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MOOSE RESEARCH CENTER REPORT

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Volume XIII
Project Progress Report
Federal Aid in Wildlife Restoration
Project W-17-4, Jobs 1.1R, 1.2R, 1.3R and 1.4R

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JOB PROGRESS REPORT (RESEARCH)

State:	Alaska		
Cooperators:	Alaska Department of Fish and Game, U.S. Bureau of Sport Fisheries and Wildlife, Kenai National Wildlife Range		
Project No.:	W-17-4	Project Title:	Big Game Investigations
Job No.:	1.1R	Job Title:	Moose Productivity and Physiology
Period Covered:	July 1, 1971 through June 30, 1972		

SUMMARY

Natality, mortality and yearling recruitment of moose (*Alces alces gigas*) were determined in four 2.6 km^2 (one square mile) pens. Calf production and survival-to-yearling were 11 percent and 0 percent, respectively, both lower than in previous years. One pen, stocked with 44 moose in autumn, contained only 14 animals the following spring because of natural mortality. At the close of the reporting period, the four pens contained 52 moose, or five per km^2 (13 per square mile). This represents a decline of 31 percent from the preceding spring. The total loss of calves was attributed primarily to the early arrival and persistence of snow cover.

The available literature in English on the hematology, blood chemistry, protein polymorphisms and endocrinology of the Cervidae was compiled and tabulated. A review of blood chemistry of moose and other Cervidae was published. Since the recurrent stated purpose of these clinically oriented studies has been evaluation of herd and range conditions, the possible analyses of data in terms of diagnostic patterns are presented. The available data demonstrate that before such management-related interpretations can be made, one must consider the effects of age, sex, season, reproductive condition, and methods of handling. Given these boundary conditions, experimental studies have demonstrated effects of nutritional level and disease on blood values in species of *Odocoileus* and *Alces alces*. Serum urea nitrogen levels (BUN) appear to be directly related to nutritional status in several cervid species. Measurements of serum albumin and hemoglobin are not sensitive indicators although they decline with severe deficiencies. A decline in serum thyroxine with nutritional restriction has been reported in *Odocoileus virginianus*. This hormone declines over winter in Alaskan moose. The metabolic shifts occurring in malnutrition and starvation as reflected in plasma nonesterified fatty acids, amino acids, ketones, and short-chain fatty acids await study in the cervids. They offer the possibility of more sensitive indicators of metabolic status. Protein polymorphisms have been described for transferrin in *Rangifer* and *Odocoileus*, and for hemoglobin in *Odocoileus virginianus*. Studies of *Alces* have shown no polymorphisms. Fibrinopeptide sequences have suggested that *Alces*, *Rangifer*, and *Odocoileus* are closely related genera.

A selected bibliography on blood chemistry of moose and other Cervidae is presented.

Weights of 70 moose of known age are presented, as are chemical and proximate analyses of important forage plants and of rumina from moose on seral birch and upland willow range. No significant differences were demonstrated in these analyses of rumina from the two ranges. Analyses of forage species indicate the need for variety in moose diets. Correlations between protein and ether extract in rumina and fecal pellets from the same moose were highly significant.

A maximum snow depth of 67 cm, with depths exceeding 50 cm for three consecutive months in most habitats, was found to be sufficient to cause high winter mortality in the Moose Research Center.

A summary of composition, production, rate of growth and shape of burn, diversity and "edge effect" in the Kenai (1947) burn is presented, as is a summary of the importance of nonbrowse foods to moose on the Kenai Peninsula.

CONTENTS

BACKGROUND

The Kenai Moose Research Center was established in 1966-1969 as a controlled environment within which to study moose-habitat interrelations. Research at the Center has stressed nutritional aspects of moose growth and productivity and quality, quantity and availability of plants eaten. LeResche (1970) and LeResche and Davis (1971) discussed the management problems considered and the approaches taken at the Moose Research Center.

OBJECTIVES

To measure natality, mortality and general condition of moose within four 2.6 km^2 (one square mile) enclosures.

To establish baselines by season, age and sex for the following serological and hematological parameters in moose and to evaluate their usefulness as indicators of nutritional status in moose:

A. calcium
B. inorganic phosphorus
C. glucose
D. urea nitrogen (BUN)
E. uric acid
F. cholesterol
G. total protein
H. albumin
I. albumin/globulin ratio
J. alpha-1, alpha-2, beta and gamma-globulins
K. bilirubin
L. alkaline phosphatase

M. lactic dehydrogenase (LDH)
N. glutamic oxalacetic transaminase (SGOT)
O. hemoglobin
P. hematocrit
Q. white blood cells
R. differential cell count (including segmenters, lymphocytes, eosinophils, monocytes, basophils)

To estimate browse production and utilization and quantitatively and qualitatively estimate consumption of all plant material by moose.

To learn changes in rumen protozoa levels in moose on various winter diets.

To learn nutritional values and digestibilities of the more common moose forage species of plants.

PROCEDURES

General Description of the Moose Research Center Facility

The Kenai Moose Research Center comprises four 2.6 km^2 (one square mile) enclosures located in the area of the 1947 burn near Kenai, Alaska. These enclosures contain representative vegetation of both burned (regenerative: predominately birch *Betula papyrifera* and white spruce *Picea glauca*) and remnant: (mixed birch-spruce-aspen *Populus tremuloides* stands). Marshland typical of summer range is included as are well-drained hillocks supporting winter browse species.

The entire area has been type-mapped into 11 vegetation types, and soil profiles of representative types have been completed. Five five-acre exclosures are present, at least one within each enclosure.

Twenty-one fenceline traps have been consturcted; 12 within pens and nine on the outside of the fenceline. Fig. 1 is a generalized map of the facility showing traps, exclosures, etc.

The log headquarters building sleeps eight, and is accessible by road during dry seasons. Two-mile-long Coyote Lake provides access by float or ski plane. The Center may be reached by light plane from Anchorage in one-half hour.

Populations of moose within the enclosures as of February 1, 1970, five months after enclosing Pens 3 and 4, were:

Pen	Cows	Calves	Bulls	Total
1	5	0	2	7
2	9	1	2	12
3	7	4	1	12
4	11	5	2	18
	32	10	7	49

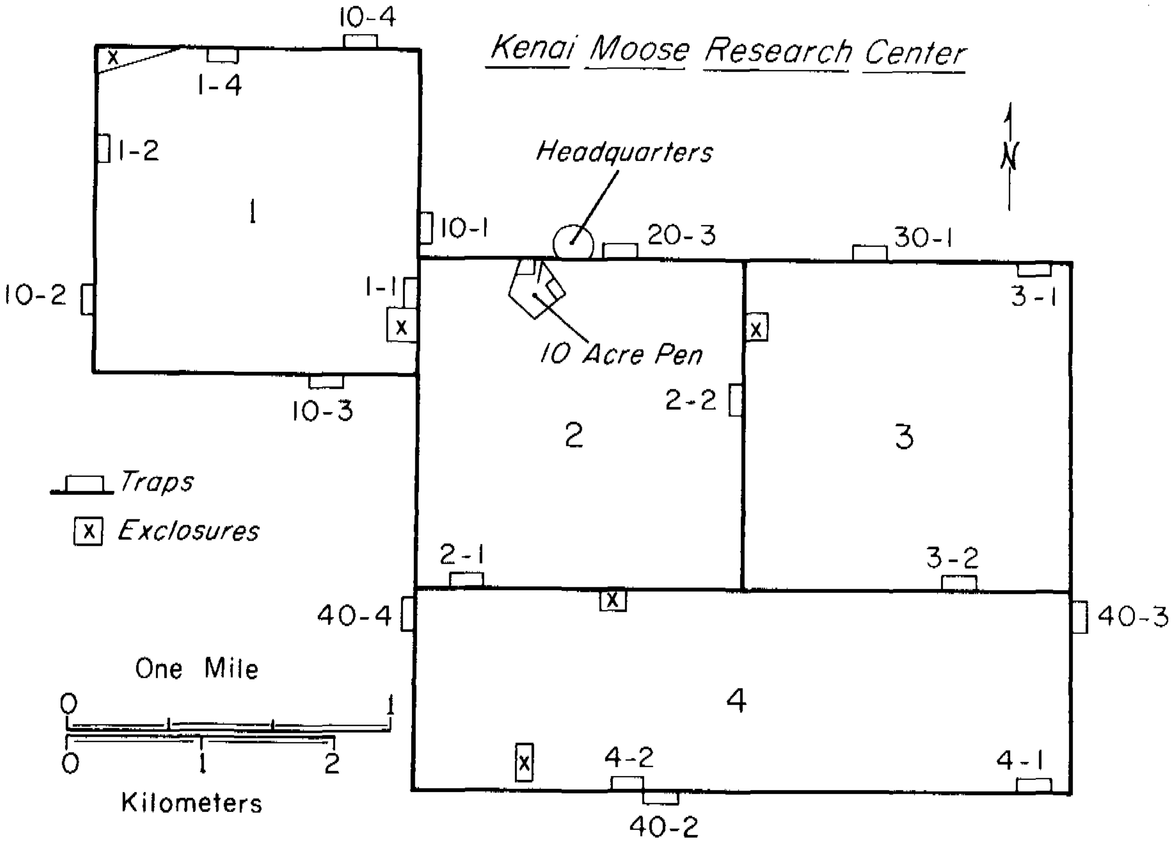

Fig. 1. Map of Moose Research Center.

Pens 1 and 2 will be left unmolested in terms of moose numbers, allowing the populations to increase, decrease, or remain constant as they will. Pen 3 will be retained at its present population level and sex structure, as representative of extra-pen populations in this area. Pen 4 will be used as an experimental pen, with abnormally high and low densities of moose present.

Table 1 is a history of major events in construction of the facility and provides reference as to timing of events leading to the current description.

Productivity and Mortality

Mortality and natality within pens are measured by daily ground observations, periodic aerial observations, trapping and use of radio-tracking devices. General condition is estimated for trapped animals by methods described below.

Blood

Blood values are determined from serum and whole-blood samples obtained from trapped and hunter-killed moose and animals immobilized for marking outside of traps (Job 1.4). Table 2 lists sources of blood material.

Blood is obtained from live immobilized animals in sterile evacuated containers by jugular venepuncture. Four or five cc of whole blood are preserved with EDTH and a thin smear is made; serum is secured by centrifugation of cooled and clotted blood. Serum is separated into: 1) a NaF tube (1.5-2 cc) for glucose determination; and 2) a 4-5 cc untreated sample for analyses of other parameters.

Analyses are performed by Alaska Medical Laboratories (Anchorage) using a Technicon Autoanalyzer SMA-12, standard hematological techniques and electrophoresis.

A review paper was prepared by LeResche, U. S. Seal (Veterans Hospital, Minneapolis), P. D. Karns (Minnesota Department of Natural Resources) and Franzmann for the International Symposium on Moose Ecology, Quebec. It is titled "A review of blood chemistry of moose and other Cervidae, with emphasis on nutritional assessment", and will appear in Le Naturaliste Canadien in fall 1973, and in "*Alces*", the symposium proceedings. A bibliography of blood studies of the Cervidae was also prepared.

Stress Evaluation

The influence of stress, particularly that which relates to excitability, on an animal during sampling procedures can influence the physiologic values obtained (Franzmann, 1972; LeResche et al., 1973b). Some values are influenced more than others and some may not be affected at all. The basic objective of this phase of research will be to correlate the physiologic values with excitability.

Table 1. Chronology of establishing the Kenai Moose Research Center.

June 1966:	Construction begun.
September-October 1967:	Browse production estimated in Pens 1 & 2. Successional plots established and read in Pens 1 & 2.
January 1967:	Pens 1 & 2 enclosed.
January 1968:	Moose in Pens 1 & 2 collared.
April 1968:	Browse utilization estimated in Pens 1 & 2.
1968:	Yearling bull introduced into Pen 1.
April 1969:	Browse utilization estimated in Pens 1 & 2.
June 1969-January 1970:	Eleven traps constructed in all pens. Blood collections begun.
June-July 1969	Successional plots established and read in Pens 3 & 4.
August 1969:	Pens 3 & 4 enclosed.
October 1969:	Two male calves introduced into 10-acre pen in Pen 2.
January-February 1970:	Numbers of moose in Pens 3 & 4 determined. Replicate count experiments conducted.
April 1970:	Browse utilization estimated in all four pens. Plots cleaned of pellets.
May 1970:	Female calf introduced into 10-acre pen in Pen 2.
August 1970:	Twenty traps complete: 11 inside pens; nine outside.
November 1970:	Two male yearlings released from 10-acre pen into Pen 2.
March 1971:	Replicate count experiments conducted.
May-June 1971:	Pellet-plots counted and cleared in Pen 1. Browse utilization estimated in Pen 1.
June 1971:	Numbers of moose in pens redetermined and calves counted.

Table 1. (cont'd.)

September-December 1971:	Pen 4 stocked with 44 moose, including orphaned calves.
June 1972:	Numbers of moose in pens redetermined and calves counted.

Table 2. Sources of moose blood for analysis: June 1969-May 1971.

Source	NUMBER OF SPECIMENS Serum	Whole Blood	Slides
Trapping at Moose Research Center:			
Pen 1	20	15	5
Pen 2	25	16	10
Pen 3	15	13	7
Pen 4	22	15	12
Outside pens	40	26	9
Total Moose Research Center	122	85	43
Hunts:			
1969-70			
GMU 15C	32	26	49
15B	13	6	21
14A	39	26	42
14B	14	6	9
1970-71			
GMU 7	7	2	0
15A	28	0	0
Total Hunts	133	66	121
Tagging:			
Bottenintnin Lake (1970)	38	23	6
Moose River Flats (1970)	61	0	0
Skilak-Tustumena Beach (1971)	3	0	0
Moose River Flats (1971)	60	0	0
Total Tagging	162	23	6
TOTALS	417	174	170

To determine the excitability stress, heart rate, respiratory rate, and rectal temperature were recorded from each moose sampled. Each individual was subjectively judged for excitability prior to and during handling. The moose is given a score of 1 (not excited), 2 (slightly excited), 3 (moderately excited), 4 (excited), 5 (highly excited), based upon observations. The ambient temperature is also recorded.

The physiologic values obtained will be tested to determine the influence of excitability, if any, upon them. A blood value that can be used as an excitability state monitor would be very useful, and would alleviate subjective evaluations.

The utilization of cellular enzyme tests will be studied to determine their relationship to excitability stress. Cellular enzymes are released when cells are destroyed during excitability, general stress, pathologic conditions, and normal cellular aging and destruction (Coles, 1967). An enzyme closely related to excitability stress would also prove useful in monitoring the relative excitability of an animal.

Hair

Hair analyses to study malnutrition and deficiencies in humans have been based upon hair shaft diameter and atrophy of hair bulb (Sims, 1968), hair root protein analysis (Crounse et al., 1970a,b), and trace element content (Strain et al., 1972). The possibility of utilizing one or more of these approaches by sampling moose hair was investigated.

For trace element analysis, 30 hair samples taken from moose in May and June were sent to Cleveland Memorial Hospital for analysis. Samples will be sent regularly throughout the year to determine if there are seasonal patterns and, if so, how they relate to blood analyses.

Root-hair protein analysis techniques are under investigation, and will be incorporated into the sampling procedure if feasible.

Weights and Measurements

Weights and measurements were obtained from trapped immobilized animals.

Chemical Analysis of Plants and Fecal Pellets

Birch, willow (*Salix* sp.), lowbush cranberry (*Vaccinium vitis idaea*), sedges and aspen (bark) were collected for nutritional analysis according to plant height, diameter and use-form class. All specimens were oven-dried at 70° C for 14 days. The following analyses were done by WARF, Inc.; Madison, Wisconsin:

Elemental: JAOAC, 51, 1003 (1968)

Protein: AOAC, 16 (1970) 11th ed.

DDM: Tilley & Terry, J. Br. Grassland Society, (2) 104 (1963), (Bovine Flora)

Ash: AOAC, 123 (1970) 11th ed.

Ether extract: AOAC, 128 (1970) 11th ed.

Fiber: AOAC, 129 (1970) 11th ed.

Snow Monitoring

Eight snow plots were established in Pens 1 and 2. One plot was located in each of the following habitat types: dense hardwoods, thin hardwoods, sedge meadow, spruce regrowth, birch-spruce regrowth (thin), birch-spruce regrowth (dense), spruce-*Ledum*, mature spruce. At approximately weekly intervals a trench was dug in each plot and thickness and general structure (e.g.: crystals, powder, ice) of each snow layer were recorded. The visibility of lowbush cranberry above snow was also recorded at this time.

Browse Production and Utilization

Browse production and utilization and plant succession are estimated using methods previously described in detail (Bishop, 1969). A canopy-cover method after Daubenmire (1959), employing exclosures, is used for successional measurements and a twig-count method with clipping is used for production and utilization estimates. During this reporting period use was estimated in all old plots in Pen 1, the 2.5 ha (10 acre) holding pen. A paper titled "Distribution and habitats of moose in Alaska" was prepared for the International Symposium on Moose Ecology by LeResche, R. H. Bishop and J. W. Coady. It will be published in autumn 1973.

Food Habits of Tame Moose

Tame moose were obtained as calves in October 1969 (two males) and May 1970 (one female). All were born in spring 1969. They were raised on natural moose range with calf starter feed (Alaska Mill Feed Co., Anchorage) fed supplementally until July 1970. The three were confined together in a 2.5 ha pen (containing a 1 ha lake) through November 1970. Summer observations were made within this pen. In November the males were released into Pen 2 with 14 other moose. "Normal range" winter observations were made of these animals. "Depleted range" winter observations were made of the female within the 2.5 ha pen, which had supported the equivalent of 82 moose per square km during the previous winter and was supporting 41 moose equivalents per square km during the winter of observations.

Tame moose were located by radio-telemetry and food intake was recorded by an observer standing 1-2 m from the moose and recording species and size of each bite eaten by pencil on an IBM optical page reader sheet or by speaking into a tape recorder. Hours of observation were distributed throughout daylight hours. Bite size in summer was recorded by estimating number of leaves ingested. Bites were classified in four categories: less than 5 leaves, 6 to 10 leaves, 11-20 leaves and more than 20 leaves. Mean number of leaves per bite in each category were taken as 2.5, 7.5, 15 and 25, respectively. Mean weight of each bite by category was then calculated as 2.5, 7.5, 15 and 25 times the mean weight of 500 randomly selected leaves from 100 separate plants. Bite size in winter was recorded by estimating length of stem ingested. Bites were classified in four categories: less than 3 inches (7.6 cm), 3 to 6 inches (15.2 cm), 6 to 12 inches (30.5 cm) and more than 12 inches. Mean length of stem in each bite category was taken to be 3.8 cm, 11.4 cm, 22.8 cm, and 38.1 cm, respectively. Thirty terminal stems of each of these lengths were then randomly clipped from six plants of each species considered. Mean weight per bite was calculated using the mean weight of the appropriate 30 stems. Biomass of food ingested per day was estimated by applying these weight/bite estimates to estimated bites/day.

A publication by LeResche and Davis, "Importance of nonbrowse foods to moose on the Kenai Peninsula, Alaska" was prepared for the Journal of Wildlife Management (37:2, in press).

Feeding Craters

Feeding crater concentrations were searched for and when found the habitat type was designated and the area of the concentration measured. Each crater was then measured in length, width, and depth. Species of plants eaten and present in each crater and their relative abundance were recorded. Also, the location of the craters within the plot was noted to determine if moose used keying characteristics before digging a crater. Snow profiles were taken at each crater concentration area.

FINDINGS

Productivity and Mortality Within Pens

Table 3 presents complete tagging, breeding, and mortality data for all moose within the enclosures. Table 4 summarizes these data in terms of numbers calving and dying. Table 5 calculates natality, yearling recruitment and change in population size for penned and unpenned populations, as summarized in Table 6.

On 1 July, 1972, populations within the 4 pens totaled 52 moose (13 per square mile). Components of the populations are tabulated in Table 7, and trends since 1968 are shown in Table 8 and Fig. 2.

These data reflect more stable population levels than might be predicted from the accompanying severe annual fluctuations in the "indicator" parameters of calf production, calf mortality and yearling recruitment. From 1968 through 1972, known June calf production in the four MRC pens has varied between 15 and 72 calves per 100 adult females (11-45% of adult moose) and yearling recruitment has varied from none to 41-45 yearlings per 100 adult females (0-33% of adult moose). Nevertheless, absolute numbers have changed only a mean of two percent in the five years since 1968. Data collected in the area surrounding the MRC (Table 5) by various workers follow a similar pattern, with estimated calf production varying from 21-48 per 100 cows and yearling recruitment

Table 3. Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 1

Moose #	Sex	Event	Date	Age	Circumstances
3	F	Weight 790 lbs.	31 August 1971	9+ years	Trapped
		With no calf	13 March 1972	9+ years	Observed
		Weight 650 lbs. with no calf	24 June 1972	10 years	Trapped
371	F	Weight 260 lbs.	31 August 1971	Calf	Roped in trap
		Last seen	4 November 1971	Calf	Observed
6	F	Weight 790 lbs.	24 August 1971	14+ years	Trapped
		Last seen alive	20 February 1972	14+ years	Observed
		Found dead	10 May 1972	15 years	Helicopter
10	F	Weight 635 lbs.	11 August 1971	4+ years	Trapped
		With no calf	6 October 1971	4+ years	Observed
		Last observed	22 May 1972	5 years	Observed
R70-8	F	With no calf	23 March 1972	3+ years	Helicopter
		Last handled	8 June 1972	4 years	Trapped
40	F	With no calf	23 March 1972	3+ years	Helicopter
		Last handled	27 June 1972	4 years	Trapped
670	F	Retagged	8 May 1972	2 years	Helicopter
		Last observed	25 June 1972	2 years	Supercub
61	F	Tagged (2 calves outside trap)	2 September 1971	9+ years	Trapped
		With no calves	23 March 1972	9+ years	Helicopter
		Last observed	10 May 1972	10 years	Helicopter

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

			PEN 1		
Moose #	Sex	Event	Date	Age	Circumstances
69	F	Tagged	8 May 1972	3 years	Helicopter
		Last handled	6 June 1972	3 years	Trapped
35	M	Last handled	27 June 1972	4 years	Trapped
43	M	Weight 1040 lbs.	4 October 1971	4+ years	Trapped
		Last handled	22 June 1972	5 years	Trapped
53	M	Tagged	15 July 1971	1+ years	Trapped
		Last Handled	28 June 1972	2 years	Trapped
55	M	Died from drug Weight 500 lbs.	10 August 1971	1 years	Trapped
58	M	Tagged	31 August 1971	1+ years	Trapped
		Last observed	20 June 1972	2 years	Helicopter
64	M	Tagged, weight 620 lbs.	2 April 1972	2+ years	Trapped
		Last handled	28 June 1972	3 years	Trapped
UC	F				
370UC	M		After June 3, 1971 these individuals were not again identified and could be dead or later tagged		
1070UC	M				
4070UC	?				

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 2

Moose #	Sex	Event	Date	Age	Circumstances
1	F	With one calf	12 August 1971	8+ years	Trapped
		With no calf	3 February 1972	8+ years	Observed
		Weight 700 lbs.	22 June 1972	9 years	Trapped
		Last trapped	28 June 1972	9 years	Trapped
2(R69-3)	F	With no calf	23 February 1972	7+ years	Observed
		Last seen (presumed dead)	23 March 1972	7+ years	Helicopter
7(R70-7)	F	With no calf	27 January 1972	8+ years	Observed
		With one calf	20 June 1972	9 years	Helicopter
		Last seen with calf	29 June 1972	9 years	Observed
9	F	With no calves	1 February 1972	9+ years	Observed
		Found dead	8 May 1972	10 years	Helicopter
52	F	With no calf	14 December 1971	4 years	Observed
		With one calf	20 June 1972	5 years	Helicopter
		Last handled	29 June 1972	5 years	Trapped
R70-2	F	Died from drug	15 July 1971	4 years	Trapped
R70-4	F	With 2 calves	5 October 1971	4+ years	Observed
		With no calves	17 December 1971	4+ years	Observed
		Last seen	28 June 1972	5 years	Observed
Raquel	F	With one calf	2 July 1971	2 years	Observed
		Fistula installed	23 August 1971	2 years	Trapped
		Fistula lost	2 September 1971	2 years	Trapped
		Weight 775 lbs.	24 June 1972	3 years	Trapped

Table 3. (cont't.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 2

Moose #	Sex	Event	Date	Age	Circumstances
62	F	Tagged	1 December 1971	19+ years	Trapped
		Paralyzed from darting, killed, weight 850 lbs.	27 January 1972	19+ years	Trapped
63	F	Tagged	22 March 1972	4+ years	Trapped
		Found dead	8 May 1972	5 years	Helicopter
66	F	Died, acute hemorragic enteritis, weight 720 lbs.	2 April 1972	9+ years	Trapped
68	F	Tagged	8 May 1972	9 years	Helicopter
		Found dead, died while calving	20 June 1972	9 years	Observed
70	F	Died, broke neck on fence during helicopter tagging	8 May 1972	5 years	Helicopter
76	F	Tagged, limps	10 May 1972	9 years	Helicopter
		With one calf	20 June 1972	9 years	Helicopter
77	F	Tagged	10 May 1972	6 years	Helicopter
		Weight 605 lbs.	23 June 1972	6 years	Trapped
UC	F	With one calf	20 June 1972	?	Helicopter
36	M	Fighting with #43M through fence	17 October 1971	4+ years	Observed
		Last seen	29 June 1972	5 years	Observed

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 2

Moose #	Sex	Event	Date	Age	Circumstances
45	M	Last seen	28 June 1972	4 years	Observed
Richard	M	Killed being lead by antlers, weight 775 lbs.	10 August 1971	2 years	Free-ranging
Walter	M	Weight 640 lbs.	23 July 1971	2 years	Free-ranging
		Died after fistula surgery	30 July 1971	2 years	Trapped
Walter, Jr. (Raquel's calf)	M	Weight 470 lbs.	28 April 1972	1- years	Trapped
		Weight 515 lbs.	24 June 1972	1 years	Trapped
54	M	Weight 355 lbs.	27 July 1971	1 years	Trapped
		Last seen (presumed dead)	23 February 1972	1+ years	Observed
65	M	Tagged	2 April 1972	1+ years	Trapped
		Last seen	28 June 1972	2 years	Observed
73	M	Tagged	10 May 1972	3 years	Helicopter
		Weight 525 lbs.	5 June 1972	3 years	Trapped
78	M	Tagged	30 June 1972	4 years	Trapped
UC	M	Last seen	30 June 1972	?	Observed

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

Moose #	Sex	Event	Date	Age	Circumstances
			PEN 2		
R70-2-70UC	?		After June 3, 1971 these individuals were not again identified and could be dead, later tagged, or still uncollared and alive in Pen 2.		
UC70UC	?				
5270UC	?				
			Pen 3		
20	F	With no calf, limping badly	12 October 1971	11 years	Observed
		Found dead	20 June 1972	12 years	Observed from helicopter
27	F	With no calf	20 June 1972	6 years	Observed from helicopter
28	F	Killed, weight 760 lbs.	12 August 1971	9 years	Dart entered vagina
38	F	With no calf	20 June 1972	18 years	Observed from helicopter
39	F	With no calf	20 June 1972	7 years	Observed from helicopter
		Weight 535 lbs.	23 June 1972	7 years	Trapped
UC	F	Observed	10 May 1972	?	Observed from helicopter
60	M	Weight 850 lbs.	31 August 1971	4 years	Trapped
		Found dead 150 meters from trap	1 September 1971	4 years	Observed

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 3

Moose #	Sex	Event	Date	Age	Circumstances
2870	F	Not bred (rectal palpation)	9 May 1972	2 years	Immobilized via helicopter
		With no calf	20 June 1972	2 years	Observed from helicopter
2771	F	Weight 155 lbs.	27 July 1971	Calf	Trapped
		Found dead	16 February 1972	Calf	Observed
67	F	Tagged, could be 2069, 3970, or UC female	8 April 1972	1+ years	Trapped
		Found dead	9 May 1972	2 years	Observed from helicopter
72	F	Tagged, could be 2069, 3970, or UC female	9 May 1972	2 years	Immobilized via helicopter
		With no calf	20 June 1972	2 years	Observed from helicopter
75	F	Tagged, could be 2069, 3970, or UC female	10 May 1972	3 years	Immobilized via helicopter
		With no calf	20 June 1972	3 years	Observed from helicopter
UC	M	Observed	20 June 1972	?	Observed from helicopter

PEN 4

Moose #	Sex	Event	Date	Age	Circumstances
22	F	With no calf	20 June 1972	7 years	Observed from helicopter
24	F	Found dead	10 May 1972	10 years	Observed from helicopter

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 4

Moose #	Sex	Event	Date	Age	Circumstances
31 (R-70-1)	F	Killed, weight 640 lbs.	25 August 1971	7 years	Trapped, did not recover from Anactine
34	F	Found dead	23 Mar 1972	14 years	Observed from air
36	F	With no calf	20 June 1972	9 years	Observed from helicopter
37	F	With no calf	20 June 1972	3 years	Observed from helicopter
R-70-3	F	Weight 680 lbs, with calf	11 August 1971	4 years	Trapped
		With no calf	20 June 1972	5 years	Observed from helicopter
A60	F	Weight 750 lbs. with calf	10 August 1971	13+ years	Trapped
		Found dead	9 May 1972	14+ years	Observed from helicopter
21	M	Found dead	26 February 1972	3 years	Observed
44	M	Found dead	9 May 1972	3+ years	Observed from helicopter
7	M	Trapped	1 September 1971	2 years	Trapped
		Observed	20 June 1972	3 years	Observed from helicopter

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 4

Moose #	Sex	Event	Date	Age	Circumstances
UC			After 3 June 1971, those individuals were not again identified and could be dead, later tagged, or still uncollared and alive in pen 4.		
2470UC					
3670UC					
R70-1-70UC					
R70-3-70UC					
4170	M	Survived to yearling	27 July 1971	1 years	Observed
		Last seen	4 February 1972	1 years	Observed
57	F	Tagged	25 August 1971	1 years	Trapped
		With no calf	16 June 1972	2 years	Observed
59	M	Tagged	1 September 1971	1 years	Trapped
		Observed	20 June 1972	2 years	Observed from helicopter
118	F	Put into Pen 4	16 November 1971	1+ years	Trapped
		With no calf	20 June 1972	2 years	Observed from helicopter
121	M	Put into Pen 4	23 November 1971	1+ years	Trapped
		Found dead	23 March 1972	1+ years	Observed from helicopter
123	F	Put in Pen 4, weight 765 lbs.	1 December 1971	?	Trapped
		With 1 calf	14 June 1972	?	Observed

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 4

Moose #	Sex	Event	Date	Age	Circumstances
126	F	Put into Pen 4, weight 790 lbs.	15 December 1971	17+ years	Trapped
		Found dead	8 March 1972	17+ years	Observed
128	F	Broke into Pen 4,	26 January 1972	?	Trapped
		With no calf	20 June 1972	?	Observed from helicopter
134	M	Put into Pen 4, weight 360 lbs.	22 March 1972	Calf	Trapped
		Found dead	23 March 1972	Calf	Observed
R-72-1	F	Tagged, put into pen 4	20 April 1972	10 years	Trapped
		Found dead	24 May 1972	10 years	Observed
71	F	Tagged	9 May 1972	3 years	Immobilized via helicopter
		With no calf	20 June 1972	3 years	Observed from helicopter
74	F	Tagged	10 May 1972	2 years	Immobilized via helicopter
		Found dead	3 June 1972	2 years	Observed
70371	F	Tagged, weight 210 lbs.	11 August 1971	Calf	Trapped
		Found dead	10 May 1972	Calf	Observed from helicopter
56	M	Tagged, weight 545 lbs.	11 August 1971	1 years	Trapped
		Found dead	25 May 1972	2 years	Observed
9671	F	Tagged and radio-collared, weight 350 lbs.	21 September 1971	Calf	Trapped
		Found dead	10 May 1972	Calf	Observed from helicopter

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

			PEN 4		
Moose #	Sex	Event	Date	Age	Circumstances
9771	F	Tagged and radio-collared, weight 320 lbs., put into Pen 4	22 September 1971	Calf	Trapped
		Found dead	14 January 1972	Calf	Observed
9871	F	Tagged and radio-collared, weight 400 lbs., put into Pen 4	29 September 1971	Calf	Trapped
		Found dead	15 January 1972	Calf	Observed
10671	M	Tagged and radio-collared, weight 350 lbs., put into Pen 4	12 October 1971	Calf	Trapped
		Found dead	27 December 1971	Calf	Observed
10771	F	Tagged and radio-collared, weight 410 lbs., put into Pen 4	12 October 1971	Calf	Trapped
		Found dead	14 January 1972	Calf	Observed
10871	F	Tagged and radio-collared, weight 385 lbs., put into pen 4	13 October 1971	Calf	Trapped
		Found dead	10 December 1972	Calf	Observed
10971	F	Tagged and radio-collared, weight 395 lbs., put into Pen 4	20 October 1971	Calf	Trapped
		Found dead	15 January 1972	Calf	Observed

Table 3. (cont'd.) Histories of individual moose in Kenai Moose Research Center enclosures, July 1971 through June 1972.

PEN 4

Moose #	Sex	Event	Date	Age	Circumstances
11071	M	Tagged and radio-collared, weight 385 lbs., put into Pen 4	21 October 1971	Calf	Trapped
		Found dead	13 January 1972	Calf	Trapped
11471	M	Tagged, weight 370 lbs.	2 November 1971	Calf	Trapped
		Found dead	6 June 1972	Calf	Observed
11571	F	Tagged, weight 440 lbs. put into Pen 4	3 November 1971	Calf	Trapped
		Found dead	9 May 1972	Calf	Observed from helicopter
12071	M	Tagged, weight 465 lbs.	23 November 1971	Calf	Trapped
		Found dead	23 December 1971	Calf	Observed
6071	M	Tagged, weight 195 lbs.	10 August 1971	Calf	Trapped
		Found dead	16 June 1972	Calf	Observed
UC small	F	Observed	20 June 1972	?	Observed from helicopter
UC large	F	Observed	20 June 1972	?	Observed from helicopter

Table 4. Moose natality, mortality, and recruitment in four one-square-mile enclosures.

	Adult F (M)	Calves	Calves lost	Yearlings recruited	Adults Died (including) long yearlings)	Net gain (+) or Loss (-) of Adults (discounting experimental manipulation)
PEN 1						
June 1972	7 (5)	0		0		
June 1971-June 1972			5		2	
PEN 2						
June 1972	8 (6)	4		0		
June 1971-June 1972			8		9	
PEN 3						
June 1972	7 (1)	0		1		
June 1971-June 1972			2	1	4	3 (1 break in)
PEN 4						
June 1972	11 (2)	1		0		
June 1971-June 1972			6		11	

Table 5. June calf crops and yearling recruitment in Moose Research Center enclosures.

Year	Calf Crop Calves/100 F	(No. F)	Yearling Recruitment Yrlgs/100 F	Population (Adult) % Gain/loss (excluding manipulations)	(No. 1+ years old)
PEN 1					
1968	83	(6)	17		
1969	0	(4) (no breeding bull)	50	+17%	(6)
1970	100	(4)	No recruitment	No change	(7)
1971	83	(6)	80	+52%	(12)
1972	0	(7)	No recruitment	No change	(12)
x̄ (not incl. 69-70)	67		37	+17%	
PEN 2					
1968	12.5	(8)	25-38		
1969	50	(8)	9	+11%	(11)
1970	30	(10)	No recruitment	-8%	(12)
1971	100	(8)	25-38	No change	(13)
1972	50	(8)	No recruitment	No change	(14)
x̄	49		12-17	No change	
PEN 3					
1969 (August)	50	(8)	0	No data	
1970	29	(7)	38	No change	(10)
1971	33	(6)	38	No change	(10)
1972	0	(7)	No recruitment	-20%	(8)
x̄	28		18	-5%	

Table 5. (cont'd.) June calf crops and yearling recruitment in Moose Research Center enclosures.

					Population (Adult) % Gain/loss	
Year	Calf Crop Calves/100 F	(No. F)	Yearling Recruitment Yrlgs/100 F		(excluding manipulations)	(No. 1+ years old)
PEN 4						
1969 (August)	83	(12)	8		No data	
1970	45+	(9)	44-56		-21%	(14)
1971	75	(8)	50		+7%	(15)
1972	9	(11)	No recruitment		-7%	(14)
$\bar{x}$	53+		26-29		-7%	
ALL PENS						
1968	43	(14)	21-29			
1969	59	(27)	11		+13%	(15)
1970	43	(30)	25-29		-10%	(39)
1971	72	(29)	41-45		+11%	(44)
1972	15	(34)	No recruitment		-7%	(48)
$\bar{x}$	42	(134)	19-20		+2%	(146)
Unit 15A (Aerial counts by Richey (unpublished) and LeRoux (unpublished) and LeResche)						
				(No. F)		
1968	47	(1520)	18 (est.)	(1520)		
1969	48	(438)	7 (est.)	(438)		
1970	ca: 30	(ca: 500)	23	(496)		
1971	21	(657)	14	(166)		
1972	28	(106)	5	(248)		
$\bar{x}$	39	(ca: 3221)	15	(2868)	-3%**	

**Kenai National Moose Range stratified random mile-square quadrant counts (unpublished) indicated populations north of the Kasilof River of 6700 ± 1410 in winter 1967, 7900 ± 1460 in winter 1971 and 5700 ± 1348 in winter 1972-73. This represents a mean annual decrease of 3 percent for the six years, disregarding the variations in weather and observers and ignoring the confidence intervals.

Table 6. Calf production, calf mortality and yearling recruitment in four 2.6km^2 (1 mi.^{2}) enclosures.

Year	Calves Produced (% of Adults)	Yearlings Recruited (% of Adults)	June-June Calf loss (%)	June Population
1969	45	10	--	62
1970	35	20	56	57-58
1971	55	33	6	75
1972	11	0	100	52

Table 7. Populations within Moose Research Center enclosures as of 20 June 1972.

	Females with					
	No Calves	1 Calf	2 Calves	Yearlings	Males	Total
Pen 1	7	0	0	0	5	12
Pen 2	4	4	0	0	6	18
Pen 3	7	0	0	0	1	8
Pen 4	10	1	0	0	2	14
All Pens	28	5	0	0	14	52

SUMMARY

	Females	Yearlings	Calves	Males	Total
Pen 1	7	0	0	5	12
Pen 2	8	0	4	6	18
Pen 3	7	0	0	1	8
Pen 4	11	0	1	2	14
All pens	33	0	5	14	52

Table 8. Summary of moose populations within Moose Research Center enclosures, 1968 through June 1972.

		Females	Yearlings	Calves	Males	Total Moose
Pen 1	January 1968	6	0	1	0	7
	June 1968	6	1	5	1	13
	June 1969	4	2	0	1	7
	February 1970	4	2	0	1	7
	June 1970	5	0	4	2	11
	June 1971	6	4	5	2	17
	June 1972	7	0	0	5	12
Pen 2	January 1968	8	0	3	1	12
	June 1968	8	4	1	1	14
	June 1969	11	1	4	1	17
	February 1970	9	0	1	2	12
	June 1970	11	0	3	2	16
	June 1971	9	3	9	4	25
	June 1972	8	0	4	6	18
Pen 3	August 1969	8	0	4	1	13
	February 1970	7	0	4	1	12
	June 1970	6	3	2	1	12
	June 1971	6	2	2	2	12
	June 1972	7	0	0	1	8
Pen 4	August 1969	12	1	10	2	25
	February 1970	11	0	5	2	18
	June 1970	9	4-5	4	1	18-19
	June 1971	8	4	6	3	21
	December 1971					44
	June 1972	11	0	1	2	14
All Pens	June-August 1969	35	4	18	5	62
	February 1970	31	2	10	6	49
	June 1970	31	7-8	13	6	57-58
	June 1971	29	13	22	11	75
	June 1972	33	0	5	14	52

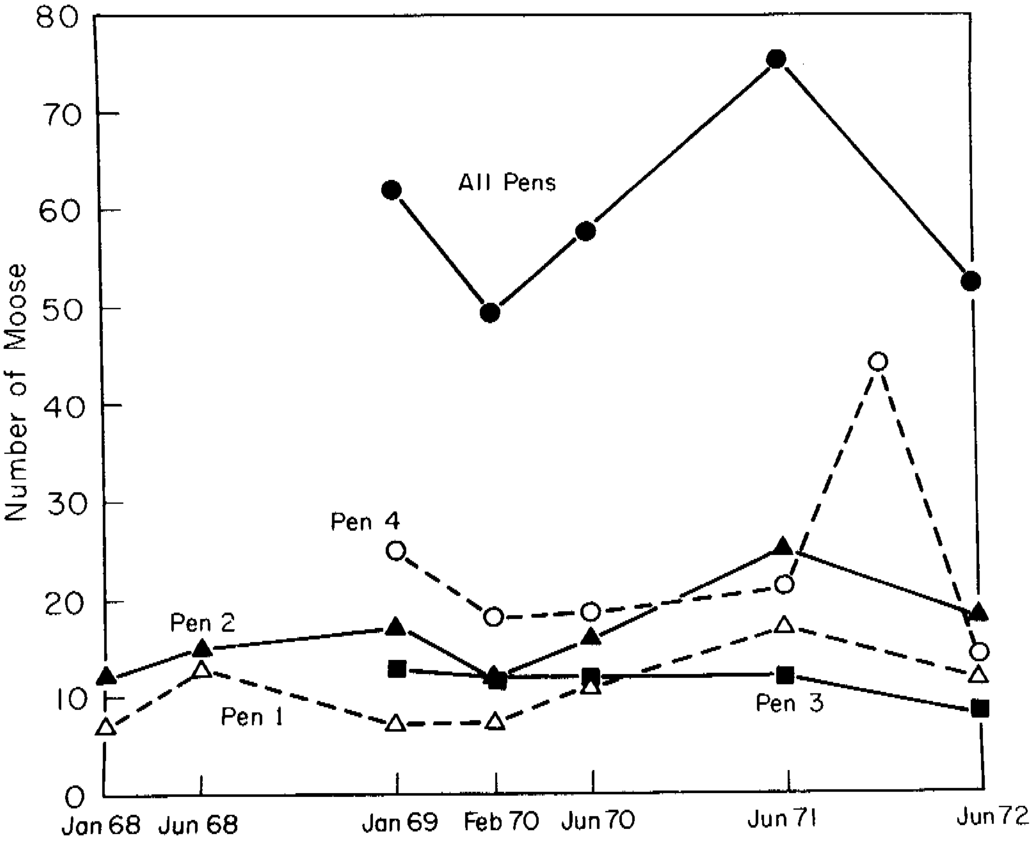

Fig. 2. Populations within Moose Research Center enclosures: 1968-1972.

varying from 5-23 per 100 cows; but total population changing only three percent per year since 1967, for a total decline of approximately 15 percent.

Both the MRC pens and the surrounding area demonstrate that long-term population levels may be more stable than annual fluctuations suggest, and that the effects of an especially "good" year or an especially "bad" year may be quickly erased by conditions in succeeding years. This apparent lack of steady trends likely reflects the relative short-term instability of a population of near maximum size.

Mortalities recorded within the pens during the reporting period are listed in Table 9. A disproportionate number of calves are represented, associated with the deliberate over-stocking of Pen 4 for the orphan calf survival study (Job 1.2R) and to the severity of the winter (LeResche and Davis, 1973).

Blood Chemistry as Indicator of Nutritional Status

Specimens of blood analyzed through June 1972 are listed in Table 2. Preliminary analyses of these data are summarized in the following publication:

Table 9. Mortalities within pens, July 1971 - June 1972.

Moose #	Sex	Age	Pen	Month - Year	Cause
60	M	4	3	September 1971	Found dead 150 meters from trap he was immobilized in on 8/31/71
20	F	12	3	October 1971-June 1972	Unknown, carcass found
28	F	9	3	August 1971	Killed with immobilizing dart (intravaginal)
67	F	1+	3	May 1972	Unknown, carcass found (winter kill)
21	M	4	4	February 1972	Unknown, carcass found (winter kill) was weak and in poor condition on 2/3/72
24	F	12	4	February 1972-May 1972	Unknown, carcass found (winter kill)
R-70-1	F	7	4	August 1971	Killed with drug
34	F	16	4	February 1972-March 1972	Unknown, carcass found (winter kill)
70371	F	calf	4	December 1971-May 1972	Unknown, carcass found (winter kill)
A60	F	15	4	December 1971-May 1972	Unknown, carcass found (winter kill)
56	M	1	4	February 1972-May 1972	Unknown, carcass found (winter kill)

Table 9. (cont'd.) Mortalities within pens, July 1971 - June 1972.

Moose #	Sex	Age	Pen	Month - Year	Cause
70171	M	calf	4	October 1971-December 1972	Unknown, carcass found (winter kill)
9671	F	calf	4	May 1972	Introduced into pen 4, carcass found
9771	F	calf	4	January 1972	Introduced into pen 4, carcass found
9871	F	calf	4	January 1972	Unknown, carcass found (winter kill)
10671	M	calf	4	December 1971	Unknown, carcass found (winter kill)
10771	F	calf	4	January 1972	Unknown, carcass found (winter kill)
10871	F	calf	4	December 1971	Unknown, carcass found (winter kill)
10971	F	calf	4	January 1972	Unknown, carcass found (winter kill)
11071	M	calf	4	January 1972	Unknown, carcass found (winter kill)
11471	M	calf	4	June 1972	Unknown, carcass found (winter kill)

Table 9. (cont'd.) Mortalities within pens, July 1971 - June 1972.

Moose #	Sex	Age	Pen	Month - Year	Cause
11571	F	calf	4	May 1972	Unknown, carcass found (winter kill)
12071	M	calf	4	December 1971	Unknown, carcass found (winter kill)
12171	M	calf	4	February 1972	Unknown, carcass found (winter kill)
126	F	advanced	4	March 1972	Unknown, carcass found (winter kill)
134	M	calf	4	March 1972	Unknown, carcass found (winter kill), found near trap next day after trapping, weak and poor.
R 72-1	F	advanced	4	May 1972	Introduced into pen and radio-collared due to pregnancy. Found carcass one month later.
74	F	1+	4	May 1972	Immobilized via helicopter, was weak and poor. Found carcass three weeks later.
6071	M	calf	4	June 1972	Unknown, carcass found (winter kill)

A REVIEW OF
BLOOD CHEMISTRY OF MOOSE AND OTHER CERVIDAE,
WITH EMPHASIS ON NUTRITIONAL ASSESSMENT

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Management of moose (*Alces alces*) throughout their range historically has relied upon the crudest assessments of habitat carrying capacity. These assessments have involved food habits studies (Peek 1973), range productivity (Seemel 1969) and utilization (Milke 1969, Telfer 1968) studies, and general population size and trend studies (Spencer and Chatelain 1953, Spencer and Hakala 1964, Rausch and Bratlie 1965). Secondary indicators of habitat's carrying capacity, as reflected in moose population characteristics, have also been relied upon. Population composition, natality and recruitment rates have been employed extensively to indicate populations' relationships with their habitat (Bishop and Rausch 1973, Pimlott 1959, Simkin 1965).

These secondary indicators in effect summarize the manifestations of nutritional, behavioral, environmental and genetic forces acting upon a population. They have been proven inadequate in situations where delicate control of moose populations is necessary. Such indicators are of little use as predictors and of even less value in understanding specific ecological relationships. Therefore, the trend in research since Peterson (1955) last summarized knowledge of moose has been toward analyses of individual primary factors rather than of their collective manifestations. This review concerns methods of measuring nutritional status of wild moose populations, and presents details of recent studies of moose blood chemistry as they relate to nutrition.

METHODS OF NUTRITIONAL ASSESSMENT

Nutritional status of individual wild animals can be assessed grossly or finely, and acutely or chronically. All body tissues reflect nutritional status and history to a greater or lesser extent, and possibilities for their analyses are as numerous as the tissues themselves. Ideally, the method for assessing nutritional status of moose populations should have several characteristics:

1. It should be sensitive to subclinical changes in nutritional status.

2. It should be specific in its indications: i.e. capable of indicating energy, mineral, protein, etc. balance.

3. It should be able to detect reasonably acute (e.g.: seasonal) changes in nutritional status.

4. It should involve tissues easily collected from both live (to allow serial collections from individuals) and dead (to allow use of hunter-killed and accident-killed specimens) moose and should be little affected by the stress of collection.

5. It should involve tissues which are easy for untrained personnel to collect and preserve, and which can be processed by standard inexpensive methods.

The broad spectrum of methods for nutritional assessment has been outlined by Jelliffe (1966). Methods we feel are potentially practical for use on moose include body weight and morphometry (LeResche and Davis 1971), analyses of urine (Blaxter et al. 1966), epithelial tissue (Squires 1963, Nutr. Rev. 1970), saliva (Murphy and Connell 1970), hair and nails (Sims 1968, Crounse et al. 1970a,b, Strain et al. 1972, Robson and El Tahawi 1971), rumen volatile fatty acid (VFA) production (Gasaway and Coady 1973) and blood constituents.

BLOOD ANALYSES - METHODS AND PATTERNS

Mammalian blood contains liquid (serum) and solid (cellular) fractions. Serology involves analyses of the chemical properties of the liquid fraction, and hematology involves analyses of the physical properties of blood cells. Both types of analyses may be related to nutrition.

Several chemical assays of serum are commonly employed in screening batteries for human patients (Table 1). These tests have been assembled to detect and discriminate between disease processes common in human populations. Interpretation of test results depends upon the magnitude of a sample's deviation from normal values, and upon the pattern of results from all tests performed. Table 1 illustrates this concept by tabulating patterns obtained in infection, malnutrition, tissue necrosis, and various organ-specific diseases. Differences in hematology also are associated with these patterns.

The most commonly measured parameters used in serological screening are those 12 measured by the "SMA-12" Technicon auto-analyzer. Patterns demonstrated in human and veterinary medicine are the following (cf: Coles 1967, Davidsohn and Henry 1969):

Electrolytes:

Calcium: Blood calcium may increase in hyperproteinemia,

Table 1. Test patterns associated with various pathological conditions.

	Disease State							
Assay	Infection	Malnutrition	Necrosis	Rapid Weight Loss	Renal Insufficiency	Hepatic Disease	Pseudohypo-parathyroidism	Hypo-thyroidism
Cholesterol		-			-	+		
Calcium		-			-		-	
Phosphorus		-	+		+	+	+	
T. Bilirubin			+	+		+		
Total Protein	+	-			-	-+		+
Albumin		-			-	-		
Uric Acid	+	-	+	+	+			
BUN		-				-		
Glucose		-+		+	+			-
LDH			+		+	+		+
Alkaline Phosphatase		+		+	+	+		
SGOT			+	+	+	+		+

See Reece and Hobbie (1972a,b) and Searcy (1969).
+ = elevation, - = depression.

hyperparathyroidism, extreme neoplasia and other abnormal conditions. Decreased calcium may result from hypoparathyroidism, vitamin D deficiency, acute or chronic renal failure, starvation associated with hypoproteinemia, parturient paresis (milk fever) and other causes. Thus, calcium depression during winter months may be related to reduced nutrition and possible hypoproteinemia and decreased vitamin D during this period. Similarly, depressed Ca may be indicative of range deterioration in certain instances.

Inorganic Phosphorus: Similarly to Ca, phosphorous is elevated in hypoparathyroidism, renal failure, and excessive vitamin D. Decreased inorganic phosphorus often results from simple lack of phosphorus intake, and as such can reflect dietary deficiencies.

Saccharides:

Glucose: Alterations in blood glucose level may be associated with pancreatic abnormalities (diabetes or insulin poisoning). Hypoglycemia may be an indication of extreme starvation, although gluconeogenesis can maintain blood glucose at high enough levels to sustain life even in severe starvation if it persists only a short while. For this reason, uric acid (a product of protein catabolism in gluconeogenesis) is sometimes a more sensitive indicator. Ketosis may be accompanied by hypoglycemia, resulting from assorted digestive or nutritional disorders (including carbohydrate deficiency).

Urea Compounds:

Urea Nitrogen (BUN): BUN level directly reflects dietary protein intake and protein absorption, and is thus a good indicator of protein energy balance. In addition, BUN may be pathologically elevated in cases of excess catabolism of body protein or in renal failure.

Uric Acid: Uric acid is a product of purine metabolism and, as such, may be increased in starvation for three reasons: 1) increased tissue protein turnover, 2) decreased renal excretion of the chemical due to acidosis, and 3) gluconeogenesis, with uric acid as a waste product.

Sterol:

Cholesterol: Cholesterol level reflects diet, dietary changes and the state of rumen metabolism. It is elevated when diets high in saturated fatty acids are consumed. Consequently, starvation conditions may result in hypocholesterolemia. Pathological conditions that may alter cholesterol levels include thyroid and hepatic disorders and nephrosis.

Proteins:

Total Protein: Total protein is a rather insensitive indicator of nutritional status for it is maintained at near-normal levels except in extreme distress. In sub-clinical cases of undernutrition, albumin is a better indicator. Most commonly, hypoprotememia is the result of trauma (wound, burns) or renal disease. Occasionally, however, it can result from gluconeogenesis and, as such, can reflect dietary insufficiencies. In cases of chronic protein starvation total protein may decrease noticeably.

Albumin: Albumin is the smallest of the serum proteins and forms 40-60 percent of the total protein. It is important as a source of amino acids and for fatty acid transport. Depressed albumin may indicate deficient protein intake or excessive protein breakdown. Decreased albumin is present in malnutrition and starvation.

Pigment:

Bilirubin: Bilirubin is a pigment liberated in the RE system by breakdown of hemoglobin. Bilirubin measurement is commonly a test of liver function, for its elevation is symptomatic of hemolytic diseases. Other conditions elevating serum bilirubin include jaundice, cardiac insufficiency and gangrenous pneumonia. Coles (1967) suggests, however, that bilirubin is elevated only slightly in severe hapatic disease in bovids, ovids and caprids.

Enzymes:

Alkaline Phosphatase: Alkaline phosphatase hydrolyzes phosphoretic esters and is concentrated intracellularly in osteoblasts, renal tubules and the intestinal mucosa. In humans, altered concentrations of this enzyme are diagnostic for bone abnormalities and liver disease. Levels normally are elevated during periods of growth and pregnancy, due to increased osteoblast activity and the enzyme's production in the placenta. Lowered levels can indicate malnutrition.

Lactic Dehydrogenase (LDH): LDH catalyzes the lactic acid-pyruvic acid conversion, occurring in most tissues. In humans, elevated LDH levels are indicative of several pathological conditions (e.g.: pulmonary or myocardial infarction, hepatitis, cirrhosis, leukemia and carcinomas).

Glutamic oxalacetic transaminase (SGOT): SGOT is elevated in cases of necrosis involving the tissues rich in the enzyme. Its concentration is especially high in the heart, liver and skeletal muscle and thus elevation is a sensitive indicator of myocardial infarction, and hepatic and muscular necrosis and stress. In cattle, SGOT elevation has been noted during starvation.

Electrophoretic fractionation of blood proteins is another common analytic technique using auto-analyzer instrumentation (e.g.: Spinco Analytrol R). This procedure separates total protein into albumin and four globulin fractions (alpha-$_1$, alpha-$_2$, beta-, and gamma-globulins) and allows calculation of albumin/globulin ratio (A/G). Changes in these values generally are indicative of these conditions:

Alpha globulins: Serum alpha-globulins are elevated during hypoproteinemia and acute cellular necrosis (especially alpha$_2$).

Beta globulins: Beta-globulin levels are elevated in pregnancy and sometimes during iron-deficient states. They may be depressed during severe infection and hepatic disorders.

Gamma globulins: The "gamma" fraction defined by electrophoresis is in reality a complex of proteins with many pathological correlations. Most generally, gamma-globulins are elevated in many infectious diseases and organ disorders.

A/G ratio: A/G ratio reflects relative change in albumin and globulin fractions and is therefore depressed in protein malnutrition and starvation. It may be elevated in cases of infection or other disorders during periods of adequate protein nutrition.

Hormones:

Thyroxine: Serum thyroxine (T_4) level reflects thyroid activity and thus is correlated directly with fasting metabolic rate and food intake. This hormone may be analyzed by the method of Nobel and Barnhart (1969).

Other Enzymes:

Creatine phosphokinase (CPK): This enzyme, similarly to SGOT, is elevated in tissue breakdown, including muscle injury and vigorous exercise (Rose et al. 1970), when it is released from skeletal muscle, heart and brain. It is an indicator of physical or mental stress as well as of trauma and perhaps nutritional stress. This enzyme can be measured by the method of Nuttall and Wedin (1966).

Changes in serum levels of other enzymes indicate presence of various disease processes and their possible locations. Use of enzymes in differential diagnosis depends upon the magnitude of elevation, the time course, the type of disease process (inflammation, necrosis, trauma, etc.) and the tissue affected. Identification of the tissue source is possible by assaying for enzymes of defined localization, Table 2. Such assays are being developed very rapidly in humans and offer great promise. Their application to moose will require direct confirmation and establishment of baseline norms, since variations between species have been documented (Zimmerman et al. 1965). Another potential use of enzyme measurements involves tissues as well as serum and may allow detection of changes in control systems (e.g.: adrenocortical activity). This might provide a more reliable index than gland weights of the functional changes in adrenal activity that are postulated to occur in response to "stress", however produced. At present, the available data on serum constituents do not provide such a correlation.

Hematology:

The basic battery of hematological values includes packed all cell volume (PCV), hemoglobin concentration, leucocyte count (WBC), erythrocyte count (RBC), and differential count of leucocytes. In general, PCV, RBC and hemoglobin levels reflect oxygen-carrying capacity and homeostasis.

Table 2. Serum enzyme tests - tissue specificity*.

Enzyme	Tissue Sources
A. High Specificity	
Acid Phosphatase	Prostate, Erythrocytes
Alanine transaminase	Liver
Arginase	Liver
Sorbitol DH	Liver
Alcohol DH	Liver
5' Nucleotidase	Hepatobiliary tract
Glutamic DH	Liver
Amylase	Pancreas, salivary glands
Lipase	Pancreas
γ-glutamyl transpeptidase	Liver
B. Moderate Specificity	
Aspartate transaminase (SGOT)	Liver, heart, skeletal muscle
Isocitrate DH	Liver, heart
Creatine Phosphokinase (CPK)	Skeletal muscle, heart, brain
C. Low Specificity	
Alkaline phosphatase	Bone, liver, intestinal mucosa, placenta, kidney
Lactic dehydrogenase (LDH)	All tissues (some isoenzyme specificity)
D. Within Cell Specificity	
Aspartic transaminase	Mitochondria form, cell sap form
Alanine transaminase	Cell sap only

*Taken from Wilkinson (1970).

Nutritional deficiencies can produce many anemias and anemia complexes that are reflected in these values. PCV reflects proportion of erythrocytes in whole blood and similarly is correlated with nutritional state. Interrelationships among all these parameters are too complex to discuss in detail here.

WBC and differential counts are useful in diagnosing various infections, intoxications, and neoplasms. Changes in absolute numbers and relative proportions of the several leukocytic cell types, when considered with other symptoms, can help differentiate among various disorders. However, individual variation makes serial bleeding of the same animal almost essential if small changes are to be detected. No direct nutritionally related changes in WBC or differential counts have been established firmly, but such information can prove of value in discovering pathology resulting from nutritional deprivation.

The patterns described occur in humans and in domestic species. Many may be expected to apply to other mammals as well. However, direct confirmation by empirical or experimental data is necessary to draw firm conclusions regarding patterns in moose. Some possible sources of artifically altered test results are indicated in Table 3. Some of these sources of artifact are peculiar to the Technicon SMA 12 systems which are sensitive to any changes altering the optical properties of serum, including lipemia (important for many carnivores--but not commonly seen in cervids), hemolysis, and high bilirubin.

The SMA 12 system, in addition, gives incorrect (low) values for serum albumin in moose blood, due to dye binding capacities. Therefore, electrophoresis is used to determine this value.

THE PROBLEM OF STRESS

Severe artifacts may result from the animal's acute physiological state when the blood is collected. These are related to recent food intake and to handling stress. The former variables are uncontrollable in wild animals, and the latter are "controllable" only to the extent they can be standardized in all animals handled. Usually this extent is slight, for individuals differ in response to drugs, traps, and handling. Thus, handling effects have been reported in every study to date (see bibliography section G). The very substantial effects of one method of handling an animal to obtain the samples are documented in Table 4. It is clear that many results depend upon whether the animal was shot, drugged, or manually restrained. These variables are at least known. More importantly, the marked effects of restraint 24 hours previously suggest that not only can short-term serial studies be seriously compromised, but that it is possible that levels in immediately obtained samples from wild animals may reflect the previous several days' activities.

A system to classify individual excitability states based on heart rate, respiratory rate, and rectal temperature has been developed for bighorn sheep (Franzmann 1972). Each individual was classified into one of five classes of excitability (not excited, slightly excited, moderately

Table 3. Possible artifactual patterns of test results.

Assay	Recent Meal	High-Protein Meal	Lipemic Serum	Old or on clot Serum	High Bilirubin	Convulsions	Detergent Contaminated Tubes	Hemolysis	Specimen Dehydration
Cholesterol		+(±)			+			+	+
Calcium			+				+		+
Phosphorous	-		-	+					+
T. Bilirubin									+
Total Protein			+	+	+		+	+	+
Albumin	+	+	+		+		+		+
Uric Acid		+	+					+	+
BUN	+	+	+					+	+
Glucose	+	+(±)	+	-					+
LDH			+	+		+		+	+
Alkaline Phophatase	+		+	+					+
SGOT			+	+		+		+	+

See Reece and Hobbie (1972a,b) and Searcy (1969).
+ = elevation, - = depression.

Table 4. Acute effects of phencyclidine and promazine administration on hematology and blood chemistry of eight pregnant, adult does* (data of Seal, Ozoga, Erickson and Verme (1972a)).

Assay (Units)	Restraint	Post Drugs	t	p
Hemoglobin (gm/100 ml)	18.6 ± 2.5	15.8 ± 2.7	4.48	.005
Red blood cells ($10^6/mm^3$)	13.3 ± 1.7	11.3 ± 1.7	3.22	.02
Hematocrit (vol. %)	49 ± 5.7	42 ± 6.9	4.02	.01
MCV (μ^3)	37 ± 3.6	37 ± 3.1	0.29	NS
MCHC (%)	37 ± 1.0	37 ± 0.7	0.36	NS
White blood cells ($10^3/mm^3$)	2120 ± 700	1500 ± 470	4.47	.005
Fibrinogen (mg/100 ml)	230 ± 35	192 ± 33	10.82	.001
Serum protein (gm/100 ml)	5.7 ± 0.7	4.9 ± 0.4	5.24	.002
SGOT (K.U.)	128 ± 26	142 ± 32	2.63	.05
CPK (I.U.)	50 ± 19	101 ± 36	5.09	.005
Sodium (mEq/L)	144 ± 6.0	142 ± 3.0	0.64	NS
Potassium (mEq/L)	4.3 ± 0.3	4.6 ± 0.5	1.32	NS
Calcium (mg/100 ml)	9.8 ± 0.5	9.7 ± 0.7	1.19	NS
Phosphorus (mg/100 ml)	6.7 ± 1.0	4.9 ± 0.9	4.50	.005
Cholesterol (mg/100 ml)	66 ± 7	58 ± 5	4.33	.005

*Studies were performed in April 1969 on eight pregnant does. The animals were guided through runways into restraint boxes and restrained manually. Blood samples were taken and then each animal was given 1 mg/kg of phencyclidine and 0.5 mg/kg of promazine by intramuscular injection. A second set of samples was taken 45 minutes later. The data are recorded as means ± standard deviation. Statistical analysis was by the t-test for paired variates.

excited, excited, and highly excited). It was concluded that classes of excitability could be established and would aid in interpreting blood values. At present, we are accumulating data based on this study to establish excitability classes for moose.

Evaluating and subsequently classifying stress states in animals may also be approached through analyses of intracellular enzymes such as LDH, SGOT and CPK, which escape into the circulatory system when cells are injured (Coles 1967). Tissue breakdown and subsequent release of these enzymes has been examined in pathologic conditions in domestic animals (Blinko and Dye 1958, Whanger et al. 1969). The influence of handling excitability on SGOT values in bighorn sheep was demonstrated, but no correlation with degree of excitability was noted (Franzmann and Thorne 1970). Another potentially useful index of handling is a combination of CPK and LDH levels which show a different time course of elevation and decline after handling and tissue damage (Seal et al. 1972a).

Immobilizing drugs have potentially contradictory effects on blood values. Many of these drugs calm the individuals being handled, decreasing excitability and stress. In addition, however, drugs may have other more discrete physiological affects due to their pharmacologic action (cf: Table 4, Harthoorn 1965, Fujita 1970). These must be experimentally determined for each species studied.

Since obtaining blood from sufficiently large samples of wild animals is difficult by any means, standardization of procedures is often extremely difficult. Nevertheless, it is extremely important to standardize methods as much as possible, and to realize that some measured values may be more plastic under stress (e.g. LDH, CPK, SGOT, glucose) than others (e.g.: BUN, uric acid, cholesterol, proteins). With these relationships in mind, it is possible to use the more plastic assays as stress indicators, while examining nutritional status using those values little affected by handling. In any event, it should be recognized at the outset that even well-documented "norms" for a wildlife population are not strictly comparable to resting normals for human or domestic species. Instead, the "normal" values are resting normals modified by the variable stress of the standardized animal handling procedure. For this reason, blood studies of wildlife are concerned with trends, and often require large sample sizes in order to document differences between populations.

BLOOD STUDIES IN WILD POPULATIONS - STRATEGY AND DESIGN

The multitude of stress-related variables, the difficulty of standardization, the need for confirmation of relationships for each species, and the lack of baseline "normal" values complicate blood studies of moose and other cervids. In essence, we may begin at the current level of knowledge and technology of human blood-nutrition relationships, but must reconfirm relationships and ascertain normal values, within the restrictions of hard-to-standardize procedures.

Until recently, blood studies of moose and other cervids were few and superficial and only sometimes related to nutrition. A systematic effort to use blood analyses to evaluate the condition of wild cervids was first reported by Rosen and Bishoff in 1952. Braend (1962) considered blood groups in moose, Nadler et al. (1967) studied serum proteins and transferrins, and Houston (1969) analyzed several serum parameters from 13 moose. Dieterich (1970) reported hematology of six moose and several other arctic mammals. More thorough nutrition-related studies have been carried out on other cervidae. Herin (1968) reported 14 blood parameters for 39 elk (*Cervus canadensis*). Weber and Bliss (1972) measured 13 parameters in wild and captive elk. Kitts et al. (1956) related age and nutrition to hematological values in black-tailed deer (*Odocoileus hemionus c.*). Seal and Erickson (1969) and Seal et al. (1972a,b) have reported on extensive studies involving nutrition - stress - blood constituent relationships in white-tailed deer (*Odocoileus virginianus*).

These studies have indeed demonstrated that blood assays in these cervids are subject to more sources of normal variation than are encountered in human studies. This has increased the complexity of interpretation substantially and has made the establishment of baseline normal values difficult. Identified variables include age, sex, reproductive status, season, and method of handling the animal. Evaluation of an animal's or a herd's condition, a primary motivation for these studies, has been confounded by these multiple sources of variation intermingled with other sources of variations in wild animals such as nutritional history, disease, and parasitism. The advent of experimental studies on animals of known condition and history (e.g.: Seal's group on *Odocoileus*; Alaskan studies on penned moose) now offers the promise of unraveling these variables and yielding the necessary information for interpretation of results from field studies.

Establishing nutrition-blood parameter correlations in moose populations involves: (a) determining boundary conditions, or those characteristics of an individual animal that must be known before blood values may be interpreted, (b) establishing normal values within these boundary conditions using standardized handling and collecting procedures and, (c) determining the nature and magnitude of changes wrought in blood values by known changes in food intake, nutrition, or related parameters.

Boundary conditions which have been identified in cervid species are tabulated in Table 5. Those demonstrated to date for moose are listed in Table 6. Species differences have become apparent in most measurements. More critical for interpretation of literature data are the many seasonal changes and the impact of handling methods. Both of these involve effects of sufficient magnitude to invalidate uncontrolled comparisons. The effect of time of day (circadian rhythms) has not been examined for any cervid species, but has been shown to be important in other mammalian species. Other conditions of possible importance include posture at time of sampling (standing or recumbent), geographic location (latitude, elevation, and climate), and perhaps genetically based intraspecies population differences.

Table 5. Demonstrated boundary conditions in Cervidae.[1,2]

Assay[3]	Species	Sex	Age	Season	Reproductive Status	Time of Day	Handling Method	Fasting or Fed
Hematology								
Hemoglobin	+	+		+	+		+	0
Red blood cells	+	+		+	+		+	0
Hematocrit	+	+		+	+		+	0
MCHC	0	0	0		0	0	0	0
MCV	+	0	0		0	0	0	0
White blood count	+						+	
Differential	+							
Chemistry								
Cholesterol	+		+	+	+		+	
Calcium			+	+				
Phosphorus		0	+	+			+	+
Bilirubin		0	+	+	+			
Uric Acid	+			+	+			
Total protein		+	+	+	+		+	
Albumin			+	+				0
Gamma globulin	+		+	+		0	+	0
Glucose	+	0	+	+	+		+	+
BUN	+	+		+				+
LDH	+		+	+				
SGOT	+		+	+			+	
Alkaline p'tase			+	+	+		+	0
CPK	+						+	0
Hormones								
Thyroxine	+			+	+		+	
Cortisol	+			+				
Insulin								
Testosterone		+	+	+	+			

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[1] Exclusive of fetal, neonatal, and first one month of life data since many differences have been documented for these periods in every mammalian species studied including white-tailed deer and moose.

[2] Genera covered include *Odocoileus*, *Alces*, *Rangifer*, and *Cervus*.

[3] A "+" indicates significant differences have been reported, while a "0" indicates no difference, and a "blank" indicates information lacking or inadequate. The initial condition is that the animals be in good health and nutrition.

Table 6. Boundary conditions in Alaskan moose.*

	Sex	Age	Pregnancy	Season
Calcium	0	+	0	+
Phosphorus	0	+	0	+
Glucose	0	+	+	+
BUN	+	0	0	+
Uric acid	0	0	+	+
Cholesterol	+	+	0	+
Total protein	+	+	+	+
Bilirubin	0	+	+	+
Alkaline p'tase	0	+	+	+
Lactic dehydrogenase	0	+	0	+
SGOT	0	+	0	+
Hemoglobin	0		+	+
Hematocrit	0		+	+
White blood count	0	+	+	

*The "0" indicates that no effects of the specified condition were observed upon the assay. The "+" indicates the occurrence of significant changes or significant differences and thus that the establishment of norms requires inclusion of this condition in formulating the data base. The effects of season are probably complicated by seasonal reproductive and nutritional factors.

The only data available concerning the latter conditions are those gathered in protein polymorphism studies, primarily designed to delineate subspecies and specific relationships (see bibliography section F). No polymorphisms in hemoglobin or serum protein patterns have been observed in several subspecies of moose (Table 7). This is in contrast to reindeer (transferrins) and white-tailed deer (transferrins and hemoglobins). There have been no reports on serum (or tissue) enzyme polymorphisms. In contrast, the polymorphisms of white-tailed deer hemoglobin are sufficient to apply to studies of subspecies relationships, selection effects, population differences, isolates, and geographic clines. In serum, the fibrinopeptides A (19 amino acids) and B (17 amino acids) are the most rapidly evolving peptides known at present and, hence, are most likely to provide information on phylogenetic relationships of closely related species and genera. Data on the sequences of fibrinopeptides A and B from moose and six other cervids (Tables 8 and 9) permit inferences concerning phylogenetic relationships among these cervids. Notably, they indicate the very close affinities of *Rangifer*, *Alces* and *Odocoileus*, with no sequence differences between the reindeer and moose and only one difference from the mule deer. Also, the three species of *Cervus* exhibited only one sequence difference, in the Sika deer. These peptides are clearly not useful for species and subspecies studies, but may allow grouping of genera at the subfamily level.

Seasonal boundary conditions in moose are especially interesting in view of seasonal changes in energy balance (Gasaway and Coady 1973). If other conditions, (sex, age, reproductive status, handling method) are kept constant, alterations in blood values caused by known seasonal changes in nutrition may be good indicators of blood-nutrition relationships. The relationships are not clear, for climatological stresses and endocrine relationships (cf: Seal et al. 1972b) also change seasonally. Nevertheless results, described below, are encouraging.

BASELINE NORMALS

It is impractical to attempt to develop baseline normal values for moose similar to those existing for humans and some domestic species. The number of individuals which must be sampled to meet boundary conditions for all population segments is prohibitive. Nevertheless, most studies of other wild cervids have presented lumped data with little or no regard to boundary conditions. Existing lumped data of moose blood values, including our own unpublished data, are presented in Table 10. It is evident that moose blood values fall in the same general range as those reported for other cervids. Little more can be said at this time, given the great variety of individuals tested and the methods used to secure samples. However, interesting apparent differences between groups of moose exist for MCV, cholesterol, glucose, BUN, albumin and serum enzymes (Table 10). Further analyses of data from Minnesota and Alaska, applying the appropriate boundary conditions, may elucidate these differences if they are real.

Table 7. Transferrin* polymorphisms in the Cervidae.

	Location	Number Animals	Observed Phenotypes	Postulated Alleles
Species				
Rangifer tarandus (0 bands in homozygotes, 0 bands in heterozygotes)				
1. Gahne & Rendel (1961)	Sweden	64	6	3
2. Braend (1964a)	Norway	132	15	6
3. Braend (1964b)	Norway	829	27	8
4. Nadler et al. (1967)	Alaska	37	Multiple	?
Odocoileus virginianus (2 bands in homozygotes, 3 bands in heterozygotes)				
1. Miller et al. (1965)	Iowa	150	3	2
2. Seal & Erickson (1969)	Minnesota	100	1	
3. Seal & Verme (Unpubl.)	Michigan	40	3	2
Alces alces (2 bands)				
1. Braend (1962)	Norway	27	1	1
2. Nadler et al. (1967)	Alaska	7	1	
3. Nadler (1968)	Canada	1	1	
4. Seal & Karns (Unpubl.)	Minnesota	150	1	1

*All phenotypes had at least two bands on electrophoresis.

Table 8. Fibrinopeptide A sequences.*

Species																			
Reindeer	Ala	Asp	Gly	Ser	Asp	Pro	Ala	Gly	Gly	Glu	Phe	Leu	Ala	Glu	Gly	Gly	Gly	Val	Arg
Moose	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mule Deer				.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Muntjak	.	.	.	.	.	.	.	Ser	.	.	.	.	Thr	.	.	.	.	.	.
Sika Deer	.	.	.	.	.	.	.	Ser	Ser	.	.	.	.	.	.	.	.	.	.
Red Deer	.	.	.	.	.	.	.	Ser	Ser	Asp	.	.	.	.	.	.	.	.	.
Elk, American	.	.	.	.	.	.	.	Ser	Ser	Asp	.	.	.	.	.	.	.	.	.

*Taken from tabulation D-95 of Dayhoff (1972). A dot indicates that the amino acid is identical with that of the reindeer in that position.

Table 9. Fibrinopeptide B sequences.*

Species																					
Reindeer	Gly	His	Leu	Ala	Asp	Tyr	Asp	Glu	Val	Glu	Asp	Asp	Arg	Ala	Lys	Leu	His	Leu	Asp	Ala	Arg
Moose	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mule Deer	.	.	.	.	.	.	.	.	.	Asp	.	.	.	.	.	.	.	.	.	.	.
Muntjak	.	.	Ser	Thr	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sika Deer	.	.	Ser	Thr	.	.	.	.	Glu	.	Glu	.	.	.	.	.	.	.	.	.	.
Red Deer	.	.	Ser	Thr	.	.	.	.	Glu	.	Glu	.	.	.	.	.	.	.	.	.	.
Elk, American	.	.	Ser	Thr	.	.	.	.	Glu	.	Glu	.	.	.	.	.	.	.	.	.	.

*Taken from tabulation D96 of Dayhoff (1972). A dot indicates that the amino acid is identical with that of the reindeer in that position.

Table 10. Blood data on moose (*Alces alces* ssp.)

Assay	*A. a. gigas*	*A. a. shirasi*	*A. a. andersoni*[3]	*A. a. gigas*[4]	
Reference	Dieterich (1970)	Houston (1969)	Karns & Seal (Unpubl.)	LeResche (Unpubl.)	
Location	Alaska	Wyoming	Minnesota	Alaska	
Number Animals	2 (3X)	13	ca: 91	ca: 520	
Type	Captive	Wild	Wild	Wild, pen	
Ages	4 mos.	10A, 3Y	Adult	Mixed	
Sex	M	4M, 9F	65M, 26F	Mixed	
Season	Summer	Winter	Oct. Dec.	Year-round (some serially sampled)	
Drugs	Restraint	Succinylcholine	Shot	Shot, succinylcholine, M-99, other	
	$\bar{x}$ ± S.D.	$\bar{x}$ ± S.D.	$\bar{x}$ ± S.E.	$\bar{x}$ ± S.D., ± S.E. 0.5	
Hemoglobin (gm/100 ml)	13.5 ± 0.4	--	13.3 ± 1.3	14.9 ± 4.7	
Red blood cells (10^6/mm^3)	5.25 ± 0.43	--	6.2 ± 1.2	--	
Packed cell vol. (Vol cells/ 100 ml blood)	38 ± 3	--	41 ± 5.8	40.4 ± 11.8	1.5
MCHC (gm/100 ml)	36 ± 2	--	35 ± 1.4	37 ± 4.0	0.4
MCV (u^3)	72 ± 7	--	59 ± 5.6	--	
Sed rate (mm/hr)	27 ± 13	--	--	--	
White blood cells (10^3/mm^3)	5.87 ± 1.13	--	--	4.19 ± 2.52	0.24
Neutrophils (10^3/mm^3)	2.46 ± 0.88	--	--	1.37 ± 0.75	0.16
Lymphocytes (10^3/mm^3)	3.10 ± 1.11	--	--	2.60 ± 0.80	0.16
Eosinophils (10^3/mm^3)	0.23 ± 0.17	--	--	--	
Cholesterol (mg/100 ml)	--	--	54 ± 10	87 ± 21	0.9
Calcium (mg/100 ml)	--	--	9.7 ± 1.3	10.6 ± 1.1	0.05
Phosphorus (mg/100 ml)	--	--	6.4 ± 1.3	5.6 ± 1.9	0.08
Bilirubin (mg/100 ml)	--	--	0.5 ± 0.1	0.4 ± 0.2	0.01
Uric acid (mg/100 ml)	--	--	0.7 ± 0.1	0.6 ± 0.6	0.03
BUN (mg/100 ml)	--	13 ± 3[1], 5 ± 1.8[2]	8.5 ± 3.2	13 ± 12	0.5
Glucose (mg/100 ml)	--	63 ± 5.7	79 ± 8	121 ± 54	2.4
Total protein (gm/100 ml)	--	6.4 ± 0.9	6.9 ± 0.7	6.9 ± 0.9	0.04
Albumin (gm/100 ml)	--	4.5 ± 1.4	3.3 ± 0.4	3.9 ± 0.7	0.03
Gamma globulin (gm/100 ml)	--	--	1.6 ± 0.6	--	0.03
Alk. phosphatase (mU/ml)	--	--	80 ± 11	81 ± 71	3.1
LDH (mU/ml)	--	--	142 ± 15	339 ± 136	6.0
SGOT (mU/ml)	--	--	59 ± 6	159 ± 59	2.6
Thyroxine (T_4) (ug/100 ml)				5.4 ± 2.3	0.15

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[1] Seven animals in July-September; [2] Five animals in October-February; [3] Sex, season and area differences found in this study. Only data on males here; [4] Sex, age and season differences.

BLOOD-NUTRITION RELATIONSHIPS IN MOOSE

Two major continuing studies of moose blood patterns are underway in North America: those of LeResche and Franzmann in Alaska and of Karns and Seal in Minnesota. Preliminary data from both are discussed here.

The Alaska study was designed to develop practical methods for assessing population/habitat relationships on different ranges throughout the state. It has used three primary sources of materials: (1) moose contained in four 2.6 km^2 enclosures at the Kenai Moose Research Center and trapped, immobilized, bled, weighed and measured periodically; (2) unenclosed moose immobilized on the Kenai Peninsula for marking, bled, measured and released and; (3) moose killed by hunters or collected for rumen VFA studies from several areas of the state.

The Minnesota study has thus far utilized hunter-killed specimens from two areas of the state, taken at two different times of year. Its objectives include testing regional differences in nutrition. In addition blood profiles are being used as indicators of the effects of parasitism, primarily by *Fascioloides magna.*

Seasonal Variation

Natural seasonal changes in diet and food intake, coupled with seasonally varying demands of pregnancy, lactation and breeding, provide an opportunity to study blood-nutrition relationships on a pseudo-experimental basis. That is, animals sampled during winter months are analagous to experimental animals on sub-maintenance diets, and those sampled during summer are analagous to animals fed high-quality rations. Seasonal energy budgets of moose calculated from weight change, food intake and value, rumen VFA production, and theoretical considerations show profits roughly from May through September and deficits from October through April (Gasaway and Coady 1973 and Figure 1). Although compounded by changes in photoperiod and resulting endocrine relationships (cf: Silver et al. 1969), pregnancy, prior dietary history and disease, certain blood values do reflect seasonal changes in energy balance in predictable ways (Tables 11-12).

Urea nitrogen varies directly in correlation with energy balance in Alaska moose (Table 11, Figure 1), reaching highest levels during seasons of positive energy balance. Similarly, October levels in 14 males from northwest Minnesota (8.5mg/100 ml) were significantly (P=.005) higher than December levels (5.7 mg/100 ml) in seven males. BUN has been repeatedly correlated with dietary protein and protein utilization balance in cervids (cf: Houston 1969, Seal et al. 1972b) and appears to be one of the best correlates, being relatively stable and unaffected by boundary conditions.

Glucose levels are also correlated with seasonal energy balance in Alaska. This is somewhat surprising in view of rapid elevation of blood glucose in handling stress. The fact that trends in glucose levels follow seasonal energy changes suggests that collection procedures can

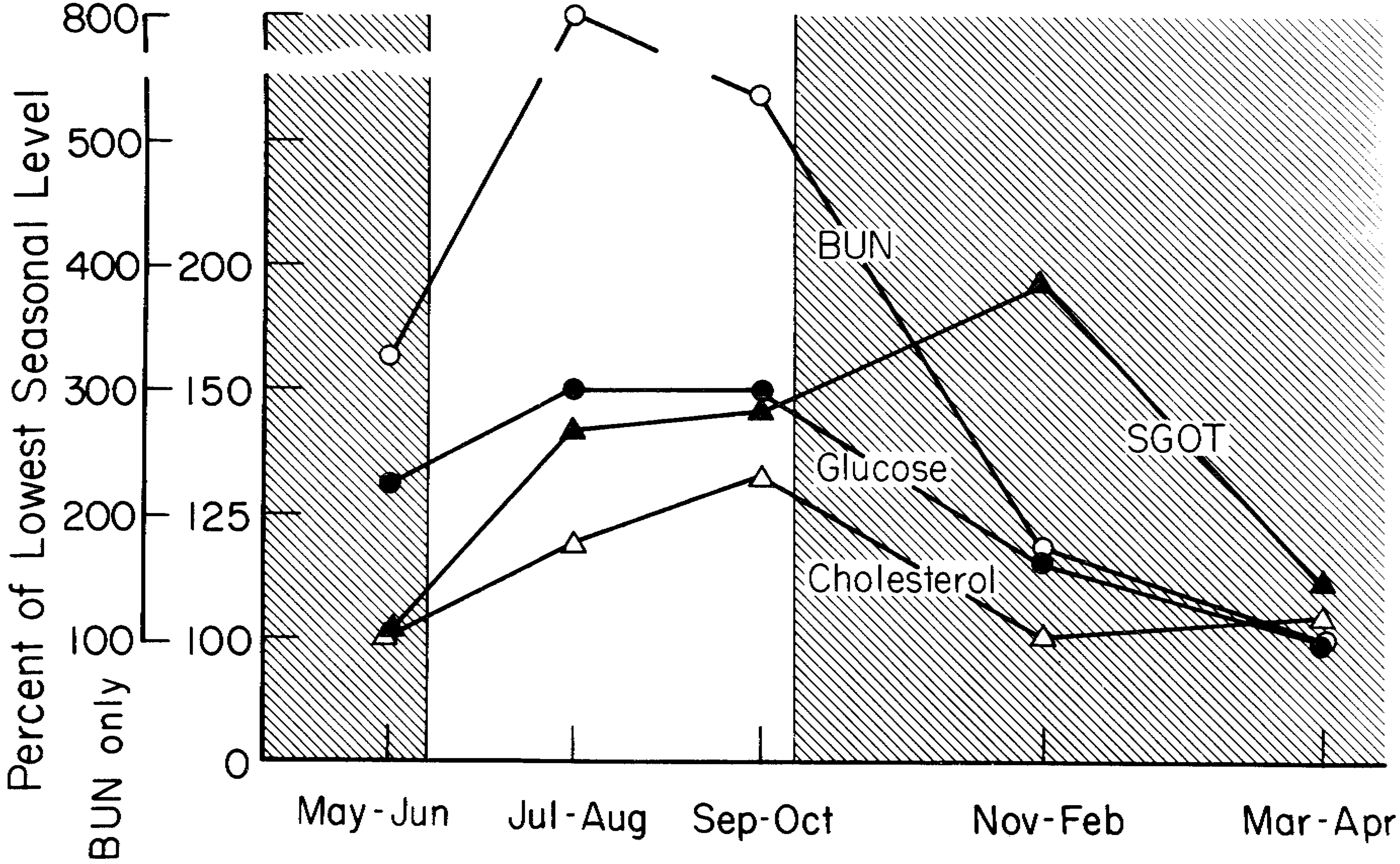

Fig. 1. Relationships of selected blood values to nutritional status of Alaskan moose.

Table 11. Seasonal variation in selected blood values in adult female Alaskan moose.[1] (Data of LeResche).

	MONTHS				
	May-June	July-Aug	Sept-Oct	Nov-Feb	Mar-Apr
n	80	30	24	109	30
Calcium (mg/100ml)	10.47 ± 0.62	10.61 ± 0.89	11.28 ± 0.80	10.8 ± 1.32	11.1 ± 0.58
BUN (mg/100ml)	(a) 13.0 ± 14.22	(a) 32.0 ± 7.54	(a) 21.3 ± 11.8	(a) 6.9 ± 4.80	(a) 4.0 ± 2.81 (a)
Glucose (mg/100ml)	(a) 118.6 ± 29.2	(a)134.9 ± 41.0	134.4 ± 49.4	(a)115.4 ± 67.7	(a) 90.8 ± 31.6 (a)
Bilirubin (mg/100ml)	0.4 ± 0.23	0.7 ± 0.34	0.8 ± 0.32	0.39± 0.3	0.33± 0.05
Cholesterol (mg/100ml)	82.5 ± 21.8	(a) 97.9 ± 17.2	(a)109.4 ± 32.9	(a) 83.0 ± 13.9	86.8 ± 12.5
SGOT mU/ml	(a) 108.1 ± 36.0	(a)153.9 ± 44.9	158.1 ± 36.7	(a)212.1 ± 46.5	(a)121.0 ± 28.7 (a)
LDH mU/ml	(a) 222.9 ± 88.3	(a)337.7 ± 108.0	345.8 ± 81.4	(a)389.7 ± 138.8	(a)291.0 ± 60.8 (a)
Total Protein (g/100ml)	6.9 ± 0.53	(a) 8.1 ± 0.66	8.2 ± 0.52	(a) 6.7 ± 0.70	6.8 ± 0.48
Albumin (g/100ml)	4.0 ± 0.47	4.7 ± 0.79	5.2 ± 0.52	(a) 3.8 ± 0.48	3.5 ± 0.43
A/G (ratio)	1.47 ± 0.38	1.54 ± 0.53	1.72 ± 0.34	1.35± 0.30	1.09± 0.28
n	92	53	46	49	no data
Thyroxine (T_4) ug/100ml	5.8 ± 3.2	5.7 ± 1.7	5.2 ± 1.6	(c) 4.5 ± 1.4 (b)	

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[1] All data are given as mean ± standard deviation. The statistical comparisons were made with the "t" test for unpaired variates.

(a) Difference between months significant at P = .001
(b) Difference between months significant at P = 0.025
(c) Difference between months significant at P = 0.05

Table 12. Serum protein electrophoresis of Minnesota adult male moose samples.[3] (Data of Karnes and Seal).

Area	N	Total Protein gm/100 ml	Albumin gm/100 ml	Gamma Globulin gm/100 ml	A/G
Northwest					
October	16	6.9 ± 0.69	3.3 ± 0.39	1.6 ± 0.56	0.93 ± 0.23
December	8	7.3 ± 0.74	3.3 ± 0.36	2.4 ± 0.72[1]	0.84 ± 0.15
Northeast					
October	14	6.5 ± 0.65	3.7 ± 0.40[1]	1.1 ± 0.37[1]	1.34 ± 0.26[2]

[1] $p \leq 0.01$

[2] $p \leq 0.001$

[3] All data are given as means ± standard deviation. The statistical comparisons were made with the "t" test for unpaired variates. The Northeast-October and Northwest-December samples were compared with the Northwest-October group.

be at least reasonably standardized, however stress-producing they might be.

Cholesterol was elevated during summer months in Alaska, suggesting a seasonal increase in dietary fatty acids. No change occurred in blood cholesterol level between October and December in northwest Minnesota. Cholesterol levels in Minnesota were significantly lower (49-56 mg/100 ml) than in Alaska (82-109 mg/100 ml), suggesting interesting differences in diet and rumen function (Peek 1973). These differences deserve further investigations.

Total protein levels in Alaska were elevated in summer and depressed in winter, probably reflecting changes in dietary protein. The significant decline in serum albumin levels between September-October and November-February further suggests a dietary influence, although no significant change in A/G ratio occurred. Total protein levels did not change significantly between October and December in Minnesota (Table 12).

SGOT and LDH levels in Alaska both peaked during winter months, suggesting generalized tissue breakdown during this period of negative energy balance. Annual lows are reached in May and June, when forage quality suddenly improves. These lows, however, are somewhat surprising, since near-term pregnancy and early lactation increase physical stress during this time. The LDH pattern in Minnesota is similar, with December levels significantly lower (204 mU/ml) than October levels (222 mU/ml). However, SGOT levels in Minnesota declined significantly from 151 mU/ml to 85 mU/ml between October and December. Serum concentrations of both enzymes were higher in Alaska than in Minnesota, perhaps due to differences in animal handling procedures. These seemingly contradictory results deserve further exploration.

Serum thyroxine (T_4) levels in Alaska (Table 11) followed the pattern described by Seal's group for white-tail does, which involved a significant decline in serum thyroxine with reduced nutrition over a three-year period in experimental animals (Seal et al. 1972b). Their studies of wild populations also yielded very low values in herds whose condition is considered poor and whose range is depleted. These studies also suggested reduced T_4 levels were due not only to low nutrition but also reflected naturally reduced metabolism and food intake in winter. Our results presented here are the first empirical evidence of such a mechanism in moose.

Hematological patterns vary seasonally in Minnesota (Table 13), with a significant decline in erythrocyte numbers and hemoglobin concentration in males from October to December. These changes are consistent with moderate normocytic anemias, which may result from protein deficiency, or with parasitic infestation aggravated by normal seasonal decline in dietary protein. Northwest Minnesota moose do carry a very heavy liver parasite load. This condition is also reflected in significantly elevated gamma globulin and depressed albumin levels, relative to those found in northeast Minnesota (Table 12).

Table 13. Hematology of adult moose from northern Minnesota (data of Karns and Seal).

SEX AREA Month	Hemoglobin (gm/100 ml)		RBC (10^6/mm^3)		Hematocrit (%)		MCV (μ^3)		MCHC (%)	
	n	$\overline{X} \pm$ S.E.	n	$\overline{X} \pm$ S.E.	n	$\overline{X} \pm$ S.E.	n	$\overline{X} \pm$ S.E.	n	$\overline{X} \pm$ S.E.
MALES										
NORTHWEST										
October	40	13.3 ± 1.28^{a}	41	$6.2 \pm 1.16^{c,k}$	29	41.3 ± 5.80^{e}	38	59.2 ± 5.63^{g}	37	34.6 ± 1.38^{h}
December	8	$11.1 \pm 1.16^{a,b,j}$	6	$5.0 \pm 0.55^{c,d}$		$30.7 \pm 2.69^{e,f,m}$	5	59.9 ± 4.82	7	$36.6 \pm 1.13^{h,i}$
NORTHEAST										
October	17	13.5 ± 2.12^{b}	22	$6.6 \pm 0.28^{d,n}$	15	39.5 ± 5.33^{f}	19	62.3 ± 4.08^{g}	12	$33.7 \pm 1.48^{i,p}$
FEMALES										
NORTHWEST										
October	8	11.6 ± 2.80	7	5.4 ± 0.73^{k}	6	33.5 ± 7.40	9	58.5 ± 6.98	9	35.7 ± 2.40
December	10	13.2 ± 1.75^{j}	9	5.7 ± 0.84	8	36.6 ± 4.31^{m}	9	59.8 ± 6.89	9	37.0 ± 2.50
NORTHEAST										
October	8	12.3 ± 2.27	7	5.7 ± 0.85^{n}	5	37.8 ± 3.77	6	59.2 ± 3.61	7	36.0 ± 1.63^{p}

g, k, n - Difference between means statistically significant at $p < 0.05$.

j, m, p - Difference between means statistically significant at $p < 0.025$.

a, b, c, f, h, i - Difference between means statistically significant at $p < 0.005$.

d, e - Difference between means statistically significant at $p < 0.001$.

Physiological Costs of Reproduction

Energy costs of pregnancy and lactation may approach 40-55 percent of maintenance levels in moose (Gasaway and Coady 1973). These costs are reflected in weight deficits of 15-20 percent in late July and 6-8 percent in October-December (LeResche and Davis 1971, LeResche unpubl.). Tables 14 and 15 illustrate how these physiological costs of reproduction may be reflected in blood values of Alaska moose.

Early-term pregnancy (October through January) resulted in a significant increase in glucose and a significant decline in cholesterol levels, by comparison with non-pregnant adult cows (Table 14). Cows in late-term pregnancy had slightly elevated glucose levels and greatly elevated levels of SGOT, alkaline phosphatase and LDH, compared to non-pregnant cows. These levels of SGOT and LDH suggest greatly accelerated tissue destruction in late-term, perhaps reflecting the combined effects of increased fetal demands and very low-nutrition forage. Alternately, these elevations might indicate fetal or placental injury during handling or increased cellular turnover at this time. In normal well-nourished humans, alkaline phosphatase is elevated in late-term pregnancy; whereas, SGOT is unchanged or slightly depressed.

Glucose elevations in pregnant animals are difficult to explain, but likely represent accommodation to fetal demands rather than enhanced energy reserves in pregnancy. Glucose in pregnant cows is depressed significantly ($P<.001$) in February-April below October-January levels. This occurs at a time when the fetus is growing most rapidly, and must represent a decline in this type of energy available for growth. Decreased cholesterol during early pregnancy might result from lipid uptake by rapidly-growing fetal myelin structure. Endocrine relationships might further be involved.

Blood values differ significantly between adult cows with no calves, those with one calf and those with twins (Table 15). These differences perhaps reflect some of the nutritional costs of rearing young. Cows with one calf tested in Table 15 weighed a mean 368 kg, significantly less than those with no calves (392 kg), in September-December. The significant increase in BUN levels from cows with no calves to those with one and those with twins is perplexing. Perhaps a hidden seasonal bias in the sample is operating, for data from all year are lumped and progressive calf loss may have resulted in cows with calves being sampled more heavily in summer months, when BUN levels are high. Alternately, the values might reflect increased protein catabolism required for lactation. Relationships are unclear.

Glucose is highest in cows with no calves, significantly lower in those with one calf, and again significantly lower in those with two calves. This most likely represents the cost of lactation, which may involve glycogen stores. SGOT and LDH are significantly elevated in cows with calves, perhaps signifying, again, greater catabolism of body tissues in lactating animals. Since lactation ceases in October or November, however, this year-round elevation is difficult to explain fully.

Table 14. Selected blood values in pregnant and non-pregnant adult cow moose, Alaska. (Data of LeResche).

	October-January				February-April				
	Pregnant		Not Pregnant		Pregnant		Not Pregnant		
	n	$\bar{X}$ ± S.D.	n	$\bar{X}$ ± S.D.	n	$\bar{X}$ ± S.D.	n	$\bar{X}$ ± S.D.	p[1]
Calcium (mg/100ml)	26	10.7 ± 0.92	44	10.7 ± 1.1	35	11.3 ± 1.8	42	11.0 ± 0.7	0
BUN (mg/100 ml)	27	5.8 ± 3.7	43	7.8 ± 5.3	35	6.1 ± 4.1	42	5.9 ± 5.1	0
Glucose (mg/100ml)	27	134.1 ± 92.2	47	107.9 ± 59.5	36	111.4 ± 55.8	43	104.3 ± 42.6	1,4
Bilirubin (mg/100ml)	27	0.35 ± 0.08	47	0.45 ± 0.35	36	0.35 ± 0.09	43	0.38 ± 0.19	0
Cholesterol (mg/100ml)	27	75.7 ± 16.9	47	90.4 ± 13.5	36	82.8 ± 10.6	43	85.2 ± 12.9	1
SGOT (mU/ml)	27	193.2 ± 55.6	46	200.0 ± 46.7	36	224.3 ± 38.8	43	153.1 ± 59.0	3
Alkaline phosphatase (mU/ml)	27	50.9 ± 26.4	47	49.1 ± 48.1	36	90.7 ± 47.8	43	54.2 ± 45.9	3
LDH (mU/ml)	27	369.3 ± 151.0	47	362.3 ± 112.0	36	413.9 ± 143.7	43	331.9 ± 115.5	3
Total protein (g/100ml)	12	6.3 ± 0.8	41	6.8 ± 0.7		No data	35	6.8 ± 0.5	0
Albumin (g/100ml)	12	3.7 ± 0.6	41	3.9 ± 0.6		No data	35	3.6 ± 0.5	0
A/G (ratio)	12	1.49 ± 0.3	41	1.36 ± 0.3		No data	35	1.12 ± 0.3	0

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[1] Values for pregnant moose were compared with those for non-pregnant moose during each of the two time periods using the "t" test for unpaired variates. Probabilities of differences were:

0 - No statistical difference during either time period. ($P \geq .05$)
1 - Pregnant vs. non-pregnant difference significant ($P < .001$) during October-January.
2 - Pregnant vs. non-pregnant difference significant ($P < .05$) during October-January.
3 - Pregnant vs. non-pregnant difference significant ($P < .001$) during February-April.
4 - Pregnant vs. non-pregnant difference significant ($P < .05$) during February-April.

Table 15. Selected blood values of adult cow moose leading and not leading calves (year-round values, Alaska). Data of LeResche.

	With No Calf			With One Calf			With Two Calves		
	n	$\bar{X}$ ± S.D.	p[1]	n	$\bar{X}$ ± S.D.	p[1]	n	$\bar{X}$ ± S.D.	p[1]
Calcium (mg/100ml)	125	10.5 ± 0.7		50	10.9 ± 0.8		5	10.3 ± 0.9	
BUN (mg/100ml)	129	12.8 ± 11.5	a	49	20.5 ± 12.7	a	5	36.0 ± 33.1	a
Glucose (mg/100ml)	130	122.6 ± 39.7		51	120.8 ± 38.2		5	114.4 ± 63.8	
Bilirubin (mg/100ml)	130	0.45 ± 0.23		51	0.59 ± 0.28		5	0.82 ± 0.63	
Cholesterol (mg/100ml)	128	86.2 ± 21.6	a,b	50	101.7 ± 26.9	a,c	5	110.4 ± 15.4	b,c
SGOT (mU/ml)	128	121.9 ± 42.0	a,b	50	147.7 ± 42.7	a	5	148.4 ± 58.2	b
Alkaline phosphatase (mU/ml)	130	85.0 ± 82.5	a	51	37.2 ± 15.2	a,b	5	86.0 ± 135.9	b
LDH (mU/ml)	128	261.5 ± 99.5	a	50	318.8 ± 88.2	a	5	396.2 ± 121.9	a
Total protein (g/100ml)	123	7.1 ± 0.7		45	7.6 ± 0.9		5	7.6 ± 0.7	
Albumin (g/100ml)	123	4.1 ± 0.6		46	4.3 ± 0.9		5	4.0 ± 0.2	
A/G (ratio)	123	1.41 ± 0.43		46	1.40 ± 0.42		5	1.08 ± 0.11	

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[1] Values for cows with no calf, one calf and two calves were compared with one another using the "t" test for unpaired variates. Probabilities of differences were:

a, b: different at $P<.001$

c: different at $P<.01$

PRESENT APPLICATIONS - NEED FOR FUTURE RESEARCH

It is abundantly clear that the full potential uses of blood analyses have not been reached. Stress of handling remains a problem, but results from Alaska indicate that sometimes trends might override these variables if methods are standardized. The problem of handling stress is insoluble in wild animals using presently available techniques, but may be minimized using tame moose and remotely-activated devices (cf: Farrell et al. 1970). Such devices might make comparisons between studies feasible in the future.

Seasonal patterns of BUN, glucose, cholesterol, proteins, and enzymes suggest that these values may be useful as indicators of nutritional status. Relationships need experimental confirmation, but eventually such indicators will allow discrimination between ranges of different qualities. Data are currently being gathered from different ranges in both Alaska and Minnesota.

The preliminary results of thyroxine assays reported here are very promising, and endocrine studies should be further pursued. We have shown that thyroxine levels vary seasonally, but do not know whether this variation is greater on lower-quality ranges, nor what the relationships between pregnancy, fetal health, and thyroid function are. Studies with animals at high and low nutritional planes, in either experimental or natural conditions, are indicated.

The only reported studies on cortisol metabolism are in the reindeer by Yousef et al. (1971). They conclude that winter acclimatization is accompanied by a decrease in half life and an increase in estimated secretion rate. No comparable data exist for other cervids. Confirmation of these results would be desirable since their method for measurement of cortisol can be influenced by increases in ketone bodies which may occur in the winter metabolic state. Simple measurement of serum cortisol is almost certainly of little value since the levels of binding proteins are low, the turnover is rapid and levels can fluctuate rapidly.

Measurements of other plasma hormone levels are not presently available. Seal's group do have data on insulin, glucagon, and TSH levels in the white-tailed deer which will be published shortly.

An area as yet barely touched is fat metabolism. Cholesterol assays show some promise, while triglycerides probably do not. The levels of both are low in cervids. Direct measurements of long-chain fatty acids, ketone bodies, pyruvate, lactate, acetate, and proprionate, especially in conjunction with rumen VFA studies, will probably provide a more direct assessment of the animal's dependence upon its fat reserves for energy.

Protein assays performed to date have been promising, but too crude to indicate precise metabolic relationships. Measurements of serum and red blood cell amino acids - especially alanine, glycine, leucine, and isoleucine - might provide valuable information on the status of protein used for gluconeogenesis. Creatine-hydroxyproline relationships have yet to be investigated in moose. Albumin-globulin relationships have successfully detected severe liver parasitism in Minnesota, and these assays will continue to have such applications.

Serum enzyme patterns have suggested seasonal changes in tissue destruction rates. Further studies might employ enzymes of higher tissue specificity in order to explain these patterns more fully.

Thus, the data currently available and the studies in progress with cervids hold considerable promise of providing the concepts and tools for evaluating condition of wild cervids and the condition of their range relative to their needs. It also appears possible to begin unraveling influences of such factors as density and social stress, separately from nutrition, upon a given population in terms of physiological response. The ability to quantitatively describe metabolic status and its endocrine regulation has increased dramatically in the past five years as the result of new exquisitely sensitive radio-immunoassay techniques. As a result, we may soon achieve the precise formulations of these mechanisms that we need in order to measure ecological and behavioral relationships of individuals and populations.

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Stress Evaluation

Stress evaluation began in May and data are insufficient for inclusion at this time. Excitability-related parameters were measured from 27 immobilized moose in May and June. Rectal temperatures ranged from 101.1°F to 108.0°F; heart rates from 52 to 140 beats per minute; and respiratory rates from 20-88 respirations per minute.

Hair Analyses as Indicators of Nutritional Status

No results are available at this time.

Weights and Measurements

Table 10 lists weights of moose obtained during this reporting period, additional weights were reported previously by LeResche (1970) and LeResche and Davis (1971). These data are summarized in Fig. 3. All available weight and morphometry data from North America are currently being analyzed for publication in 1974.

Nutritional Analyses of Plants, Rumina, and Fecal Pellets

Results of these analyses are presented in Tables 11-13.

Table 11, although based on few samples from a single site at one season, suggests the importance of variety to moose. This principle is discussed at length by LeResche and Davis (1973) and below (Food Habits of Tame Moose).

Chemical and proximate analyses of rumina of moose from lowland seral birch ranges and upland willow ranges show no significant differences between the two groups (Table 12), suggesting that the analyses performed were inappropriate to detect such differences. Volatile fatty acid (VFA) production rates might better reflect such nutritional differences (Gasaway and Coady, 1973).

Table 13 suggests that fresh fecal pellets might prove valuable in estimating relative levels of nutrients in rumina of animals from different areas. Correlations between protein and ether extract in rumina and pellets were highly significant ($P<.001$), and the correlation of caloric contents was significant at $P<.03>.02$.

Snow Monitoring

Snow studies initiated in late winter 1971 (LeResche and Davis, 1971) were continued in the winter of 1971-1972, and snow depths are listed in Table 14. Snow conditions during 1971-1972 were more severe than those during the previous winter. A maximum snow depth of 67 cm was recorded, and depths of 50 cm or greater were present for three consecutive months in five of the eight snow plots.

Although 67 cm of snow is not a great amount when compared with other parts of Alaska where moose are abundant, it is sufficient to

Table 10. Weights of moose handled at Moose Research Center traps, July 1971 - June 1972.

						Weight	
Date	Moose #	Pen*	Sex	Age	Remarks	Kg	lbs
15 July 1971	70-2	2	F	4	No calf	298	655
15 July 1971	53(70)	1	M	1	--	211	465
15 July 1971	88	0	F	9	Lactating	357	785
23 July 1971	Walter	2	M	2	Tame	291	640
27 July 1971	5271	2	M	calf	Died in winter	70	155
27 July 1971	2771	3	F	calf	Died in winter	70	155
27 July 1971	5470	2	M	1	Died in winter	161	355
10 Aug. 1971	43	1	M	4	--	473	1040
10 Aug. 1971	A60-71	4	M	calf	Died in winter	89	195
10 Aug. 1971	89	0	F	4	Lactating	400	880
10 Aug. 1971	A60	4	F	14	With calf	341	750
10 Aug. 1971	55	1	M	1	--	228	500
11 Aug. 1971	5670	4	M	1	Died in winter	248	545
11 Aug. 1971	70371	4	F	calf	Died in winter	95	210
11 Aug. 1971	R 70-3	4	F	4	With calf	309	680
11 Aug. 1971	10	1	F	4	Lactating	289	635
12 Aug. 1971	1-71	2	F	calf	Died in winter	84	185
12 Aug. 1971	90-A	0	F	8	With calf	434	955
12 Aug. 1971	90-71	0	F	calf	--	118	260
24 Aug. 1971	6	1	F	14+	With calf, died in winter	359	790
12 Aug. 1971	28	3	F	9	No calf	345	760
25 Aug. 1971	R 70-1	4	F	9	With calf	291	640
25 Aug. 1971	R 701-71	4	M	calf	Died in winter	84	185
31 Aug. 1971	3	1	F	9	With calf	359	790
31 Aug. 1971	371	1	F	calf	Died in winter	118	260
1 Sept. 1971	9171	0	M	calf	--	148	325
2 Sept. 1971	61	1	F	9	Lactating	355	780
14 Sept. 1971	93	0	M	3	--	364	800
19 Sept. 1971	9571	0	F	calf	--	175	385
21 Sept. 1971	9671	4	F	calf	Died in winter	159	350
22 Sept. 1971	9771	4	F	calf	Died in winter	145	320
29 Sept. 1971	9871	4	F	calf	Died in winter	182	400
5 Oct. 1971	100	0	F	13	In estrus	430	945
7 Oct. 1971	101	0	F	5	In estrus	345	760
7 Oct. 1971	102	0	F	13	In estrus	400	880
8 Oct. 1971	103	0	M	1	--	268	590
11 Oct. 1971	104	0	F	1	--	284	625
12 Oct. 1971	106	0	F	7	With calf	395	870
12 Oct. 1971	10671	4	M	calf	Died in winter	159	350
12 Oct. 1971	10771	4	F	calf	Died in winter	186	410
13 Oct. 1971	10871	4	F	calf	Died in winter	175	385
20 Oct. 1971	10971	4	F	calf	Died in winter	180	395
20 Oct. 1971	109	0	F	9	With calf	420	925
21 Oct. 1971	11071	4	F	calf	Died in winter	175	385
27 Oct. 1971	112	0	F	2	--	291	640

Table 10 (cont.)

Date	Moose #	Pen*	Sex	Age	Remarks	Kg	Weight lbs
3 Nov. 1971	11571	4	F	calf	Died in winter	200	440
2 Nov. 1971	11471	4	M	calf	Died in winter	168	370
4 Nov. 1971	116	0	F	11	--	261	575
4 Nov. 1971	117	0	F	2	--	466	1025
17 Nov. 1971	119	0	F	3	--	311	685
23 Nov. 1971	12071	4	M	calf	Died in winter	211	465
1 Dec. 1971	123	4	F	4	No calf in 1972	348	765
15 Dec. 1971	126	4	F	10	--	359	790
15 Dec. 1971	125	0	F	--	With calf	373	820
27 Jan. 1972	62	2	F	19	--	386	850
22 Mar. 1972	134	4	M	calf	Died in few days	164	360
2 Apr. 1972	66	2	F	10	Died in trap, fetus	327	720
2 Apr. 1972	64	1	M	1	--	282	620
25 Apr. 1972	138	0	F	3	Pregnant	355	780
26 Apr. 1972	132	0	F	--	--	318	700
28 Apr. 1972	Wally Jr.	2	M	calf	Supplementally fed	214	470
24 June 1972	Wally Jr.	2	M	Yrlg.	Supplementally fed	234	515
5 June 1972	73	2	M	3	--	239	525
22 June 1972	1	2	F	8	No calf	318	700
23 June 1972	77	2	F	6	No calf	275	605
23 June 1972	39	3	F	7	--	243	535
24 June 1972	Rachel	2	F	3	No calf	352	775
24 June 1972	3	1	F	9	No calf	295	650
28 June 1972	72A	3	F	2	No calf	225	495
1 Aug. 1972	45	2	M	3	--	384	845

* Pen "0" indicates moose trapped outside pens.

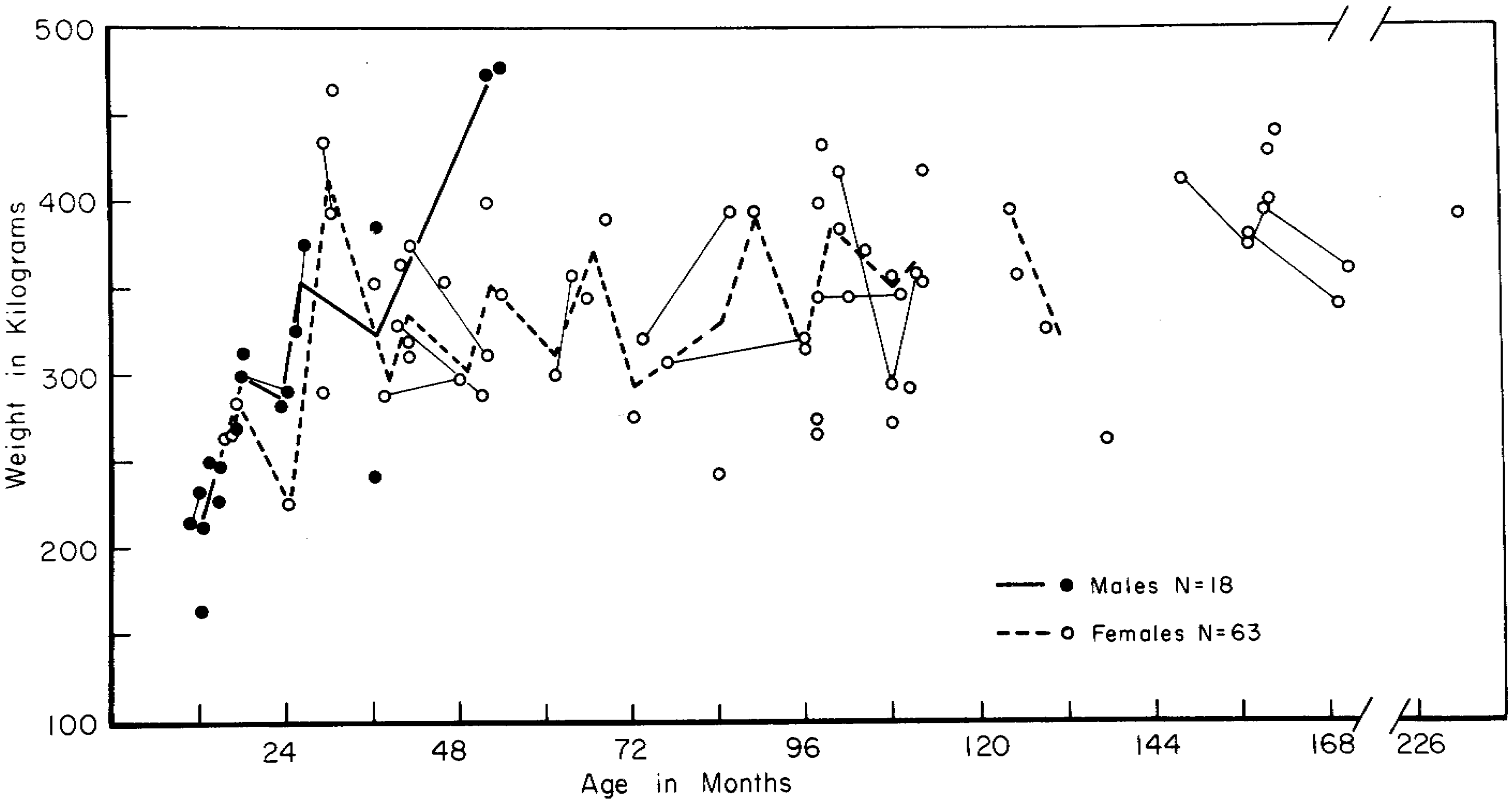

Fig. 3. Weights of 81 moose of known age from the northern Kenai Peninsula. Thick solid lines show seasonal mean weights of males to 48 months age. Dotted lines show seasonal mean weights of females to 132 months age. Thin solid lines connect sequential weights of individual animals at various ages, and reflect seasonal fluctuations in weight.

Table 11. Nutritional values of plants collected in May 1971.

	Analyses n	Protein %	Ether Extr. %	Ash %	Carbohydrates %	Fiber %	Digestible[1] dry matter %	P %	Ca %	K %	Mg %	Na %	Al ppm	Ba ppm	Fe ppm	Sr ppm	B ppm	Cu ppm	Zu ppm	Mn ppm	Cr ppm
B. papyrifera																					
Stems	8	8.8	14.6	1.8	49.7	30.8	36.9	0.23	0.38	0.34	0.17	0.027	31	93	78	25	16	9	141	283	<1.5
P. tremuloides																					
Stems	8	9.1	4.9	2.3	54.3	26.0	39.5	0.22	0.66	0.61	0.15	0.015	16	63	46	53	17	8	80	69	<1.5
Bark	3	3.3	3.1	8.6	59.2	59.2	48.6	0.03	1.30	0.35	0.18	0.024	36	109	32	109	17	5	152	80	<1.5
V. vitis-idaea																					
Whole plants	3	5.4	2.1	2.1	67.0	17.6	50.1	0.09	0.63	0.34	0.17	0.008	148	57	100	10	17	4	14	828	<3.0
Carex aquatilis																					
Whole plants	1	5.4	2.2	3.6	53.0	31.6	-	0.10	0.15	0.92	0.10	0.010	47	51	547	15	3	2	26	>800	<3
Alnus crispa	3	8.6	1.4	1.3	54.1	24.1	32.5	0.16	0.45	0.33	0.14	0.010	28	57	56	34	12	7.2	28	98	1.5
Ledum palustre	3	7.6	8.5	2.0	56.0	22.9	43.1	0.12	0.66	0.38	0.17	0.018	180	81	197	11	26	7.4	26	713	3.0

---

[1] Bovine flora

Table 12. Analyses of rumen contents of moose shot on the Kenai Peninsula (Units 7 and 15A), November - December 1971.

	$\bar{x}$ seral birch range (n=6)	$\bar{x}$ willow range (n=8)
Protein (%)	6.1	6.6
Ash (%)	1.5	1.5
Ether Extr. (%)	5.0	2.5
Fiber (%)	43.9	43.9
Carbohydrates (%)	43.6	45.5
Calories/100 g	245	230
DDM (%)	16.3	15.2
P (%)	0.16	0.16
K (%)	0.14	0.14
Ca (%)	0.38	0.49
Mg (%)	0.070	0.070
Na (%)	0.093	0.092
Al ppm	22	15
Ba ppm	57	53
Fe ppm	225	198
Sr ppm	27	45
B ppm	13	13
Cu ppm	6.9	8.4
Zu ppm	107	118
Mn ppm	233	163
Cr ppm	1.5	1.5±

Table 13. Correlation of nutrient content of fecal pellets with that of rumens collected from the same animal. November - December 1971.

(n)	r	p
Protein (5)	0.8835	<.001
Ash (5)	0.3093	>.10
Fat (ether extr.) (5)	0.9828	<.001
Crude fiber (5)	0.4200	>.10
Carbohydrates (5)	0.4200	>.10
Calories (5)	0.7128	.03>.02
Phosphorus (5)	-0.2300	>.10
Potassium (5)	0.2703	>.10

Table 14. Snow depth (cm) in each of eight habitat types, Kenai Moose Research Center, winter 1971-1972.

	November				December				January			February				March				April				May
	5	12	19	24	3	9	16	23	5	19	25	2	8	20	28	7	14	20	28	5	11	19	27	7
Mature Hardwoods (dense)	11	11	9	11	15	19	29	28	33	32	32	47	44	42	40	39	44	42	38	46	44	43	36	Tr.
Mature Hardwoods (thin)	13	15	13	15	19	23	33	33	36	32	34	52	51	50	50	50	56	57	51	58	55	56	42	Tr.
Sedge	13	18	12	16	20	25	37	34	44	29	27	43	42	41	38	39	43	44	38	43	44	46	33	Tr.
Spruce regrowth	14	18	13	15	20	25	39	36	46	46	45	58	56	57	55	57	60	58	54	62	61	60	47	Tr.
Birch-Spruce (thin)	17	16	13	15	21	24	37	32	43	43	43	62	58	58	55	51	56	55	51	58	57	56	47	Tr.
Birch-Spruce (dense)	13	15	11	13	17	24	33	29	43	46	43	55	56	56	50	51	55	53	47	53	52	57	39	Tr.
Spruce-ledum	*	9	*	6	10	13	15	19	46	39	39	57	55	57	53	56	61	60	56	58	61	67	51	Tr.
Mature Spruce	8	8	5	7	9	13	23	23	26	24	24	36	34	34	34	33	34	36	30	36	33	30	26	Tr.

*Not checked.

cover some important forage plants, including lowbush cranberry (*Vaccinium vitis-idaea*). Lowbush cranberry may be an important sustaining winter browse plant in this area (LeResche and Davis, 1973) and its nonavailability could adversely affect wintering moose. Because of the greater snow depths this past winter *Vaccinium* was visible for a much shorter period than during the previous winter. It was no longer visible in December and remained snow-covered until April or May except in the dense birch habitat type where it was visible in late March under the bases of spruce trees. The extensive covering of *Vaccinium* by snow may cause greater crater digging activity by moose (see Feeding Craters section, this report).

Browse Production and Utilization

This project segment returned fully to the Bureau of Sport Fisheries and Wildlife in May 1971, when John L. Oldemeyer began work. He has reported his findings in Annual Progress Reports (Oldemeyer, 1972, 1973a) and a review publication (Oldemeyer, 1973b). An abstract of Oldemeyer's work during this reporting period appears below:

> The Kenai Field Station of the Denver Wildlife Research Center was established in May 1971 with the primary objective to study moose habitat on the Kenai National Moose Range particularly at the Moose Research Center.
>
> A brief history of the Moose Research Center and moose and habitat research that has taken place up to this time is given.
>
> Twenty sites in each of four one-square-mile pens were chosen for intensive research. All sites in Pens 3 and 4 were sampled for browse density and frequency of occurrence and for birch production. Summarized data for the density and frequency sample are presented; however only preliminary production analysis has been started.

Several aspects of moose habitat were reviewed in depth in a publication prepared during this period (LeResche et al., 1973a). Conclusions relative to the seral habitat of the Moose Research Center are reproduced below:

Fire-mediated habitats are the most ephemeral of Alaskan moose habitats; yet, they support the greatest population explosions and among the greatest densities of moose in the state. The earliest specific publications concerning moose management in Alaska (Spencer and Chatelain, 1953; Leopold and Darling, 1953a and b; Chatelain, 1951, 1952) correctly stressed the correlation between dense moose populations and forest fires.

The ecological effects of fires in Alaska are extremely complex (cf. Lutz, 1956; Slaughter et al., 1971; Viereck, in press) and cannot be considered in detail here. Lutz (1956) presented a diagrammatic representation of normal courses of post-fire succession in Alaskan taiga. Viereck (in press) modified the chart and we reproduce his chart here

(Fig. 5). The course of succession and the seral community's value to moose are determined by a multitude of site (soils, temperature, moisture, slope and exposure), fire (severity, mode of travel, duration) and miscellaneous (natural reseeding sources, size of openings created) factors. The general successional courses producing maximum benefits to moose populations are those involving paper birch-willow-aspen shrub thickets.

Fires have probably always been common in Alaska, but have increased in frequency and area burned since modern settlement (Hardy and Franks, 1963). Viereck (in press) maintains there are very few Interior forests that survive burning long enough to reach what can be considered climax stage. Barney (1971) suggests that 600,000 to 1,000,000 ha burned annually from 1900-1940. Even with modern fire control, a mean of approximately 400,000 ha annually have burned between 1940-1969 (Barney, 1971). The general trend in the past three decades has been toward an increase in numbers of fires (1,138 in the 1940's, 2,583 in the 1950's and 2,380 in the 1960's in Interior Alaska) but a decrease in the total area burned (5,018,000 ha in the 1940's, 4,330,000 ha in the 1950's, 2,590,000 ha in the 1960's) and the area burned per fire. Increased fire control capabilities have thus perhaps decreased the benefits of civilization to moose.

<u>Characteristics</u> - Several factors determine the impact a fire-created successional community will have on moose populations: (1) species composition, (2) size of burn and per-area standing biomass and production of available browse, (3) rate of attaining a) above snow and b) above moose-reach heights and (4) amount and distribution of mature communities remaining, diversity of seral communities created and distribution of mature communities remaining (e.g.: "edge effect" created).

Composition - The species re-invading burned areas in Alaska most often tend to be the same species present before the fire (Fig. 5). This results from re-sprouting or growth of root suckers (Spencer and Hakala, 1964; Viereck, in press). Stands are often nearly monotypic in shrub species (cf. Table 15), with birch or aspen (on the warmest, driest sites) predominating. Spruce encroachment usually occurs slowly (Viereck, in press) in the Interior, but sometimes almost immediately (e.g.: on some stands on the Kenai Peninsula). Although willows are often among the first recolonizers, they generally do not achieve great numbers or production, perhaps because of consistent utilization by moose. Aspen may be similarly affected. Spencer and Hakala (1964) described how moose and plant competition had altered the proportion of aspen in the Kenai (1947) burn. It apparently decreased from 96.5 percent of the standing shrub biomass in 1952 (Spencer and Chatelain, 1953) to less than 1 percent in 1967 (Table 15). Wet lowland and permafrost sites are usually less thoroughly burned (Viereck, in press) and thus may rapidly recover by vegetative reproduction to a composition similar to that existing before the fire. Willows, blueberry (*Vaccinium* sp.) and dwarf birch (*Betula nana*) tend to be more numerous in these stands.

The exact composition of species recolonizing a burn may depend upon the timing of the fire relative to plant phenology (Viereck, in press). Willow species produce seeds that are viable for only a matter

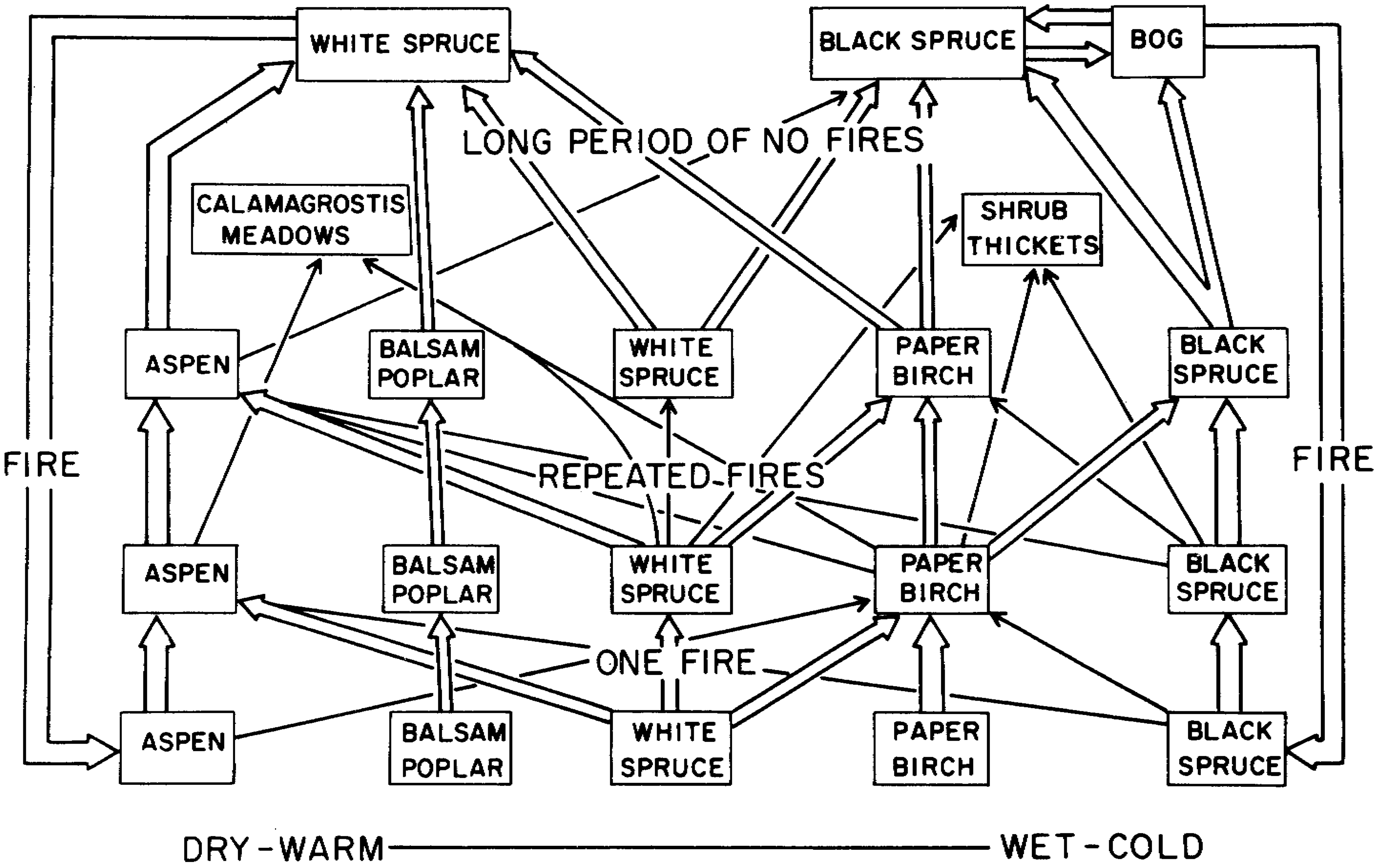

Fig. 5. Diagrammatic representation of normal post-fire succession in Alaskan taiga (from Viereck, in press.)

Table 15. Characteristics of shrub standing crop and production on Kenai burn 20 years after the 1947 fire. Modified from Seemel 1969.

Species	Community	Stems/ hectare	Annual Production g/hectare
Betula papyrifera	Dense Birch	80,046	479,348
" "	Medium Birch	47,221	315,987
" "	Thin Birch	34,381	249,316
" "	Spruce-birch	19,296	118,118
" "	Spruce Regrowth	6,775	35,226
Populus tremuloides	Dense Birch	237	202
" "	Medium Birch	339	348
" "	Thin Birch	541	875
" "	Spruce-birch	200	224
" "	Spruce Regrowth	168	224
Viburnum edule	Dense Birch	114	101
" "	Spruce-birch	89	90
Salix spp.	Dense Birch	1,641	9,233
" "	Medium Birch	1,196	6,193
" "	Thin Birch	692	3,747
" "	Spruce-birch	469	2,255
" "	Spruce Regrowth	652	2,109
Alnus crispa	Thin Birch	319	718
Betula nana	Spruce Regrowth	8,772	9,008
Totals:	Dense Birch	82,038	488,884
	Medium Birch	48,756	322,528
	Thin Birch	35,933	254,656
	Spruce-birch	20,054	120,687
	Spruce Regrowth	16,367	46,567

of weeks, and various species produce seeds at different times of year. Further, some species (paper birch, white spruce) produce "bumper" seed crops only once in several years (Viereck, in press), and the year the burn occurs might thus affect species composition of the resulting seral community.

There is little detailed information directly relating species composition of burn regrowth to subsequent moose population densities. However, observations suggest that the higher the proportion of first, willow, and second, birch shrubs produced, the greater the moose densities that will result during early years of succession.

Production - Biomass production of shrubs can be prodigious following burns in Alaska. Seemel's (1969) studies 21 years after the Kenai (1947) burn indicate annual production of nearly 500 kg/ha in the densest shrub *B. papyrifera* stands (Table 15). Standing crop is also large, with 82,000 shrub stems/ha estimated in the most dense stands. Both production and standing crop, as well as composition, vary considerably with individual stand (cf.: Table 15), and thus the proportions of various communities and variously-productive stands in a burn also influence moose numbers.

Productivity and quantity of available browse are seldom limiting factors to moose densities in large burns in Alaska. In the Kenai (1947) burn of 127,600 ha, Seemel (1969) estimated that more than eight moose/km^2 in a 2.6 km^2 enclosure used only 18.3 - 22.8 percent of the estimated annual shrub production, depending upon community. Spencer and Chatelain (1953) in contrast, had estimated that utilization by only 1.7 moose per km^2 on the same burn in 1952 was 45 percent of the annual production of aspen, then virtually the only shrub present. Since then plant production has exceeded moose production in relative terms, even though moose densities achieved the highest level ever recorded. Spencer and Hakala (1964) suggested that adequate densities of moose might retard succession in seral shrub habitats under certain conditions. We feel that these densities are seldom reached and never persist. Although moose may alter relative abundance of species in seral communities, we know of no instance where they have retarded succession over a large burned area. In the case of the Kenai burn, moose populations appeared to peak at the very high level of 4-6 moose/km^2 in the most productive habitat, at about the same time Seemel made his estimates. Within four 2.6 km^2 enclosures, populations remained relatively static at 4.6 - 5.4 moose/km^2 (before calving) over a three-year period, and utilization probably did not exceed Seemel's estimate (LeResche and Davis, 1971).

Isolated smaller burns serving as winter concentration areas for moose are sometimes retarded in succession and, on occasion, "over-utilized" by immigrant moose. Succession on the 1320 ha Kenai Lake burn (1959) has been effectively retarded by wintering moose, with most shrubs being browsed to snowline annually. This burn is unusual in that it is situated in the midst of nearly-mature range that wintered many moose until the late 1950's, and is about 20 km from the nearest edge of the larger Kenai burn (1947). Because fires are frequent throughout most of Alaska, small burns are often near other burns of various ages, and are therefore not subjected to intensive use by large concentrations of moose from a vast area. Furthermore, small isolated burns do not produce widespread moose population explosions sufficient to alter succession. Thus, in most cases, post-burn succession in large burned areas seems to proceed at a rate little different from what it would in the absence of moose. The course of succession may well be altered, however.

Rate of Growth - The sooner recolonizing shrubs achieve a height that makes them available to moose during winter, the sooner moose population explosions occur. Conversely, the more rapidly shrubs mature into trees, the shorter is the productive life of the burn. Spencer and Chatelain (1953) estimated that the Kenai burn (1947) produced significant browse by 1950, and that by 1953 moose had increased four-fold. Moose densities peaked on the burn about 1967-1969, and may have experienced the first stages of a decline in the winter of 1971-1972; however, they remain very high today.

Rates of growth differ between burns and within large burns, depending upon species present and site and climatological variables. Within the Kenai (1947) burn, heights of *B. papyrifera* plants in adjacent stands ranged from 1 m to almost 7 m in 1970. We do not know whether some sites were recolonized by paper birch later than others or whether growth rates alone account for the differences.

Hakala et al. (1971) predicted that browse would "continue to improve" on areas burned on the Kenai Peninsula (1969) for 23-25 years after the burn, as has been the case with the 1947 Kenai burn area. Moose densities could be expected to remain high for this period, and then decline as happened after a series of fires in the 1880's and 1920's (Spencer and Hakala, 1964). The limited information available, then, suggests that the "useful life" of a burn as moose habitat in Alaska is usually less than 50 years, and that moose densities peak 20-25 years after the burn.

Shape of Burn, Diversity and "Edge Effect" - The degree of interspersion of communities, or amount of "edge effect", produced by a fire is very important in determining the fire's effect on moose populations. Great discontinuity of burning is desirable because it provides, (1) cover (mature) habitat close to feeding habitat, (2) increased variety of alternate forage species and (3) staggered maturation rates of individual stands.

The forest edge ecotone allows moose both to invade a heterogeneous burn sooner than a large homogeneous burn and to achieve higher year-round densities. The distance a moose will continually move from cover into open feeding areas likely varies with season, age, sex, reproductive status, snow characteristics and a multitude of other factors. It appears certain, however, that increased mature forest edge will hasten establishment of moose in a new burn. The rate of moose increase on the Kenai (1947) burn, described by Spencer and Chatelain (1953) as 400 percent in five years, was probably near the maximum attainable because of the tremendous amount of edge created. It is problematical whether immigration from nearby areas had a significant effect (LeResche, 1973).

Once the moose population is established, small stands of mature timber (30-40 m tall birch, white spruce and aspen in the 1947 Kenai burn) provide year-round escape cover and winter refugia from deep snow. In addition, these stands provide alternate food sources that may be of considerable importance to the maintenance of high moose densities. LeResche and Davis (1973) showed that *Vaccinium vitis-idaea* plants were important to moose in winter and remained available more consistently in mature stands than in adjacent seral stands on the Kenai.

Shrub-forest ecotones are not the only important edges created by fires. Shrub-sedge and shrub-aquatic ecotones are also important at various times of year. Brush bordering summer feeding bogs, for example, can be excellent cover habitat for young calves (LeResche, 1966). Dense shrubs bordering small, drying potholes are preferred habitat for adults in late fall, when they dig craters in snow to feed on cured sedge leaves.

The optimum amount of edge and/or the optimum size and shape of individual burned stands in Alaska is difficult to determine because moose densities depend upon so many variables. The Kenai burn (1947), however, appears to represent, if not the ideal, at least the most productive large area of moose habitat known to us. Densities of moose exceeding 4/km^2 have been achieved over most of the burn (vs densities of ca 0.08/km^2 in similar unburned areas (Spencer and Chatelain, 1953) through a combination of high forage production, generally mild winters, abundant alternate foods (especially *V. vitis-idaea*), edge effect, and adjoining upland ranges.

The fire burned 127,600 ha of approximately 260,000 ha, and has regenerated into several paper birch and birch-spruce communities (Table 15). The entire burn has not been analyzed, but detailed type maps have been constructed of the reasonably-representative 1024 ha enclosed by the Kenai Moose Research Center enclosures.

A type map of 254 ha of this mixed habitat, prepared 20 years after the burn (Fig. 6), was analyzed for sizes of individual stands and amount of ecotone between each of the 11 communities distinguished (Tables 16-17). A "stand" was defined as a contiguous area of one community, regardless of shape, and ecotone was simply taken as the length of mapped margin between stands.

The 254 ha contains 624 individual stands ranging in size from .02 ha to 18.4 ha (Table 16). Mean stand size is 0.41 ha, and 86 percent of all stands are less than 0.5 ha in area; only 8 percent of the stands are larger than 1 ha, and only 2 percent larger than 5 ha. Remnant mature stands comprise 118 ha, or 46 percent of the area. This mature forest is extremely segmented, comprising 411 stands distributed throughout the area.

The large number of stands and their irregular shapes have produced tremendous amounts of ecotone (Table 17) --112 km in the 2.5 km^2 area. Mature communities have about 99 km of "edge", sharing 59 km of this with the various seral shrub communities. Shrub communities themselves are surrounded by about 103 km of ecotone, bordering on mature forest and on other seral communities.

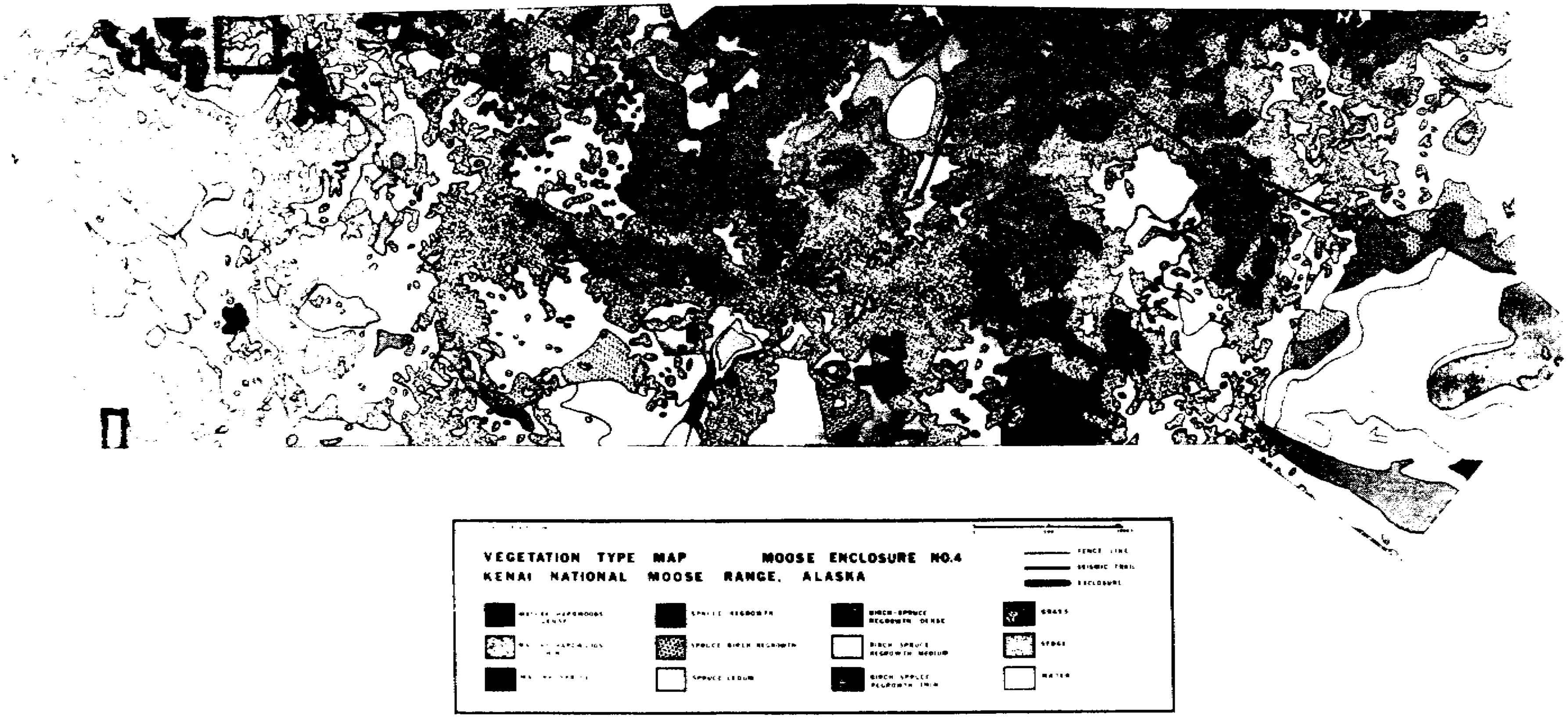

Fig. 6. Vegetation type map of 25+ ha of the 1947 Kenai burn.

Table 16. Sizes of 624 stands of 11 communities in 254 ha of the Kenai, Alaska (1947) burn, mapped in 1967, Kenai Moose Research Center, Pen 4.

Community	Number Stands	Total Area ha	$\bar{x}$ area/ stand-ha	Range ha/stand	No. Stands of Area					
					.5ha	.5-1.0ha	1.1-2.0ha	2.1-5ha	5-10ha	10ha
Dense Mature Hardwoods	22	43.07	1.96	.05-12.9	9	5	2	3	2	1
Thin Mature Hardwoods	383	70.69	0.18	.02-18.4	368	7	4	1	1	2
Mature Spruce	6	4.54	0.76	.02- 3.9	5				1	
Spruce Regrowth	10	19.29	1.93	.14-11.6	4	2	2	1		1
Spruce-Birch Regrowth	33	17.83	0.54	.02- 2.3	22	5	5	1		
Spruce-Ledum	6	5.39	0.90	.23- 2.5	3	1	1	1		
Dense Shrub Birch	23	7.30	0.32	.21- 1.3	20	1	2			
Medium Shrub Birch	40	41.16	1.04	.03- 8.9	24	7	4	2	3	
Thin Shrub Birch	77	31.28	0.41	.02- 6.2	62	7	5	2	1	
Grass	19	1.82	0.10	.02- 0.4	19					
Sedge	5	12.05	2.41	.07-10.2	3	1	0			1
Totals	624	254.42	0.41	.02-18.4	539	36	25	11	8	5
Percent of total stands					86%	6%	4%	2%	1%	1%

Table 17. Amount of ecotone (in meters) between 11 plant communities in 254 ha of the Kenai, Alaska (1947) burn mapped in 1967, Kenai Moose Research Center, Pen 4. (Figure 6).

Community	Dense Mature Hardwoods	Thin Mature Hardwoods	Mature Spruce	Spruce Regrowth	Spruce-Birch Regrowth	Spruce Ledum	Dense Shrub Birch	Medium Shrub Birch	Thin Shrub Birch	Grass	Sedge	Water
Dense Mature Hardwoods		17,581	325	206	356	-	711	1,728	2,642	51	-	-
Thin Mature Hardwoods			305	2,541	2,795	-	3,150	22,764	22,967	508	178	-
Mature Spruce				-	-	76	203	1,016	406	-	76	-
Spruce Regrowth					3,455	1,524	305	457	1,524	661	356	-
Spruce-Birch Regrowth						203	1,067	4,522	4,472	813	102	-
Spruce-Ledum							-	102	280	-	1,931	-
Dense Shrub Birch								3,303	1,016	-	-	-
Medium Shrub Birch									3,303	457	508	-
Thin Shrub Birch										457	102	-
Grass											-	152
Sedge												356
	23,600	72,789	2,407	11,029	17,785	4,116	9,755	38,167	37,169	3,099	3,609	508

Total Edge = $\frac{224,033 \text{ m}}{2}$ = 112.0 km

This 2.5 km^2 by no means represents an extreme case, but rather is a fair sampling of the entire 260 km^2 area affected by the burn. By extrapolation, then, the Kenai burn (1947) produced over 60,000 separate stands, more than 11,000 km of ecotone and 128,000 ha of new shrub communities. It is not surprising that moose densities achieved such a high level as a result of this fire.

Moose Use - Seral burn habitats are extremely important wintering ranges once growth is sufficient to provide available browse above the snow. Some burns (the Kenai burn [1947], for example) receive an influx of moose from upland ranges in early winter, and support very dense wintering concentrations. Others (in the upper Little Chena drainage near Fairbanks, for example) support moose during late summer and fall, but may be virtually deserted when moose move down into denser forests and riparian stands in November and December. The most diversified burns (Kenai 1947) also support significant densities of moose during calving, summer and rutting periods and have relatively high resident populations throughout the year.

Food Habits of Tame Moose

The results of this study, as excerpted from LeResche and Davis (1973), are presented below.

ABSTRACT

Food intake of three tame moose (*Alces alces gigas*) was observed on the Kenai Peninsula, Alaska, during summer on normal range and during winter and spring on normal and depleted range. Plant species and bite sizes were recorded for 49,308 bites consumed. Food eaten varied between summer and winter, and moose ate a greater variety of forage than previously realized. Birch (*Betula papyrifera*) leaves comprised 56 percent (by number of bites) of the summer diet, forbs 25 percent, grasses, sedges and aquatics 10 percent, and willow (*Salix* spp.) 5 percent. Winter diet on range that had supported average moose densities for the area (15 per square mile) was 72 percent birch twigs, 21 percent lowbush cranberry (*Vaccinium vitis-idaea*) and 6 percent willow and alder (*Alnus crispa*). On depleted winter range, stocked for 18 months with abnormally high moose densities, birch twigs comprised only 22 percent of the diet. The bulk of bites taken were of lowbush cranberry (51 percent) and foliose lichens (*Peltigera* spp.) (23 percent). In May, moose consumed 10-30 times as much cranberry and lichen as birch. Availability of understory forage species during part of the winter is probably an important factor in supporting the very high moose densities found on this range.

INTRODUCTION

Analyses of moose range commonly stress abundance, production and use of large woody shrubs (Aldous and Krefting, 1946; Krefting, 1951; Spencer and Chatelain, 1953; Spencer and Hakala, 1964; Houston, 1968). This emphasis occurs because browse is the only food available to moose in winter over much of their range and winter range is classically considered a limiting factor for moose populations, and because range survey methods depend on the ease by which one can visually estimate browse conditions (Cole, 1963).

Emphasis on woody shrubs has persisted despite an impressive array of evidence that moose are extremely catholic in their tastes. Especially in spring and summer, they consume forbs, grasses, mushrooms, lichens, and practically all other floral components of their environment. Murie (1934) reported a great variety of foods taken on Isle Royale. Peterson (1955) listed more than 100 species and groups of plants taken at least occasionally by moose. Houston (1968), although stressing that browse was the most important food class during all seasons in Wyoming, demonstrated that moose ate significant quantities of grasses, sedges, rushes and forbs in spring and summer.

This paper reports that moose on heavily utilized range in south-central Alaska ate considerable proportions of decumbent lowbush cranberry (*Vaccinium vitis-idaea*) and lichens during winter, despite an abundance of available and unused woody browse. Furthermore, only about 65 percent of their food consumption in summer was from erect browse species.

Summer Foods

Fifty-six percent of more than 28,000 bites taken by the three tame moose in July and August consisted of birch leaves. Utilization by individuals ranged from 49-65 percent birch leaves. Five percent of bites were of willow species. Moose took all leaves, most bark and stems up to 2 cm diameter from the willow they discovered. Four percent of bites were leaves and twigs of dwarf birch (*Betula nana*). Thus, during summer, 65 percent of all bites taken were parts of woody browse plants.

The remaining one-third of summer forage was primarily forbs (25%), grasses (3%), sedges (4%) and aquatics (3%). Alder, aspen, lowbush cranberry, lichens and mushrooms (mostly *Boletus* spp.) were taken in trace amounts.

Moose consumed different nonbrowse species as the season progressed, apparently according to plant phenology. In late May and June, they ate newly emergent marsh-growing forbs, especially cloudberry (*Rubus chamaemorus*) and sundew (*Drosera rotundifolia*). Moose gathered in groups in muskegs to feed on these species in their pre-flower and early flowering stages. Moose in boggier areas consumed newly emergent sedges (*Carex* spp.; *Eriophorum* spp.) and horsetails (*Equisetum* spp.) during this period.

Fireweed (*Epilobium angustifolium* and *E. latifolium*) was a favored food during July. Moose selected plants in the pre-flower stages, and consumed flowered plants (late July and August) only rarely. Along with lupine (*Lupinus nootkatensis*), fireweed contributed most of the forb biomass consumed during summer. These two species were also the most abundant forbs present during this period.

Lupine was the dominant forb food from the date we first saw moose consume it (10 July) through late August. Lupine was abundant and the plants relatively large (20-25 cm in height) for several weeks before the moose first began to eat the species. During the period of consumption, moose selected almost exclusively plants in the pre-flower state.

Mushrooms, especially *Boletus* spp., were abundant during the summer of 1970, and apparently were eaten whenever encountered by moose. Fifty other nonbrowse plant species consumed in summer are listed in Table 2.

Winter Foods

Winter feeding habits of moose on normal range varied significantly from those of animals confined to a small area of depleted range. We did not collect quantitative data from tame moose until February, but rather observed wild animals during September-January. Plants consumed were essentially the same as those taken during late winter with one exception. During this entire period, when snow depth was less than ca:30 cm, moose dug craters to secure large, still succulent, *Carex* plants from boggy areas around marshes and river banks.

Tame moose on normal winter range consumed 72 percent birch stems in February-May. Most of the remaining plant material eaten was lowbush cranberry--21 percent by number of bites and by biomass. Lowbush cranberry was available throughout the winter, being emergent from the snow in most habitats on most days. The multitude of dead-fallen burned spruce poles and the dense lower branches of new growth conifers shielded lowbush cranberry plants from deepest snow. Moose commonly dug craters under these obstructions and often kneeled beside them to feed on lowbush cranberry plants.

In addition to birch, moose browsed 6 percent willow and alder, in approximately equal proportions. A few bites of the large foliose lichen *Peltigera* spp. were consumed on normal range, as were some miscellaneous forbs--primarily wintergreen (*Pyrola secunda*) and dwarf dogwood (*Cornus canadensis*) after snow melt.

The moose on depleted range ate only 23 percent browse during February-May. Almost all lichens were taken in May when snow cover was absent from most of the ground surface. Thus, lichens were essentially a spring food, and not a winter staple. In late April and during May, however, lichens made up more than half the diet, with cranberry comprising almost all other food. Lichens consumed were almost entirely the large foliose *Peltigera* spp., which is very abundant ground cover in many areas of the burn. Other genera (especially *Cladonia* spp.) were also consumed.

Results of nutritional and elemental analyses of food species collected in May are presented in Table 11.

DISCUSSION

Snow is a paramount factor in seasonal distribution and numbers of mammals in the north (Formozov 1946). Moderate snow conditions on the northern Kenai Peninsula lowlands contribute significantly to the land's exceedingly high carrying capacity for moose. The range produces more than 180 kg (400 pounds) of available browse per acre annually in the most productive areas (Bishop 1969). While this great biomass of woody browse is doubtless important, it is only slightly used at current high moose densities, and similar habitat elsewhere in Alaska supports many fewer moose on a year-round basis. Other moose populations believed to approach the 1947 Kenai burn group in year-round density are the Matanuska Valley herd and the small, recently-established population near Yakutat. These areas are characterized in most years by snows arriving late in fall and disappearing or settling early in the spring. Non-woody plants are thus available to these populations during most months of most years. In contrast, moose populations on the vast seral ranges of interior Alaska do not reach densities approaching those on the northern Kenai Peninsula. Many interior situations present higher quality (predominantly willow--Milke 1969) browse ranges; however, snow cover is early, persistent, and often deep. The long period during which Interior moose must eat only woody browse is probably an important factor in limiting moose densities.

An almost complete loss of calves in much of the 1947 Kenai burn during the winter of 1971-72 corroborates this thinking. During this winter, lowbush cranberry was covered by snow in all habitat types by mid-December. The snow did not settle or melt appreciably in the succeeding weeks, and by late February all 35 calves in the Moose Research Center enclosures were dead. Surveys in the vicinity of the Center showed a calf:cow ratio of .02 (n = 186 cows). Calves died inside and outside our enclosures with rumens full of birch, and with body weights decreased 27 - 34 percent from September-November weights.

Axiomatically, food quality and digestibility are as important as quantity and availability in determing ungulate densities (cf: Klein 1970), and quality of browse species is related to successional state (Cowan et al. 1950). Under the best conditions, woody browse usually contains less than 10 percent crude protein, 1-7 percent crude fat, 40-60 percent carbohydrates (NFE) and 20-40 percent cellulose (crude fiber) (cf: Kelsall 1968, Milke 1969, Houston 1968). Kelsall does report analyses of eight willow species with a mean of more than 20 percent protein, but this is higher than other reports. In protein levels, at least, the woody parts of all common browse species provide barely adequate maintenance levels of nutrition as judged from domestic ruminants (Swenson 1970) and other wild cervids (Ullrey et al. 1969, Luick et al. 1971). Thus, population levels of moose confined to woody browse for long periods may suffer accordingly.

Depletion or virtual elimination of some browse species--willow, aspen and highbush cranberry in the Kenai burn--may not only reduce the proportion of higher-protein forage, but also does reduce variety available in winter. Variety itself is important to ruminants, for digestibility of forage is sometimes altered strikingly by addition of other material to a one-species diet (eg: Mellenberger et al. 1971).

Nonwoody browse and succulent species were consumed in quantity by moose when snow cover allowed. The several important nonbrowse species increased crude nutrient intake as well as providing variety. *Peltigera* lichens contain nearly 20 percent protein and more than 9 percent ash (Kelsall 1968). Lowbush cranberry, the most important nonwoody winter food, contains 67 percent carbohydrates and protein levels approximately equivalent to those in woody browse species.

It is instructive to calculate nutrient contents of several diets containing various proportions of browse and nonbrowse forage. Moose eating only birch consume approximately 9 percent protein, 15 percent fat, 50 percent carbohydrates and 2 percent ash. This diet is only 37 percent digestible, as estimated using bovine flora (WARF Institute). By substituting 25 percent lowbush cranberry for some birch (thereby approximating the 75:25 proportions of birch and cranberry eaten on "normal" Kenai winter range), protein and fat intake decreases somewhat, but carbohydrate level increases to 54 percent and digestibility is enhanced, even discounting any synergistic effects.

A 50 percent birch, 25 percent cranberry and 25 percent *Peltigera* diet (approximating the February-May average on "depleted" Kenai winter range) provides 10.7 percent protein, 3.7 percent ash and 57.7 percent carbohydrates--increases over a pure birch diet--but a decreased proportion of fat. In any event, biomass of available forage is increased when nonbrowse plants are available, and this additional plant material is at least equal to birch browse in nutrition.

We have concluded that the exceedingly high moose densities on the 1947 Kenai burn range result not only from high annual production of woody browse, but also from the normally moderate snowfall and short duration of snow cover sufficient to restrict consumption of nonbrowse species. Seral ranges with good ground cover of lowbush cranberry and *Peltigera* lichens will likely have a very high carrying capacity for moose if snowfall and duration of snow cover permit access to these plants during at least part of the winter. Nonbrowse plants not only increase biomass of forage available, but also provide higher protein, ash, carbohydrate and digestibility levels, as well as enhanced variety.

Feeding Craters

Three concentrations of feeding craters examined in mature hardwood habitat within the Moose Research Center enclosures contained 84 craters, or 19 per hectare. One concentration examined in sedge/spruce-*Ledum* habitat contained 47 craters, or 58 per hectare. Mean dimensions of craters measured are listed in Table 18. Locations of craters relative to surrounding objects are tabulated in Table 19.

Several difficulties were encountered in determining what species moose ate in the craters and what plants were present. Pawing tore apart vegetation to the extent that it was uncertain whether it had been

Table 18. Dimensions of moose feeding craters in mature hardwood and sedge/spruce-*Ledum* habitat types.

	Mean (cm)				Range (cm)		
	n	Length	Width	Depth	Length	Width	Depth
Hardwoods	84	183	102	36	76-381	36-178	22-56
Sedge/spruce-*Ledum*	47	180	120	20	76-483	28-198	10-31

Table 19. Location of individual moose craters in relation to surrounding objects.

	Hardwoods	Sedge/ Spruce-*Ledum*
in open	31%	62%
near windfall	16%	-
near birch	26%	-
near spruce	10%	13%
near aspen	11%	-
near stumps	10%	-
near alder	-	26%

fed upon or merely pawed. Granular snow at the base of craters often caved in, covering the vegetation, and light snowfalls covered many plants. Because of this, plants eaten from craters in hardwood habitat types were not recorded. In a few cases craters were not dug deep enough to reach vegetation (see Table 20).

RECOMMENDATIONS

1. Moose populations in the northern Kenai Peninsula should be managed on the assumption that they are near maximum levels and slowly declining. No increase can be sustained by the present habitat, although some can be expected within 3-5 years in the 1969 burn area.

2. Annual changes in production and recruitment should be interpreted primarily in light of long-term trends, with the knowledge that, in areas of high population densities, these parameters may fluctuate widely year-to-year.

3. Experimental studies should be performed to confirm suspected correlations between nutritional status and blood parameters in moose. These studies should include the evaluation of handling stress and its influences on blood values obtained.

4. Blood thyroxine levels should be further studied in relation to metabolic state.

5. All available weight and morphometry information should be consolidated and published.

6. The correlations between chemical values of pellets and rumina of moose on different quality ranges should be further investigated with a view toward determining whether simple pellet analyses might provide an index of range quality.

7. Snow depths should be routinely monitored in all habitat types. Data collected to date should be consolidated with food habits information and snow data from Interior Alaska (Coady's) and conclusions drawn concerning the relative importance of snow conditions to moose in these two regions.

8. Further data should be gathered concerning feeding craters with a view toward determining whether or not crater numbers and characteristics are indicative of relative snow-induced stress on moose populations.

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Table 20. Plant species present and fed upon in moose feeding craters.

Plant Species	Percent craters with species present		Percent craters in which species was fed upon
	mature hardwood	sedge/spruce-*Ledum*	sedge/spruce-*Ledum*
Vaccinium vitis-idaea	68	34	15
Ledum palustre	20	36	-
Rosa acicularis	20	-	-
Lycopodium spp.	8	-	-
Betula papyrifera	4	-	-
Salix spp.	-	79	72
Carex spp.	-	70	36
Equisetum spp.	-	trace	-
No species reached	13	4	-

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JOB PROGRESS REPORT (RESEARCH)

State: Alaska

Cooperators: Alaska Department of Fish and Game, U. S. Bureau of Sport Fisheries and Wildlife--Kenai National Moose Range, and Alaska Cooperative Wildlife Research Unit

Project No.: W-17-4 Project Title: Big Game Investigations

Job No.: 1.2R Job Title: Moose Behavior

Period Covered: July 1, 1971 through June 30, 1972

SUMMARY

Total mortality of orphaned and unorphaned moose calves during the winter of 1971-72 precluded assessment of differential mortality. Eight orphaned calves lost a mean of 35 kg from autumn until their deaths in December or January, or 20 percent of their original body weight. After apparently being deserted by their mothers in late winter calves aggregated in large groups containing only calves.

Variations in aggregating behavior are related to breeding activities, mother-young relations, the male social system, the sex ratio of the population, and external influences of forage, topography and cover. Aggregations from midwinter through spring are primarily related to the extrinsic factors of forage location and cover. In addition the solitary nature of the cow with calf may facilitate the calf's protection from predation and access to the best forage available to the cow. Aggregations during the pre-rut, rutting, and post-rutting periods probably can be attributed to internal behavior patterns associated with breeding and possibly the establishment and maintenance of social systems, as well as to environmental factors, including access to high quality forage supplies in early winter which serves to provide the moose with added sustenance prior to the severe winter periods where forage accessibility is restricted.

Although the social system among moose populations appears to be primitive when compared to the highly gregarious systems of wapiti, red deer and caribou, the differences in aggregation patterns among the three populations studied here indicate that the species is highly adaptable to a variety of conditions. The successful adaptation to different habitats, which range from mountainous, forested terrain where plant communities are relatively stable, to alpine tundra, and to undulating boreal forest where successful occupation is primarily dependent upon the transitory seral stages, must be considered a major influence upon the social system and the aggregation patterns described herein.

CONTENTS

BACKGROUND

LeResche and Davis (1971) discussed the importance of moose (*Alces alces*) behavior to population dynamics and moose management practices. Of special note are the importance of the cow-calf bond to calf survival during the first winter, and the seasonal dynamics of moose aggregations. Migratory behavior is considered separately under Job 1.4R (LeResche and Davis, 1971 and this report).

Proper management of moose populations sometimes requires harvesting females as well as bulls. Calves orphaned when their mothers are taken by hunters may present special management problems. If survival or physical condition of calves is significantly affected by loss of the mother, hunting regulations may have to be modified to take this into consideration.

High mortality of moose calves may occur even when the mother is present. In an area near Palmer, Alaska, in 1965, over 55 percent mortality of calves occurred during the first five months after birth (LeResche, 1966). The greatest mortality occurred within two weeks after birth, when approximately 26 percent of the calves were lost. Calf losses during severe winters may also be high. In the Yakutat area of Alaska, for example, nearly 60 percent of the calves observed in December 1968 were lost before counts were again made in May 1969 (Rausch, 1971). However, the mortality rates of calves without mothers may be even higher. Altmann (1958), who did her work in Wyoming, stated that moose calves without mothers rarely survive the winter. In Alaska several populations of moose have been established by transplanting calves which were raised in captivity. Data on mortality of these calves before release and hunting data on the established populations are available (Burris, 1971). These calves were released in areas with no moose or low moose populations and good habitat conditions. The transplants were successful, but actual mortality rates from the time of release are not known.

Orphaned calves surviving until spring may be in poorer condition than calves with mothers and therefore be more subject to mortality by disease, accidents, or predation.

The mother's presence may cease to be a significant factor in calf survival and condition sometime between fall and spring. If large enough samples of calves can be obtained at different times, a comparison of survival rates between samples will be useful for management purposes.

Behavior patterns of moose calves will obviously be altered by loss of the mother. Social stress may increase due to attempts by orphaned calves to associate with other moose or even other species. When a calf loses its mother, the calf may revert to the generalized following response of its earlier life (Altmann, 1958). It will probably be rejected by other moose and possibly injured. Altmann (1958) cited an example of a healthy orphan moose calf being put into an area with a bison herd. The calf tried to join the herd and was gored by a bison cow, although there were no obstacles to its escape.

Weaning of calves may be nearly complete by the rutting season, but calves may depend on their mothers for guidance in feeding. In deep snow conditions calves may expend more energy without a mother to break trail for them. Social interactions may cause calves to be driven out of optimum feeding areas under deep snow conditions.

OBJECTIVES

To gain information on survival rate, physical conditions, and causes of mortality of moose calves orphaned at various times in the fall and winter; to compare this information with survival, condition, and causes of mortality of calves having mothers.

To study certain aspects of the behavior of orphaned calves and compare to the behavior of calves having mothers.

a) Social interactions

b) Activity patterns and movements

c) Feeding

To examine the seasonal dynamics of moose aggregations on the Kenai Peninsula and compare them with groupings in other parts of North America, in reference to habitat and population characteristics.

PROCEDURES

Orphan Calf Survival

The study was conducted at the Kenai Moose Research Center on the Kenai Peninsula. Most of the work was done in Pen number 4. During the summer of 1971, this pen contained eight adult females, six calves, five to seven yearlings, and three adult males. In the fall and winter (1971-72), moose numbers reached a maximum of at least 40 animals due to introductions of moose from outside the pens. High winter mortality reduced the Pen 4 population to 13 or 14 moose by June of 1972.

Most observations were made in Pen number 4. One lone calf was observed in Pen number 3 for several days in February 1972. Additional observations of lone calves and calves with cows were made in areas outside the Moose Research Center.

Between September 21, 1971 and November 23, 1971, eleven calves were trapped from the area outside the Moose Research Center. These calves were released in Pen number 4. When the mothers were also trapped, they were released outside the pens. One calf that was born in Pen number 4 was orphaned when its mother died from a drug overdose. This calf was also used in the orphan project.

When a calf was trapped, it was weighed and measured and a blood sample was taken. All trapped calves were ear tagged and collared for identification. Seven of the calves were equipped with radio collars.

After being introduced into Pen number 4, calves were frequently located by one of the following methods: (1) radio-tracking, (2) snow tracking or accidental sightings from the ground, and (3) aerial sightings.

When a calf was sighted, its location was plotted on a map. The map location was often determined by using a hand compass and counting paces to fencelines or other permanent landmarks.

An attempt was made to determine what vegetation was eaten most extensively by the calves. The following methods were used to study feeding: (1) identifying plant after observing calf feeding, (2) locating calf and backtracking in snow to see what plants were eaten, and (3) collecting rumen samples from dead calves for later analysis.

Behavior patterns that were observed include:

1. Activity patterns
    a. feeding (duration and frequency)
    b. resting (duration and frequency)
    c. movements (rate, frequency, snow depth, and habitat)
2. Social interactions
    a. frequency of contact
    b. type of contact
    c. description of animal or group contacted

Dead calves were thoroughly examined. If the carcass was not decomposed, it was weighed, measured, and autopsied. The area around a carcass was investigated for tracks made by the calf or other animals. In some cases, backtracking in the snow helped to determine rate of movement and activity prior to death.

Materials collected from dead calves included: (1) femur for marrow fat determination, (2) mandible for measurement and tooth eruption, and (3) rumen sample to be analyzed.

Data analysis will include: (1) comparisons including percent fat in femur marrow and rumen analysis between winter-killed calves and calves which died of other causes and (2) comparisons of behavior patterns of orphan calves in Pen 4, lone calves observed outside the pens, and calves having mothers.

Moose Aggregations

We follow Bergerud and Manuel (1969) in defining an aggregation as any group of animals which occur within reasonable proximity to each other. The problem of determining whether these aggregations were dictated by external factors such as topography or forage supplies, or whether they are in fact social groups wherein individuals interact among each other (Etkin, 1964) will be discussed.

Most aggregations discussed in the literature were located by aerial search using a Piper Supercub, Aeronca Champ, or Bell G3B helicopter. In addition, summer observations in southwestern Montana were made from vantage points where moose could be readily located from the ground due to the open nature of the area. In Minnesota, summer observations included moose using lakes, streams and ponds, as investigated from a canoe and also by air. All Alaska data were obtained by aerial search. Information from southwestern Montana was obtained from 1958-60 and from 1965-67, from Alaska between 1970-72, and from Minnesota between 1967-70. Aggregations have been grouped according to different periods representative of moose phenological patterns, i.e., calving period, summer, pre-rut, rut, post-rut, early winter, midwinter, late winter and spring. These periods seemed to be the most likely times when group sizes would vary for one reason or another.

Moose were classified according to the following criteria: bulls were identified by presence of antlers or antler pedicels and lack of the white vulvar patch (Mitchell, 1970); cows were identified by lack of antlers or pedicels and presence of the white vulvar patch; calves were identified on a basis of size (usually there was a mature cow present to compare sizes with) and the short snout length characteristic of young-of-the-year animals. Because the nature of the terrain precluded close observation of moose, no classifications were attempted in northeastern Minnesota after January 1, when most bulls were either shedding or had shed antlers. Some individuals were identified according to sex and age in southwestern Montana during the winter. Groups were classified as bulls only, cows only, bulls and cows, cows and calves, and bull-cow-calf groups for purposes of analysis. Only groups in which all individuals were classified were included in the analysis of sex-age groups.

Characteristics of Moose Populations and Habitat

The Kenai, Alaska, moose population is migratory, and spends summer months at or above timberline in the Kenai Mountains. Cow:calf ratios averaged 100:44 from 1968 to 1970 in June (LeResche, 1970), and the bull: cow ratio averaged 20:100. Hunting seasons are open for bulls with limited cow permits. Population density is over 3.6 moose per square mile (Evans et al., 1966). Moose are generally readily visible from the air in this area of Kenai birch (*Betula papyrifera* var. *kenaica*), quaking aspen (*Populus tremuloides*), and black spruce (*Picea mariana*), which was burned over in 1947 (Spencer and Hakala, 1964), and is generally a low forest.

The southwestern Montana moose population probably moves shorter distances, usually along a drainage (Knowlton, 1960), and occupies more densely forested habitats which are not as amenable to aerial observation as those in the Kenai. Populations may spend all but late winter in mountainous terrain, at which time they commonly use the narrow willow (*Salix* sp.) bottoms along drainages. Cow:calf ratios averaged 100:45 and sex ratios approached equality (Stevens, 1966, 1970). Hunting seasons are by either-sex permit with cows and bulls taken in similar proportions (Stevens, 1971).

Population densities range near 0.43 moose per square mile, but Stevens pointed out that these figures are misleading because an undetermined amount of unsuitable habitat has been included in the estimates. Generally, these moose are dispersed until winter and then may occur in winter concentrations at densities of up to 25 moose per square mile. A typical wintering situation would be several to 25 moose in a willow bottom of each drainage. It should be mentioned that the winter ranges of the Jackson Hole (Houston, 1968) and Red Rock Lakes National Wildlife Refuges (Dorn, 1970) are more extensive than commonly occurs through southwestern Montana.

The northeastern Minnesota ranges are probably the most densely vegetated, and least suitable to search from the air. Population densities were approximately two moose per square mile (Peek, 1971), the cow:calf ratios averaged 100:47 over a four-year period, and sex ratios approached equality. These moose appear to be non-migratory (Van Ballenberghe and Peek, 1971). No hunting occurred during the observation periods and human-caused mortality was probably negligible. It is evident that these moose populations vary considerably in characteristics, and habitat.

FINDINGS

Orphan Calf Survival

Between September 21 and November 23, 1971, 11 calves were trapped and introduced into Pen 4 without their mothers. A calf which was born in Pen 4 was orphaned on August 25, 1971, when its mother was accidentally killed. This calf also became part of the orphan project (See R70171, Table 1).

In November and December 1971, calves were located and observed for varying lengths of time. Their locations were plotted on a map of Pen 4. Observations were made of feeding and other activity patterns, and social interactions.

Between December 10, 1971, and January 15, 1972, nine of the 12 orphan calves in Pen 4 were found dead. The average weight loss for eight of these calves was 19.8 percent (Table 2). The ninth calf (No. R70171, Table 1) was born in Pen 4 and weighed 185 pounds on August 25, 1971. When found dead in December 1971, this calf weighed 220 pounds. The calf probably gained weight after the initial weighing, then lost weight prior to death.

None of the other three orphan calves in Pen 4 were seen alive later than December 8, 1971. Two of these calves were found dead during helicopter tagging in the pens on May 9 and 10, 1972. The final project calf was found dead on June 6, 1972. It was not possible to determine the time of death of these three calves.

In Pen 4, four calves with mothers had been observed during the fall and early winter. None of these calves were seen alive later than December 19, 1971. Two of the calves had been trapped and marked during the summer of 1971. Their carcasses were found in May and June 1972. An unmarked calf carcass was also found in Pen 4 in June 1972.

Several dead calves were found in the other pens and in the area adjacent to the moose pens during aerial and ground surveys. Many cows known to have had calves in 1971 were seen in late winter without calves. No yearlings were seen in the pens during the summer of 1972. Calf mortality in the moose pens during the winter of 1971-72 was almost certainly 100 percent.

The 100 percent mortality of calves in Pen 4 was unforeseen and very few of the early observations were of calves with mothers. Therefore, it was not possible to compare the behavior of orphan and non-orphan calves in the same pen during the same time period.

Many dead calves found in the pens and in several other areas were autopsied, weighed, and measured. Femurs and rumen samples were collected. Some of the femur marrow values are given in Table 1. Rumen samples have not yet been analyzed.

Aerial surveys and general observations during the winter of 1971-72 seemed to indicate that more lone calves were seen than could be accounted for by the number of hunter-killed cows. It is possible that calves become weak under severe winter conditions which limit food availability and hinder movements. Perhaps they are then abandoned by their mothers. In Pen 3 at the moose pens, a lone calf was tracked and observed from the ground for several hours between February 10 and February 16,

Table 1. Data on project calves.

Moose Number	Sex	Date Trapped	Weight When Trapped	Date Found Dead	Weight at Death	Condition of Carcass	% Fat-Femur Marrow
9671	F	9-21-71	159 kg	5-10-72	--	Hide and hair intact	--
9771	F	9-22-71	146 kg	1-14-72	118 kg	Frozen	--
9871	F	9-29-71	182 kg	1-15-72	152 kg	Legs, ears, stiff body soft	--
10671	M	10-12-71	159 kg	12-27-71	123 kg	Partially stiff	9.1
10771	F	10-12-71	186 kg	1-14-72	139 kg	Frozen	--
10871	F	10-13-71	175 kg	12-10-71	142 kg	Fresh	8.0
10971	F	10-20-71	180 kg	1-15-72	145 kg	Frozen	--
11071	M	10-21-71	175 kg	1-13-72	143 kg	Fresh	7.1
11471	M	11-2-71	168 kg	6-6-72	--	Maggot infested	--
11571	F	11-3-71	200 kg	5-9-72	--	Maggot infested	--
12071	M	11-23-71	211 kg	12-23-71	170 kg	Odor	8.3
R70171*	M	8-25-71	84 kg	12-29-71	100 kg	Legs, ears stiff	8.4
2771**	F	7-27-71	70 kg	2-16-72	107 kg	Fresh	7.6

* Born in Pen 4, orphaned August 25, 1971.
**Born in Pen 3. Later abandoned by mother.

Table 2. Weight losses of eight calves.

Moose Number	Sex	Weight when trapped kg (lbs.)	Weight at death kg (lbs.)	Weight loss kg (lbs.)	Weight loss (%)
10871	F	175 (385)	142 (313)	33 (72)	18.7
12071	M	211 (465)	170 (375)	41 (90)	19.4
10671	M	159 (350)	123 (270)	36 (80)	22.9
11071	M	175 (385)	143 (315)	32 (70)	18.2
10771	F	186 (410)	139 (305)	48 (105)	25.6
9771	F	145 (320)	118 (260)	27 (60)	18.8
10971	F	180 (395)	145 (320)	34 (75)	19.0
9871	F	182 (400)	152 (335)	30 (65)	16.2
	$\bar{x}$ kg (lbs.)	177 (389)	142 (312)	35 (77)	19.8

1972 (see No. 2771, Table 1). No other moose were seen near the calf during this period. The calf died on February 16, apparently of malnutrition. The calf was seen with its mother on December 14, 1971, but had been seen alone as early as January 26, 1972. The mother was seen again during a helicopter survey of the moose pens on March 23, 1972. She has also been observed and trapped at later dates.

Moose Aggregations

The results are presented below as they will be published in:

Peek, J. M., R. E. LeResche and D. R. Stevens. 1973. Dynamics of moose aggregations in Alaska, Minnesota, and Montana. J. Mammal. (in press).

The other authors' affiliations are: Department of Entomology, Fisheries and Wildlife, University of Minnesota (St. Paul); and U. S. National Park Service (Estes Park, Colorado), respectively.

RESULTS

Annual Variation in Group Size

Group sizes reflected the relative density of the three populations, being highest on the Kenai and lowest in southwestern Montana (Table 3). Summer aggregations were smallest, while the post-rutting aggregations were largest. In addition, the Kenai population tended to aggregate in March and April. Analysis of variance indicated significant differences in group sizes between populations and between seasons within populations at the 90 percent level of probability.

Group sizes varied most on the Kenai, where groups of 1-12 were observed between July and November, and again in March and April. Greatest variation in the Minnesota population occurred from October through early January. Distributions at this time ranged from one to seven moose. Variations in the Montana population was greatest during the post-rut-March period. Both variation in group size and average group size data suggest that the fall and winter periods may be identified as the periods when these moose populations were most aggregated.

Distribution of Single Individuals

Cows occurred as single individuals more frequently than did bulls. The exceptions to this occurred during the rut in the Montana and Minnesota populations and in January and February in the Kenai population (Table 3). Both sexes were least gregarious in summer in the Montana and Minnesota populations and in January and February in the Kenai population. Both sexes were most gregarious during the pre-rut, rut, and post-rut periods. The percentage of male-female aggregations dropped rather abruptly after the rutting period in the Kenai population; and more slowly in the other two populations. The percentage of cows occurring as groups of two or more individuals was higher on the Kenai than

Table 3. Distribution of aggregations by sex.

	Period	Total Number Groups	Males Alone		Males with Other Males		M - F(c)		Females alone (c)		Other Females		Percent Female Calves Solitary	Percent Males Seen Alone	Percent Females Seen Alone
			#	%	#	%	#	%	#	%	#	%			
Minnesota	June-August	139	58	42	3	2	2	1	75	54	1	1	100	92	96
	Early Sept.	23	5	22	2	9	7	30	9	39	-	-	60	36	56
	Late Sept.-early Oct.	27	8	30	1	4	9	33	8	30	1	4	40	44	44
	Late Oct.-November	228	25	11	32	14	59	26	95	42	17	7	81	22	55
	December	232	30	13	26	11	34	15	130	56	12	5	94	33	74
Montana	May-June	108	25	23	14	13	3	12	53	49	3	3	100	60	77
	July-August	147	51	35	9	6	8	5	76	52	3	2	100	75	87
	Late Aug.-early Sept.	89	28	31	12	13	13	15	35	39	1	1	100	53	71
	Sept. 16-Oct. 15	87	29	33	2	2	22	25	30	34	4	5	57	55	54
	Oct. 16-November	27	5	19	2	7	5	19	15	56	0	0	71	42	75
	December	124	19	15	9	7	14	11	76	61	6	5	93	45	79

Table 3. (cont'd.) Distribution of aggregations by sex.

	Period	Total Number Groups	Males Alone		Males with Other Males		M - F(c)		Females alone (c)		Other Females		Percent Female Calves Solitary	Percent Males Seen Alone	Percent Females Seen Alone
			#	%	#	%	#	%	#	%	#	%			
Kenai	May-June	317	41	13	9	3	17	5	200	60	50	16	94	61	75
	July	267	36	13	24	9	60	19	108	34	39	12	94	30	52
	August	324	39	12	22	7	77	24	149	46	37	11	95	28	57
	Sept. 1-15	250	21	8	13	5	83	33	86	34	47	19	87	18	40
	Sept. 16-Oct. 15	100	3	3	2	2	34	34	36	36	25	25	66	9	38
	Oct. 16-November	95	1	1	1	1	42	44	29	31	22	23	65	2	31
	December	69	4	6	0	0	5	7	44	64	16	23	96	44	68
	January	99	17	17	2	2	4	4	65	65	11	11	95	81	81
	February	36	3	8	0	0	0	0	29	81	4	11	100	100	88
	March	593	30	5	7	1	21	4	414	70	125	21	100	52	74
	April	540	54	10	4	1	41	8	314	58	127	24	93	55	65

on the other two areas, probably reflecting both the higher density and the disparate sex ratio of the Kenai population. The data suggest that the bull may be identified as the more gregarious of the sexes.

Aggregation Patterns for Bulls

The mean group size for Kenai bulls was highest in July and August, dropped during the pre-rut and rutting periods, increased slightly during the post-rut period, dropped during the winter and then increased in March. This was contrasted by the tendency for bulls in the Montana and Minnesota populations, which tended to be lowest in the summer periods and during the rut, and highest during the post-rutting and early winter periods.

Variation in group sizes was greatest in summer in the Kenai population. Variation in the Minnesota population was uniformly low until the post-rut and early winter period. Although classifications ceased after December, the variation of all groups observed in midwinter suggested that bull-only group sizes declined during this period. The Montana populations showed greatest variability in grouping of bulls in May-June, and during the post-rut and early winter periods. Bulls in the Minnesota and Montana populations characteristically aggregated more in late fall than did the Kenai bulls.

Aggregation Patterns for Cows

Differences between aggregating behavior among cows from the three populations were great. Cows from the Montana population were most gregarious during the post-rut and December periods, although at no time was there an apparent pronounced tendency to aggregate. The Kenai cow population tended to aggregate during the pre-rut, rut, and post-rutting periods and to disperse during the winter.

Variation in group size was uniformly low in the Montana and Minnesota populations, and pronounced in the Kenai population. While variation for bulls appeared greater in the Montana and Minnesota populations, variation for cows was greater in the Kenai population, indicating the difference was related to the differences in sex ratio.

Aggregation Patterns for Cow-Calf Groups

There was less tendency for cows with calves to aggregate with other moose than for cows without calves in the three populations (Table 3). The average group size ranged between 2 and 3 for all three populations, indicating that the cow-calf or cow-twin calf group was most frequently observed. Cows with calves in the Minnesota and Montana populations did not appear to aggregate with other moose at any time except during the pre-rut and post-rutting periods. Cows with calves aggregated more frequently at all times of the year in the Kenai population, especially during the migration periods of spring and fall (LeResche and Davis, 1971).

Aggregation Patterns for Cow-Bull Groups

Groups comprised of both sexes were most frequently observed in the pre-rut, rut, and post-rut periods, but the sexes aggregated more frequently in the Kenai population than in the other two populations. Aggregations of both sexes in summer commonly included an adult cow and a yearling bull (yearling bulls may be identified by antler development, Peek, 1961). Aggregations during the rut were of adult bulls and cows, probably associated most frequently for breeding purposes. Cows with calves were associated with bulls in the Montana and Minnesota populations from the pre-rutting period on. The Kenai cows with calves also associated with bulls during summer months and during the migration period.

Aggregations Above and Below Timberline, Kenai

Flights made in June and July, August, and March on the Kenai included observations of moose above and below timberline (Table 4). In all cases but one, group sizes and variation in group size was greatest above timberline than below. The one exception, cow-calf groups seen in June below timberline as compared to those seen in July above timberline, may have been associated with migration activities.

DISCUSSION

The milk group was considered as the basic social unit in moose (de Vos et al., 1967), and other aggregations appear to be relatively loose-knit and transitory (Houston, 1968). Interaction among animals within aggregations during summer and late winter appears to be minimal most of the time, with individuals often appearing to ignore each other. The cow-calf group, plus the aggregations associated with breeding appear to be true social units, as defined by Etkin (1964).

The causes of aggregation have been suggested to be defense against predators (Lack, 1968; Goss-Custard, 1970), as well as to the pattern of food availability in terms of food item dispersion and seasonal variation in abundance (Crook and Gartlan, 1966). Variations in aggregation size in moose appear to relate to extrinsic factors such as those above, plus snow depth and hardness, vegetative cover, and intrinsic factors such as sex of animal, breeding activities, aggressive behavior, family care, group life (Tinbergen, 1953) and possibly the sex ratio. Population density did not appear to influence trends in aggregation changes through the year, although the largest group sizes and greatest variation within periods did occur with the densest population.

Influence of Sex Ratio on Aggregation Behavior

Differences between the Kenai population and the other two populations in aggregating behavior of females may be partially attributable to the disparate sex ratio on the Kenai as compared with the nearly equal sex ratios of the other two populations. Cows were definitely more gregarious on the Kenai than elsewhere. Groups of cows without

Table 4. Summary of above (AT) and below (BT) timberline aggregations of moose in August, March, and June-July, Kenai Peninsula, Alaska.

Date	AT or BT	Number of male groups	Number of moose	Group $\bar{X}$	Range	Number of female groups	Number of moose	Group $\bar{X}$	Range	Number of male female groups	Number of moose	Group $\bar{X}$	Range
August	AT(2)[1]	32	58	1.81	1-8	80	154	1.92	1-12	44	197	4.48	2-11
	BT(2)	29	40	1.38	1-3	63	70	1.11	1-6	17	37	2.18	2-6
March	AT(2)	18	40	2.22	1-10	81	130	1.60	1-8	12	66	5.50	2-15
	BT(4)	29	29	1.00	--	389	506	1.30	1-6	10	30	3.00	2-5
July	AT(4)	51	85	1.67	1-7	124	198	1.60	1-8	58	221	3.81	2-5
June	BT(2)	11	13	1.18	1-2	52	73	1.40	1-4	4	10	2.50	2-4

Date	AT or BT	Females-calves		Group $\bar{X}$	Range	Males-females-calves		Group $\bar{X}$	Range	All Groups[2]		Group $\bar{X}$	Range
		Number of groups	Number of groups			Number of groups	Number of moose			Number of groups	Number of moose		
August	AT(2)[1]	20	48	2.40	2-6	2	9	4.50	4-5	173	466	2.62	1-12
	BT(2)	38	80	2.11	2-4	1	3	3.00	-	146	230	1.58	1-6
March	AT(2)	15	49	3.27	2-13	-	-	-	-	126	285	2.26	1-15
	BT(4)	43	99	2.30	2-6	-	-	-	-	477	673	1.41	1-6
July	AT(4)	32	73	2.28	2-4	2	7	3.50	3-4	267	584	2.19	1-13
June	BT(2)	19	47	2.47	2-7	-	-	-	-	86	143	1.66	1-7

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[1] Number of flights.
[2] Includes some not classified according to sex or age.

calves occurred frequently at all seasons except in February and March. While cows with calves were less social, even in early summer, groups were observed. This period would be considered that when the cow would be most protective of the calf (Altmann, 1958). The Kenai bull population appeared to associate more readily with cows than the other two bull populations in question, and less frequently with other bulls, when ranges in group sizes are considered. This was especially apparent during the fall and winter periods. The data indicate that the high percentage of cows and low percentage of bulls in the Kenai population tends to influence aggregating behavior by causing cows to be more gregarious and by causing the sexes to mix more frequently during the year than was observed in the other two populations.

Influence of Predation Upon Aggregation Size

Adult moose in prime condition appear to be relatively immune to predation, but aged or diseased individuals and calves are vulnerable (Mech, 1966; LeResche, 1968). In northeastern Minnesota and Ontario, the incidence of moose remains in wolf (*Canis lupus*) scats is higher in summer than in winter (Halverson, 1969; Pimlott et al., 1969). This suggests that predation is most important when aggregation sizes are lowest, in summer, and also among the cow-calf groups which are the most solitary. In addition, the late winter-early spring periods of low aggregation size in northeastern Minnesota are periods when that population is probably at its poorest physiological status, following the winter period, and presumably includes more vulnerable animals than in early winter or fall. It is therefore possible that the solitary and well dispersed nature of the moose population, especially during periods when individuals would be most vulnerable, may be attributable in part to the influence of predation.

Undoubtedly the highly aggressive nature of the cow immediately after parturition, and the tendency to remain with the calf rather than to conceal it, are predator-induced responses. It appears that the forested terrain which these species occupy during summer months favors the solitary mode of defense against predation, where vulnerable individuals remain dispersed and assumedly less easy to locate. Cows with young calves are not uncommonly found on small islands or in swampy areas (Rausch, 1959; Peek, 1971) which probably favor the maneuverability of the long-legged moose over its potential predators.

Although wolves are not present in the southwestern Montana area, and may not have been a major influence upon moose habitat selection or mortality because of the abundance of other Cervidae (Cowan, 1947; Murie, 1944), the fact that cows are seen in relatively open cover with newborn calves in this area (Peek, 1961) suggests that the aggressive nature of the cow would facilitate calf survival if wolves were present.

The tendencies of cows to be aggressive prior to calving, to withdraw from disturbances, and to defend the calf were factors which Geist (1963) considered to inhibit development of any greater social organization beyond the "milk group" in the Wells Gray Provincial Park, British Columbia population. In addition, aggressive interaction between cows has been observed during the rut by Altmann (1959:423), Geist (1963:412) and Peek (1961). This aggressiveness was considered by Geist (1971:124) to be an antiwolf adaptation. The solitary tendency may be related to this same influence or possibly to a need to minimize intraspecific competition for scarce forage sources, or both.

Influence of Breeding Activities on Aggregation Behavior

Aerial searches during the actual breeding period would provide observations of both sexes searching for mates, rutting groups, bands of young individuals, and cows which had mated (Altmann, 1959). The pre-rutting period is the first time since winter that increases in aggregation size are readily apparent in the data. Bulls are least apt to be seen alone during the period, cows without calves tend to associate with other individuals more, but cows with calves are still solitary. The tendency is for groups of cows and bulls to decline in size during the rutting period, suggesting that pre-rutting and post-rutting period groups are larger and more variable in size than the rutting group. Actually, it appears that the separation of pre-rutting, rutting, and post-rutting periods would be artificial, since it may be expected that groups representing each phenological period may be present at any time after breeding starts. The possibility exists that pre- and especially post-rutting groups are aggregating for purposes other than these associated with breeding.

Aggregations which contain bulls during this period tend to be largest, so the period of the year when the highest amount of social interaction occurs is also the period when bulls appear to be most gregarious. Post-rutting aggregations are especially large. The period of actual receptivity to breeding in the cow moose is quite short and most cows are probably bred within a ten-day period centering upon October 1 (Edwards and Ritcey, 1958). Spermatogenesis, indicative of androgen secretion, extends uninterrupted from early September through November and may have a significant influence upon male behavior until antler drop in early January (Rausch, 1959; Peek, 1961; Houston, 1968). It is likely that pre-rutting and post-rutting aggregations serve to bring males together for purposes of social display. Observations of bulls in November and December in Minnesota suggest that they are highly aggressive at that time. Very often, antler polishing and jousting, plus other activities which may be interpreted as display towards conspecifics are observed. The possibility exists that dominance heirarchies among males are established at this time. In summer, males appear less antagonistic and less gregarious. This is contrasted by the antagonistic nature of the female which coincides with and explains their solitary nature. The tentative conclusion which may be drawn is that moose populations tend to be more patriarchal than matriarchal in nature, since it appears that the bull is the most social of the two sexes, and appears to govern what social interaction exists within a population. The bull tends to seek out other individuals for purposes of social display which is not the case with the female, whose social interactions center around breeding and family care. If dominance heirarchies are established or maintained in late fall and early winter, the purpose may be indirectly related to reproduction through selection of habitat which facilitates survival and maintenance of condition. Moose in northeastern Minnesota tend to disperse into small groups and to occupy the more dense covers of sparse forage in late winter. Undoubtedly there is a premium in occupying the cover which provides best forage as well. It is possible that the more dominant males select prime wintering areas and tend to exclude younger animals. This exclusion process is probably usually a passive interaction, wherein the more aggressive animals occupy the best bedding and feeding sites, causing the subordinate to search for other areas. In this connection, it is significant that des Meules (1964) reported that once suitable bedding sites were used up within a yard in Quebec, moose occupying the area moved out.

Influence of Environment on Aggregation Behavior

The largest group sizes in the Kenai, and in northeastern Minnesota occurred when moose were occupying the most open cover, whether it be alpine tundra above timberline, or recently cutover shrub communities. While both populations were aggregating during the reproductive and post-reproductive periods, and most certainly the use of open cover where individuals would be able to observe each other more easily would be important, the Montana population appeared to aggregate to some extent in winter while occupying the relatively open cover afforded by willow bottoms. Moose occupying douglas fir (*Pseudotsuga menzieseii*) in winter tended to be more solitary than those occupying willow bottoms (Stevens, 1970 and Knowlton, 1960). Dassman and Taber (1956) noted that deer (*Odocoileus hemionus*) which inhabit dense cover usually form small groups or are solitary. Pruitt (1960) found barren-ground caribou (*Rangifer tarandus*) occurred in smaller bands on taiga winter range than on tundra summer range. Thus this tendency to aggregate into larger groups may also have a psychological basis, wherein the larger group replaces the role of vegetative cover for the individual (Crook, 1970). Because moose groups are so loose knit, individuals seemingly being oblivious to one another in late winter, such an explanation does not completely explain this tendency. In winter the deeper snows on mountainsides cause moose to move into the willow bottoms and lower ranges (Edwards and Ritcey, 1956) and also place the animal in contact with an abundant and highly palatable forage source. Thus it appears that topography, snow depth, and forage supplies play a major role in aggregating moose in mountain areas.

This does not appear to be the case in the relatively even terrain in boreal forests. Here successful occupation of late winter cover with sparse forage sources is facilitated by the dispersal of the population as Houston (1968) and Geist (1971) suggest.

Conclusions

It is concluded that the variations in aggregating behavior are related to breeding activities, mother-young relations, the male social system, the sexual composition of the population, and external influences of forage, topography and cover. Aggregations from midwinter through spring are primarily related to the extrinsic factors of forage and cover. In addition the solitary nature of the cow with calf may facilitate its protection from predation and access to the best forage available to the cow. Aggregations during the pre-rut, rutting, and post-rutting periods probably can be attributed to internal behavior patterns associated with breeding and possibly the establishment and maintenance of social systems, as well as to environmental factors, including access to high quality forage supplies in early winter which serves to provide the moose with added sustenance prior to the severe winter periods where forage accessibility is restricted.

Although the social system among moose populations appears to be primitive when compared to the highly gregarious systems of wapiti (*Cervus canadensis*), red deer (*Cervus elaphus*) and caribou, the differences in aggregation patterns among the three populations studied here indicate that the species is highly adaptable to a variety of conditions. The successful adaptation to different habitats, which range from mountainous forested terrain where plant communities are relatively stable, to alpine tundra, to undulating boreal forest where successful occupation is primarily dependent upon the transitory seral stages must be considered a major influence upon the social system and the aggregation patterns described herein.

RECOMMENDATIONS

1. Further studies should be undertaken to determine the importance of the cow-calf bond to overwinter calf survival during "normal" winters.

2. Consideration should be given to encouraging or requiring the harvest of calves when accompanying cows are killed in areas of high moose populations.

3. Aggregation behavior should be studied in other parts of Alaska with moose populations having sex ratios less skewed toward females, in order to determine whether change in aggregation behavior might reflect important changes in population size or productivity.

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JOB PROGRESS REPORT (RESEARCH)

State: Alaska

Cooperators: Alaska Department of Fish and Game, U. S. Bureau of Sport Fisheries and Wildlife (Kenai National Moose Range)

Project No.: W-17-4 Project Title: Big Game Investigations

Job No.: 1.3R Job Title: Development and Testing of New Techniques

Period Covered: July 1, 1971 through June 30, 1972

SUMMARY

A one-stage rumen fistulation procedure was not successful on two tame moose. Mean monthly femur-marrow fat contents of calf moose from January through May ranged from 11 to 6 percent. Adult femur-marrow fat levels ranged from 13 to 94 percent (monthly means) on a year-round basis. A manuscript on precision and accuracy of aerial moose censusing was submitted for publication during the reporting period.

CONTENTS

BACKGROUND

Moose (*Alces alces*) research and management require methods of estimating numbers and of handling, marking and following animals. These techniques necessarily vary with species, location and nature of the management/research problem. The Moose Research Center, with known numbers of confined animals, provides a unique test-ground for numbers-related techniques and for methods and equipment whose effectiveness can be learned only by relocation of animals.

LeResche and Davis (1971) summarized present knowledge of and needed future work on techniques of aerial censusing, chemical immobilizing, radio-tracking, pellet-count censusing and marking moose for movement studies. LeResche and Lynch (1973) reported on a moose trap developed at the Moose Research Center and used to capture free-ranging moose in Alberta.

Van Dyne (1968) reviewed techniques for measuring dietary preferences and digestibilities of foods selected by large herbivores. Previous studies at the Moose Research Center have utilized techniques involving observation of free-ranging animals (LeResche and Davis, 1973 and this report, Job 1.1), estimating food intake by observing browsed plants (LeResche and Davis, 1971 and Oldemeyer, 1973), rumen contents analyses of shot animals (LeResche and Davis, 1971), fecal analyses (this report, Job 1.1), and in vitro trials. To carry out in vivo digestibility trials, rumen-fistulated animals were needed.

Collection of femurs and analysis of their marrow for fat content has been done extensively and rather indiscriminately in Alaska in recent years. Neiland (1970) reported a simplified "dry-weight" method of estimating fat content in bone marrow, and many femurs have been analyzed since then. The potentialities and shortcomings of using marrow fat to indicate nutritional status are reviewed by Cheatum (1949) and Bischoff (1954). Consolidation of data from various parts of Alaska was needed to allow at least crude interpretation of moose femur-marrow fat values.

OBJECTIVES

To develop and/or test techniques for: aerial censusing, pellet-count censusing, immobilizing, radio-tracking, and marking of moose; to develop a technique for implanting permanent rumen fistulae in moose; and to establish baselines for interpreting femur-marrow analyses of moose.

PROCEDURES

Procedures followed were essentially the same as those described by LeResche and Davis (1971). In addition, bone-marrow data were collected from several areas of the state and tabulated. Rumen fistulae were implanted in two tame 14-month-old moose by Dr. R. Herin, Colorado State University. A 4 cm long incision was made in the left abdominal wall approximately 15 cm dorsally from the spine and 5 cm posteriorly from the last rib. The rumen was pulled through the incision (Fig. 1) and sutured to the incision margin in a circular pattern. The rumen was incised within the sutures and the base flange of the fistula plug device (Fig. 2) was folded and inserted into the rumen. The sleeve flange was then placed over the tube, pulled tight against the abdominal wall (thereby squeezing the rumen and wall between the two flanges) and the cable clamp was tightened. The plug was inserted and the animal revived. The first attempt took two hours, the second, 20 minutes.

FINDINGS

Results of aerial-census evaluation experiments are presently in manuscript form as: LeResche, R. E. and R. A. Rausch. Accuracy and precision of aerial moose censusing. (Under review at J. Wildl. Mgmt.).

Radio tracking gear, as described by LeResche and Davis (1971) proved successful in the orphan calf survival study, reported in Job 1.2R (this report).

One moose (Walter) died from the effects of prolonged chemical immobilization (M-99) during the first fistulation procedure. The flanges from the fistula plug assembly implanted in the second moose (Raquel) caused tissue necrosis, and the plug was rejected in approximately ten days. The fistula itself healed satisfactorily, but the hole closed completely about 18 months after the surgery.

Fat levels of femur-marrows of 106 calves and 60 adults are presented in Table 1 and Fig. 3. More data should be consolidated and analyzed (eg: those from Coady, 1973) before conclusions are drawn.

No further findings concerning technique development and testing are available at this time.

RECOMMENDATIONS

1. The one step rumen fistulation procedure is not indicated for moose. Two-stage procedures should be tested.

Figure 1. Rumen being pulled through incision in abdominal wall.

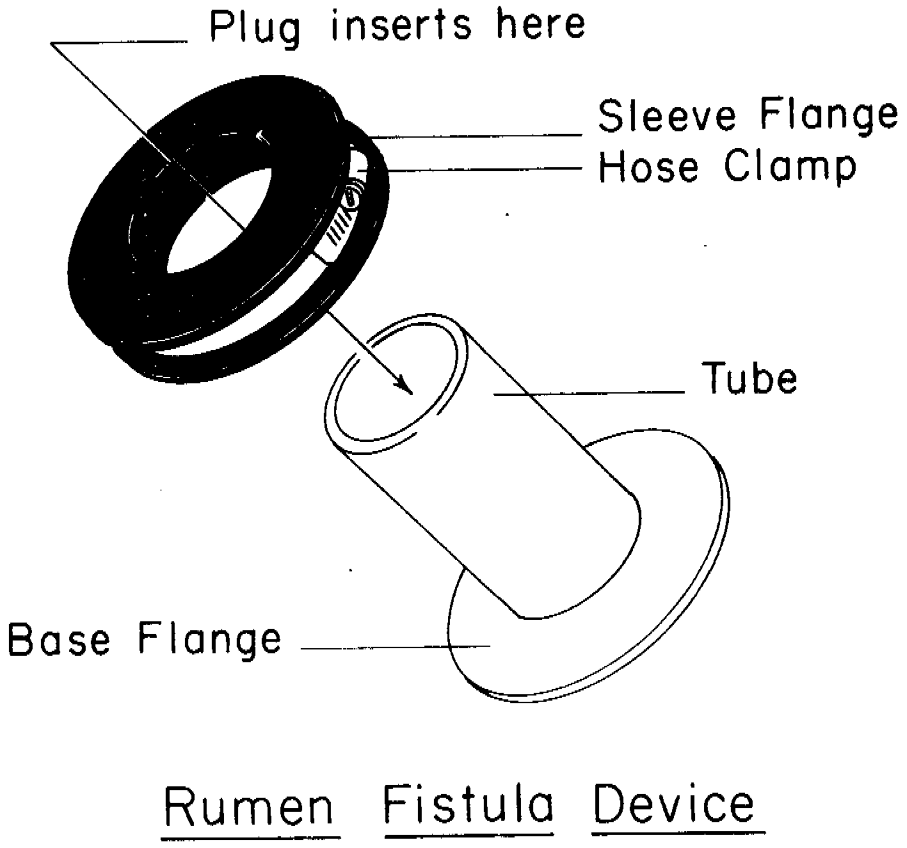

Figure 2. Schematic drawing of rumen fistula device tested at Moose Research Center.

Table 1. Fat levels (expressed as percentage dry weight--cf: Neiland, 1970) of moose femur marrow collected in various months of the year. Males and females are lumped, "calves" are animals from birth through the following May 31, and "adults" are all older animals. The tabulation includes only those animals killed by man or other predators and not those obviously suffering from malnutrition or disease. The levels therefore approximate "normal" levels for the time and place collected.

	Calves			Adults		
Month	n	$\overline{x}$ (% dry weight)	range	n	$\overline{x}$	range
June	2	22	2-41	1	45	-
July	None			3	82	81-85
August	None			2	86	75-93
September	None			2	94	94-94
October	None			1	29	(rutting bull)
November	None			1	91	-
December	None			1	85	-
January	8	11	7-37	7	67	35-90
February	26	10	6-28	7	77	57-92
March	35	8	6-25	14	75	27-92
April	33	8	5-16	3	71	63-76
May	2	6	3-9	4	13	8-20

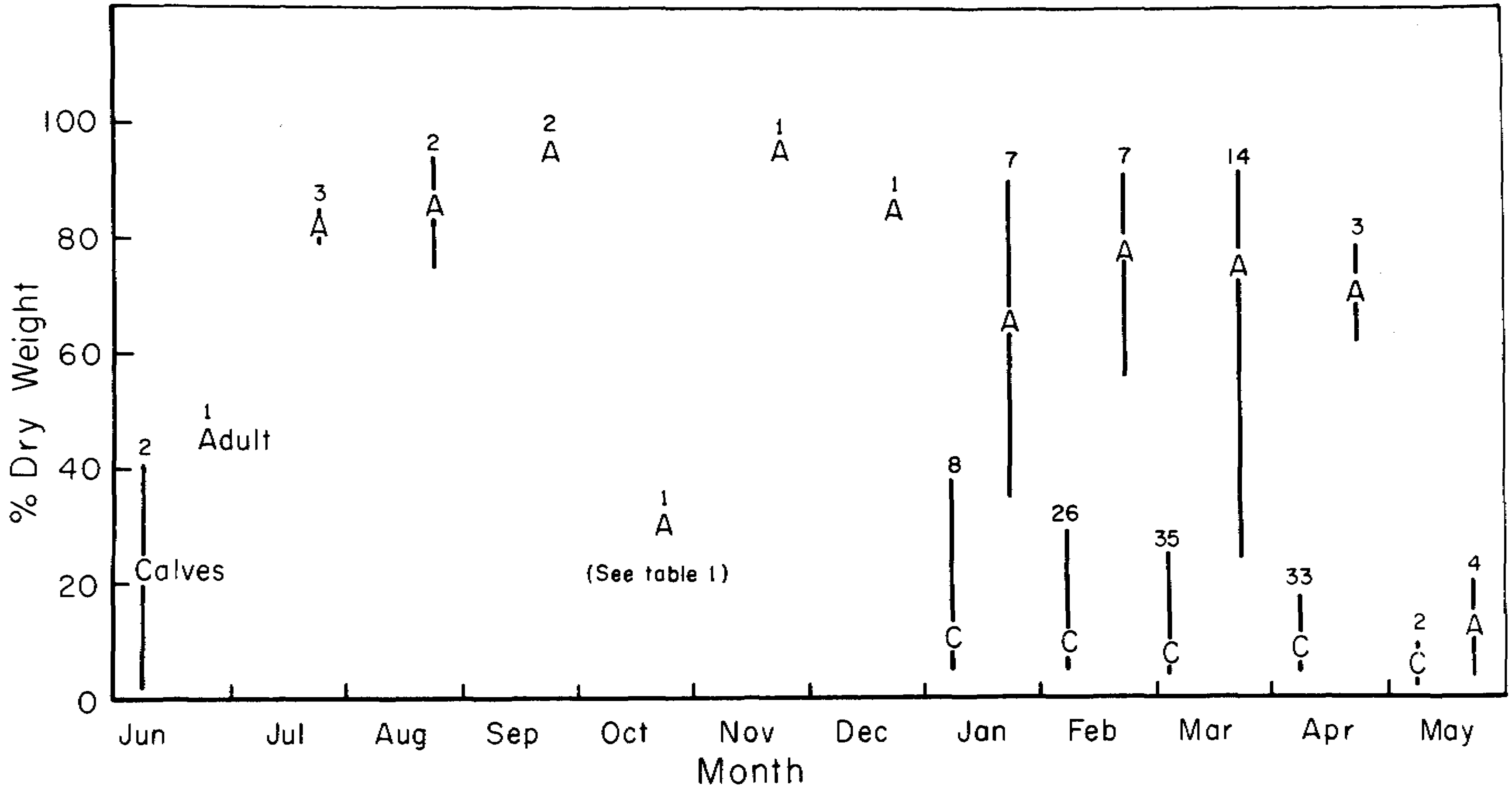

Figure 3. Percent dry weight of femur marrow in adult (A) and calf (C) moose during months of the year. Letters (A or C) indicate mean, vertical lines show ranges and numbers above lines indicate sample sizes.

2. Femur marrow fat analyses done in the future should be consolidated and similarly summarized, to provide more valid guidelines for interpretation. Fat values for marrow of animals suspected to have suffered from malnutrition should be separately summarized. Marrow analyses on calves of the year are uniformly low and not valuable for determining comparative nutritional status.

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JOB PROGRESS REPORT (RESEARCH)

State:	Alaska		
Cooperators:	Alaska Department of Fish and Game; U. S. Bureau of Sport Fisheries and Wildlife; Kenai National Moose Range		
Project No.:	W-17-4	Project Title:	Big Game Investigations
Job No.:	1.4R	Job Title:	Kenai Peninsula Moose Population Identity Study
Period Covered:	July 1, 1971 through June 30, 1972		

SUMMARY

Thirty-eight moose were marked and released outside the Moose Research Center, bringing the total number marked to 321. Two hundred fifty-one resightings of collared moose occurred, bringing the total to 664. An analysis of migrations and population mixing of moose on the Kenai Peninsula and a review of moose migrations in North America were published.

CONTENTS

BACKGROUND

Moose (*Alces alces*) in the lowland areas of the northern Kenai Peninsula receive considerable hunting pressure in the few restricted areas where access exists. In late fall, moose herds in these areas characteristically have a low proportion of bulls, and trophy-size bulls are extremely rare. Although lowland areas contain a higher proportion of calves within the herd, calf production in some years is lower than anticipated (eg: 33 calves:100 cows in November 1970). Most of the area in question is seral birch (*Betula papyrifera*) range remnant from the 1947 burn, and birch browse is in great abundance. However, substantial numbers of moose have died during severe winters in the area. Population estimates by personnel of the Kenai National Moose Range suggest substantial numbers of moose (7900 ± 1400 minimum north of the Kasilof River in early 1971), but concern has been expressed regarding the numbers and welfare of the "lowland" moose, especially in relation to hunting pressure.

The moose traditionally using climax willow (*Salix* sp.) ranges in foothills and mountains, but wintering on the lowland areas, receive little hunting pressure. These groups characteristically exhibit a high bull:cow ratio and a low proportion of calves.

With the formalization of moose management plans for the Kenai and the designation of certain areas as trophy, foot-hunting and maximum sustained yield hunting areas, delineation of these various groups, their interactions, their seasonal movements, and their calving and breeding sites, has become imperative. Further, the proposed classification of more than one million acres of the area as wilderness, as well as the possibility of a limited access road bisecting part of the area, require specific knowledge of the migrations of these moose. Descriptions of populations and their movements would 1) allow harvesting of desired portions of specified moose herds and prevent harvesting of trophy-class bulls while they are away from trophy-management areas (and often antlerless), 2) prevent unnecessary restriction of activities (eg: by wilderness designation) in areas of key winter range, where habitat manipulation might someday become necessary, 3) contraindicate development of small areas seasonally crucial to large numbers of moose (eg: during calving, rutting, or wintering) and 4) provide valid data relative to possible obstructions presented by future proposed highways and other projects.

The literature contains few major studies of moose migrations and/or movements, and the studies that have been undertaken have shown that such movements vary with the population studied. Goddard (1970) reported an Ontario study similar to ours. His recoveries were few (59 of 328 marked moose) but he documented movement from summer to winter ranges (done previously by Edwards and Ritcey, 1956; Kraft, 1964; and Houston, 1968) and suggested there was no net movement into heavily hunted areas.

Phillips and Berg (1971), with many relocations (2,000) of few (27) radioed Minnesota moose, recorded individual home ranges of 2-10 square miles, winter confinement to less than 100 acres, average daily movement of 0.60 miles, identical mean daily movements of cows and bulls, and 0.5-21 mile movements from winter to summer ranges. VanBallenberghe and Peek (1971) also radio-tracked moose in Minnesota. They showed summer localization, winter confinement by snow, adjacent winter and summer ranges of an individual, and a rapid 12-mile movement by a rutting bull. Mercer and Kitchen (1968) described dispersal of moose introduced onto the Labrador Peninsula. LeResche (1968) and LeResche and Davis (this report; Job 1.2R) reported localization of parturient females and their new calves, and LeResche (1970) suggested internal triggering as a factor in moose migrations. Bishop (1970) reported that a Tanana Flats (Alaska) calf-tagging study suggested that both resident and migratory individuals were present in these lowlands in spring. Didrickson (pers. comm.) reported adult moose tagged in the Matanuska Valley (Alaska) moved nearly 60 miles on occasion.

OBJECTIVES

To identify populations and key habitat areas and to learn seasonal patterns of movement by moose on the Kenai Peninsula.

PROCEDURES

Table 1 lists moose marked during the reporting period. Except where noted, moose were captured in fenceline traps (LeResche and Lynch, 1973), marked and released. Thirty-eight reconnaissance flights made during the period are listed in Table 2.

FINDINGS

Resightings of marked moose are listed in Table 3. LeResche (1972) prepared a summary and analysis of resightings through June 1971. No further analysis is available at this time.

A review prepared as part of this job is reproduced below. It will be published in _Le Naturaliste Canadien_ in autumn, 1973.

Table 1. Sex, age, location, and markings of moose tagged on the Kenai Peninsula from July 1, 1971 through June 30, 1972.

	Males	Females	Sex?	Calves	Total
Moose Research Center	5*	30**	0	2***	37
Miscellaneous****		1			1
				Total	38

* Two males marked with quad-colored collars; three with solid blue; all had silver Saflag in left ear.

** Twenty-two females marked with white collars; eight collared with quad-colored collars; all had silver Saflag in right ear.

*** One male calf tagged with silver Saflag in left ear; one female calf tagged with silver Saflag in both ears.

****This cow was mired down in the mud near Hidden Lake. Tagged when rescued.

Table 2. Reconnaissance flights by Alaska Department of Fish and Game searching for collared moose July 1, 1971 through June 20, 1972.

Date	Area	Collared Moose Located*
1 Sept 71	Mystery Creek	6 MRF, 1 Unk
14 Sept 71	Mountains between Big Indian Creek and Thurman Creek	16 MRF
1 Sept 71	Moose River Flats	1 MRF
23 Sept 71	Mystery Creek	1 BL, 5 MRF
8 Nov 71	Swan Lake Canoe System and vicinity	1 Unk, 1 BL, 6 MRC, 3 MRF
9 Nov 71	Moose Lake vicinity	1 MRF, 1 MRC, 1 Unk
8 Nov 71	North of MRC	2 MRC, 1 Unk
8 Nov 71	North side Kenai River west of Skilak Lake	1 Unk
12 Nov 71	East of Bear Lake (GMU 15A)	1 BL, 4 MRF, 2 MRC, 1 Unk
3 Jan 72	Slikok-Funny River Road	0
3 Jan 72	Tustumena-Skilak Benchland	0
3 Jan 72	Bottenintnin Lake-Skilak outlet	1 MRF, 3 Unk
3 Jan 72	Mystery Creek Basin	0
18 Jan 72	Swan Lake Canoe System-MRC area	1 MRC, 1 Unk
18 Jan 72	MRF	0
18 Jan 72	Skilak Loop-Skilak Lake outlet	1 MRF, 1 BL, 1 Unk
11 Feb 72	Mountains north of Thurman Creek	2 MRF
11 Feb 72	Sterling Hwy Mile 60-Mile 100	2 Unk
3 March 72	Sterling Hwy Mile 100-Mile 75	0
3 March 72	Swanson River Road-MRC area	1 MRC
3 March 72	Eastern MRF area and Mystery Creek	0
3 March 72	Skilak Loop	1 MRC, 2 MRF
29 March 72	Tributaries on west side of Resurrection Creek	1 MRF
29 March 72	Chickaloon River and Big India Creek	6 MRF
29 March 72	Skilak Loop	1 BL
29 March 72	Mile 62-90 Sterling Highway	0
7 April 72	Slikok Lake	0
7 April 72	Moose Creek (Tustumena Lake)	1 TB
7 April 72	Funny River-Killey River	0
7 April 72	Skilak Loop	1 MRF, 1 Unk
7 April 72	Sterling Highway Mile 75-90	2 Unk
19 April 72	Mountains north of Thurman Creek	1 MRF
25 April 72	Skilak outlet area	1 Unk
15 May 72	Moose River Flats	1 MRC, 26 MRF, 3 Unk
15 May 72	Bottenintnin Lake	2 Unk
14 June 72	Swan Lake Road-MRC area	0
14 June 72	Moose River Flats	3 MRF
14 June 72	Tustumena-Skilak Benchland	0
	Total	123

*Code:	
Tagged at Moose River Flats:	MRF
Tagged at Moose Research Center:	MRC
Tagged at Bottenintnin Lake:	BL
Tagged at Tustumena Benchland:	TB
Part of markings lost so exact tagging site unknown:	Unk

Table 3. Resightings of collared moose occurring from July 1, 1971 through June 30, 1972.

Tagging Location	July 71		Aug 71		Sept 71		Oct 71		Nov 71		Dec 71		Jan 72		Feb 72		Mar 72		Apr 72		May 72		June 72		Total
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
Skilak-Tustumena Benchland																				1					1
Mystery Creek 1968		3	1	1					2	2		1		6		2			1			2	1	2	24
Moose River Flats	2	3		5	11	20		2	5	30	1	1		4		5	2	12	1	3		29		5	141
Moose Pens			1	1						12				4				4		2		3	1	3	31
"Bot." Lake			1	3		2				4		2	3	5		2		1	1	2		1			27
Not Properly Identified									1	5	2	2	2	8		3						3	1		27
																									251

Moose Migrations in North America

by

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Movements of moose (*Alces alces* ssp.) have long fascinated North American naturalists and scientists, but have been poorly understood until recently. Some early naturalists believed changes in abundance were actually mass migrations to and from large areas (eg. Merrill 1916, Heape 1931). Others, perhaps correctly, believed that moose they observed remained life-long in one very small area (Seton 1909, 1929, Bailey 1930). Still others, unable to discern a pattern in recorded observations, concluded that moose were nomadic, their movements being without pattern during most of the year (Heape 1931). Some observers recognized patterns of movement, and saw cause-and-effect relationships between movements and snow, rainfall, food quantity, food quality or even feces-tainted range (Heape 1931, Hosley 1949, Peterson 1955). Only recently have more definitive studies in British Columbia (Edwards and Ritcey 1956), Montana (Knowlton 1960), Minnesota (Berg 1971, Van Ballenberghe and Peek 1971), Wyoming (Houston 1968), Ontario (Goddard 1970), and Alaska (LeResche 1972) revealed the true complexity of the migration phenomenon in moose.

Moose populations in North America vary from the extremes of sedentary to truly migratory. Every degree of migratory behavior in between the extremes seems represented on the continent. Differences in behavioral patterns are certainly correlated with habitat and terrain occupied, but may also be related to taxonomic form, annual variations in weather, and population structure. The central questions with regard to moose migrations are these:

1. How is migratory behavior, or lack of it, related to habitat, terrain and taxonomy?

2. What are the immediate mediating causes of migratory behavior; snow, forage, internal stimuli?

3. What role does tradition play in movement patterns of individuals and populations?

4. What is the adaptive value of migratory behavior where it exists, and why is it absent from some populations?

This review considers migration in North American moose in light of these questions. Migratory behavior is defined as movement between separate seasonal home ranges, regardless of distance traveled. Local movements (within a home range) and dispersals into new areas and newly-created habitat are also discussed.

LOCAL MOVEMENTS

The common denominator of an individual's use of space is its "home range", considered in this review to be the area in which the individual accomplishes its normal activities during a given period of time. "Home range" and related concepts of localized activity have been defined and redefined as often as any terms in animal ecology and behavior (Burt 1940, Godfrey 1954, Kaufman 1962, Jewell 1966, Mohr and Stumpf 1966). My present definition ignores the fine points but allows comparisons between reported moose studies. Local movements occur within the home range. Home range may shift seasonally, and individuals may occupy more than one home range in a year. Territories, or defended areas, have never been reported for moose (Geist 1963) with the possible exception of cows with calves (Altmann 1958, LeResche 1966).

Size of Home Ranges

Seasonal home ranges of moose are consistently small throughout North America. Casual observations and formal studies all have concluded that, regardless of how far moose habitually move between seasons, home range during a given season seldom exceeds 5-10 km^2. This is true in areas where moose migrate and where they are primarily sedentary; and in all habitats studied.

Peterson (1955) felt that moose in Ontario (*A. a. americana*) frequently passed a lifetime in an area of 32-800 km^2 (a radius of 2-10 mi^2). DeVos (1956) reported summer home range was about 6.0 km^2 for a cow with a calf occupying lowlands in Ontario, and Goddard (1970) characterized more in similar Ontario habitat as having "relatively small" winter and summer home ranges.

Telemetry studies in Minnesota habitat characterized by low relief and mixed deciduous and deciduous-coniferous forests have confirmed very small home ranges in both winter and summer (*A. a. andersoni*). Berg (1971) and Van Ballenberghe and Peek (1971) reported summer home ranges averaging 4.6-14.3 km^2 (the latter made 75 percent of their relocations within 2.6 km^2) and winter home ranges averaging 2.0 km^2. Van Ballenberghe and Peek (1971) observed an adult female that remained in a 2.4 ha area for 25 days in January and February. They concluded that "winter home ranges consisted of a series of (very small) high use areas connected by wanderings of various distances".

Moose (*A. a. shirasi*) in more mountainous areas of the western United States, similarly, have small home ranges. Houston (1968) and Knowlton (1960) studied seasonally migratory populations in Wyoming and Montana, respectively. In Wyoming, 24 of 25 moose studied had summer home ranges less than 3.8 km^2, and 35 of 39 had winter ranges this small.

In Montana, summer home ranges varied between 2 and 8 km^2. Stevens (1970) also felt that moose he studied in another area of Montana were "relatively sedentary" in winter.

Alces alces gigas in Alaska have seasonal home ranges similar in size to other subspecies. Murie (1944) described an adult cow that spent most of her time throughout the year in 8 km^2 near a road. LeResche (1966) estimated summer home ranges of 4-5 km^2 for females with calves in one migratory population. Another migratory population had summer-fall above timberline home ranges of less than 32 km^2, and an apparently resident lowland population occupied home ranges year-round of less than 20 km^2 (LeResche 1972 and unpubl. data).

Sex, Age and Home Range Size

Collectively, studies to date indicate that calves and their attending cows have smaller home ranges for a short time following parturition than do other moose, and that yearlings have larger home ranges than other moose. Home ranges during rut seem to vary with the sex structure of the population.

Summer home ranges of cows with calves in various areas are summarized in Table 1. Altmann (1958), McMillan (1954), LeResche (1966), LeResche and Davis (1971), and Berg (1971) documented extremely small home ranges of cows and newborn calves in Wyoming, Alaska and Minnesota. These home ranges seem to increase beginning when the calf is one to three weeks old (Berg 1971, LeResche and Davis 1971), until summer, summer-fall and winter home ranges are equivalent to those of cows and bulls. Houston (1968) and Saunders and Williamson (1972) could show no differences between size of seasonal home ranges of cows and bulls in Wyoming and Ontario. McMillan (1954), Peek (1962) and Berg (1971) found no differences between eventual summer home ranges of cows with calves and cows without calves. LeResche (1966) did note such a difference, but this was likely due to the fact that cows without calves began their fall migration during his observations. Knowlton (1960) suggested from scant evidence that bulls' summer home ranges were about four times as large as those of cows with calves.

Knowlton (1960), Houston (1968), Berg (1971) and LeResche and Davis (1971) showed that, during rut, bulls' movements on summer-fall range became erratic, and home range increased accordingly. This change is more properly considered a transition into another area of activity (i.e.: "rutting home range") than a true change in summer home range. Rutting home range of females may be a function of their abundance in the population relative to bulls (Houston, 1968). This idea is substantiated by my observations in areas of Alaska with very few bulls (circa 10-20 bulls:100 cows). Cows in these areas become much more active and mobile during rut than those described by Houston in Wyoming, where bull:cow proportions approached 81:100.

Data on yearling home ranges are limited and contradictory, but do suggest they may be larger than those of older moose. Seton (1909) believed young bulls wandered erratically over a wider area than mature

Table 1. Home ranges of moose cows with calves. Modified from Berg, 1971.

	Time Interval	Home Range Area (km2)	Reference
Montana	6 July-23 September	2.2	Knowlton 1960
Wyoming	6 June-15 September	5.1	McMillan 1954
Ontario	15 August-31 October	6.0	DeVos 1956
Minnesota	11 June-22 August	5.9	Van Ballenberghe & Peek 1971
Minnesota	15 May-1 October	15.4	Berg 1971
Minnesota	15 May-1 October	16.9	Berg 1971
Alaska	6 June-31 October	8.4	LeResche 1966

animals. Houston (1968) maintained yearling moose in Wyoming had no "established" home ranges and moved further and more erratically than older animals. Pimlott (1959) and Simkin (1965) showed that, in Newfoundland and Ontario, yearlings were more vulnerable to hunting than other moose, and suggested larger home ranges might be a contributing factor. However, Saunders and Williamson (1972), in Ontario, found no significant difference related to age in linear movements of tagged moose.

Especially in light of the contrast between individual constancy of home ranges in adult moose and the species' tendency to disperse and explore (below), it seems logical that young moose should have larger home ranges (or broader local movements) than older animals. This remains to be confirmed by more precise studies, however.

Tradition and Home Ranges

Moose in all areas of North America tend to return to the same individual home ranges year after year. Since Seton (1909) spoke of moose's "judgement founded on their memory of the country", study after study has confirmed traditional use of the same areas by the same individuals, and suggested that patterns persist over several generations.

DeVos (1956) observed a tagged calf returning as a yearling to the area of its birth after a winter's absence. Knowlton (1960) noted that the same concentration areas were used each winter in mountainous areas of Montana. Geist (1963) recognized that individual moose returned each year to their "accustomed summer range" in British Columbia.

Houston (1968) confirmed strong individual tradition among Wyoming moose. His study included both Type B and Type A populations, and demonstrated that marked individuals from the Type A group returned year after year to permanent summer home ranges. He believed that the Type B group, similarly, had permanent summer ranges. Specific winter home ranges were used annually by members of the Type A population. Type B animals were apparently less attached to specific winter ranges, although still traditional to a great extent. Twenty of 33 (61%) marked animals returned to established home ranges for at least two consecutive years. Five others (15%) returned only in alternate winters, and the remaining 24 percent had not returned within one or two winters. Houston felt that the severity of winters influenced the return of the Type B group. Berg (1971) conclusively demonstrated that radio-marked moose in Minnesota lowlands returned to their established summer-fall and winter home ranges for at least two consecutive years. Each individual (males and females were included) migrated annually between two established home ranges.

Studies in Alaska since 1963 have confirmed strong traditionality in many areas by following marked calves and adults (Bishop 1969a, 1969b, LeResche and Davis 1971, LeResche 1972). This traditional use is demonstrated both by populations (Fig. 1, 2) and by individuals (Fig. 3). Figure 2 shows seasonal locations over a 2 1/2 year period of collared moose from groups marked at various times of year in different areas of the Kenai Peninsula (Fig. 1). The figure includes moose from three

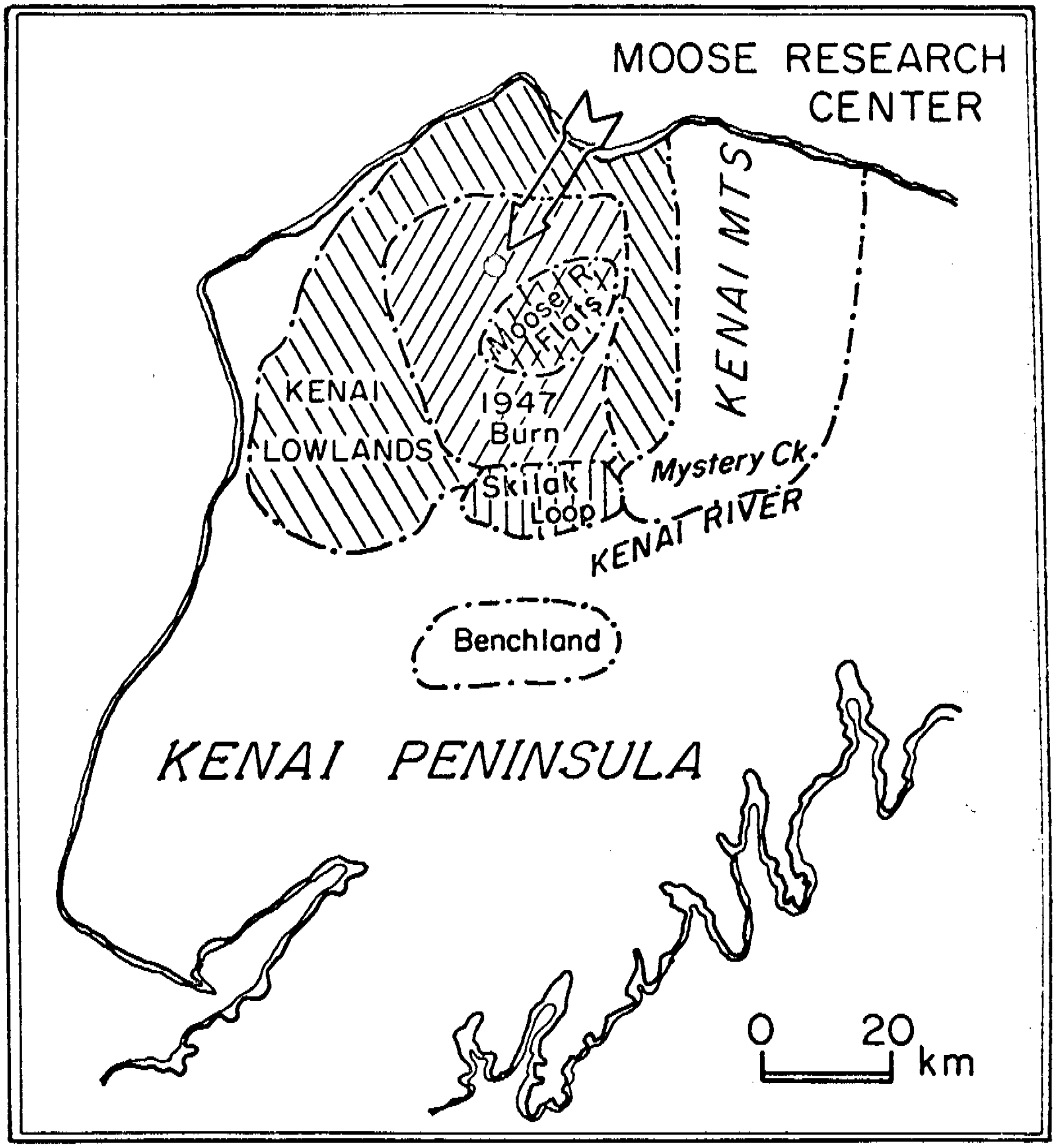

Fig. 1. Locations of seasonal ranges on the Kenai Peninsula, Alaska.

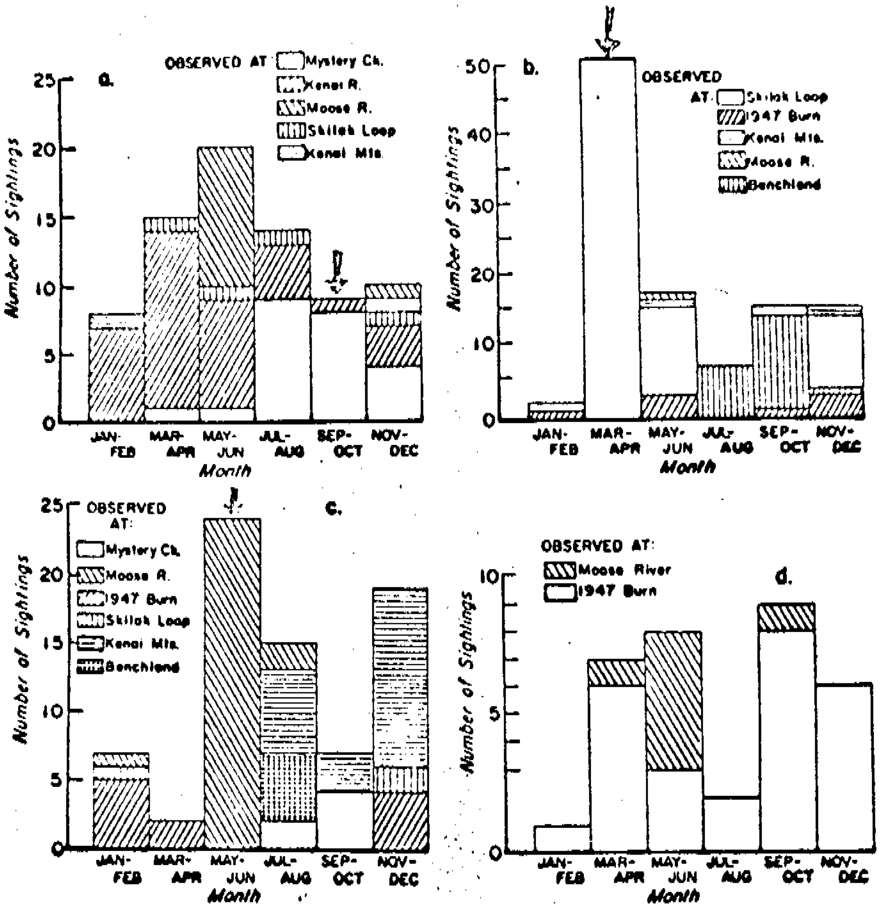

Fig. 2. Bimonthly locations of groups of moose tagged at four locations on the Kenai Peninsula, Alaska: (a) marked at Mystery Creek in October, (b) marked at Skilak Loop in March, (c) marked at Moose River in May and June, (d) tagged at 1947 burn in all months. (From LeResche 1972).

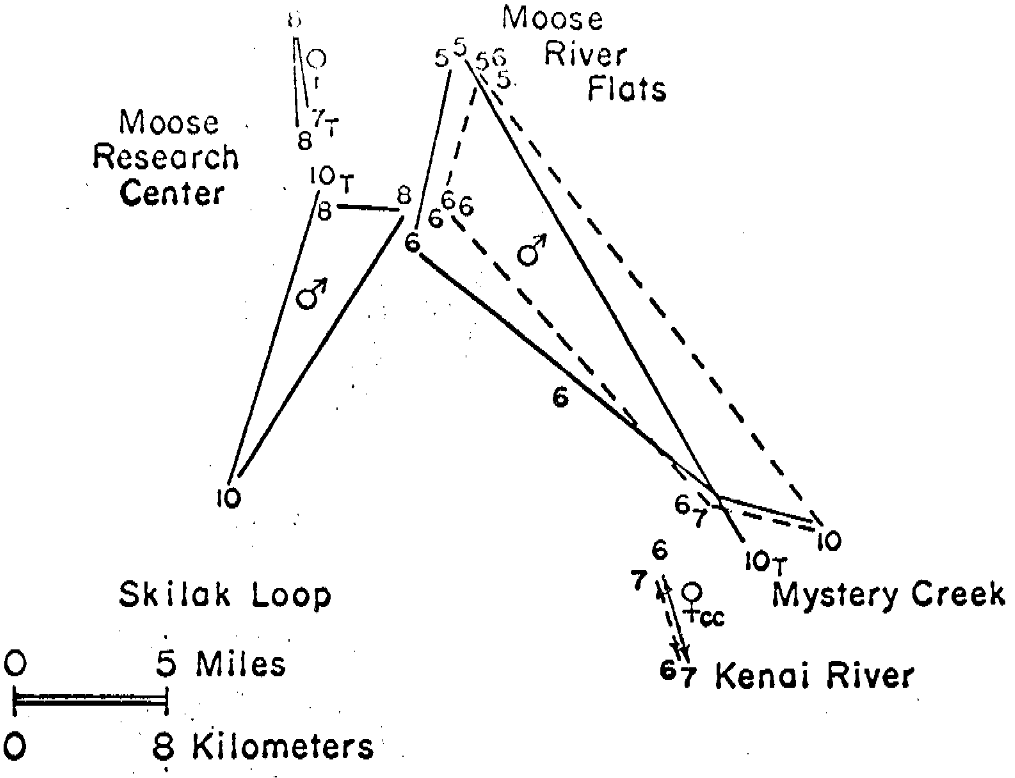

Fig. 3. Migration patterns of two male and two female moose over a two-year period on the Kenai Peninsula, Alaska. "T" is tagging site, digits are monthly resighted (1=January, 12=December), "cc" indicates two calves present. (From LeResche 1972).

migratory groups (a, b, c) and a predominately resident population (d). Each group concentrated annually in the area they were marked. At other times of the year, some groups were widely dispersed. Groups a, b and c represent animals with traditional autumn (rutting), winter and early summer (calving) ranges, respectively.

Individuals of each group had fixed spring, summer and autumn ranges (Fig. 3). These respective ranges were occupied at rather constant time intervals for the period of the study (LeResche 1972).

MOVEMENTS BETWEEN SEASONAL HOME RANGES

"Migration" is most commonly taken to mean regular annual movements of some distance, involving return to at least one common area during each annual cycle. The many regular shifts between seasonal home ranges reported for moose populations in North America are true migrations in this sense. Much confusion has arisen because not all populations are migratory, and because migratory and resident groups not infrequently occupy common areas during part of the annual cycle, and sometimes during rut. The interactions between migratory populations (or population segments) and resident populations (or segments) lead to seasonal aggregations and segregations, and therefore affect habitat relationships and population dynamics. Any consideration of the significance of migrations to moose populations must consider these factors.

All seasonal movement patterns reported for moose in North America represent one of three general types (Fig. 4): Type A; short distance movements between two seasonal ranges with little change in elevation; Type B; medium to long distance movements between two seasonal ranges with significant differences in elevation between high summer-fall ranges and lower winter ranges, and; Type C; medium to long distance movements between three distinct seasonal ranges with significant differences in elevation between high summer-fall ranges and lower winter and spring ranges. These types do not represent absolutely distinct patterns, but rather form a continuum, (Table 2). These patterns differ in timing and regularity, distance traveled, change in elevation involved, and number of seasonal home ranges visited annually. All represent seasonal oscillations between at least two areas or habitats, however.

Timing and Regularity of Movements

Timing varies between individual populations, and probably reflects differences in general seasonal climatic changes and habitats. In addition, timing varies year-to-year in some populations, perhaps reflecting annual climatic differences.

Localized (Type A) populations in northwest Minnesota moved 2-6 km from summer-fall to winter ranges in late November, and all returned within a 10-day period in April in one spring (Berg 1971). In similar habitat in northeast Minnesota, moose occupy a series of high-use winter areas beginning in January, and wander short distances between these areas until May-June, when they become localized on summer ranges

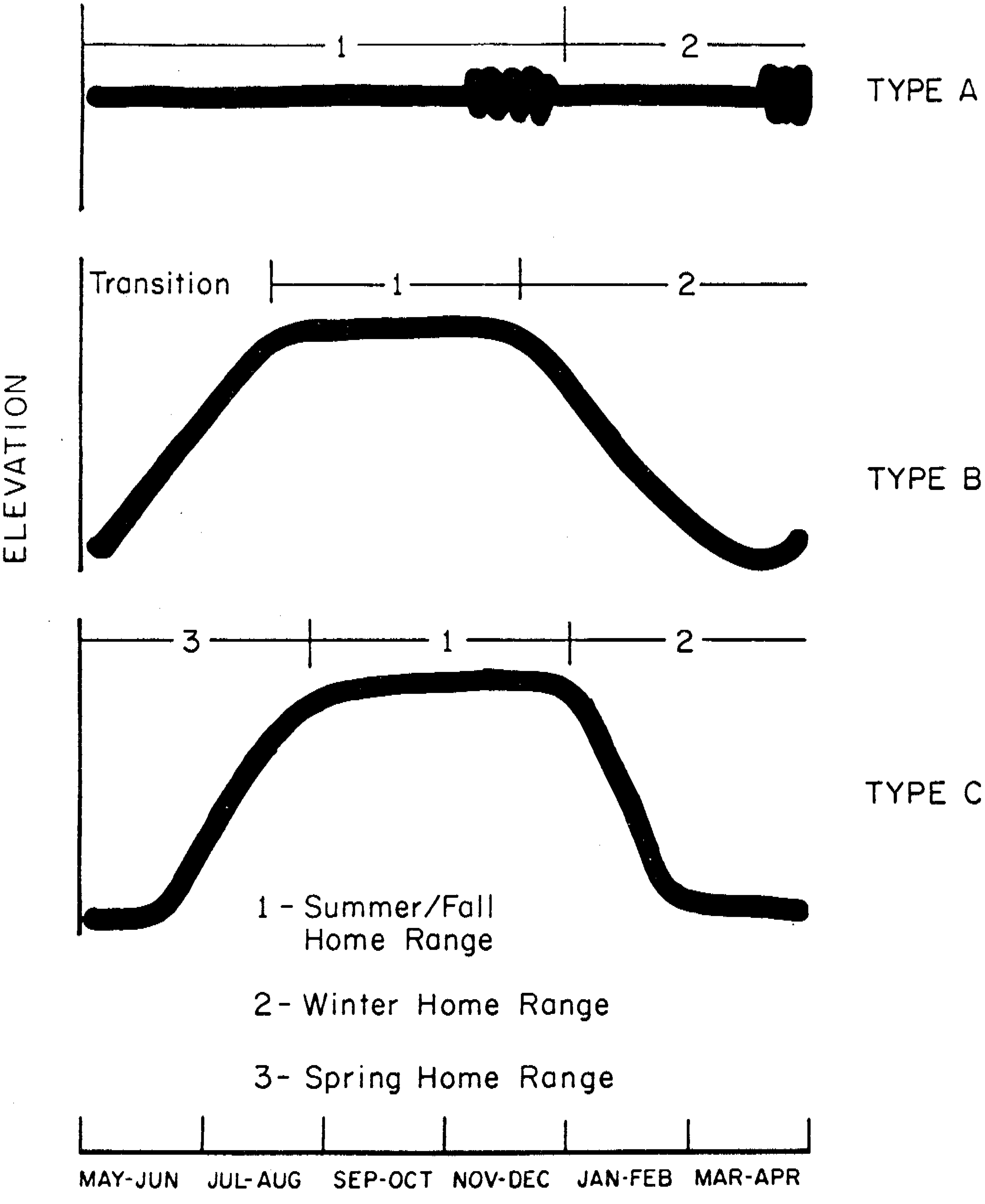

Fig. 4. Types of moose migration patterns reported from North America. Broken line in Type A representation indicates periods of movement. "Transition" period in Type B may be longer or shorter than shown, and represents winter home range habitat.

Table 2: Summary of seasonal movements of moose in North America. Because methods of study and reporting results vary, designation of migration type is necessarily arbitrary. Designations are made to help structure consideration of the many separate situations represented.

Location (study)	Summer/Fall range (elevation-m)	Distance between (km)	Winter range (elevation-m)	Distance between (km)	Spring (calving) range (elevation-m)	Distance between (km)	Migration type	Remarks
N.E. Minnesota (Van Ballenberghe and Peek, 1971)	coniferous-deciduous mosaic (500-700)	local (2-6km)	coniferous-deciduous mosaic (500-700)	local (2-6km)			A	Local shifts in winter home range depending upon weather
N.W. Minnesota (Berg, 1971)	open willow	2-10km	mature willow/ hardwoods	2-10km			A	Definite, rapid but short-range seasonal shifts-no vertical component
Wyoming (Houston, 1968)	floodplain willow (2200-2300)	8-16km	floodplain willow (2200)	8-16km			A	Share winter-spring range with larger Type B group (below)
British Columbia (Edwards & Ritcey, 1956)	subalpine forests (2400)	?	subalpine forests (2400)	?			A	Both groups represent small resident segments of a much larger Type B population
British Columbia (Edwards & Ritcey, 1956)	lowland burns (500)	?	lowland burns (500)	?			A	See above
Tanana Flats, Alaska (Bishop, 1969)	lowland mosaic (200-250)	local ?	lowland burns (200-250)	local ?			A	Share spring-summer & some winter range with Type C population
Kenai, Alaska (LeResche, 1973)	lowland mosaic (75-100)	local 0-16km	lowland burns (75-100)	local (0-16km)	same as summer-fall		A	Share spring & some winter range with Type C population (below)

Table 2: Continued

Location (study)	Summer/Fall range (elevation-m)	Distance between (km)	Winter range (elevation-m)	Distance between (km)	Spring (calving) range (elevation-m)	Distance between (km)	Migration type	Remarks
Northwest Territories (Barry, 1961)	tundra (0±)	to 170km	riparian willow ?	to 170km			A-B	Move along rivers long distances, with little change in elevation
Arctic North Slope, Alaska (Alaska Dept. Fish & Game, 1973)	riparian willow & tundra (100-200)	0-75km	riparian willow (200-600)	0-75km			A-B	Move along rivers long distances, with little change in elevation; some cross crest of Brooks Range through high passes
British Columbia (Edwards & Ritcey, 1956)	subalpine forests (2400-2500)	20-60km	lowland burns (500-700)	20-60km			B	Share winter & spring-summer ranges with two Type A populations (above)
Montana (Knowlton, 1960)	subalpine meadows & upland willows (3000)	2-7km	riparian willow (2000)	1-7km			B	Very short movement; but great elevational difference
Kenai, Alaska (LeResche, Unpubl.) (benchland residents)	alpine tundra & upland willows 1000±	2-20km	riparian willow (500-800)	2-20km			B	Share spring-summer range with much larger Type C group (below)
Wyoming (Harry, 1957; Houston 1968)	upland forest (3300)	15-40km	floodplain willow (2200-2300)	15-40km			B	Type A in some years, depending upon snow. Shares winter range with smaller Type A group (above)

Table 2: Continued

Location (study)	Summer/Fall range (elevation-m)	Distance between (km)	Winter range (elevation-m)	Distance between (km)	Spring (calving) range (elevation-m)	Distance between (km)	Migration type	Remarks
Kenai, Alaska (LeResche, 1973)	upland willows (600-750)	30-40km	lowland burns (80-100)	20±km	lowland bogs (80±)	13-20km	C	Share ranges with groups of Types A & A-B (above)
Tanana Flats, Alaska (Bishop, 1969)	upland willows (1000)	30-50km	lowland burns (200-500)	20±km	lowland bogs (200-300)	15km	C	Share ranges with Type A group (above)

(Van Ballenberghe and Peek 1971). Wyoming moose, representing both Type A and Type B groups, move onto winter ranges from mid-December to mid-January; then return to spring-summer ranges from late March to mid-April (Houston 1968). Type B groups have left this range by mid-June. More northerly groups with Type A movements (Kenai, Alaska; LeResche 1972 and Tanana Flats, Alaska, Bishop, 1969) follow roughly the same schedule in their local movements.

Timing varies considerably annually and regionally among Type B and Type C groups. Moose in mountainous British Columbia move rapidly from late winter range to summer range in April (Edwards and Ritcey 1956). In one year, the migration was complete by mid-April. In other years it was still in progress in May, a lull in movement (attributed to cold weather) having occurred in the interim. In contrast, movement from upland summer ranges to lower wintering areas is normally a gradual process in this population, occurring from mid-September until abrupt upward movement begins again in April. Progression of the migration varied between years, perhaps due to differences in snow accumulation.

In Montana, moose from a Type B group first arrived at lowland winter concentrations between mid-December and mid-January, and continued to drift slowly onto winter ranges as late as March (Knowlton 1960). Return to summer range is more rapid, occurring mostly in May and June.

Two Type C populations in Alaska return to summer-fall ranges later than moose in Montana and British Columbia, and remain on them for a shorter time. Movement to upland summer-fall ranges is gradual, in contrast to that in Montana and B. C., and is not complete until rut, in late September and October. Conversely, movement from upland ranges to winter ranges is sudden, and may occur as early as mid-November. This, too, contrasts with the slow winter-long descents described in Montana and B. C.

Movements in Interior Alaska (Tanana Flats) are similar in all respects to those at Kenai, except that ascent to summer-fall areas may not be detectable until as late as early September. In both locations in Alaska, timing of the precipitous fall downward migration varies year-to-year, apparently depending upon snowfall. In at least one instance at Kenai, major downward movement was delayed until January.

Environmental and Physical Distances between Seasonal Ranges

Distances between seasonal ranges can be considered as horizontal distances, elevational distances, or environmental distances. To be adaptive, movements must involve a change in environment, or travel an "ecological distance" from one environment to another. As suggested by Edwards and Ritcey (1956), a change in elevation accomplished by a relatively short horizontal movement may result in environmental changes similar to those resulting from extremely long latitudinal migrations. In regions where juxtaposition of disparate habitats is extreme, only short horizontal movements may be necessary to realize the maximum environmental changes practicable. In vast flat areas of homogeneous habitat, no reasonable migration can achieve a significant environmental change.

Seasonal migrations reported in North America involve horizontal movements of from one to more than 170 km, and include examples of all distances in between. No distinct relationship--direct or inverse--is evident between elevational shift and horizontal movement. Rather, the horizontal and elevational distances traveled are linked to environmental differences achieved at each location studied.

The shortest horizontal and elevational distances traveled occur, by definition, in Type A populations. In low-relief Minnesota habitats, distances between summer and winter home ranges are only 0-10 km, although definite and regular seasonal movements do occur (Van Ballenberghe and Peek 1971, Berg 1971). Of the 11 winter home ranges documented by Berg, three were adjacent to, and two were included within summer-fall home ranges of the same individuals. No spectacular advantages accrued to the moose that moved these short distances, for habitat was similar (though <u>not</u> equivalent) on both ends of the movements.

Type A movements in other areas, although covering only short horizontal and elevational distances, may involve large ecological changes. Resident moose both at Kenai and at Tanana Flats, Alaska, redistribute seasonally on lowland ranges, moving only a few kilometers. In so doing, however, they move from open bogs to mature hardwood forests, dense seral shrub ranges, or riparian willow habitats (LeResche et al., this volume).

The two northernmost populations listed in Table 2 (Northwest Territories and Arctic North Slope, Alaska) both spend summer on tundra and intertidal ranges near the Arctic Ocean. Both groups undergo medium to long distance horizontal movements along river courses. These movements have small elevational components, but involve major ecological change, from exposed areas where survival in winter might be difficult (Miller et al., 1972), to riparian willow habitat which offers more available forage in winter and protection from weather. These movement patterns are considered as intermediate between Types A and B.

Type B movements, which involve a change in elevation and nearly always a rather major ecological change, may involve as little as a 2 km horizontal movement (Table 2). These movements are characteristic in mountainous terrain, and typically proceed between high subalpine or upland forests (summer-fall range) and low seral shrub or riparian habitat (winter range). The longest horizontal movements, in British Columbia and Wyoming, are 60 km and 40 km, and also involve the greatest change in elevation (Edwards and Ritcey 1956, Harry 1957, Houston 1968). The British Columbia population moves from subalpine forests 2400-2500 m elevation to lowland burns 500-700 m elevation. Migratory moose in Jackson Hole, Wyoming, move from upland forests as high as 3300 m to flood plain willow communities 2200-2300 m elevation. Similar ecological movements are accomplished with shorter horizontal and elevational movements by moose in Montana and Alaska (Knowlton 1960, LeResche unpubl.). In the Gravelly Mountains, Montana, moose move between subalpine meadows and upland willows at 3000 m and riparian willow about 1000 m lower, while traversing only 2-7 km horizontally in the steep terrain. In the Kenai Peninsula "benchland", a group of moose moves from subalpine willows and alpine tundra at 1000 m elevation to riparian willow communities at 500-800 m, traversing only 2-20 km horizontally. This group sometimes oscillates between the habitats (depending upon whether bare ridges exist above timberline) several times in winter, in a manner similar to that described by McDowell and Moy (1942) in Montana.

Both Type C populations in Alaska move elevationally 500-800 m and horizontally 30-50 km between summer-fall and winter ranges; and 0-300 m and 20 km between winter and spring ranges. These movements are important environmentally in terms of habitat (Table 2) and climatological variables (Coady, this volume).

Traditional Routes of Travel

Because specific home ranges are used repeatedly by individuals, we might expect routes of travel to be similarly traditional. The little data available suggest this is the case. Knowlton (1960) described the following of drainage patterns and Houston (1968) diagrammed routes repeatedly used which also followed topographic features. Edwards and Ritcey (1956) believed that migrations retained the same essential elements year after year.

Berg (1971) and LeResche (1972) present evidence that individual moose repeatedly use the same routes of travel between seasonal ranges. In Minnesota, Berg radio-tracked a cow and a bull and found that each followed the same routes during spring and fall movements. LeResche's information from Alaska is partially included in Figure 3, which illustrates movements of three individuals over 2 1/2 years. The individual moose were observed often enough during seasonal movements to suggest that routes they followed were at least very similar from one year to the next.

Segregations, Aggregations and Seasonal Movements

Seasonal movements of moose alter the spatial relationships between individuals and groups, as well as redistributing moose in relation to their habitats. When animals of different ages, sexes, and reproductive conditions move differentially, migrations cause a reordering of group makeup. When migratory and "resident" groups converge or diverge, aggregations and segregations occur. The social and demographic changes resulting from such interactions are often overlooked when causes of migrations are sought.

Population segments may differ in timing and extent of seasonal movements, or in whether they migrate at all. Many studies have shown that "migratory" and "resident" populations may share the same ranges at any time of the year. Houston (1968) studied a "resident" (i.e. remaining in his study area year-round) Type A group and a "migratory" (i.e. visiting the study area only in winter) Type B group in Wyoming. These moose were aggregated during most winters, but extent of ingress by the Type B group was related to snow conditions. Type B moose were about twice as numerous as resident individuals. Edwards and Ritcey (1956) described migrations of a vast majority of moose they studied in

British Columbia, but noted "a few" moose were year-round residents on this group's summer and winter ranges. A similar situation is present in the Tanana Flats, Alaska (Bishop 1969b), where one Type A group remains in lowlands all year (but redistributes seasonally), and a larger Type C group moves between various upland ranges and the lowlands. Both groups aggregate on lowland spring calving ranges. Another small segment of the population remains in upland areas throughout the year, redistributing seasonally and mixing with Type C groups in autumn.

"Resident" and migratory groups interact in a complex manner on the Kenai Peninsula (Fig. 2). The "resident" (Type A) lowland group intermingles with the Type C migratory groups on winter and spring areas. The Type C groups, in addition, congregate with upland "residents" (Type B) in summer and fall, on upland ranges. Probably 40-50 percent of the moose involved undertake Type C movements, about 40 percent are Type A lowland "residents", and the remaining 10-20 percent have Type B movement patterns.

Segregations and aggregations assume greater social importance when they involve distinct age and/or sex classes of the population. Definite segregations by sex, age, and reproductive status have not been reported in Type A populations although redistribution of bulls during rut and of yearlings has been suggested above. Seasonal movements in these populations seem to involve all classes of animals.

Social segregation is common in some Type B and Type C moose populations. Peterson (1955) noted that cows, calves and yearlings tended to move to upland ranges later in the spring than bulls in Montana and British Columbia. Moose summering in upland ranges in British Columbia had higher twinning rates, and perhaps higher pregnancy rates, than those resident in the lowlands (Edwards and Ritcey 1958). This suggests a differential movement pattern between females of different reproductive capacities.

Figure 5 illustrates progression of seasonal movements by bulls and cows of a Type C population studied on the Kenai Peninsula, Alaska (LeResche 1972). Bulls leave lowland spring ranges beginning in May and June, and all reach upland ranges by early July. Cows without calves are delayed in comparison to bulls, but precede cows with calves to upland ranges. Many cows with calves do not leave lowland home ranges until August, and many never travel as far into the hills as bulls. Rutting occurs after the bulls drift slightly downward, to elevations where cows are concentrated. Sexual segregation reoccurs after rut, when many cows begin downward movement to winter home ranges and most bulls return to the highest upland ranges. Full intermixing is not reestablished until all animals congregate on winter ranges, usually by January.

During spring, summer and early winter, this migratory population is largely segregated from the Type A group of almost equal size, which remains in the lowlands. There are significant differences in sex, age and reproductive success between the Type C and Type A groups. Bull:cow ratio may approach 60-80 in the Type C groups; whereas, it is 20-40 in

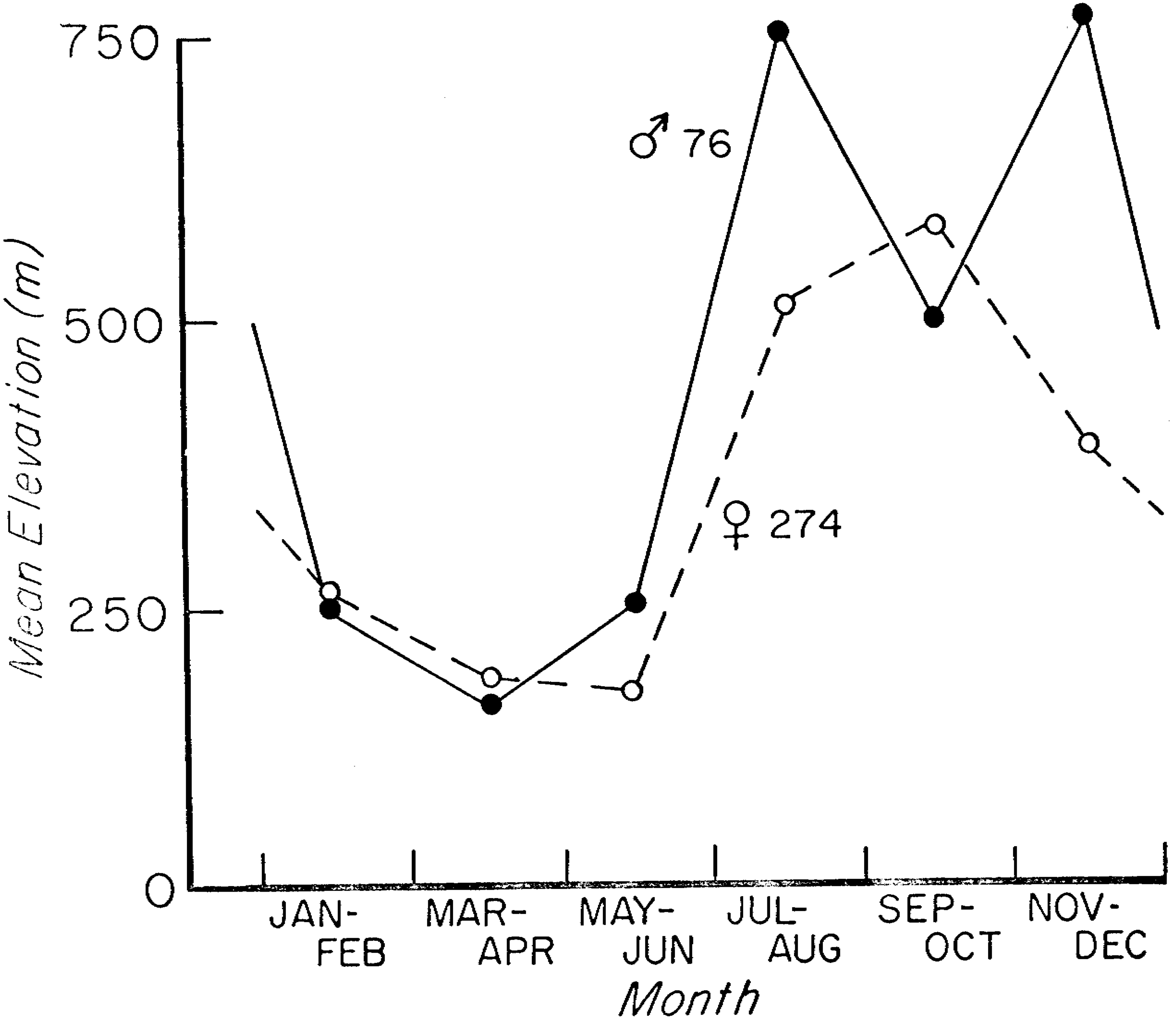

Fig. 5. Mean bimonthly elevations where bulls and cows were sighted in a study of a Type C moose population on the Kenai Peninsula, Alaska. (From LeResche 1972).

the "resident" group. Type C animals are significantly older (LeResche 1970), and calf:cow ratios are significantly lower in the Type C groups. These differences result from the more intense hunting that occurs on the lowlands, but may also reflect changes in movement patterns with age.

Type C groups on the Kenai segregate from other Type C groups as well as from lowland residents. Because individuals return annually to traditional summer-fall ranges, in specific upland drainages, breeding groups tend to retain separate identities year after year. Many of these groups contain only 100-500 moose, and are composed of the same individuals each autumn. During other times of the year, individuals may be far apart (LeResche 1972).

Mediating Factors in Seasonal Movements

Proximate factors that initiate or halt migrations may be climatological or botanical and may involve "internal clock" mechanisms. Almost all descriptions of seasonal movements by moose have noted correlations with one climatological or habitat-related factor or another. Such presumptive data show that primary mediating factors differ between situations. There is recent evidence that internal time cues are also involved.

Weather, and particularly snow conditions, are the most often reported mediating factor in moose migrations. Formozov (1946) and Nasimovitch (1955) have reviewed the influence of snow on distribution and movements of mammals, including moose. Snow depth and characteristics definitely affect local movements and habitat selection by moose throughout North America, and cause "yarding" in many instances (Seton 1909, Heape 1931, Peterson 1955, Edwards 1956, Harry 1957, Van Ballenberghe and Peek 1971). Snow-moose relationships vary according to many factors, which are discussed in depth by Coady in this volume. In general, snow causes or restricts movements by altering the energy cost of traveling or living in a habitat, and by altering the availability of forage.

"Rigor of the winter" alters location of winter range of a Type B moose group in Wyoming (Houston 1968). The migratory group only wintered in Houston's lowland study area during more severe winters. Knowlton (1960) believed that winter snow depths in Montana initiate movements downward from upland summer ranges. Edwards and Ritcey (1956) concluded that temperature is the "basic factor" mediating Type B movements in British Columbia, but that snow depth alters the effects of temperature. Spring movements halt when temperature drops in this region, and resume with a rise in temperature. However, no upward movement occurs during warm periods in winter because snow depths prevent it.

Peek (1962) felt that precipitation affects summer distribution of moose in Montana, where greater use of upland habitats occurs in dry summers.

Abundance and quality of available forage change with snow conditions and with habitat. Hosley (1949:15) concluded that "depth of snow and the resulting effect on food availability....determine the locations of moose in winter." Stevens (1970) described yarding of Montana moose due to snow conditions and movements from the yards after available forage was exhausted.

Springtime movements from winter ranges may be mediated by disappearance of snow or by phenology of growing plants. Probably both factors are important. The abrupt shift from downward drift to rapid upward migration in spring described for Type B populations in British Columbia (Edwards and Ritcey 1956) and Montana (Knowlton 1960) suggests a sudden release by disappearance of snow rather than a movement initiated by new plant growth. Knowlton, nevertheless, concludes that "greening up" of forage initiates spring movements. In contrast, Type C Kenai Peninsula groups move from winter range onto spring concentration areas in April and May and then disperse slowly to upland summer-fall ranges beginning in June. Most snow disappears from upland ranges in May, so this movement is more likely related to plant phenology.

It is impossible to know whether seasonal movements would occur without proximate climatological and phenological stimuli. However, there is some evidence of internally mediated migratory behavior in moose. Sexual stimuli cause movements of bulls preceding and during rut. Houston (1968) postulated that the extent of movements of cows might be similarly affected, being perhaps "a function of the density of breeding males."

My studies of moose enclosed in four 1 mi^2 (2.6 km^2) pens near Kenai, Alaska, indicate that these moose have migratory tendencies consistent with actual movements of unenclosed moose. Most individuals were born outside the pens and now are enclosed on the Kenai lowlands near the interface between a major spring range (where Type A and Type C populations aggregate), and an extensive lowland wintering area (Fig. 1). Animals enclosed in the pens are from both Type A and Type C populations. The movements of unenclosed moose are described above and by LeResche (1972). Sightings of enclosed moose along fencelines over a 34 month period were analyzed for directional tendency (i.e.: a moose sighted along the north fenceline of a pen had a northward tendency, etc.). Frequency of sightings of moose along north, east, south and west fencelines differed significantly by time of year (Table 3), and directional tendency was consistent with known migrations of unenclosed moose.

During seasons of most significant migrations by unenclosed moose (e.g.: movement to calving concentration areas in March and April and migration to upland summer and rutting areas in July-August), locations of enclosed moose differed most from those predicted by X^2 expectations under a null hypothesis of no seasonal change in distribution (Table 3). During February-April, within pen locations were weighted north and west (the direction of movement from wintering to calving areas) to contribute 44 percent to the X^2 value. In July and August, when unenclosed moose were migrating east and south to upland summer rutting ranges, enclosed moose were seen more often than expected along east and south fencelines. This deviation from expected values contributed 27 percent to the total X^2 value. Similarly, a westerly trend within the pen contributed 18 percent to X^2 during the months (November - January) when unenclosed moose were gradually moving westward from rutting to wintering areas.

Table 3. Proportions of 757 observations of moose along enclosure fencelines by season and compass direction. Kenai Moose Research Center. May 1969 - March 1972.

	Fenceline				Number of
Season	North	East	South	West	Observations
Nov. - Jan.	.21	.18	.43	.18	112
Feb. - Apr.	.36	.20	.24	.20	80
May - June	.15	.33	.31	.11	150
July - Aug.	.07	.38	.49	.06	175
Sept. - Oct.	.18	.33	.43	.07	240
Total Observations					757

n.b. Proportions of animals along each fenceline differ significantly by season (P .001; X^2=70.43, 12df).

During pre-calving, calving and post calving periods (May - June) and during pre-rut and rut (September - October) unenclosed moose are essentially resident in calving and rutting areas. During these periods enclosed moose differed but little from expected distribution patterns, thereby suggesting no migratory tendency (Table 4).

Enclosed moose are, of course, influenced by the external stimuli of day length, temperature, plant phenology, etc. Nevertheless, the directional tendencies they exhibit are appropriate only in light of patterns (probably learned) cued by internal timing mechanisms. For example, in autumn the penned moose are already present on winter range, and are not affected by snow or vegetation on upland ranges. Still, their directional tendency is in the direction necessary to move from upland ranges to winter ranges.

DISPERSALS

There can be little doubt that moose have evolved as an opportunistic species, adapted to dispersing into subclimax habitats periodically created by fires and other disturbances (Geist 1971). This ability is manifest in prehistoric and more recent extensions of moose distribution throughout North America (cf: Anderson 1924, Peterson 1955, Mercer and Kitchen 1968, LeResche et al. this volume, Krefting this volume, Dodds this volume, Kelsall and Telfer this volume). It is further suggested by the countless instances of increases and declines in areas of subclimax forests (eg. Leopold and Darling 1953, Peterson 1955, Lutz 1960, Spencer and Hakala 1964).

In fact, actual extensions of range have sometimes been more apparent than real in recent centuries (cf: Lutz 1960, Barry 1961, LeResche et al. this volume). Instead, supposed "dispersals" have in reality been only increases in previously low density populations. Nevertheless, true range extensions certainly have occurred, sometimes with the aid of transplants, in Western and Southeastern Alaska (Alaska Department of Fish and Game 1973, LeResche et al. this volume) and parts of Canada.

It is perhaps a moot point what proportion of large increases in moose numbers is due to immigration and what proportion results from increased productivity of resident moose. However, some recent studies indicate there is at least a short period of delay before apparent "immigration" occurs into an area of vacated habitat. The basis for this delay is likely the traditionality of movement patterns discussed here.

Goddard (1970) concluded from an eight-year study of marked moose in Ontario that there was no net movement of moose into heavily hunted areas. He felt that sustained harvest from the heavily hunted area depended upon enhanced production rather than immigration. We observed a similar pattern during early years of state management of moose in Alaska. Intensive hunting along road systems (especially in the Matanuska Valley and near Kasilof, Kenai Peninsula) significantly decreased roadside resident (Type A) populations. Late winter densities

Table 4. Seasonal directional tendencies of enclosed and unenclosed moose. Kenai Peninsula, Alaska. 1969-72. "Statistical expectation" is the expected chi-square value with null hypothesis of no directional variation by season, and relative movement is included only when observed frequently exceeds expected by more than 20 percent.

	Enclosed Moose		
Season	Movement Relative to Statistical Expectation	Percent Contribution to X^2	Activity of Unenclosed Moose
Nov. - Jan.	West	18%	Slow westward migration to wintering areas.
Feb. - Apr.	North/West	44%	Northwestward migration to calving areas.
May - June	None	4%	Occupation of calving areas
July - Aug.	South/East	27%	Eastward migration to summer and rutting areas
Sept. - Oct.	East	7%	Rutting

remained high due to an influx of Type C moose, but in summer and autumn, when Type C groups were away, populations were depressed from previous levels. There was no evidence of a significant influx of outside moose into the Type A populations. Both these examples suggest a delay in filling hunter-created niches in Type A populations.

The rate at which newly-created habitat is colonized by moose is poorly known. Spencer and Chatelain (1953) and Spencer and Hakala (1964) document increase in moose numbers on the 128,000 ha Kenai (1947) burn area. Spencer and Chatelain (1953) believe that increase was probably about fourfold from 1950-1953, and it occurred "largely as a result of diversion of moose from other wintering areas". Spencer and Hakala (1964) estimate an increase from 2,000 moose in 1949 to 4,500 in 1955, which represents an increment of 9 to 21 percent annually. Whichever of these estimated increases is most accurate, it is entirely possible that reproduction by previously resident moose on the areas in question accounted for the entire increase in numbers. Neither publication reports a concurrent decrease of moose numbers in nearby areas, from which they feel immigrants originated.

The best information on moose dispersals comes from Labrador (Mercer and Kitchen 1968). Animals introduced in southeast Labrador in 1953 have since expanded into an area of about 4,400 km^2, at a rate of about 10 km per year. Simultaneously, moose occurring naturally in southwest Labrador spread northeast at the rate of 13 - 24 km per year. Rate of dispersal depends on quality and quantity of habitat available, of course, as well as on intensity of other limiting factors, such as disease, hunting and climate. It is interesting to note, however, that true dispersals (as opposed to increases in density) are often relatively slow.

THE CENTRAL QUESTIONS

How is migratory behavior related to habitat, terrain and taxonomy?

No precise relationships are evident, for often several general movement patterns are present in a single population of moose occurring in one habitat. In general, however, the most complex movement patterns occur in areas with the greatest compression of disparate habitats and climates. This situation almost always involves hilly or mountainous terrain, where different climates and biota are very close to one another. Only local movements (Type A) have been reported from the flattest terrain studied, in Minnesota and Ontario. An exception occurs in the arctic, where long migrations occur in relatively flat areas. Here, however, summer habitats are probably absolutely uninhabitable in winter. In Ontario and Minnesota travel over great distances would achieve little change in climate or habitat. This pattern is confused, however, by resident (Type A) populations occurring in almost all areas studied--including those areas where more complex movement patterns (Types B & C) occur.

There is no evidence that any of the four subspecies of North American moose has consistently different migratory behavior than any other.

What are the immediate mediating causes of migratory behavior?

Seasonal movements are mediated by snow conditions, available forage and a combination of both. There is some evidence for internally mediated migratory tendency. Autumn movements from summer-fall to winter ranges are most often attributed to snow accumulation; whereas, reverse spring movements are associated with disappearance of snow and "greening up" of forage. Weather changes during migration periods sometimes alter the speed and progress of movements.

What role does tradition play in migratory patterns?

Tradition is strong in movement patterns of individual moose. Movement patterns of populations change over time, but similarly contain strong elements of tradition. Specific home ranges and specific routes of travel are used on an annual basis by individuals in all areas studied. Overall annual movement patterns of populations and population segments change little year-to-year during periods when habitat relationships remain relatively stable. The extent and timing of movements vary with climatological and phenological events, but the pattern remains constant.

The rates and mechanisms of establishing migration patterns in newly-created habitats are obscure. It is probable that several years pass before traditional patterns are changed and new patterns established. Young moose and rutting bulls move most erratically. These animals might thus be the pioneers of new movement patterns.

What is the adaptive value of migratory behavior?

The result of migrations is alteration of individuals' environments. Movements change physical (climatic), biotic (forage and interspecific) and social (intraspecific) relationships. It is within these relationships that we must search for the ultimate benefits accrued from migratory behavior. Relationships changing seasonally are responsible for annual movement patterns; those changing over decades or centuries are ultimately responsible for dispersals. In the final analysis, species seek the environmental relationship in which they have the greatest reproductive potential. Movement patterns will thus be selected for if they have reproductive value (MacArthur 1972). Basic to reproduction is survival, and basic to survival is energy balance. Movement patterns will thus be selected for if they place individuals in a favorable energy balance (cf: West 1960, Cox 1961, 1968). The influences of forage quantity and quality and climatic variables on energy balance of moose are extremely complicated but are now at least partially understood (Gasaway and Coady, this volume, Oldemeyer, this volume, Coady, this volume). In the grossest terms, the energy advantages achieved by a moose migrating from deep snow to less deep snow, from non-available forage to available forage, or from less nutritious forage to more nutritious forage are intuitively obvious. We can expect more thorough accounting of these relationships once energy costs and benefits of seasonal environments are measured precisely.

Social factors are even less well understood than physical and extraspecific biotic factors of migrations. Their consideration is clouded by the fact that movements achieving overwhelmingly beneficial climatic or forage relationships might result in decreasing social benefits. The converse--social benefits being important enough to override unfavorable climatic or biotic relationships--might also occur. Social benefits are presently difficult to measure, but may be sought in aggregations and segregations that occur as the result of movement patterns. The most generally apparent aggregations are breeding aggregations and winter concentrations; the most obvious segregations are post-parturition segregations of cows with calves and segregation of populations during breeding.

Aggregation for breeding is necessary to reproduction, and all movement patterns must result in this one aggregation. The larger "herd", which might be intermixed on calving or wintering areas, often splits into many localized rutting populations. These populations are segregated from one another during breeding. This results in significant pre-rut movements by some segregated population segments. Several parameters, such as summer distribution of population segments and bull:cow proportions, influence these "gametic migrations," but in all cases their adaptiveness is obvious. Less obvious are the benefits derived from segregation of small populations year after year in traditional breeding ranges. Perhaps such distributions insure best use of "spotty" habitats (upland riparian willow stands, for example). In addition, regular return to traditional breeding grounds by the same individuals insures contact during the rutting season, and perhaps allows efficient social patterns to develop and persist.

In some reported cases, upland Type A populations aggregate with Type B or Type C populations, which have migrated from the lowlands, for rut. These groups might interact for only the late summer-fall period each year. In contrast, lowland Type A populations are generally isolated during rut, in lowland areas that Type B and C groups have left. Perhaps this segregation preserves genetic tendencies for both localized (Type A) and long-distance (Types B & C) migratory behavior in the same large area. Localized behavior may be adaptive only when a substantial portion of a population leaves during part of the year. It may be especially adaptive to reproducing females; whereas, the benefits of migration might be greatest to other individuals. Thus, both types of behavior are retained in the same area.

It is difficult to ascribe social adaptiveness to movements that result in aggregations on winter range; probably selection pressure for these patterns originates largely in climatic and forage advantages. Nevertheless, aggregations do occur in late winter (cf: Peek et al. ms) in large expanses of good habitat where clumping is probably not required by snow or forage conditions. Social advantages of these groupings might perhaps be sought in predator-prey relationships or socialization of short yearlings before their rejection by cows.

Summer segregation of some migratory populations by sex and reproductive status might have social advantages. Part of the adaptiveness of this pattern certainly derives from localization of cows in relatively "predator-safe" habitats at a time when travel is difficult for new calves; contrasted with the forage (energy balance) advantages of upland habitats to animals unencumbered with young. Perhaps social advantage also derives from minimizing contact between young calves and moose other than their dams, at the time when their first socialization occurs.

MANAGEMENT CONSIDERATIONS

Moose migration patterns have significant influence on designation of special-use lands (eg. wilderness areas, recreational areas, highway routes) and development of hunting seasons and limits. Annual movements are especially important when they involve travel from inaccessible areas to roadside areas. Segregation of localized traditional breeding groups and the slowness of dispersal into social niches further complicates hunter management. The root of most migration-related management problems lies in management of land areas rather than moose populations. Their solutions lie in learning the nature and timing of movement patterns and the geographical origins of the groups and population segments involved.

Management problems are unique to each situation, but several general examples will illustrate their nature. Traditionality of seasonal home ranges and slowness of dispersal into vacated home ranges greatly influence hunter management along road systems where there are "resident" populations and in upland drainages where the same individuals breed repeatedly. In such situations, these groups must be considered as isolated populations rather than as portions of larger reservoirs of animals, and must be harvested only within their limited annual increments.

When lands are designated for special uses--to protect certain moose "herds" or to provide for trophy hunting of large bulls, for example--it is essential to understand seasonal movement patterns of all segments of the group in question. Without such understanding, critical habitats (eg. winter range, calving areas) outside the designated area might be destroyed, thereby affecting any moose from the "protected" area that might use them seasonally. Similarly, "trophy" areas near "maximum sustained yield" areas are futile if trophy animals migrate to the latter areas during hunting seasons. Conversely, maximum sustained harvest management will fail in situations where moose are not present in accessible areas when hunting is allowed. Benefits from intensive habitat manipulation for production of moose to be harvested may be minimal if lands important to the same moose at other times of the year are not also appropriately manipulated or protected.

Finally, knowledge of moose movements is critical to planning compatible human developments. Construction of a single highway or pipeline barrier across a major migration route could affect moose over tens of thousands of square kilometers. Misuse of a very small critical seasonal range for only a month each year could result in the disruption of thousands of moose over a vast area. These possibilities are not hypothetical, but very real in some areas (cf: LeResche 1972). Where migrations do occur, managers must realize that free movement is of major importance to healthy moose populations.

RECOMMENDATIONS

1. No more moose should be tagged on the northern Kenai Peninsula other than at the Moose Research Center traps.

2. No further reconnaissance flights should be made for the sole purpose of locating marked moose, but sightings of marked animals seen incidentally to other flights should be recorded.

3. Recommendations of LeResche and Davis (1971) should be followed.

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