective hunting strategies can be effective in managing moose to realize their socio-biological potential and allow maximum meat and trophy production. Harvests can be adjusted by: modifying season length and timing, weapon type, limiting the number of licences issued, or requiring hunters to be selective by establishing specific target sex and age classes. If, on the other

Alces

hand, the objective is to maximize recreational hunting opportunities, then managers could consider: liberal pre- and post-rut seasons, reducing hunter efficiency, requiring several hunters to share one moose, and targeting for a lower density population, thereby decreasing success rates.

Population Density

Moose densities in North America are generally low (0.1 - 0.5/km^2) in systems where wolves (*Canis lupus*) or bears (*Ursus* spp.) are unexploited (Bergerud 1992). Mean densities of 19 moose populations in Alaska and Yukon where both predators were lightly exploited was 0.15 ± 0.02 vs. 0.62 ± 0.94/km^2 for 15 populations where bears and wolves were heavily harvested (Gasaway *et al.* 1992). In systems where moose are the primary prey of wolves, Bergerud and Snider (1988) reported moose densities of 0.25 ± 0.38/km^2 for 11 hunted populations, and Crête (1987) reported 0.37 ± 0.25/km^2 for four unhunted populations. In multi-ungulate systems, where deer (*Odocoileus spp.*) or elk (*Cervus canadensis*) are more vulnerable, moose densities commonly reach 0.6 - 1.3/km^2 (Carbyn 1983; Crête 1987; Bergerud and Snider 1988). In contrast, Cederlund and Sand (1991) reported hunted densities in south central Sweden with no predators approximate 1.5 moose/km^2 or close to the 2.0/km^2 density considered by Crête (1987) to be the North American food carrying capacity (K) in a predator-free environment.

Recently disturbed, high quality habitats have the potential to produce higher moose densities when predation pressure, among other mortality factors, is low. In most jurisdictions, substantial numbers of moose are removed annually in such areas by hunting, thereby depressing densities (Eason 1985). Repopulation may be a slow process according to Gasaway *et al.* (1980) and is initiated primarily by offspring of the area's survivors. No dispersal was reported by Gasaway *et al.*

(1980) at densities of 0.20 moose/km^2, whereas, Ballard *et al.* (1991) documented a dispersal rate of 60% (9 of 15) in an adjacent study area at a density of 0.60 moose/km^2. Management strategies in these areas should focus on retaining a minimum density of 0.2 to 0.3 moose/km^2 to sustain or increase future populations and align harvest levels with existing densities. Consideration could be given to managing low and high density populations separately (Gasaway *et al.* 1980; Cederlund *et al.* 1987). This may require a refinement of management areas depending on overall objectives.

Hunting Season Timing

Season opening dates can influence the magnitude and age structure of the harvest. Where selective hunting is not imposed and the season begins in mid September at or during the rut, the harvest can be taken very quickly (Ritcey 1974). Prime aged bulls are the most mobile and, therefore, the most vulnerable (Bubinek and Timmermann 1982, Timmermann and Gollat 1982). A rut dominated by sufficient prime bulls should be short (2-3 weeks), since a high proportion of cows are bred in their first heat. Consequently, the majority (+ 85%) of calves will be born the latter part of May, ensuring a maximum pre-winter development period. Early winter aggregates of bulls and cows can also lead to excessive harvests from hunters using modern all terrain vehicles (Ward and Larsen, pers. comm. 1992). Managers should develop harvest strategies which control the harvest of prime breeding males and females during these vulnerable periods. Sex differential seasons for example can be effective in spreading the hunt over a longer period of time and reducing the danger of overharvesting (Ritcey 1974).

Adult Sex Ratio

North American harvest strategies often concentrate on removal of males (Baker 1975).

Alces

Where trophy hunting is practiced the pressure may be further concentrated on prime bulls (Cowan 1974). Taiga or woodland moose often carry out a wide searching effort, a ritual courtship, and pair association, prior to breeding. The sex ratio required to assume full reproductive participation of females depends on population density and breeding effectiveness of bulls (a function of age). Swedish studies reported by Markgren (1974) suggest low bull/cow sex ratios can only be tolerated at high densities. North American moose, however, which use advertising calls to extend their contact orbit, may be more effective in mate search than Scandinavian moose which do not vocalize (Cowan 1974). The minimum bull/cow ratios that will ensure the breeding of all receptive females is not known. Values from published modelling studies suggest ratios for taiga moose with densities of > 0.30 moose/km² should not fall below 50/100 (Crête *et al.* 1981, Nygren 1984) Where densities are below 0.30/km², adult sex ratios should be closer to parity. Schwartz (pers. comm. 1991) recommends 20 - 30 bulls per 100 cows for tundra moose. Ward and Larsen pers. comm. (1992) believe a ratio of 30 bulls/100 cows is sufficient to ensure that all cows are bred in the Yukon. At present, these values are a "best guess," as nowhere in North America, to my knowledge, have low pregnancy rates as a result of unbalanced sex ratios, been reported. In addition, no studies have yet demonstrated that a reduced proportion of bulls causes a change in pregnancy rates. Younger bulls are physiologically capable of breeding receptive cows during their first estrus in the absence of dominant older bulls (Schwartz *et al.* 1982). Concern, however, has been expressed that low bull/cow ratios could influence conception dates and neonate sex ratios (Bishop and Rausch 1974; Crête *et al.* 1981).

Prime bulls may function as social inducers to help initiate and stimulate ritual courtship and ovulation (Schwartz pers. comm.

1991). Miquelle (1991) suggested scent urination by mature bulls may attract cows and induce ovulation. He observed subadult bulls (*A. a. gigas*) do not scent urinate, yet attempt to acquire some of its benefits by obtaining attractive odours from mature bulls. Knowles (1984) also reported subadult teen bulls wallowing in prime bull rut pits. Crichton (pers. comm 1992), however, in the fall of 1982, observed a young bull, estimated at 2.5 yrs., accompanied by a cow on the Bloodvein River, Manitoba. The bull dug, urinated, and wallowed in a rut pit, followed by the cow wallowing in the same pit. Schwartz *et al.*(1990) speculated that sex pheromones may play a role to synchronize the rut, and possibly assist in inducing estrus.

Intuitively, a balanced social structure should include a sufficient proportion of prime bulls whether it be for breeding purposes, retention of genetic diversity, maintaning social order, or for viewing enjoyment as mature type specimens. Close scutiny of the age structure of the harvested component is nessesary to ensure adequate numbers of animals are maintained in the prime breeding age. Herds should be socially balanced to attain maximum in utero productivity. When the mean age of harvested bulls is consistently <4 years concern is warranted (Crichton 1992). Additional studies appear justified in determining the role of this social class in the overall social structure of a population.

Harvest Rates

Gross productivity is defined by Simkin (1974) as the percentage of the population that could be removed annually on a sustained yield basis if all of the young that were conceived were successfully borne, and survived to the hunting season. Estimates for North America range from 24 to 25% (Simkin 1974). For example, if the pre-parturition herd numbered 100 moose and 33 calves were dropped, then the gross productivity would be 33/133 x 100, or 24.8%. The rate of increase in this

Alces

example is 33%.

Predation appears to be the major limiting factor for moose (Gasaway *et al.* 1983, Bergerud and Snider 1988, Ballard *et al.* 1991). Bergerud (1992) has argued that there is a stabilizing recruitment for each population that balances the natural mortality of adults. For moose, he suggests the stabilizing recruitment at 6-9 months is 25 calves/100 cows. If hunting elevates the annual mortality of adults, and more than 25 calves/100 females is needed to stabilize recruitment, then moose will need to space themselves more widely to stabilize predation. Consequent moose mortalities will be lower. Higher harvest rates up to 25% are only possible when natural mortality is almost absent, as the maximum observed finite rate of increase is 1.30 (range 1.15 - 1.30) for North American moose (Keith 1983, Van Ballenberghe 1983). Cederlund and Sand (1991) reported a rate of increase of nearly 1.5 for a Swedish moose population with a winter density of 1.3 moose/km², no predation losses and an annual hunter yield approaching 50%. They speculated that further selective harvesting of low productive females (i.e. those without calves) in conjunction with higher pressure on bulls and calves could boost yields to 60%.

Respecting wolves, moose/wolf ratios of 75-100 moose/wolf should result in increasing moose populations, ±50/wolf in stability, while 25 per wolf will result in declining moose populations (Bergerud pers. comm. 1992, Gasaway *et al.* 1983) assuming no alternate prey base. Managers thus must consider predator management as an intergal component of any moose management plan.

A knowledge of productivity, adult sex ratio, and estimates of annual losses are required to determine if a harvestable surplus exists. North American harvest rates show large variations between jurisdictions ranging from 2% to 16% of the estimated prehunt population (Crête 1987). If population growth is the objective, harvest rates should be sex

and age specific, and generally fall under 10%. Strategies could include: the protection of prime breeding animals (especially cow moose so that calf production is enhanced), directing hunting pressure to animals in the herd with the lowest reproductive potential (i e. young bulls and calves), and reducing non-hunting losses. To be successful, any selective harvest strategy will require hunter education (Timmermann 1992).

ACKNOWLEDGEMENTS

REFERENCES

ADDISON, R. B., J. C. WILLIAMSON, B. P. SAUNDERS, and D. FRASER. 1980. Radio-tracking of moose in the boreal forest of northwestern Ontario. Can. Field Nat. 94:269-276.

ADDISON, E. M., M. L. WILTON, R. F. McLAUGHLIN, and M. E. BUSS. 1985. Trends in natality and calf mortality of moose in south central Ontario. Alces 21:1-16.

ALTMANN, M. 1956. Patterns of social behaviour in big game. Trans. N. Amer. Wildl. Conf. 21:538-45.

————. 1960. The role of juvenile elk and moose in social dynamics of their species.

Alces

Zoologica 45(1):35-39.

BABCOCK,W.H., J.F. KIMBALL, J.A.RENSEL and M.L. WOLF. 1982. Management alternatives for Utah moose. Alces 18:235-257.

BAILEY, T. N. 1978. Moose populations on the Kenai National Moose Range. Proc. N. Am. Moose Conf. Workshop 14:1-20.

————, and A.W. FRANZMANN. 1983. Mortality of resident vs introduced moose in confined populations. J. Wildl. Manage. 47:520-523.

BAKER, R. A. 1975. Biological implications of a bulls-only moose hunting regulation for Ontario. Proc. N. Am. Moose Conf. Workshop. 11:464-475.

BALLARD, W. B., J. S. WHITMAN, and D. J. REED. 1991. Population dynamics of moose in south - central Alaska. Wildl. Monogr. 114 : 1-49.

BANNIKOV, A. G. 1970. Moose in the USSR and its exploitation. Finnish Game Research 30:273-276.

BERGERUD, A. T. 1992. Rareness as an antipreditory strategy to reduce predation risk for moose and caribou. Pages 1008-1021 in D. Mc Cullough and R. H. Barrett, eds. Wildlife 2001; Populations. Elsevier applied Science.

————. 1989. Rareness as an antipredator strategy to reduce predation risk. Trans.19th IUGB Congress, Trondhiem. 1:15-25.

————, and J. B. SNIDER. 1988. Predation in the dynamics of moose populations: a reply. J.Wildl. Manage. 52:559-564.

————, W. WYETT, and J. B. SNIDER. 1983. The role of wolf predation in limiting a moose population. J. Wildl. Manage. 47:977-988.

BISHOP, R. H., and R. A. RAUSCH. 1974. Moose population fluctuations in Alaska, 1950 - 1972 Naturaliste can. 101:559-593.

BLOOD, D.A. 1974. Variation in reproduction and productivity of an enclosed herd of moose (Alces alces). Trans. Int. Congr. Game Biol. 11:59-66.

BOER, A. H. 1987. Reproductive productivity of moose in New Brunswick. Alces 23:49-60.

————. 1992. Fecundity of North American moose (Alces alces): A review. Alces Suppl.1:1-10.

BOWYER, R. T., J. L. RACHLOW, V. VAN BALLENBERGHE, and R. D. GUTHRIE. 1991. Evolution of a rump patch in Alaskan moose: an hypothesis. Alces 27:12-23.

BUBENIK, A. B. 1972. North American moose management in light of European experiences. Proc. N. Am. Moose Conf. Workshop 8:276-295.

————. 1971. Social well-being as a special aspect of animal sociology. Int. Conf. on the Behav. of Ungulates and its Relation to Management, Calgary, Alta. Mimeo - 25pp.

————. 1984. Behavioural significance of the moose bell. Alces 19:238-245.

————. 1985. Reproductive strategies in Cervides: Pages 367-373 in P. F. Fennesy and K. R. Drew,eds. Biology of deer production. Royal Soc. New Zealand Bull. 22.

————. 1987. Behaviour of moose (Alces alces) of North America. Swedish Wildl. Res. Suppl. 1:333-366.

————, and H. R. TIMMERMANN. 1982. Spermatogenesis in the taiga moose of north central Ontario - a pilot study. Alces 18:54-93.

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

CARBYN, L., 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. J. Wildl. Manage. 47: 963-976.

CAUGHLEY, G. 1976. Wildlife manage-

Alces

ment and the dynamics of ungulate populations. Pages 183-246 *in* T.H. Coaker ed. Applied biology. Academic Press, London.

CEDERLUND, G., and H. K. G. SAND. 1991. Population dynamics and yield of a moose population without predators. Alces 27:31-40.

———, F. SANDEGREN, and K. LARSSON. 1987. Summer movements of female moose and dispersal of their offspring. J. Wildl. Manage. 51:342-352.

CLUTTON - BROCK, T. H., F. E. GUINNES, and S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Chicago, Ill. 387 pp.

COADY, J. W. 1982. Moose. Pages 902-922 *in* J. A. Chapman and G. A. Feldhamer, eds. Wild Mammals of North America. The Johns Hopkins Univ. Press, Baltimore.

COURTOIS, R., and M. CRÊTE. 1988. Déplacements quotidiens et domaines vitaux des orignales du sud - ouest du Québec. Alces 24:78-89.

COWAN, I. M. 1974. Management implications of behaviour in the large herbivorous mammals. Pages 921-934 *in* V. Geist and F. Walters, eds. The behaviour of ungulates and its relation to management, Vol. 1. IUCN New Ser. Publ. 24, Morges, Switzerland.

———, W. S. HOAR, and J. HATTER. 1950. The effects of forest succession upon the quality and upon the nutritive values of woody plants used by moose. Can. J. Zool. 28:249-271.

CRÊTE, M. 1982. Évaluation des modifications apportées à la réglementation de la chasse à l'orignal au Québec de 1971 à 1981 et perspective d'avenir. Alces 18:329-356.

———. 1987. The impact of sport hunting on North American moose. Swedish Wildl. Res. Suppl. 1:553-563.

———. 1988. Forestry practices in Québec and Ontario in relation to moose population dynamics. For. Chron. Pp. 246-250.

———, R. J. TAYLOR, and P. A. JORDAN. 1981. Optimization of moose harvests in southwestern Québec. J. Wildl. Manage. 45:598-611.

CRICHTON, V. 1988. In utero productivity of moose in Manitoba. Alces 24:143-149.

———. 1992. Six year (1986/87 - 1991/92) summary of in utero productivity of moose in Manitoba, Canada. Alces 28:201-211.

CUMMING, H. G. 1974. Annual yield, sex and age of moose in Ontario as indices to the effects of hunting. Nauraliste can. 101:539-558.

DE VOS, A. 1956. Summer studies of moose in Ontario. Trans. N. Am. Wildl. Conf. 21:510- 525.

———, P. BROKX, and V. GEIST. 1967. A review of social behaviour of the North American cervids during the reproductive period. Am. Midl. Nat. 77(2): 390-417.

DENNISTON, R. H. 1956. Ecology, behaviour and population dynamics of the Wyoming or Rocky Mountain moose. Zoologica 41:105-18.

DODDS, D. G. 1958. Observations of pre-rutting behaviour in Newfoundland moose. J. Mamm. 39:412-416.

EASON, G. 1985. Overharvest and recovery of moose in a recently logged area. Alces 21:55-75.

———. 1986. Aerial sexing of moose calves and implications. Alces 22:181-200.

EDWARDS, J. 1983. Diet shifts in moose due to predation avoidance. Oecologia 60:185-189.

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

FARO, J. B., and A. W. FRANZMANN. 1978. Productivity and physiology of moose on the Alaska Peninsula. Alaska

Alces

Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep. Proj.W-17-9 and W-17-10. 29pp.

FRANZMANN, A. W. 1981. *Alces alces*. Pages 1-7 *in* Mammalian Species No. 154. The American Society of Mammalogists.

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

FRYXELL, J. M., W. E. MERCER, and R. B. GELLATELY. 1988. Population dynamics of Newfoundland moose using cohort analysis. J. Wildl. Manage. 52:14-21.

GARTON, E. O., M. D. SAMUEL, and J. M. PEEK. 1985. Analysis of home ranges. Alces 21:77-89.

GASAWAY,W.C., S. D. DUBOIS, and K.L. BRINK. 1980. Dispersal of subadult moose from a low density population in interior Alaska . Proc. N. Am. Moose Conf. Workshop 16:314-329.

———, R. O. STEPHENSON, J. L. DAVIS, P.E.K. SHEPHERD, and O.E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84.50pp.

———, and S.D. DUBOIS. 1985. Initial response of moose (*Alces alces*) to a wildfire in interior Alaska. Can. Field Nat. 99:135-140.

———, ———, R.D. BOERTJE, R.J. REED, and D. T. SIMPSON. 1989. Response of radio-collared moose to a large burn in central Alaska. Can. J. Zool. 67:325-329.

———, 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.

GEIST, V. 1963. On the behaviour of the North American moose (*Alces alces andersoni* ,Peterson 1950) in British Columbia. Behaviour, 20:377-416.

———. 1974. On the evolution of reproductive potential in moose. Naturaliste can. 101:527-537.

GODDARD, J. 1970. Movements of moose in a heavily hunted area of Ontario. J. Wildl. Manage. 34:439-445.

HAAGENRUD, H., and L. LORDAHL. 1979. Sex differential in populations of Norwegian moose *Alces alces* (L). Medd. Norw. Viltiforsk 3 (6):1-19.

HARMEL, D. E. 1982. Effects of genetics on antler quality and body size in white-tailed deer (*O. virginianus*). Pages 339-348 *in* R. D. Brown, ed. Antler development in Cervidae. Caesar Kleberg Wildl. Res. Inst., Texas A & I Univ., Kingsville.

HATTER, J. 1950. The moose of central British Columbia. Ph.D. dissert., Wash. State Univ., Pullman, 359pp.

HAUGE, T. M., and L. B. KEITH. 1981. Dynamics of moose populations in northeastern Alberta. J. Wildl. Manage. 45:573-597.

HOSLEY, N. W. 1949. The moose and its ecology. U. S.Dept. Int., Fish and Wildl. Serv., Wildl. Leafl. 312:1-51. Wash., D.C.

HOUSTON, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming.Tech.Bull. Grand Teton Nat. Hist. Assoc. 1:1-110.

———. 1974. Aspects of the social organization of moose. Pages 690-696 *in* V. Geist and F. Walther, eds. The behaviour of ungulates and its relation to management.IUCN Publ.NS 24 (2): 690-696.

KEITH, L. B. 1983. Population dynamics of wolves. Pages 66-77 in L.N. Carbyn, ed. Wolves *in* Canada and Alaska:their status,biology,and management. Can. Wildl. Serv. Rep. Ser. 45, Ottawa.

KELSALL, J. P. 1963. The moose, *Alces alces americana* (Clinton), of Fundy National Park, New Brunswick. N.E. Fish

Alces

and Wildl. Conf., Portland, ME. 15pp.

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.Sc. Thesis, Univ. of Alaska, Fairbanks. 93pp.

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 Dept. of Renewable. Resour. Rep., Whitehorse. 105pp.

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

LYNCH, G. M. 1976. Some long-range movements of radio-tagged moose in Alberta. Proc. N. Am. Moose Conf. Workshop 12:220-235.

_____. 1991. That's no bull. Rolfe's Annual Alberta Hunting Guide, Edmonton, Alta. P. 43.

_____, and L. E. MORGANTINI. 1984. Sex and age differential in seasonal home range size of moose in north central Alberta, 1971-1979. Alces 20:61-78.

MARKGREN, G. 1969. Reproduction of moose in Sweden. Viltrevy 6 (3): 1-299.

_____. 1972. At'erfynd av markta algar. Sven. Jakt. 110:274-277.

_____. 1974. The question of polygamy at an unbalanced sex ratio in the moose. Pages 756-758 *in* V.Geist and F. Walther, eds. The behavior of ungulates and its relation to management, IUCN Publ. NS 24 (2):756-758.

_____. 1982. Moose populations along a climate gradient across Sweden. Nat. Swedish. Environ. Protection Board Rep. 1571, Stockholm. 52pp.

MIQUELLE, D. G. 1990. Behavioral ecology of moose in Denali National Park and Preserve, Alaska. Thesis., Univ. Idaho,

Moscow. 152pp.

_____. 1991. Are moose mice? The function of scent urination in moose. Am. Nat. 138(2):460-477.

_____, J. M. PEEK, and V. VAN BALLENBERGHE. 1992. Sexual segregation in Alaskan moose. Wildl. Monogr. 122:1-57.

MOISAN, G. 1952. Investigations on moose population. Pages 25-43 *in* General report of the Ministers of Game and Fisheries for the fiscal years 1950-51 and 1951-52. Quebec Dept. of Fish and Game 151pp.

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

MURIE, A. 1934. The Moose of Isle Royale. Univ. Michigan Mus. Zool., Misc. Publ. No.25. Univ. Michigan Press, Ann Arbor. 44pp.

MYTTON, W. R., and L. B. KEITH. 1981. Dynamics of moose populations near Rochester, Alberta, 1975-78. Can. Field Nat. 95:39-49.

NYGREN, T. 1984. The relationship between reproduction rate and age structure, sex ratio and density in the Finnish moose population. Trans XVI Int. Congr. Game. Biol., Strbske Pleso. 1983.

PEEK, J. M. 1962. Studies of moose in the Gravelly and Snowcrest Mountains, Montana. J. Wildl. Manage. 26: 360-365.

_____. 1971. Moose habitat selection and relationships to forest management in northeastern Minnesota. Ph.D. Thesis, Univ. of Minn. 250pp.

_____, R. E. Le RESCHE, and D. R. STEVENS. 1974. Dynamics of moose aggregations in Alaska, Minnesota and Montana. J. Mamm. 55:126-137.

_____, V. VAN BALLENBERGHE, and D. G. MIQUELLE. 1986. Intensity of interactions between rutting bull moose in central Alaska. J. Mammal. 67:422-426.

Alces

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

————. 1974. A review of the general life history of moose. Naturaliste can. 101:9-21.

PETERSON, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Nat. Park Serv. Scien. Monogr. Ser. No. 11. U.S. Gov. Printing office, Wash, D.C. 210pp.

PHILLIPS, R. L., W. E. BERG, and D. B. SNIFF. 1973. Moose movement patterns and range use in northwestern Minnesota. J. Wildl. Manage. 37:266-278.

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

RAUSCH, R. A. 1959. Some aspects of population dynamics of the railbelt moose populations, Alaska. M. Sc. Thesis , Univ. of Alaska, Fairbanks. 81pp.

————, and A. BRATLIE. 1965. Annual assessments of moose calf production and mortality in south central Alaska. Proc. Western Assoc. State Fish and Game Comm. Ann. Meet., 45:140-146.

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

RITCEY, R. W. 1974. Moose harvesting programs in Canada. Naturaliste can. 101: 631-642.

ROLLEY, R. E., and L. B. KEITH. 1980. Moose population dynamics and winter habitat use at Rochester, Alberta, 1965-77. Can. Field Nat. 94:9-18.

ROUSSEL, Y. E., E. AUDY, and F. POTVIN. 1975. Preliminary study of seasonal moose movements in Laurentides provincial park, Québec. Can. Field Nat. 89:47-52.

ROUNDS, R. R. 1978. Grouping characteristics of moose (Alces alces) in Riding Mountain National Park, Manitoba. Can. Field Nat. 92:223-227.

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.

SAUNDERS, B. P., and J. C. WILLIAMSON. 1972. Moose movements from ear-tag returns. Proc. N. Am. Moose Conf. Workshop 8:177-184.

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

SCHWARTZ, C. C. 1992. Techniques of moose husbandry in North America. Alces Suppl. 1: 177-192.

————, and H. J. HUNDERTMARK. 1993. Moose reproduction. J. Wildl. Manage. (in press).

————, A. B. BUBENIK, and R. CLAUS. 1990. Are sex-phermones involved in moose breeding behaviour? Alces 26:104-107.

————, W. L. REGELIN, and A.W. FRANZMANN. 1987. Seasonal weight dynamics of moose. Swedish Wildl. Res. Suppl. 1:301-310.

————,————, ————. 1982. Male moose successfully breed as yearlings. J. Mamm. 63 (2):334-335.

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.

SKUNCKE, F. 1949. Algen, studier jaktock rard. P.A. Norstedt and Sons, Stockholm, Sweden. 400pp.

SPENCER, D. L., and E. F. CHATELAIN. 1953. Progress in the management of the moose in south central Alaska. Trans. N. Amer. 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.

Alces

Can. Field Nat. 101:103-104.

STRANDGAARD, S. 1982. Factors affecting the moose population in Sweden during the 20th century, with special attention to silviculture. Swedish Univ. Agric. Sci., Dep. Wildl. Ecol. Rep.8, Uppsala, Sweden. 31pp.

STRINGHAM, S. F. 1974. Mother-infant relations in moose. Naturaliste can. 101:325-369.

SYLVEN, S., M. ASPERS, J. A. ERIKSSON and M. WILHELMSON. 1979. Regulated harvesting of the moose population - a simulation study. Swedish Univ. Agric. Sci. Dept. Annual Breeding and Genetics Rep. 33. 51pp.

TELFER, E. S. 1984. Circumpolar distribution and habitat requirements of moose (Alces alces). Pages 145-182 *in* R. Olson, R. Hastings, and F. Geddes, eds. Northern Ecology and Resource Management. Univ. Alta. Press. 438pp.

TIMMERMANN, H. R. 1987. Moose harvest strategies in North America. Swedish Wildl. Res. Suppl. 1:565-579.

_____. 1992. Moose hunter education in North America - a review. Alces Suppl. 1:65-76.

_____, and R. GOLLAT. 1982. Age and sex structure of harvested moose related to season manipulation and access. Alces 18:301-328.

_____, and J. G. McNICOL. 1988. Moose habitat needs. For. Chron. June 1988. Pp. 238-245.

_____, and H. WHITLAW. 1992. Selective harvest in North Central Ontario - a progress report, 1983-90. Alces 28: 137-163.

Van BALLENBERGHE, V. 1977. Migratory behaviour of moose in southcentral Alaska. Proc. Int. Congr. Game Biol. 14:103-109.

_____. 1983. Rate of increase in moose populations. Alces 19:98-117.

_____, and J. M. PEEK. 1971. Radio telemetry studies of moose in northeastern Minnesota. J. Wildl. Manage. 35:63-71.

VERME, L., and J. OZOGA. 1981. Sex ratio of white-tailed deer and the estrus cycle. J. Wildl. Manage. 45:710-715.

WILSON, E. O. 1975. Sociobiology, the new synthesis. Harvard Univ. Press, Cambridge, Mass. 697pp.

WRIGHT, B. S. 1956. The moose of New Brunswick. A Report to the Minister of Lands and Mines, N.B. 63pp.

Alces