DYNAMICS OF MOOSE POPULATIONS IN THE AOSERP STUDY AREA IN NORTHEASTERN ALBERTA

by

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Minister of the Environment
222 Legislative Building
Edmonton, Alberta

and

The Hon. John Roberts
Minister of the Environment
Environment Canada
Ottawa, Ontario

Sirs:

Enclosed is the report "Dynamics of Moose Populations on the AOSERP Study Area in Northeastern Alberta".

This report was prepared for the Alberta Oil Sands Environmental Research Program, through its Terrestrial Fauna Technical Research Committee (now the Land System), under the Canada-Alberta Agreement of February 1975 (amended September 1977).

Respectfully,

W. Solodzuk, P.Eng.
Chairman, Steering Committee, AOSERP
Deputy Minister, Alberta Environment

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DYNAMICS OF MOOSE POPULATIONS ON THE AOSERP STUDY AREA IN NORTHEASTERN ALBERTA

DESCRIPTIVE SUMMARY

The physical disturbances to the landscape and the additional human activity attending oil sands development are expected to have significant impacts on the population dynamics and ecology of big game species in the AOSERP study area. These populations constitute renewable natural resources having economic, social, recreational, aesthetic, and scientific values. Preservation and management of this big game resource require information on the natural control and regulation of populations, interaction with man, effects of disturbances from oil sands development on population dynamics, and detailed information about range preferences in the oil sands area of Alberta.

One aim of this research was to determine baseline information on the population dynamics and distribution and abundance of big game populations in the AOSERP study area. A second aim was to identify those environmental factors and intra- and interspecific interactions which have the greatest impact on distribution and abundance.

Specific objectives of this study were to: (1) describe and quantify the baseline states of moose; determine sex and age ratios, densities, distribution during the various seasons, recruitment, and mortality; (2) describe and quantify all interactions between moose and the vegetation-landform complex including seasonal use of habitats and forages, and quantification of preferences; and (3) describe and quantify the effects of carnivores on moose, normal mortality, human exploitation, and carnivore predation.

This report has been reviewed and accepted by the Alberta Oil Sands Environmental Research Program.

W.R. McDonald

W.R. MacDonald, Ph.D
Director
Alberta Oil Sands Environmental
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ABSTRACT

Intensive studies of moose were conducted on a 25 000 km^2 study area in northeastern Alberta from January 1976 to June 1978. Sixty-six moose (*Alces alces*) were radio-collared and another eight were colour-marked only. The population is either stationary or slowly declining. An estimate of 4595 (0.18/km^2) for the entire study area was obtained in the winter of 1977-78. Moose were largely absent in winter from the Birch Mountains and the jack pine area north of the Firebag River. There was a significant increase in the proportion of yearlings in the population between the winters of 1975-76, as a result of higher reproduction and/or calf survival in 1975-76. Our best estimate of the combined yearling and adult sex ratio was 30:70. There was a significant inverse relationship (r^2 = 0.62) between age of radio-collared bulls and dates of antler drop. Seasonal shifts between winter and summer home ranges were made by 34 (76%) of 45 moose; 13 (38%) of these movements exceeded 20 km. No significant differences in home-range size were found between sexes and seasons. Three distinct periods of increased movement among bulls were observed; April-May, September-October, and December-January. Cow movements were more leisurely and less well-defined. Spring (May-June) calf-cow ratios among radio-collared cows ≥3 years old averaged 88:100. Calf production as indexed by calf-cow ratios was similar in spring (May-June) 1976 and 1978, but autumn ratios were higher in 1977 than 1976. Calves constituted 30% of the winter populations in 1975-76, 18% in 1976-77, and 20% in 1977-78. The annual survival rate of calves of radio-collared cows was 0.27. Survival of these calves was lowest in the first month of life (0.61) and rose in subsequent months (0.95). An estimated 29% of calf losses were due to wolf predation. The annual survival rate of radio-collared yearlings and adults averaged 0.75. A second estimate of 0.76 to 0.77 was obtained independently from demographic and kill data for the entire study area population in 1977-78. Hunting and wolf predation were the main causes of mortality. Wolves consumed an estimated 61 to 66% of the yearlings and adults dying in 1977-78. Visual observations of radio-collared moose suggested that: (1) moose were least gregarious from April to August; (2) a significant increase in cow-bull associations occurred in September and lasted through November; (3) in November young bulls (1.5 to 2.5 years old) were associated with cows more than were older bulls; (4) bull association with other bulls increased significantly in November; and (5) cows with calves associated with other adult moose significantly less than did single cows. Uplands were used more than lowland from June through September, but upland use increased significantly in October. Lowland use rose in November and December, more so by bulls than cows, but decreased from January to March as snow depth increased. Snow depths were greatest within lowland covertypes. Lowland usage on winter home ranges (December-March) was significantly related ($r^2 = 0.60$) to availability. Decreased snowfall in winter 1976-77 resulted in increased lowland usage in February and March. Lowland use rose markedly and peaked in April and May. If there are "critical" habitats for moose, they are likely the open lowlands which apparently provide the first high quality food in spring. The rate of exploitation of moose in this region cannot likely be raised without producing a major population decline. The most promising means of increasing the allowable harvest would be to reduce the high early mortality of calves.

ACKNOWLEDGEMENTS

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During this study numerous people assisted us; to all we extend our thanks. J. Jorgenson, T. Fuller, R. Rolley, J. Cary, B. Mytton, and R. Frokjer deserve special mention for collecting and analyzing data. The skill and concern for safety shown by the principal engineers and pilots, J. LeRoux, F. Wiskar, D. Peterson, L. McCallam, B. Hardy, and P. Beaulac, were much appreciated. The help of K. Thirwell, R. Weatherill, G. Kemp, C. Boyle, and D. Hadler in facilitating day-to-day operation is gratefully acknowledged.

2. STUDY AREA

When AOSERP was established, a geographic area of about 25 000 km^2 was designated as the program's study area. There were two smaller study areas (Figure 2), Bitumount (1685 km^2) and Syncrude (324 km^2), lying within the AOSERP study area, and over which census flights were conducted each winter.

The AOSERP study area is within the Boreal Forest. Stringer (1976) described its vegetation, geologic history, and soil types. In general, lowlands are covered by a mixture of sedge (*Carex*) meadows, willow (*Salix*) flats, and tamarack (*Larix laricina*) and black spruce (*Picea mariana*) muskegs. Well-drained uplands are forested with mixed and solid stands of aspen (*Populus tremuloides*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and white birch (*Betula papyrifera*); balsam poplar (*Populus balsamifera*) occurs mostly along river valleys. From maps provided by the Alberta Forest Service, it is estimated that less than 1% of the 25 000 km^2 study area had burned during the past 25 years.

Elevations vary from 300 m along the Athabasca River to 600 m at Muskeg Mountain on the east side and 800 m in the Birch Mountains on the northwest. Except for the eastern and northern slopes of the Birch Mountains, most changes in elevation occur gradually. There are few lakes on the study area, except in the Birch Mountains and north of the Firebag River.

Mean daily temperatures at Fort McMurray during 1944 to 1970 ranged from 16°C and 15°C in July and August to -22°C and 17°C in January and February. Annual snowfall averaged 140 cm from 1944 to 1970. The maximum overwinter snowfall was 297 cm in 1971-72. In the winters of 1975-76, 1976-77, and 1977-78, snowfall totalled 130, 152 and 123 cm, respectively. The winter of 1976-77 was mildest despite its greater snowfall, half of which fell after 10 March and melted quickly; mean monthly temperatures during January to March were 10 to 15 degrees above normal.

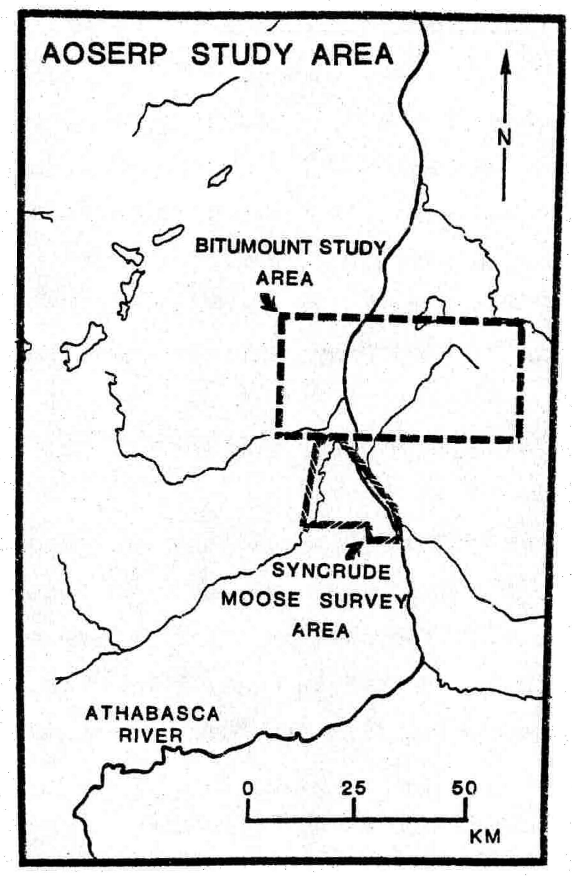

Figure 2. Study areas surveyed for moose in winter.

The only town within the study area is Fort McMurray which grew from approximately 6000 people in 1968 to nearly 30 000 by 1978. Two native villages, Fort MacKay and Anzac, each contain 200 residents.

Travel on the study area in summer is largely restricted to Highway 63 and the Athabasca, Clearwater, Richardson, and Firebag rivers. In winter, the area is used primarily by trappers and native hunters who travel along cutlines by snowmobile.

3. METHODS

3.1 TAGGING AND RELOCATION OF MOOSE

All moose were darted and immobilized from a helicopter, mainly a Hughes 500C. Various dosages of (1) etorphine hydrochloride (M99), (2) a mixture of M99 and xylazine hydrochloride (Rompun), and (3) a mixture of fentanyl citrate and Rompun were used. Hyaluronidase (Wydase) was occasionally added to the latter two mixtures to shorten induction time (Haigh et al. 1977). Outside incisors (C_1) were pulled for ageing (Sergeant and Pimlott 1959) and ear tags were attached. Radio (150-153 MHz) and colour-coded collars were placed on 66 moose; another eight received colour-coded collars only.

Radio-collared individuals were relocated from a Cessna 180 or 185 equipped with two four-element yagi antennas. Initial radio-contact was normally made 600 to 1200 m AGL at distances up to 16 km. Relocations were made at 1 wk intervals in 1976, and 2 wk intervals thereafter. There was a 2.5 mo gap between relocations in 1977 from mid-April to the end of June. The time, location, habitat, activity, and number and sex of associates of radio-collared moose were recorded. All locations were plotted on 1:50 000 forest cover maps and later converted to metric grid coordinates to facilitate computer analyses.

3.2 CENSUS FLIGHTS

Moose were counted on the Syncrude area (Figure 2) in February 1977 and in December and March 1977-78 from a helicopter flying east-west transects at 0.4 km intervals. These surveys were flown at an altitude of 95 to 100 m AGL and an airspeed of 80 to 96 km/h.

On the Bitumount study area, a helicopter was used to search stratified random quadrats of 2.6 km^2. In January 1976, these quadrats were stratified by dominant vegetation and proximity to the Athabasca River valley (Jacobson 1978). In February 1977, stratification was based on the moose distribution as observed during fixed-wing transects flown 2 wk earlier (Jacobson 1977). The stratified random-quadrat surveys were flown at an altitude of 46 to 91 m AGL and an airspeed of 81 to 106 km/h (Jacobson 1978; Cook and Jacobson 1978).

The Bitumount study area was flown with fixed-wing aircraft in January 1977 and in December and March 1977-78. Transects were flown east-west at 0.8 km intervals, altitudes of 95 to 100 m AGL, and airspeeds of 120 to 144 km/h. Population estimates from fixed-wing surveys of the Bitumount study area and helicopter surveys of the Syncrude survey area were based upon the total number of moose observed and the ratio of marked (radio-collared) observed to total marked moose present (a simple Petersen estimator).

In February 1978, fixed-wing transects were flown east-west at 5 km intervals over the entire AOSERP study area.

3.3 DETERMINATION OF SEX

The vulva patch could be used only to sex moose (Mitchell 1970) during helicopter surveys. None was flown on the Bitumount study area in winter 1977-78, and the presence of antlers or a calf had to be relied on to indicate sex. The proportion of antlerless bulls was estimated from the timing of antler drop among the radio-collared animals.

3.4 SURVIVAL RATES

Survival rates of yearling and adult radio-collared moose were calculated by Trent and Rongstad's (1974) method. Two separate estimates were made: the first involved only those moose whose fates were known; the second included individuals with whom radio contact was lost. In the latter case, survival rates were averaged which assumed that (1) all were dead and (2) all were alive.

Survival rates for calves of radio-collared cows were calculated as for yearling and adults. It was assumed that calves which disappeared from such cows during May-March had died. Although lone calves might survive, none was observed during this study. Calf survival to winter was also calculated from three demographic statistics: the calf-cow ratios during summer and winter, and the intervening adult survival rate.

3.5 AVAILABILITY AND USAGE OF VEGETATION TYPES

The availability of vegetative covertypes was determined from AOSERP maps and 1977 aerial photos. These were sampled systematically along east-west lines drawn at 9.7 cm (5 km) intervals across the Bitumount study area. The transects were partitioned into 0.5 cm (0.26 km) sections and the number of millimetres of each covertype per section was measured. It was thus possible to estimate mean availability and variance of vegetation types.

Three lowland and four upland covertypes were recognized. Lowlands were open bog-willow-tamarack, willow-tamarack-black spruce, and black spruce; there was a gradient here from wetter and more open to drier and more treed types. Upland covertypes were aspen-white spruce, aspen, jack pine mix, and jack pine; soil moisture graded from mesic to xeric.

4. RESULTS AND CONCLUSIONS

4.1 POPULATION DENSITY AND TRENDS

Bibaud and Archer (1973) surveyed 230 km^2 of the minable portion of the oil sands region (Figure 1) in January 1973. An area of 95 km^2 lay within what later became the Bitumount study area (Figure 2); there, 23 moose or 0.24/km^2 were observed (Table 1). In January 1976, a stratified random-quadrat survey of the Bitumount study area estimated 0.22 moose/km^2 (Jacobson 1978). One year later, in February 1977, a similar survey gave 0.19 moose/km^2 (Cook and Jacobson 1978). These surveys suggest that the winter population was stationary or declining slowly during 1973 to 1977.

Petersen-index calculations (Bailey 1951, 1952), based on sightings of radio-collared moose during fixed-wing transects in January 1977, December 1977, and March 1978, suggested a population increase on the Bitumount study area between the winters of 1976-77 and 1977-78 (Table 1). In January 1977, 17 of 33 to 37 radio-collared moose on the area were observed for an estimate of 0.21 to 0.24/km^2. In December 1977 and March 1978, an observation was made of nine of 17 and eight of 15 radio-collared moose for estimates of 0.28/km^2 and 0.26/km^2. Although the apparent 12% rise in population was not statistically significant, it is believed that a real increase did occur. Survey conditions were similar in both years, but more moose were seen during winter 1977-78; 277 and 265 were observed in December 1977 and March 1978, compared to 193 in January 1977.

The difference in 1977 between density estimates of 0.21 to 0.24 and 0.19/km from Petersen-index and stratified block counts, respectively, (Table 1) probably reflects the inability to see all moose within blocks despite intensive search.

In February 1977, 0.08 moose/km^2 were estimated to occur on the 324 km^2 Syncrude survey area: all six radio-collared animals present were observed during the helicopter transects. The mean estimate for December and March in the following winter was 0.37/km^2;

Table 1. Population and density estimates for moose in the 1685 km^2 Bitumount study area.

Year	Month	Census method	Aircraft used	Moose Population estimate	90% C.L.[a]	Moose/km^2
1973	Jan[b]	Counts within random quadrats	Helicopter			0.24
1976	Jan[c]	Counts within stratified random quadrats	Helicopter	367	275 to 459	0.22
1977	Jan[d]	Peterson-index calculation based on proportion of radio-collared moose sighted	Fixed-wing	355 to 399	259 to 631	0.21 to 0.24
1977	Feb	Counts within stratified random quadrats	Helicopter	320	243 to 397	0.19
1977	Dec[d]	Peterson-index calculation based on proportion of radio-collared moose sighted	Fixed-wing	473	313 to 971	0.28
1978	Mar[d]	Peterson-index calculation based on proportion of radio-collared moose sighted	Fixed-wing	443	288 to 962	0.26

[a] C.L. = Confidence Limit.

[b] From Bibaud and Archer (1973), a total of 37 2.6 km^2 quadrats were surveyed on the study area.

[c] From Jacobson (1978), this population estimate did not include a 1.6 km wide strip on the western boundary of the study area.

[d] The actual number of radio-collared moose on the study area was between 33 and 37; population estimates and confidence limits were calculated for both numbers. In December 1977 and March 1978, the actual number of radio-collared moose present was known from radio-relocation flights immediately before the census.

five of 10 radio-collared individuals were seen. While the confidence limits are wide, the difference here is statistically significant, and the trend similar to that noted above on the Bitumount study area.

Fixed-wing transects were flown at 5 km intervals over the entire AOSERP study area (25 000 km^2) in February 1978, and 510 moose were observed (Figure 3). Since the mean population estimate for the Bitumount study area in the winter of 1977-78 was 458, and 0.111 was the proportion seen there on the above transects, the total number of moose on the AOSERP study area was calculated to be 4595 (510/0.111) or a density of 0.18/km^2.

4.1.1 Seasonal Distribution of Moose in the AOSERP study area

While searching for woodland caribou (*Rangifer tarandus*) during February 1976, moose seen in the Birch Mountains and the jack pine area north of the Firebag River (Figure 2) were recorded. North-south transects at 1.6 km intervals were flown in a Cessna 185 at airspeeds and altitudes similar to later survey flights over the Bitumount study area. Assuming 50% observation efficiency (the average from three fixed-wing surveys over the Bitumount study area, as discussed below), densities of 0.03/km^2 and 0.11/km^2 were calculated for the Birch Mountains and jack pine area, respectively. These densities were much lower than the 0.22 moose/km^2 calculated for observations on the entire AOSERP study area during February 1978 (Figure 3) and likewise indicated that few moose were present in the Birch Mountains and jack pine area.

The relative scarcity of moose in the Birch Mountains is probably a winter phenomenon. For example, eight times as many moose were seen there in summer per hour of flying than in winter. Furthermore, as discussed later, seven radio-collared animals either moved into the mountains in spring or out in autumn. On the other hand, there is no indication that moose numbers change seasonally in the jack pine area; densities there appear to be consistently low.

The Muskeg Mountain area (Figure 1) lies just east of the AOSERP study area, and thus was not covered by the transect flights

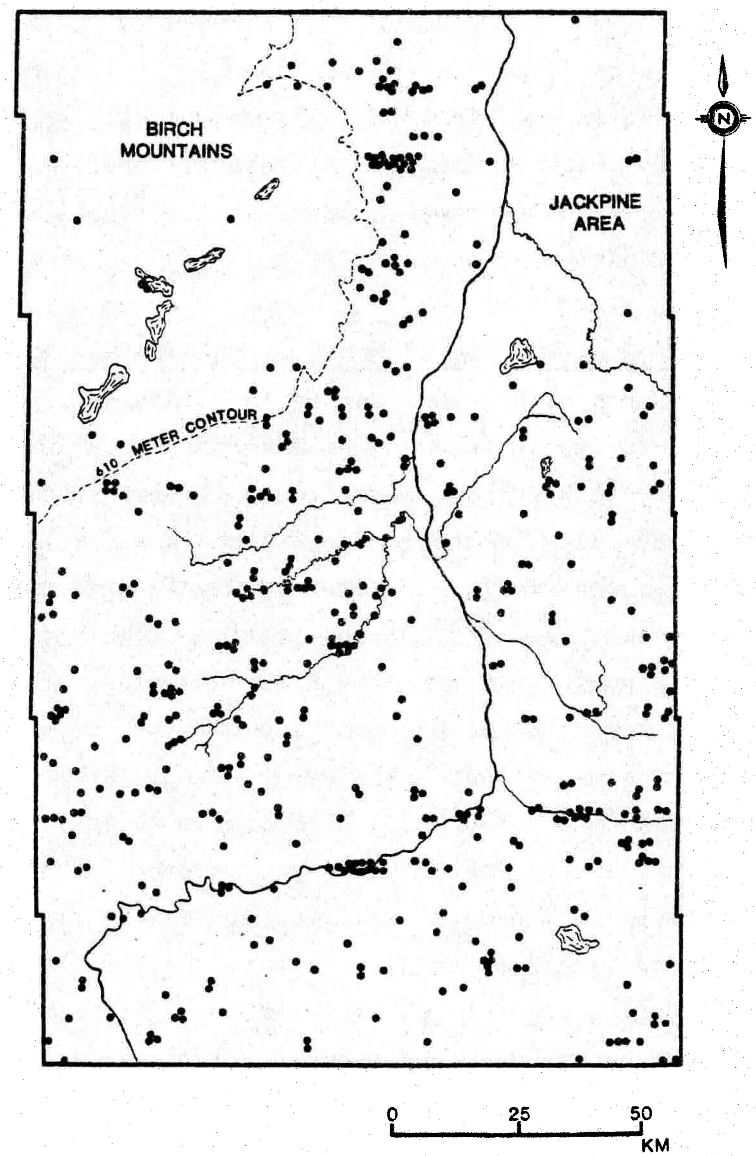

Figure 3. Distribution of moose observed during an aerial (fixed-wing) survey of entire AOSERP study area in February 1978; transects were at 5 km intervals.

in February 1978. However, movements of nine radio-collared moose in spring and autumn suggested that overwinter densities there, as in the Birch Mountains, were low.

4.2 AGE AND SEX STRUCTURE

Twenty-two of the 23 (96%) yearling and adult moose collared in the winter of 1975-76 were ≥3.5 years old (Table 2). By the following winter, a significant increase ($p < 0.01$) in yearlings had reduced the proportion of moose ≥3.5 years old to 62% (29 of 47).

As will be shown below, this marked rise in yearling recruitment reflected improved calf survival during 1975-76. The age distribution from both winters indicated that not since 1970 and 1971 had recruitment to the yearling cohort been so high. Although no conscious attempt was made when darting moose to be age selective, other than avoiding calves, the age distributions shown in Table 2 may be biased through differential vulnerability to capture. It is unlikely, however, that such vulnerability changed between the two winters, and the increased proportion of yearlings during the second winter was doubtless real.

The observed sex ratio among yearlings and adults changed progressively from 26:74 in January 1976 to 33:67 in February 1977 and 44:56 in December 1977 (Table 3). The January 1976 ratio was significantly different ($p < 0.02$) from that in December 1977. It is believed that this apparent change was caused by a difference in relative visibility of the sexes due to different sampling times during these two winters. Bulls frequented open lowlands in December more than did cows (see Section 4.9), and hence were more observable at that time. By February, both sexes were in similar habitats and probably equally visible. It is therefore suspected that the proportion of bulls was overestimated in the December 1977 survey.

Although it did not likely bias sex-ratio information, the age-related timing of antler drop could affect comparisons of sex ratios between populations having different age distributions. A significant relationship (Figure 4) was found between age of bull and date of

Table 2. Age distribution among yearling and older moose marked during winters of 1975-76 and 1976-77 on or near the Bitumount study area. Age determined from tooth sectioning[a].

Sex	Winter	Age (Years)										Total
		1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	
Bulls	1975-76				1	2	2		1		1	7
	1976-77	3	1	2			1	6	1	1	3	18
Cows	1975-76	1		2	2	2	4		2	2	1	16
	1976-77	12	2	1	3	1	2	3		3	2	29
Total	1975-76	1		2	3	4	6		3	2	2	23
	1976-77	15	3	3	3	1	3	9	1	4	5	47
Percent	1975-76	4						96				
	1976-77	33[b]						62				

[a] Sergeant and Pimlott 1959.

[b] Significantly different from combined yearlings and 2 year olds in 1975-76. ($p < 0.01$).

Table 3. Sex ratio of adult and yearling moose observed during aerial surveys on the Bitumount study area.

Year	Month	Aircraft used	Total moose observed	Unsexed adults	Unknown sex or age	% Bulls among adults and yearlings (±95% C.L.[a])	Bulls/100 cows among adults and yearlings
1976	Jan	Helicopter	82		5	26 ± 12	35
1977	Feb	Helicopter	128	3		33 ± 9	49
1977	Dec	Fixed-wing	277	81[b]		44 ± 6	77

[a] C.L. = Confidence Limits.

[b] Moose were sexed from the helicopter in January and February using the vulva-patch criterian (Mitchell 1970). Sex was determined from the fixed-wing aircraft in December by the presence or absence of antlers: based on dates of antler drop by radio-collared bulls during fall 1976-77 and 1977-78, 33% (27) of the 81 antlerless adults were bulls and 67% (54) were cows.

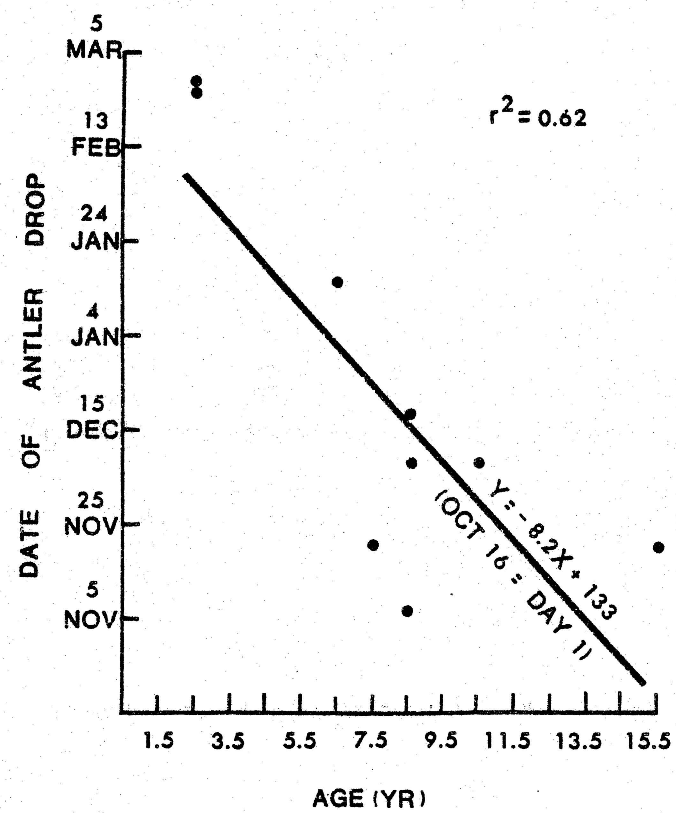

Figure 4. Relationship between age of bull moose and date of antier drop in the AOSERP study area.

antler drop, with older bulls shedding antlers in November and 2 year olds as late as March. Early winter (November-December) surveys frequently use the presence or absence of antlers to distinguish sex, thereby assuming that most, if not all, males have retained antlers. The appropriateness of this assumption will obviously vary with the existing age distribution. Fuller and Keith (in press b) noted a similar relationship among woodland caribou in this same region.

4.3 SIZE AND COMPOSITION OF MOOSE GROUPS

Observations of radio-collared moose during relocation flights provided information on association with other moose. Operationally, two or more moose were considered to be associated if they were <100 m apart. Because sex of many associates of radio-collared animals could not be determined from the fixed-wing aircraft during December-April, a detailed analysis of association was not attempted during that period.

It was found, as did Peek et al. (1974), that moose were least gregarious from April to August, groups averaging 1.1 among bull groups (n = 157) and 1.6 among cows (n = 317). Single animals accounted for 88% of bull observations, with the remainder evenly divided between multiple-bull and bull-unknown sex associations. Fifty-four percent of the cow observations were of single animals, 32% were of cow-calf groups, and 11% were of cow-unknown sex associations.

Bull-cow associations increased significantly in September with onset of the rut and remained common through November. Thirty-five present of the 125 observations of radio-collared bulls during September-November were bull-cow groups. The peak of rutting, as determined by back-dating calving 20 dates, 240 to 246 days (Peterson 1955), was 13 September to 12 October.

There may be age-related differences in the timing of bull-cow associations. Among radio-collared bulls, yearlings and 2 year olds were seen least frequently with cows in September (two of eight) and most frequently in November (four of six); whereas 11 of 29 older bulls (38%) were with cows in September, but just nine of 36 (25%) in November. The November differences are statistically significant. Mytton and Keith (in press) found a similar relationship at Rochester, Alberta.

Associations of radio-collared and other bulls increased significantly in November. The size of groups containing either a radio-collared bull or a radio-collared cow was highest during this post-rutting period, averaging 2.0 (n = 92) and 2.2 (n = 172), respectively. The largest group was observed in November and consisted of eight animals.

Presence or absence of a calf seemed to be the most important factor affecting the associations of radio-collared cows. Cows with calves associated with other adult moose significantly less than did cows without calves (Figure 5). Such behavior was particularly evident during November to March, the period when mean group size tended to be largest. The reclusiveness of cow-calf groups has also been noted by Peek et al. (1974) and Van Ballenberghe (in press).

An age-related difference in bull-cow associations existed in November, when cows ≥9 years old were with bulls during 38% of 26 relocations compared to 12% of 65 relocations of younger cows.

4.4 SEASONAL HOME RANGE

To determine seasonal home ranges, all radio locations of each animal were first plotted sequentially. This gave an overview of moose movements on an individual basis and disclosed if and when obvious shifts in home range had occurred. In this way, arbitrary designations of seasonal ranges by calendar dates were avoided, and the innate variations between individuals were also taken into account. The criterion for a shift in home range was that an animal moved into an area spatially distinct from that previously occupied, and remained there for at least 1.5 mo.

Seasonal shifts in home range were exhibited by 76% (34 of 45) of radio-collared moose; most were between winter and summer ranges. Such shifts were of two general kinds (Figure 6): (1) 38% were >20 km and largely represented movements between winter ranges near the Fort Hills (Figure 1) and summer ranges of higher elevation in the Birch Mountains or Muskeg Mountain area; and (2) 62% were shorter movements between winter and summer ranges, distances between range centres averaging only 6 km. These movements were not associated with an elevational change.

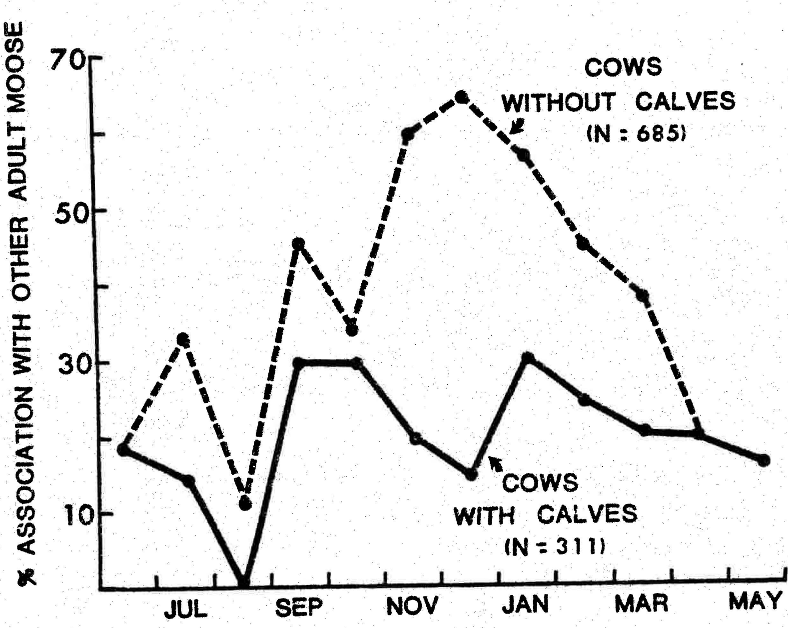

Figure 5. Percent association of radio-collared cows, with and without calves, with other adult moose in the AOSERP study area.

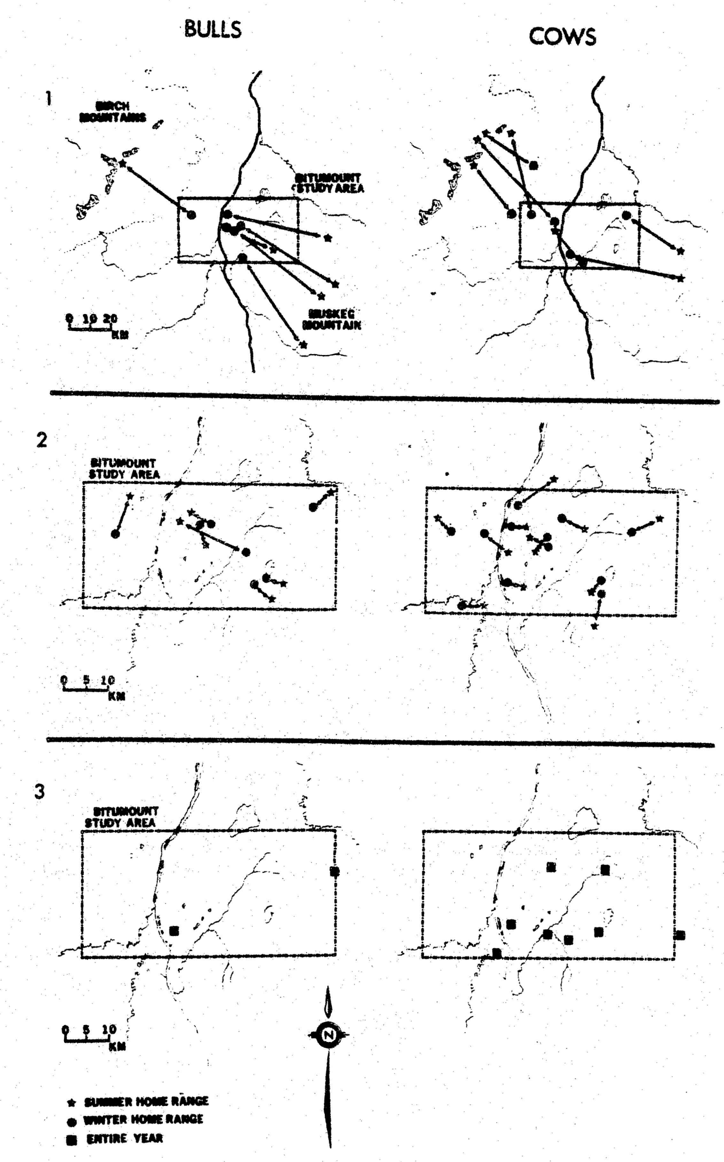

Figure 6. Patterns of range use among radio-collared moose in the AOSERP study area. Moose exhibited: (1) long-range (≥20 km); and (2) short-range shifts between winter and summer ranges; or (3) no seasonal shift.

There was considerable individual variation in the time of shifts between summer and winter ranges. Movements from summer to winter ranges were most variable. This was also noted in south-central Alaska by Van Ballenberghe (1978). No consistent difference in timing between the sexes could be detected. The earliest moves to winter range occurred in the study area in late September and early October; the latest occurred in February. The majority of summer-to-winter range shifts were in December and January. The mean date of arrival on winter ranges during winters 1976-77 and 1977-78 was 31 December. Arrivals were significantly earlier in the winter of 1977-78 (mean 13 December) than in the winter of 1976-77 (mean 12 January). The greater snowfall during November to December 1977 versus 1976 (65 cm versus 36 cm) may have prompted earlier movements. Dates of departure from winter ranges averaged 2 April, but extended from late March to early June. Movements to summer range commenced with the spring thaw and loss of snow cover. The mean date of arrival on the summer range in 1976 was 19 May; information is lacking for 1977 and 1978.

The apparent size of winter and summer home ranges, using the minimum-perimeter-polygon method (Mohr 1947), increased with the number of relocations and was highly variable for any given number (Table 4). About all that can be safely concluded from these data is that moose in the AOSERP study area usually have seasonal home ranges exceeding 20 km^2, and that winter and summer ranges are probably of similar size. In addition, no difference in home range size of bulls and cows could be detected. The mean size of the annual home range of 10 moose which did not make seasonal shifts was 97 km^2 (range 60 to 183 km^2), based on 28 to 71 relocations.

4.5 MOVEMENTS WITHIN AND BETWEEN HOME RANGES

Radio-collared moose were relocated at approximately 1 wk intervals during 1976 and at 2 wk intervals thereafter. The frequency distributions of distances moved between successive fixes in 1976 and 1977 (Figure 7) were not significantly different and the data were pooled.

Table 4. Mean home range[a] size of radio-collared moose on the entire AOSERP study area during the winters of 1975-76 and 1977-78, and the summers of 1976 and 1977.

No. of radio-locations used to estimate home range size	Winter[b] home range size (km^2)			Summer[c] home range size (km^2)		
	Mean	Smallest and largest ranges	No. of ranges	Mean	Smallest and largest ranges	No. of ranges
4-5	12	1-59	17	9	1-21	19
6	21	1-73	12			
7	22	1-87	16			
8-9	28	3-131	12			
10-15	30	3-111	12	37	18-97	7
15-25				57	12-141	6

[a] Determined by minimum-perimeter-polygon method (Mohr 1947).

[b] Mean date of arrival on winter range during 1976-77 and 1977-78 was 31 December. Mean date of departure from winter range during 1976 and 1978 was 2 April. Thus, the mean number of days on winter range was 92.

[c] Mean date of arrival on summer range in 1976 was 19 May. In 1977 there were no relocations prior to 30 June. No summer range calculations were made for 1978. Relocations after 31 August were not included in summer range calculations.

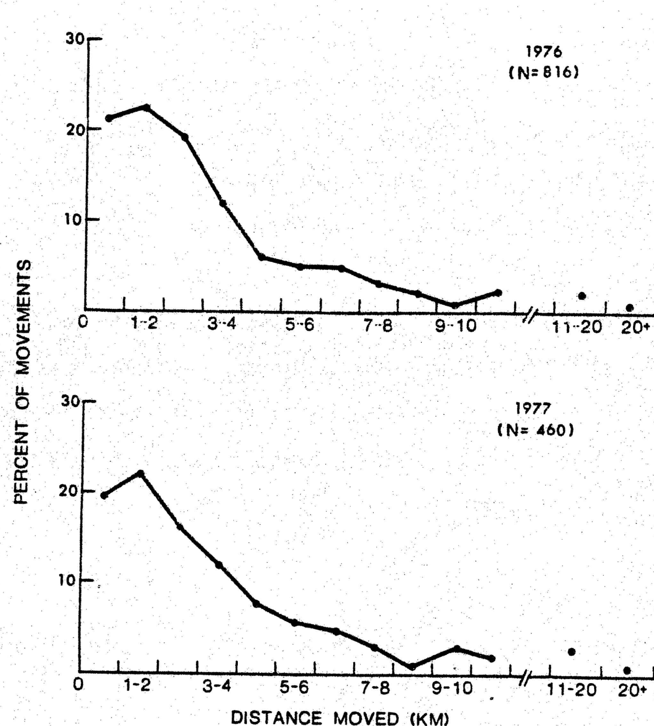

Figure 7. Frequency distribution of movements between successive fixes taken at approximately 1 wk intervals in 1976 and 2 wk intervals in 1977. Total number of movements is given in parentheses.

As an index to the relative magnitude of sex- and time-specific movements, the percentage that exceeded 5 km (Figure 8) within 2 wk intervals throughout the year was determined. Overall, 26% of 521 bull movements exceeded 5 km compared to a significantly lower 19% of 956 cow movements. The difference was caused mainly by a high proportion (48%) of bull movements exceeding 5 km in September and October; only 16% of cow movements were so long at that time. During the 2.5 mo immediately preceding this period, bull movements were much less (8% >5 km) whereas cow movements were about the same (19% >5 km).

There were three distinct periods of increased movements among bulls. The first occurred in April and May with shifts from winter to summer range; the second was in September and October with the rut; and the third came in December and January when most moves to winter range took place.

Cow movements, on the other hand, were less well-defined. The absence of apparent movement peaks during seasonal range shifts in April-May and December-January resulted from the more leisurely rate of travel by cows. Only 50% of their moves over a 2 wk period exceeded 5 km during range shifts, compared to 76% of moves by bulls.

4.6 CALF PRODUCTION

Newborn calves were first observed on 21 May 1976 and 17 May 1978. All initial observations of calves with radio-collared cows were made by 9 June in both years. First observation dates averaged 22 May (n = 7) in 1976 and 24 May (n = 13) in 1978. In 90% of these cases, less than eight days had passed since a previous observation of the radio-collared cow.

Eighteen of 20 (90%) first observations of newborn calves of radio-collared cows were in lowland covertypes. Average straight-line distance between first and second observations of newborn calves, six to nine days later, was 1.7 km (n = 10).

Differences in calf production may exist within the AOSERP study area. In May to June 1976, a significantly higher calf-cow ratio was noted in the Birch Mountains (122 calves/100 yearling and adult cows) than on the Bitumount study area (50 calves/100 cows; n = 22 cows).

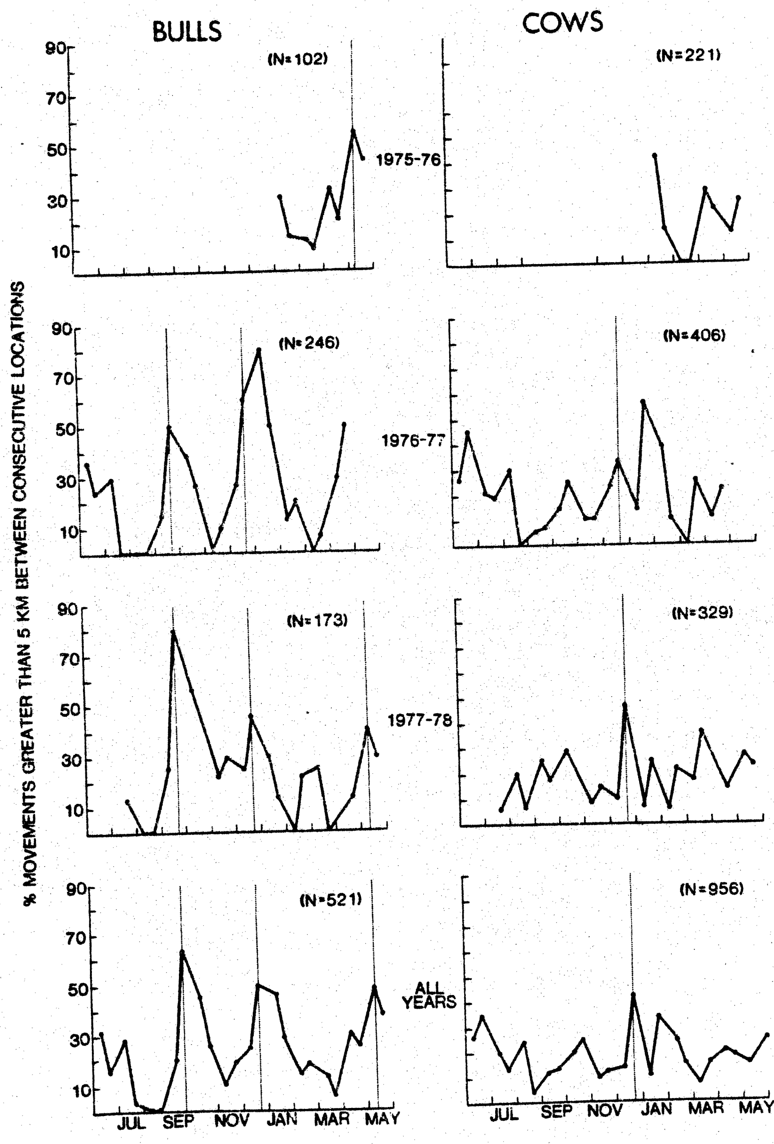

Figure 8. Percent of movements by moose greater than 5 km within approximately 2 wk intervals in the AOSERP study area. Total number of movements is given in parentheses.

There were too few observations in the Birch Mountains in 1977 and 1978 to make a similar comparison. The higher calf-cow ratios among cows migrating to and from the Birch Mountains is consistent with the findings of Mytton and Keith (in press), who noted higher calf production among migratory cows at Rochester, Alberta. Edwards and Ritcey (1958) observed higher in utero pregnancy and twinning rates in years when their samples allegedly contained more migratory cows summering at high elevations.

Calf-cow ratios among radio-collared cows were not significantly different from those among unmarked cows (Table 5); Faro and Franzmann (1978) likewise found no differences in Alaska. This suggests that winter tagging did not adversely affect calf production. In addition, no subsequent change could be detected in calf-cow ratios among cows immobilized and tagged two or more winters earlier.

Calves of our radio-collared cows were missed on 10% (n = 52) of relocation flights during 1 June to 15 September. Gaseway (1977, Appendix 3) estimated that calves were missed during 7 to 11% of their observations of radio-collared cows.

Small sample sizes precluded a detailed look at age-related differences in calf production. Elsewhere, reproductive rates of yearling cows tend to be lower and more variable than those of older cows (Pimlott 1959; Simkin 1965; Markgren 1969; Blood 1974). Four of the six radio-collared yearlings produced a single calf as 2 year olds.

Between-year differences in calf production are suggested by data from the Bitumount study area (Table 6). Most of the radio-collared cows resided there. Although calf-cow ratios and twinning rates were probably similar in the spring of 1976 and 1978, the calf-cow ratio in the autumn of 1976 was about one-third that in the autumn of 1977 ($p = 0.12$).

Winter census flights over the Bitumount study area and Syncrude survey area provided additional information on recruitment of calves (Table 7). Data from both study areas agree closely; calves averaged 30% of the winter population in 1975-76, 18% in 1976-77, and

Table 5. Observed calf production and twinning rates of radio-collared and unmarked cows in the AOSERP study area.

Observation dates	Radio-collared Calves/100 yearling and adult cows	Radio-collared Twinning rate[a]	Unmarked Calves/100 yearling and adult cows	Unmarked Twinning rate[a]	Total Calves/100 yearling and adult cows	Total Twinning rate[a]
21 May to 22 Jun 1976	64 (14)[b]	29 (7)	25 (8)	0 (2)	50 (22)	22 (9)
17 May to 22 June 1978	100 (19)	36 (14)	80 (10)	33 (6)	93 (29)	35 (20)
Means	82 (33)	33 (21)	53 (18)	17 (8)	72 (51)	29 (29)
23 June to 21 Sept. 1976	25 (12)	0 (3)	83 (12)	10 (10)	54 (24)	8 (13)
30 June to 28 Sept. 1977	72 (25)	13 (16)	58 (19)	10 (10)	66 (44)	12 (26)
Means	49 (37)	7 (19)	71 (31)	10 (20)	60 (68)	10 (39)

[a] Twinning rate is the number of cows with twins divided by the number of cows with calves.

[b] Sample size (cow numbers) is given in parentheses.

Table 6. Observed calf-cow ratios and twinning rates among radio-collared moose (≥3 years old) on the Bitumount study area in the spring of 1976 and 1978, and the autumn of 1976 and 1977.

	1976		1977	1978
	May-June	September	September	May-June
Calves/100 cows	75 (12)[a]	25 (12)	76 (21)	100 (11)
Twinning rate[a]	29 (7)	0 (3)	14 (14)	44 (9)

[a] Sample sizes (cow numbers) are given in parentheses.

[b] Twinning rate is the number of cows with twins divided by the number of cows with calves.

While the causes of calf mortality remain largely unknown, it is possible to estimate the amount due to wolf predation. Using (1) a February 1978 population estimate of 4595 moose in the AOSERP study area; (2) 20% (919) calves in the population (Table 7); and (3) a survival rate of 0.39 for calves from 1 June to 15 February (calculated from the mean annual survival rate of 0.27), 2356 (919/0.39) calves were estimated to be in the study area on 1 June. T. Fuller (personal communication) estimated at least three calves were consumed per wolf annually. The estimated 166 wolves present in the study area (Fuller and Keith in press a) would then consume a minimum of 498 calves in 1 year. This amounts to about 21% of the 1 June calf population, and 29% of total annual mortality.

It is suspected that black bears (*Ursus americanus*) may cause appreciable calf mortality in the study area, as appears to be the case on the Kenai Peninsula in Alaska (Franzmann and Peterson 1978). This suspicion is based on the fact that bears were numerous and calf hair was noted in early-summer bear scats.

4.8 YEARLING AND ADULT SURVIVAL

Annual survival rates of radio-collared yearlings and adults whose fates were known were 0.82 in 1976, 0.74 in 1977, and 0.78 in 1978 (Table 10); the mean was 0.78. If animals whose radio-collars stopped functioning (i.e., fate unknown) are included, the mean annual survival rate becomes 0.72. The grand mean from the two sets of estimates is 0.75. No sex-specific differences in survival could be detected.

The two main causes of the 18 mortalities (Table 11) among the radio-collared yearlings and adults were native hunting (7) and wolf predation (7). Most (89%) losses occurred from October through April.

4.9 COVERTYPE USE

Covertype "use" refers simply to the presence, as recorded from the air, of radio-collared moose in a particular covertype. The

Table 10. Survival rates of radio-collared yearling and adult moose in the AOSERP study area during 1976, 1977, and 1978.

Year	Time period	Interval (days)	No. of radio-collared moose	Interval survival rate[a]	365 day survival rate
1976	27 Jan.-31 Dec.	339	39	0.83	0.82
1977	1 Jan.-31 Dec.	365	46	0.74	0.74
1978	1 Jan.-22 Jun.	173	23	0.89	0.78
Mean					0.78

[a] Using the analysis described by Trent and Rongstad (1974).

Table 11. Mortality among radio-collared yearling and adult moose in the AOSERP study area.

Cause of death	Age	Sex	Approximate Date of Death
	1.5	F	7 Jan. 1977
	2.5	M	11 Feb. 1977
	2.5	F	17 Nov. 1977
	3.5	F	18 Apr. 1978
Hunting	5.5	F	25 Oct. 1977
	7.0	F	25 Apr. 1976
	8.5	F	19 Apr. 1978
	10.5	F	8 Mar. 1977
	12.5	F	17 Dec. 1977
	1.5	M	29 Jan. 1977
	6.5	M	18 Jan. 1977
	6.5	M	30 Jan. 1977
Wolves	7.5	F	5 Nov. 1976
	8.5	F	5 Dec. 1977
	8.5	M	15 Jan. 1978
	11.0	F	17 Jun. 1978
Unknown	2.0	F	23 Apr.-30 Jun. 1977
Fighting	12.5	M	21 Oct. 1976

best information on covertype availability comes from the Bitumount study area where 40% was lowland (Table 12). Lowlands comprised a somewhat higher percentage of the total AOSERP study area (perhaps 50%), as did uplands forested with jack pine. The absence of adequate vegetation maps prevented us from determining availability over this larger area.

Because of movements described earlier, the percentage of moose relocations on the Bitumount study area varied seasonally. Eighty-three percent of all relocations during January-April were made there, 68% during May-August, and 72% during September-December. Hence, the availability of covertypes in the Bitumount study area probably reflected their overall availability for radio-collared moose.

There were major seasonal differences in use of upland and lowland covertypes (Table 12). Sixty to 64% of all locations (n = 655) were in the uplands from June through September, with aspen and aspen-white spruce being the dominant covertypes used. Jack pine and mixed-jack pine cover received its highest usage in this period.

In October, use of upland cover increased significantly, with the aspen-white spruce covertype accounting for all of the increase.

In November and December, upland usage decreased significantly, as moose were observed more often in open bog-willow-tamarack or willow-tamarack-black spruce lowlands. It was found that there was a significantly higher use of lowlands by bulls than cows during this period (Figure 9). As noted earlier, aerial surveys conducted during November to December will likely show higher ratios of bulls to cows than those conducted later, as bulls are more observable in such open lowlands.

Use of uplands rose in January and continued to rise through March. Aspen use increased most, but use of aspen-white spruce increased also. While seasonal trends were similar between years, significantly higher lowland usage occurred in the winter of 1976-77. In February and March 1977, 47% of the relocations were in lowlands compared to 29% and 33% in 1976 and 1978.

A marked shift into the lowlands occurred in April and May, when 60% and 72% of all relocations were made there. All three lowland

Table 12. Percent usage of different covertypes as indicated by location of radio-collared moose in the entire AOSERP study area from February 1976 to June 1978.

Cover type	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Mean monthly Usage	Availability[a]
Jack pine	8	6	6	9	2	0	2	1	0	3	0	4	3	5
Jack pine mix[b]	8	17	16	9	11	13	5	8	12	9	8	6	10	2
Aspen[c]	30	25	27	20	24	19	16	26	27	31	12	6	22	29
Aspen-White Spruce[d]	14	13	15	23	35	23	18	15	15	23	20	12	19	24
Total upland usage	60	61	64	61	72	55	41	50	54	66	40	28	54	60
Open muskeg-Willow-Tamarack	6	4	10	12	9	14	24	17	17	12	18	19	14	15
Willow-Tamarack-Black Spruce	13	17	10	13	9	18	24	13	6	11	20	18	14	13
Black Spruce	21	18	16	14	10	13	11	20	24	11	22	35	18	12
Total lowland usage	40	39	36	39	28	45	59	50	47	34	60	72	46	40
Total number of locations	122	157	167	209	180	150	128	130	175	213	219	133		

[a] Availability applies to Bitumount study area only.

[b] Combines jack pine-aspen, jack pine-spruce, and jack pine-aspen-spruce mixes.

[c] Includes white birch and balsam poplar.

[d] Includes spruce-only stands.

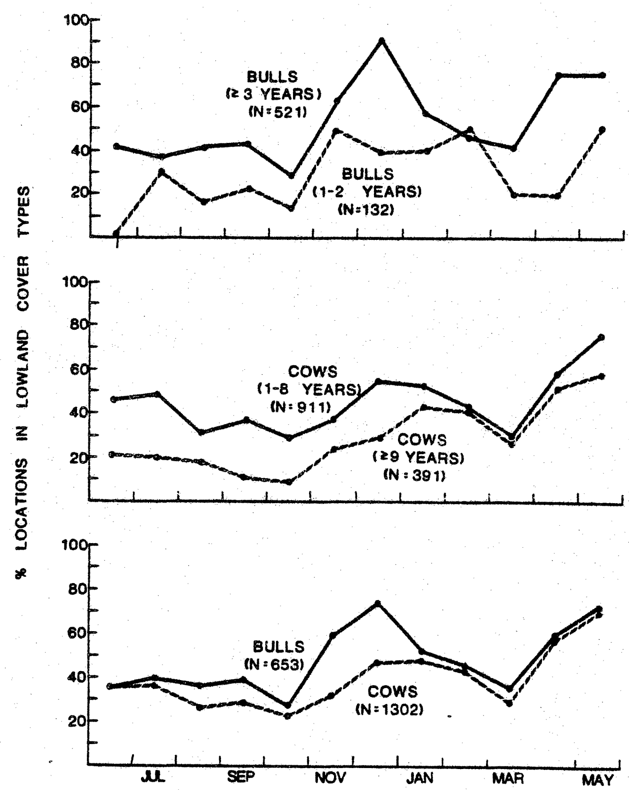

Figure 9. Sex and age differences in use of lowland covertypes by radio-collared moose in the AOSERP study area. Total number of observations is given in parentheses.

covertypes received increased use in April, but black spruce accounted for nearly all of the increase in May. The corresponding decreased use of uplands was most notable in aspen.

Coinciding with the April move into the lowlands were apparent changes in the activity of radio-collared moose. For example, the percentage of moose bedded when relocated decreased continuously from 44% in March (Figure 10). Presumably other activities, such as feeding and movement, increased during this period.

Older bulls (≥3 years old) tended to use lowlands more than did young bulls (1 to 2 years old) (Figure 9). This difference was most notable in December when nearly 90% of the older bulls were found in lowland covertypes, but only 40% of younger bulls were there. Cows too showed age-related differences (Figure 9), with cows (≥9 years old) using lowlands significantly less during June-December.

Sex- and age-related differences in covertype usage appeared to be least during January to March (Figure 10). The present authors also checked for differences between cows with and without calves, but found none.

As with movements and home ranges, covertype usage exhibited much individual variation. For example, use of lowlands on winter range varied from 0% to 86% (Figure 11). Sixty percent of this variation could be explained by lowland availability.

A significant relationship existed between lowland availability within individual winter ranges and lowland use (Figure 11). The regression line's slope of 0.74 was not significantly different from 1.0 ($p = 0.21$), but this suggests some selection for lowlands on winter range. Similar individual variation in covertype usage existed on summer ranges, but the relationship between use and availability was not statistically significant ($p = 0.12$).

4.10 EFFECTS OF SNOW

Coady (1974) stated that depth, density, and hardness of snow were probably its most important characteristics to moose. The present authors measured snow depth only.

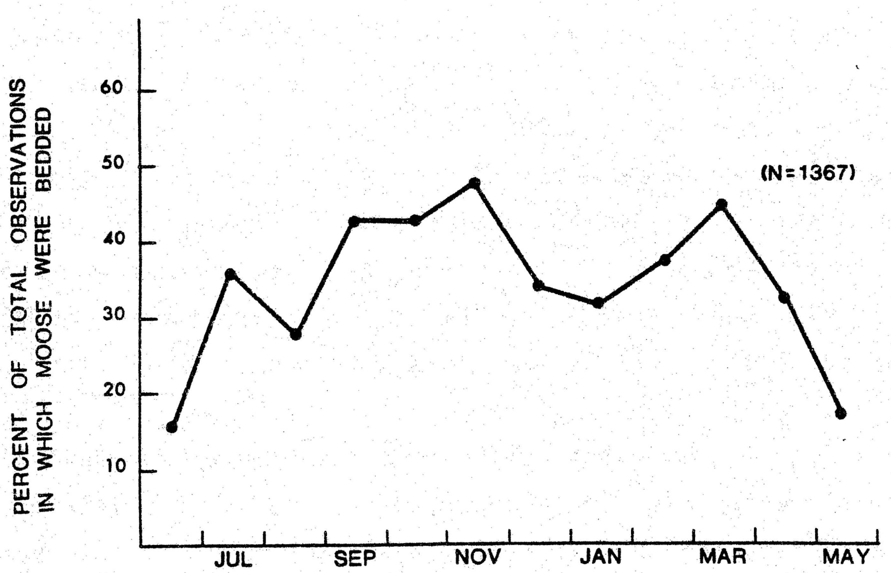

Figure 10. Seasonal changes in bedding activity of radio-collared moose in the AOSERP study area. Total number of observations is given in parentheses.

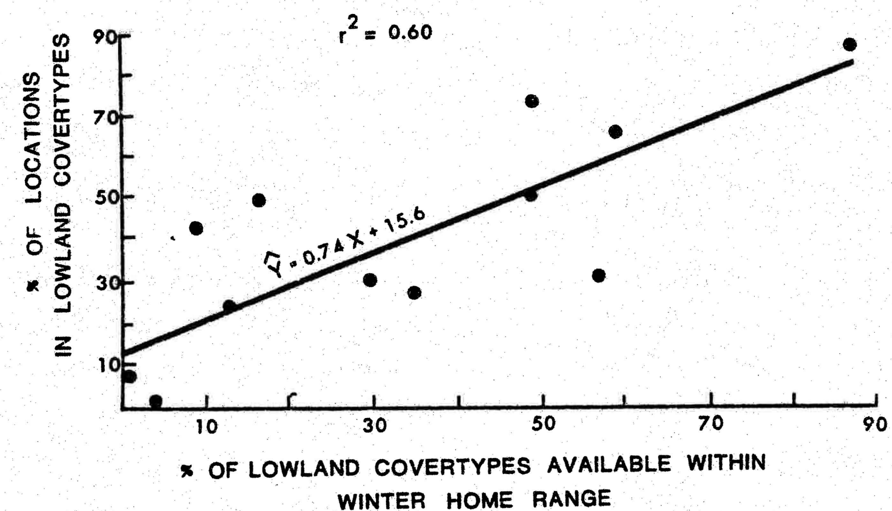

Figure 11. Relationship between the use and the availability of lowlands within winter ranges of moose in the AOSERP study area. Only animals for whom there were 10 or more locations on a water range were included.

One likely effect of increased snow depth, already noted, was the earlier return to winter ranges in 1977-78. The movements out of the Birch Mountains and Muskeg Mountain areas each winter are toward areas with shallower snow. Depths in the Birch Mountains and Muskeg Mountain area averaged 10 to 15 cm more than on winter ranges in the Bitumount study area (Atmospheric Environment Services. Unpublished data).

Snow depths tended to be shallower on uplands than on lowlands in the AOSERP study area (Fuller and Keith in press c; Nowlin 1978), and the difference probably grew as winter progressed. Fifty percent of the January moose locations (n = 130) were on uplands versus 53% in February (n = 175) and 66% in March (n = 213) (Table 12).

The lower use of uplands in February to March 1977, compared to 1976 and 1978, coincided with decreased snow depth. Snowfall through 17 March was only 60 cm in 1977 compared to 117 cm in 1976 and 102 cm in 1978.

Month-end snow depths at Fort McMurray between 1944 and 1972 averaged 28 cm in December, 36 cm in January, 38 cm in February, and 28 cm in March; maximums were 58, 66, 64, and 53 cm, respectively. From the works of Nasimovitch (1955), Kelsall (1969), Ritcey (1967), and Prescott (1968), Coady (1974) concluded that snow depths up to 70 cm cause little or no restriction of movement. If this is correct, movements by moose in the AOSERP study area are rarely restricted.

4.11 MORTALITY FROM HUNTING

To assess the rate of harvest of moose in the AOSERP study area, information is needed on both sport hunting (mid-September through late November) and native hunting (year-round). In neither case was there mandatory registration of moose kills.

Information on sport hunting was gathered through a questionnaire and follow-up telephone survey to members of the Fish and Game Association at Fort McMurray. They accounted for 70 to 80% of all licenses sold there annually. Information on native hunting was obtained from Fort MacKay through repeated conversations with the village chief.

Hunter success was measured during the 1976 season and areas of hunting activity were identified by distributing a questionnaire in April 1977. A follow-up telephone survey was conducted from November through February 1977-78. This survey tested non-response bias in the 1976 questionnaire, and also provided information on the 1977 hunting season.

Seventy-three percent of respondents bought moose hunting licenses compared to 61% of non-respondents (Table 13). Twenty-eight percent of licensed respondents were successful compared to 16% of licensed non-respondents. After correcting for numbers of non-respondents in the sample, the 1976 hunting season results were compared with those of 1977.

The only significant difference between years was the percentage of members buying moose hunting licenses (Table 14), i.e., 63% in 1976 and 52% in 1977. The success rate of licensed hunters was 0.19 in 1976 and 0.26 in 1977.

In the questionnaire, and during the telephone survey, successful hunters were asked for the location of their kills. Sixty percent (n = 40) were either off highway 63 south of Fort McMurray, or along the Clearwater River (Figure 1). These areas are most accessible. Other locations included: the Athabasca River north of Fort McMurray; the Firebag River; fly-in lakes in the Birch Mountains; and off Highway 63 north of Fort McMurray (Figure 2). Eighty-five percent of all reported kills were within the AOSERP study area.

Phillips et al. (1979) conducted a study of recreational activity on the AOSERP study area and found that 48% of the hunters did not reside there. In 1976, these "non-residents" had a success rate of 0.14 compared to 0.18 among residents.

Native hunting success was hard to monitor. Despite numerous visits to Fort MacKay, it was not possible to obtain a complete record of moose killed by natives. The village chief estimated that 18 moose were harvested in the year starting May 1977. It is assumed that equal numbers were taken by residents of Anzac, which is similar in size to Fort MacKay and the only other native village in the study area.

Table 13. Characteristics of respondents and non-respondents to a moose-hunting questionnaire by members of the Fort McMurray Fish and Game Association in 1976[a]. Sample sizes given in parentheses.

Category	Percent		Probability of difference (X^2 test)
	Respondents	Non-respondents	
% Buying moose hunting licenses	73 ± 8 (115)	61 ± 8 (132)	0.05
% Of active hunters hunting in the Fort McMurray area vs. elsewhere in province	89 ± 7 (82)	96 ± 5 (53)	0.14
% Of licensed hunters	28 ± 10 (80)	16 ± 8 (73)	0.10

[a] Information on non-respondents was obtained in a follow-up telephone survey of 1976 Fish and Game Association members.

Table 14. Results of the hunter questionnaire (1976) and telephone survey (1977) of the Fort McMurray Fish and Game Association. Sample size is given in parentheses.

Category	1976[a]	1977[b]	Probability of difference (X^2 test)
% Buying moose hunting licenses	63 ± 6 (247)	52 ± 8 (160)	0.02
% Of active hunters hunting in the Fort McMurray area vs. elsewhere in province	95 ± 4 (135)	93 ± 7 (59)	0.66
% Of licensed hunters successful	19 ± 6 (153)	26 ± 10 (70)	0.25

[a] Overall percentages obtained by correcting for the number of non-respondents in the sample (see Table 13).

[b] Because of direct telephone contact, there were no non-respondents in 1977.

Trappers were another source of hunting mortality. Fox and Ross (1979) interviewed 28 trappers in the AOSERP study area and found that 50% regularly took moose. The 55 active trappers on the study area would therefore take at least 28 moose annually.

Little is known of the ages of moose shot by hunters. It was observed that calves were rarely taken by sport hunters, but some were killed with cows by native hunters and trappers.

In 1977, 792 resident (non-alien) moose licenses were sold in Fort McMurray. Using this information and that given above on sport, native, and trapper hunting, the number of yearling and adult moose harvested in the year starting 15 May 1977 was calculated as between 351 and 433 (Table 15).

By adding consumption rates of moose by wolves, the total yearling and adult mortality was obtained. Fuller and Keith (in press a) estimated that wolves annually consumed about 15% of the yearling and adult moose within the 1289 km^2 area occupied by their Muskeg River pack. This 15% included any other natural mortality, as the pack visited all known moose carcasses within their territory. Numbers of yearling and adult moose present in the AOSERP study area on 15 May 1977 can be calculated from the 15 February 1978 estimate of 4595 moose (3676 yearling and adults) (Table 7), and a 15 May to 15 February survival rate of 0.80 (calculated from the mean annual survival rate of 0.75). The 15 May estimate of 4595 (3676/0.80) multiplied by the 15% consumption rate yields an estimate of 689 yearling and adult moose consumed by wolves during the year starting 15 May 1977.

In total, between 1040 and 1122 yearling and adult moose were estimated to have died from May 1977 to May 1978 in the AOSERP study area, an annual mortality rate of 23 to 24%. This compares with an independent estimate of 25% annual mortality from the radio-collared sample.

Table 15. Calculated mortality among yearlings and adult moose in the AOSERP study area.

Source of mortality	Type of population parameter	Parameter value
	Number of moose hunting licenses sold at Fort McMurray[a]	= 792
	Proportion hunting moose in the Fort McMurray area (Table 14)	= 0.93
	Number hunting moose in the Fort McMurray area (792 x 0.93)	= 737
	Moose hunting success rate (Table 14)	= 0.26
Sport hunting	Number of moose killed by Fort McMurray license holders (737 x 0.26)	= 192
	Proportion of hunters in the AOSERP study area that actually reside within the area	= 0.52
	Total number of moose harvested in AOSERP study area by hunters not residing within the area, assuming a success rate same as resident (192/0.52 - 192)	= 177
	Total number of moose harvested in AOSERP study area by hunters not residing within the area, assuming a success rate of 0.14[c] (0.14/0.26 x 177)	= 95
	Approximate number of active trappers in the AOSERP study area[a]	= 55
	Proportion harvesting moose regularly on trapline[c]	= 0.50
Trappers and Natives	Number of moose harvested by trappers (55 x 0.50)	= 28
	Number of moose harvested by natives of Fort MacKay and Anzac[d]	= 36
	Total number of moose harvested by natives and trappers (28 + 36)	= 64

continued...

Table 15. Continued.

Source of mortality	Type of population parameter	Parameter value
	Number of moose in AOSERP study area on 11 Feb. 1978[c]	= 4595
	Proportion yearlings and adults in moose population[f]	= 0.80
	Number of yearling and adult moose in AOSERP study area on 11 Feb. 1978 (4900 x 0.80)	= 3676
	Average yearly survival rate of radio-collared yearling and adult moose[g]	= 0.75
Wolves	Survival rate from 15 May to 15 Feb. as calculated from yearly survival rate	= 0.80
	Estimated number of yearling and adult moose alive on 15 May 1977 (3676/0.80)	= 4595
	Proportion of yearling and adult moose consumed yearly by wolves[h]	= 0.15
	Number of moose consumed by wolves during 1 year beginning 15 May 1977 (4595 x 0.15)	= 689
Total	Mortality from wolves, sport hunting, and trappers and natives depending on way of estimating kill by hunters not residing in AOSERP study area 689 + (192 + 177) + 64 or 689 + (192 + 95) + 64	= 1122 or 1040
	Annual mortality rate of yearling and adults alive on 15 May 1977 in AOSERP study area (1122/4595) or 1040/4595)	= 0.24 or 0.23

continued...

Table 15. Concluded.

[a] Information provided by the Fort McMurray Fish and Wildlife Office. Number of moose licenses sold combines regular and Zone-1 male.

[b] Success rates reported by Phillips et al. (1979).

[c] Calculated by Fox and Ross (1979).

[d] Marcel Ahaysou, chief of the village of Fort MacKay, estimated that 18 moose were harvested by his village. This figure was doubled to allow for natives residing in the village of Anzac.

[e] A total of 510 moose were observed in the entire AOSERP study area during the ungulate survey; 53 were observed in the Bitumount study area. The 53 amount to 0.111 of the mean population estimate for the Bitumount study area during the winter of 1977-78. Assuming equal visibility of moose on both areas, then the total number of moose in the entire AOSERP study area was 4595 (510/0.111).

[f] Calves constituted 20% of the winter of 1977-78 population in the Bitumount study area and the Syncrude moose survey area. Thus, yearling and adults constituted 80%.

[g] The mean survival rate of radio-collared yearling and adult moose was 0.72 when moose whose radio-collars had stopped functioning were included, and 0.78 (Table 10) when only those moose whose fate was known were used.

[h] Calculated by Fuller and Keith (in press a).

5. DISCUSSION

5.1 POPULATION ESTIMATES

The use of the Petersen estimates deserves further comment. The present authors were surprised in January 1977 to observe 17 of the 33 to 37 radio-collared moose present in the Bitumount study area. This fixed-wing transect survey was intended only to show the late-winter distribution of moose as a basis for stratifying random quadrats in February.

The immediate cost (excluding radio-collaring) of obtaining Petersen estimates from fixed-wing aircraft was less than half that of random-quadrat estimates from helicopters ($4000 versus $10 000). In addition, Petersen estimates are inherently more accurate. The ratio of observed-to-total radio-collared moose present, or observation efficiency, should be unbiased by such factors as poor snow conditions, dense cover, etc., which tend to cause underestimates of populations by census methods dependent upon total counts on sample areas.

It is not felt by the present authors that the coloured radio-collars increased observability of the marked moose on winter surveys. In short, an animal was first observed, then it was noticed whether or not it was collared. Faro and Franzmann (1978) believed, however, that colour-collared moose were more conspicuous in late May and early June, however.

Observation efficiency is undoubtedly affected by aircraft type and vegetative cover. On the study area, observation efficiency averaged 50% from a fixed-wing, but at Rochester it averaged 65% from a helicopter (Rolley and Keith in press). The Rochester study area was also more open and with fewer conifers than the Bitumount study area.

5.2 RATE OF POPULATION INCREASE

Estimates of moose densities in the Bitumount study area between 1973 and 1978 (Table 1) suggested a stationary or slowly declining population. As noted earlier, slightly higher numbers in the winter of 1977-78 were related to greater snow depths which apparently increased seasonal ingress from other section in the AOSERP study area.

As an alternative check on the status of the moose population, its rate of increase (r_s) and stable age distribution were calculated from estimates of age-specific survival and fecundity in the radio-collared sample. [The interative technique described by Caughley (1977:110) was used.] Mean annual survival rates of calves and older individuals were 0.27 and 0.75, and fecundity averaged 66 calves/100 2 year old cows and 88/100 older cows. The resulting exponential rate of increase (r_s) was -0.189 annually, or a finite rate of increase (λ) of 0.83. This predicted decline of 17% annually would occur upon stabilization of the population's age distribution at 12% yearlings, 11% 2 year olds and 77% older individuals. The latter comprised 73% of the sample of 70 yearling and older moose darted during 1976-77 (Table 2).

A second rate of increase was similarly calculated using the highest yearling and adult survival rate of 0.76 estimated for the the entire AOSERP study area from demographic and kill data (Table 15). In this case, r_s was -0.177 (λ = 0.84); a predicted decline of 16% annually.

It seems clear from the above analyses, and density estimates since 1973, that the moose population in this region is at best stationary, and probably declining. Although information from elsewhere on yearling and adult survival is scarce, the two independent estimates of 0.75 and 0.76 to 0.77 annually are close to the 0.74 and 0.87 (Coady 1976) and 0.84 (Didrickson and Taylor 1978) reported from Alaska. The unhunted predator-free population at Rochester, Alberta, had a combined yearling and adult survival rate of 0.84 annually (Mytton and Keith in press).

The data on reproduction, though limited, suggest rates comparable to most other moose populations in Canada and Alaska (summarized by Simkin 1974; Rolley and Keith in press). However, the exceptionally high rates of reproduction at Rochester (Rolley and Keith in press; Mytton and Keith in press), 300 km south, were well above those in the AOSERP study area. Calf-cow ratios and twinning rates among radio-marked adult cows observed largely within 1 wk after calving were 166/100 and 88% at Rochester, and 88/100 and 37% at Fort McMurray. The present authors do not believe these reproductive indices reflect different range conditions--there was no obvious impact of moose on the abundant browse in either area. A more likely explanation is that the lower winter temperatures at Fort McMurray increased energy demands sufficiently to depress fecundity and/or neonate survival. Rolley and Keith (in press) found through multiple regression that 76% of annual variation in percent calves at Rochester was associated with numbers of days during preceding winters with (1) mean temperatures below -12°C and (2) snow depths exceeding 25 cm. During 1966-76, the number of days annually with mean temperatures below -12°C averaged 53% more at Fort McMurray than at Rochester; whereas days with snow depths above 25 cm averaged 10% less. If the above regression primarily indicates reproductive change, then about one-third of the reduction in the ratio of newborn calves to cows at Fort McMurray versus Rochester can be ascribed to lower winter temperatures.

The single most important difference between the stationary or decreasing population and others that are increasing appears to have been lower calf survival. Annual survival of calves at Rochester, for example, averaged 0.54 compared to 0.27 in the study area. This difference undoubtedly reflects the largely predator-free environment at Rochester. It was earlier estimated that wolves could account for at least 29% of annual mortality of calves in the AOSERP study area. The present authors strongly suspect that a substantial amount of the high early mortality there (39% within the first month) was caused by black bears. It has been shown recently that black bears are major predators on elk calves in Idaho (Schlegel 1976) and moose calves in Alaska (Franzmann and Peterson 1978; Franzmann and Schwartz 1978).

An immediate practical implication of the foregoing conclusions is that the rate of exploitation of moose in the AOSERP study area likely cannot be raised without producing a major population decline. This assumes that hunting mortality and predation are not compensatory, an assumption that is becoming increasingly accepted (Keith 1974). The most promising means of improving the rate of increase, and hence allowable harvest, would be to reduce the early mortality of calves. Before this can be done, however, more must be known about the factors involved in such losses.

5.3 COVERTYPE USE

The greater use of taller and denser upland cover in summer has been noted by Van Ballenberghe and Peek (1971) and Peek et al. (1976), and may be related to a higher protein content of browse there. Oldemeyer (1974) reviewed the nutritive value of browse and stated that protein is generally considered the most important plant nutrient. Laycock and Price (1970) and Vallentine and Young (1959) (cited in Oldemeyer 1974) found a higher protein content of plants growing under a canopy than in the open.

Peek et al. (1976) also suggested that taller and denser cover might reduce harassment of moose by larger diptera.

A significant rise was noted in upland usage in October. This may be the result of bulls moving into uplands while searching for cows (Peek et al. 1976). Upland use by bulls increased by 11% from September to October, whereas cows increased their use by 5%. Berg and Phillips (1974) observed increased use of "tall-mature" forest cover in October in northwestern Minnesota during 1970, but not during 1971.

A shift to open lowlands in November to December was made by both bulls and cows (Figure 10), but more so by the former. Peek et al. (1976) stated that use of open areas in early winter probably is related to the bull's need to recover fat reserves lost during the rut, or at least to decrease rate of weight decline. November and December are also the months when aggregations were largest. Mytton and Keith (in press), Lynch (1975), and Gasaway (1978) likewise observed high use of open lowlands in late fall and early winter.

The later winter (January to March) shift from lowland to upland habitat seems to be related primarily to rising snow depths. Houston (1968), Chamberlin (1972), and Telfer (1970) also reported greater usage at that time of areas having less snow.

The dramatically increased use of lowlands in spring (April to May) recorded by the present authors was noted earlier in northeastern Minnesota (Berg and Phillips 1974). Movements into open covertypes also occurred in New Brunswick (Kelsall and Prescott 1971) and Wyoming (Houston 1968). This increased use of open areas has been tied to their earlier snowmelt and green-up (Houston 1968; Phillips et al. 1973; Berg and Phillips 1974). There is probably a need to obtain high quality forage among cows in late stages of pregnancy and the negative energy balance afflicting both sexes throughout winter (Gasaway and Coady 1974). It may well be that such open areas, predominantly lowlands, comprise the most critical element in the year-round habitat of moose.

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