THE IMPORTANCE OF THE COW-CALF BOND TO OVERWINTER MOOSE CALF SURVIVAL

by
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THE IMPORTANCE OF THE COW-CALF BOND TO OVERWINTER MOOSE CALF SURVIVAL

A

THESIS

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BY

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ABSTRACT

Observation of penned and free-ranging moose on the Kenai Peninsula, Alaska, are presented for the period 1971-75. Winter behaviors that are reported include individual time/activity patterns, feeding behavior, and daily movements; and social behaviors of aggregation, association, interaction, and cow-calf behavior. The feeding sequence of cratering for ground vegetation and the use of bark from windthrown aspen trees are described. In 1975, aggregations apparently occurred in response to provision of a concentrated food source by mechanical habitat manipulation. Extremely high moose densities resulted with considerable turnover. Frequent bond disruption and high calf mortality are documented. A general hypothesis is advanced that the importance of the bond for calf survival diminishes with declining conditions. The decline of the Kenai Peninsula moose population during the period of study is attributed primarily to declining habitat quality in combination with conditions of colder winter temperatures, and deeper and more persistent snow cover.

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INTRODUCTION

Direct behavioral observation of wild animals in their natural environment has been employed for many years to document and describe their behavior and life histories. Most of these studies consist of observations of a single population for a few years. Only recently have these techniques been applied to wildlife management. For this purpose, observation of a single species under a variety of environmental conditions is often required. The principle behind such an approach is that certain behavior patterns can be used as indices of herd health and of the relationship of the population to its habitat. Stress conditions will cause deviations in the usual behavioral life history of the species.

Moose behavior can be expected to vary considerably as moose traditionally occupy range where the available browse changes in quantity and quality. The most nutritious moose browse occurs in early seral stages (Cowan et al. 1950, Peterson 1955, Krefting 1974a). While some areas contain vegetation in such stages on a somewhat permanent basis, e.g. river basins, many more animals are supported by areas undergoing secondary succession following disruption of late seral or climax vegetation. Wildfire has been the major agent resulting in creation of moose habitat in

Alaska (Spencer and Chatelain 1953, LeResche et al. 1974). Although the nature and timing of regeneration is a complex process (Lutz 1953, Viereck 1973), many burned areas have produced a large quantity of high-quality moose browse for many years. However, as the vegetation matures or grows out of reach of moose, the habitat remains optimal for a relatively short time. Thus, local moose populations in Alaska may undergo large fluctuations in number as the location of suitable habitat shifts. The nutritional status of individuals in the population varies with the carrying capacity of the habitat, so certain features of the life history of moose can be expected to vary also.

Reproductive success of moose has been linked to range quality (Pimlott 1959, Markgren 1969), but maternal behavior has not been studied in connection with the changes in habitat quality. The cow and calf constitute the only long-term bond in the species, with the two associating during the first year of the calf's life. If the cow again gives birth, the yearling is usually chased away it may remain in association with the cow until the fall rutting period (Altmann 1960).

The winter period, when the cow and calf are together, is most likely a critical time for calf survival. The nutritive value of forage is at an annual low and nutritional stress may be imposed by snow which buries some food sources, decreases availaility of others, and increases the energy expenditure necessary to move to obtain woody browse.

There is a widespread belief that calves are very dependent on their mothers for winter survival. This belief seems to be based on limited and scattered bits of evidence rather that any prolonged observations of cows with calves. This belief has caused problems in managing moose populations because the general public is averse to shooting cow moose and leaving orphans to starve in the winter. However, cow-calf behavior and calf survival can be expected to vary with the severity of snow and weather conditions, range condtions, and predator densities. An understanding of the nature of the cow-calf bond under various conditions is needed so that sound management decisions can be made.

Winter conditions and decreasing habitat quality on the Kenai Peninsula, have resulted in high calf mortality and a general population decline in recent years (Bishop and Rausch 1974, LeResche et al. 1974, Oldemeyer et al. in Franzmann and Arneson 1975). Behavioral indices of these conditions have included frequent disruption of the cow-calf bond before death of the calf and variations in daily activity patterns in comparison with more favorable conditions. This study was designed to observe different behavior patterns of cow-calf pairs to determine the nature of the cow-calf bond which resulted in successful or unsuccessful calf-rearing. In Mt. McKinley National Park, my aim was to observe interactions between the cow and yearling before or after parturition in a situation where winter range conditions were more favorable to calf survival. These behavioral observations may aid in diagnosing declining conditions similar to those on the Kenai Peninsula and making management decisions.

STUDY AREA

I conducted research on the Kenai Peninsula, Alaska, located between Prince William Sound and Cook Inlet in southcentral Alaska (Figure 1). I made the bulk of my observations within the enclosures of the Moose Research Center (MRC), a co-operative research project of the Alaska Department of Fish and Game (ADFG) and the U.S. Fish and Wildlife Service, Kenai National Moose Range (KNMR - See Figure 2). During the winter of 1974-75, the KNMR staff carried out a vegetation rehabilitation project in the Willow Lakes area. This consisted of crushing the vegetation with LeTourneau tree crushers (method described in Hakala et al. 1971). During February and March, I observed concentrations of moose in the 23 km^2 Willow Lakes area (Figure 3).

I observed cows and yearlings during the spring of 1975 in Mount McKinley National Park, Alaska (Figure 1). The topography, habitat, and general conditions in the area have been adequately described by Dixon (1938) and Murie (1944). Based on aerial surveys conducted in recent years, high concentrations of moose occur within the extreme eastern portion of the park, east of the Teklanika and Sushana drainages (S. Buskirk, pers. comm.). Most of my observations took place in this area within 1-7 km of the park road.

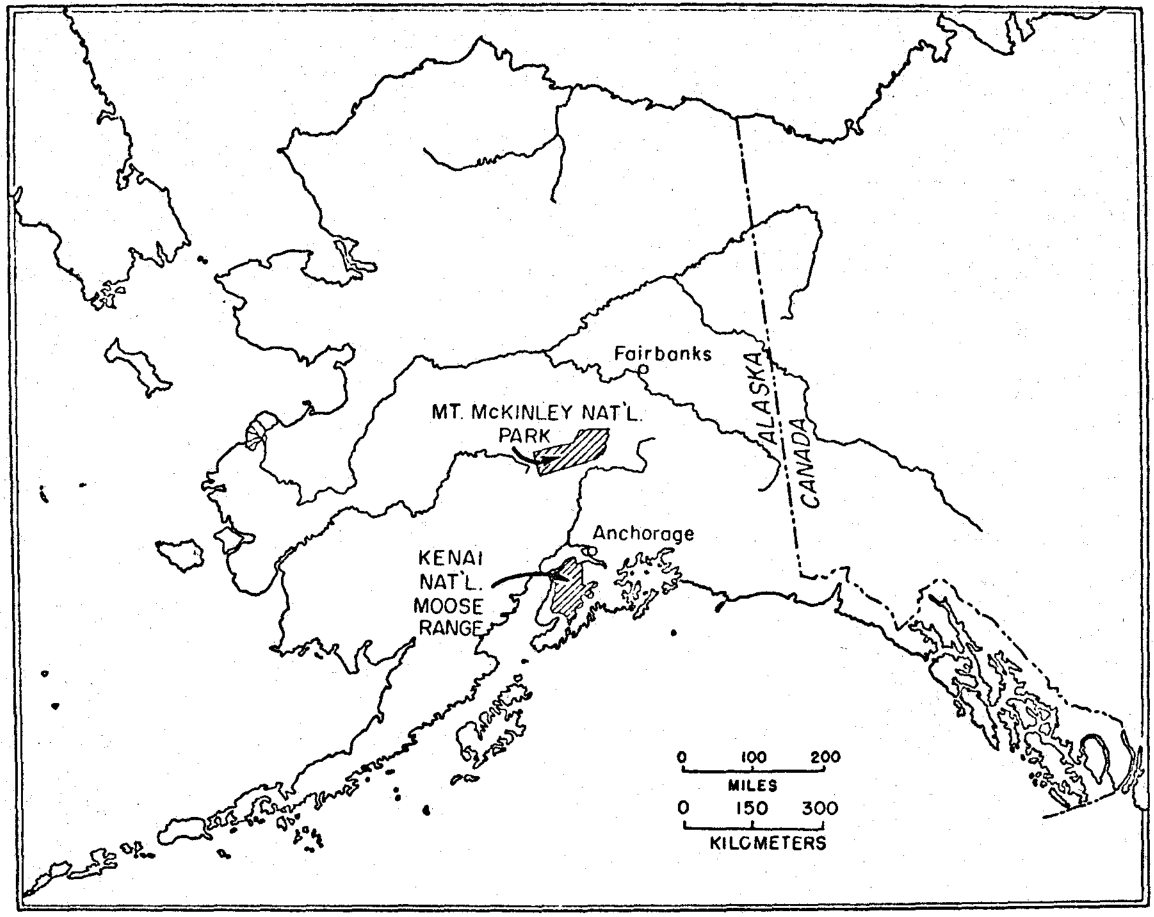


Figure 1. Map of Alaska with study areas indicated.

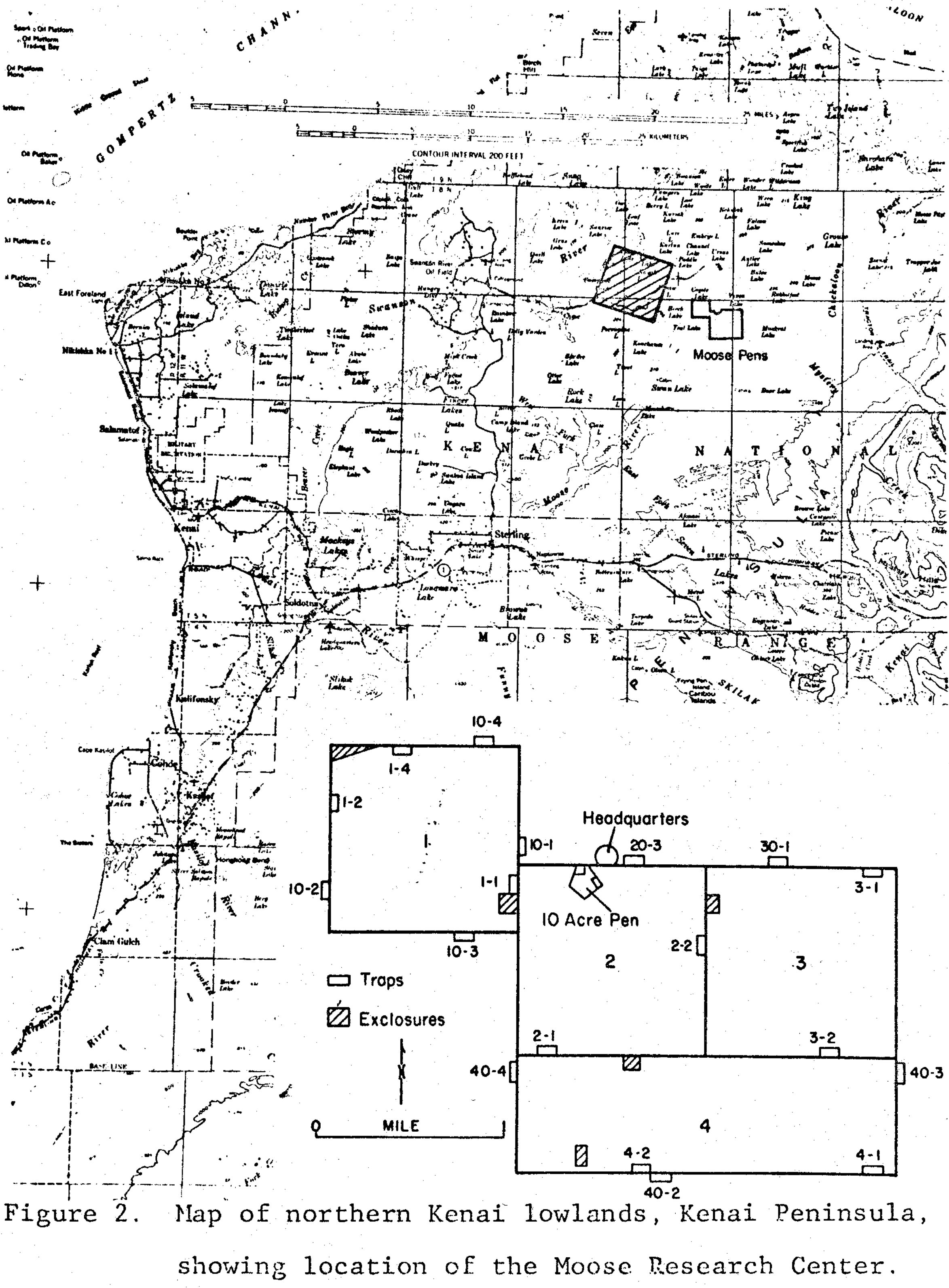
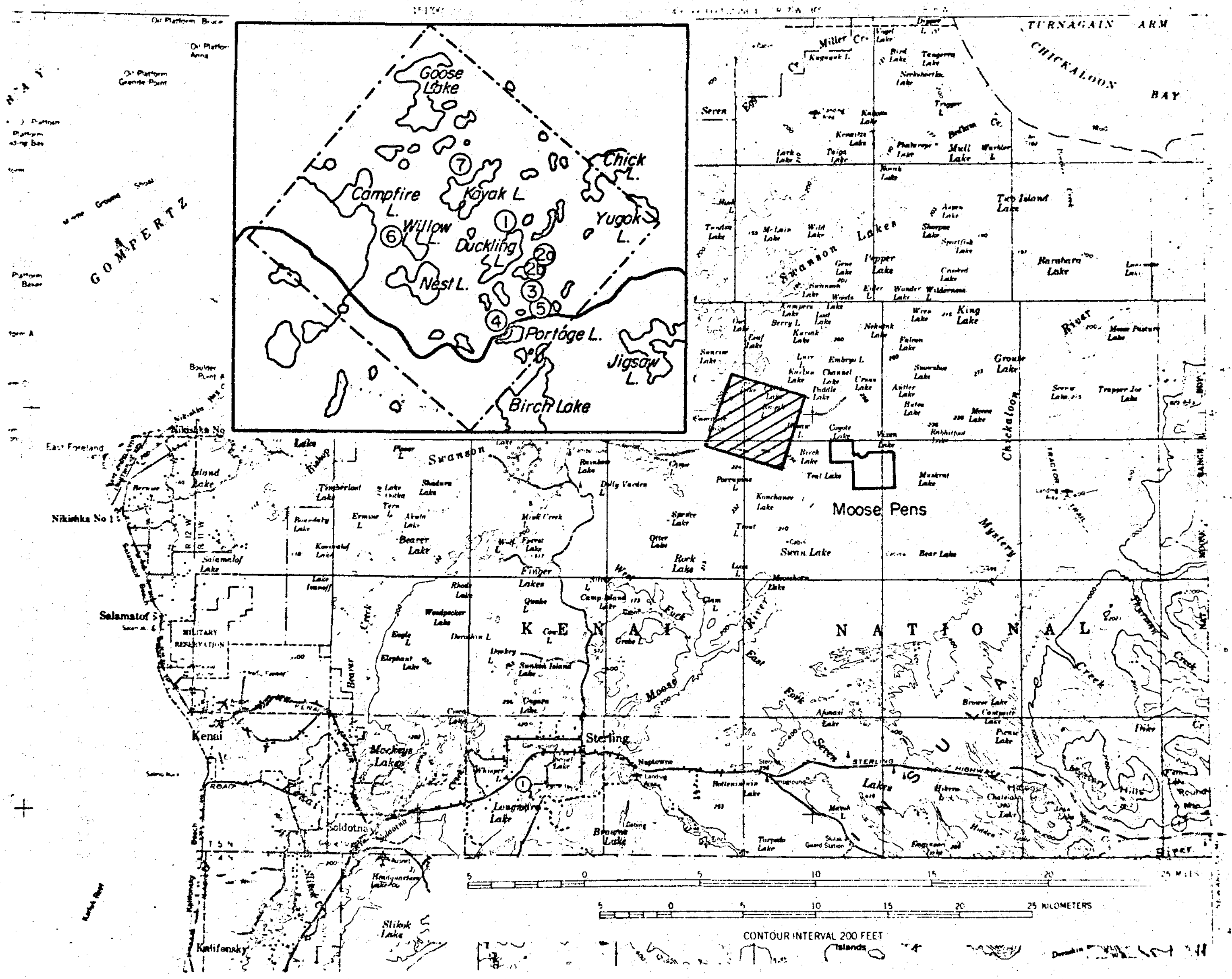


Figure 2. Map of northern Kenai lowlands, Kenai Peninsula, showing location of the Moose Research Center. Inset illustrates general layout of facilities.

Figure 3. Map of northern Kenai lowlands, Kenai Peninsula, showing location of Willow Lakes Rehabilitation Area, where approximately 820 ha were rehabilitated by mechanical crushing of vegetation during the winter of 1974-75. Numbered areas are areas of moose aggregation.


Goose Lake
Chick L.
Campfire L.
Kayak L.
Yugok L.
Willow L.
Duckling L.
Nest L.
Portage L.
Jigsaw L.
Birch Lake
①
2a
2b
③
④
⑤
⑥
⑦
TURNAGAIN ARM
CHICKALOON BAY
GOMPERTZ
Swanson Lakes
Moose Pens
KENAI NATIONAL
Mystery Creek
Chickaloon River
Sterling
Soldotna
Kenai
Kalifonsky
Salamatof
Nikishka No 1
East Foreland
Swan Lake
Mackeys Lakes
Longmere Lake
Skilak Lake
STERLING HIGHWAY
MILITARY RESERVATION
CONTOUR INTERVAL 200 FEET
25 KILOMETERS
25 MILES

Spencer and Hakala (1964) and Bishop and Rausch (1974) have described the Kenai Peninsula in detail. The study areas were located in the Kenai lowlands on the west side of the peninsula. The north portion of these lowlands is a plain of some 7680 square kilometers, composed of flats, low ridges, hillocks, muskegs, and more than 1000 lakes. The plain is glacial in origin and now consists of a thick sheet of glacial deposition along with water-laid sands and gravels. A thin loess mantle extends over much of the area. The general elevation is in the range 15 to 100 meters.

The climate of the region has characteristics of both continental and maritime zones, although moderating influences of Cook Inlet diminish rapidly with increasing distance from the coast. Annual precipitation ranges from 40 to 50 cm and average annual snowfall ranges from 135 to 150 cm. Cushwa and Coady (1976) characterized snow depths as ranging near 40 cm for short periods of time and seldom reaching 60 cm. Winter thaws are common and bare ground may be exposed at any time.

Mean annual temperature is 1° C. The growing season averages 88 days, usually beginning about 11 June and ending 6 September.

In general, white spruce (Picea glauca), paper birch (Betula papyrifera), and quaking aspen (Populus tremuloides) dominate the forest vegetation on the better-drained soils of the lowlands. Poplars (Populus balsamifera and Populus tricocarpa), black spruce (Picea maritima), willow (Salix spp.), and green alder (Alnus crispa) grow on the wetter sites and in the better-drained areas that have been burned repeatedly. Muskegs are covered by sphagnum moss (Sphagnum spp.), low shrubs, and a few black spruce.

A major factor influencing species composition of habitats and habitat distribution on the peninsula is the history of repeated wildfires. The area enclosed by the pens of the MRC and the Willow Lakes Rehabilitation Area (WLRA) were both located within the 125,455 ha area that was burned in June, 1947. The area enclosed at the MRC is considered to contain vegetation representative of the entire burn. LeResche and Davis (1971, 1973) described the vegetation of the enclosures:

> These enclosures contain representative vegetation of both burned (regenerative: predominantly birch and white spruce and black spruce) and remnant (mixed birch-spruce-aspen stands). Marshland typical of summer range is included as well as well-drained hillocks supporting winter browse species.

Oldemeyer et al. (in Franzmann and Arneson 1975) described the ground vegetation in both burned and unburned stands as dominated by lowbush cranberry (Vaccinium vitis-ideae), bunchberry (Cornus canadensis), rose (Rosa acicularis), twinflower (Linnea borealis) and fireweed (Epilobium latifolium).

Hinman (in Rausch and Bishop 1968) type-mapped the area of the MRC into eleven vegetation types. He noted that each vegetation type involved few species, but that the distribution of types was complex. He attributed this complexity to typical features of valley-glaciated topography which included a great many small hills, small muskegs, and rapid changes in soil and vegetation types, and to the number of islands of unburned vegetation in the area after the 1947 fire.

Freeman (in Rausch and Bishop 1968) found the upland soils to be fairly uniform. Naptowne soils, on which remnant or regrowth birch were the dominant vegetation, cover 85 percent of the area, while Tustumena soils, supporting only spruce regeneration, underlie 5 percent of the area. Wet soils and lakes account for 7 and 3 percent of the remaining area, respectively. Upland soils have low fertility status, although Naptowne soils are much higher in some nutrients.

The 1947 Burn and the moose population in the burn area has been studied by several researchers. Spencer and Chatelain (1953) reported the rapid build-up of the numbers of moose wintering in the burn following the fire. Spencer and Hakala (1964) described later changes in the density of moose and productivity of the forage. The density of moose increased steadily from 1945-59, and at a slower rate thereafter, although the population stabilized and declined slightly following winter losses in 1954,1955, and 1960.

A major purpose of studies at the MRC is to define the relationships of the Kenai moose and its habitat. Research conducted within the Pens and nearby areas of the Kenai has been reported in LeResche 1970, LeResche and Davis 1971, LeResche et al. 1973, Franzmann and Arneson 1973, Johnson et al. 1973, LeResche et al. 1974, Franzmann and Arneson 1974, and Franzmann and Arneson 1975.

Bishop and Rausch (1974) summarized moose population dynamics from 1950-1970. Based on aerial censusses and composition counts conducted after 1964, the Kenai moose population appears to have increased or at least remained stable until 1971. LeResche et al. (1973) stated that the moose population in the 1947 Burn peaked in the years 1967-69 and began decreasing in 1971-72. Aerial surveys flown between 1971 and 1975 suggest that the population has continued to decline (Appendix A). This decline in numbers during the period 1971-74 amounted to 26 percent in ADFG Game Management Units 15A and 15B, with most of the decline taking place in 15A, the northern lowlands of the peninsula (ADFG 1975).

An account of the effects of the 1947 Burn on the moose population as well as the effects of the moose population on its browse supply appears in LeResche et al. (1974). They considered the rate of increase of the moose population in the burn to be near the maximum attainable, due mainly to the effects of the tremendous amount of "edge" in the resulting pattern of interspersed habitat types. They concluded that the 1947 Burn appeared to represent

> if not the ideal, at least the most productive large area of moose habitat known to us . . . through a combination of high forage production, generally mild winters, abundant alternate foods (especially *Vaccinium vitis-ideae*), edge effect, and adjoining upland ranges.

Although densities supported by the Burn at one time may have been maximal, all indications are that the area has lost its value as good winter range. Based on analyses of winter forage species for nutrient content and browse utilization studies, Oldemeyer et al. (in Franzmann and Arneson 1975) concluded that the most apparent change on the range of the northwestern Kenai was that of species composition. They demonstrated the importance of variety in the diet of moose, and characterized the range as formerly multispecies habitat, but now dominated by paper birch, a relatively poor winter forage.

METHODS

I made most of my observations at the MRC from January through April, 1975. Dave Johnson made similar observations in the winters of 1971-72 and 1972-73 (Johnson, unpub.) and these have been incorporated into discussion sections. In addition to penned moose, Johnson also made late-winter observations around the town of Soldotna in 1972.

Throughout the winter of 1974-75, I made observations in Pens 1, 2, and 4 at the MRC. A history of the populations within the pens from September, 1971, through September, 1974, is included in Appendix B. Most adult moose within the pens had been marked previously by the MRC staff and were readily identifiable by numbered neck collars and/or colored plastic ear tags. Several cows and calves were trapped and outfitted with radio collars in the fall of 1974 (Table 1).

I located radio-collared moose by use of a hand-held loop antenna and portable receiver. Fairly accurate map locations could be obtained by utilizing the detailed vegetation-type maps of the pens. Moose were often located as I travelled through the pens or snow-tracked them when conditions permitted. Whenever possible, moose were snow-tracked between sightings to determine 24-hour movement patterns. The distance moved by the moose was

Table 1. Cows and calves observed in the Moose Research Center during the period January-April, 1975. Approximate dates of death are given when known.

Moose #	Type	Pen	Collar Type	Approx. date of death
40	Cow	2	Radio	1 March, 1975
119	Calf	2	Radio	14 Jan., 1975
79	Cow	2	Radio	-
117	Calf	2	Radio	1 Feb., 1975
R-70-8	Cow	1	Radio	-
116	Calf	1	Radio	Late Jan. - early Feb.
-	Calf	2	Unmarked	?
670	Cow	2	#670	-
-	Calf	2	Unmarked	Late Jan.
138	Cow	Outside	4-color	-
-	Calf	Outside	Unmarked	Late Jan.

estimated by pacing on snowshoes.

In January and early February, emphasis was placed on observing cow-calf pairs; later, the thrust of the study was to obtain long-term daylight observations of individuals in the pens and observations in the WLRA.

I was able to observe large numbers of moose in the WLRA where mature vegetation had been mechanically crushed. I attempted to age and sex all animals, although only a few had been collared previously by ADFG personnel and were thus easily identifiable as individuals.

The types of observations made on all moose, when possible, included:

1) Activity patterns
    a) Feeding (duration, frequency, food type consumed)
    b) Resting (duration, frequency)
    c) Movements (distance, terrain, habitat, snow conditions)
2) Interactions of individuals
3) Aggregations
4) Miscellaneous behaviors - comfort movements: stretching, shaking, yawning, attention postures, yawning, sniffing

Whenever I observed cow-calf pairs, I paid attention to behavior that might give evidence of the nature of the bond between the two. In general, food habits, synchrony of activity and rest, distances between the two while feeding or resting, and separations were recorded. I specifically looked for the following behaviors on the part of the cow:

1) Provision of food to the calf
   a) Breaking off browse plants
   b) Uncovering ground vegetation
2) Breaking trail in deep snow
3) Active defense of the calf
4) Close approach to the calf regularly or when disturbed
5) Vocalizations

Specific behaviors by the calf that I particularly looked for included:

1) Selection of food that the cow was feeding upon
2) Close approach to the cow regularly or when disturbed
3) Nursing attempts
4) Following when travelling
5) Vocalizations
6) Behavior when separated from the cow

In the WLRA, I paid particular attention to aggregation and association behavior, both of which are defined in the Results sections. Occupation and movement in and out of areas of concentration was monitored for a portion of the winter. I noted the percentage of animals active of all animals visible at 15-minute intervals. I also recorded the occurrence of collared moose and persisting groups. Distance precluded an accurate description of food habits.

Selection of the area to be observed depended on the availability of large numbers of moose and the desire to see the changing pattern of occupation in a single area. Thus, when only a few moose were seen in an area repeatedly, I shifted observation to a new area, determined by aerial observations of concentrations of moose. I recorded additional sightings on or near Swanson River Road and on the way to and from sites of long-term observation.

In Mt. McKinley National Park, I looked for the behaviors of the cow and yearling already mentioned for the cow and the calf. In particular, careful attention was paid to behavior at the time of the break-up of the cow-yearling association.

Observations were made with 7 x 35 wide-angle binoculars. I used both a 35 mm Single Lens Reflex and 16 mm movie camera. Either a pocket tape recorder or notebook was used for recording observations.

Disturbance by observer

Murie (1934) summarized his impressions of the senses of moose by saying that "hearing and smell are highly efficient . . . vision is somewhat deficient." I found this description to be accurate and had difficulty making undetected appproaches through heavy brush or on snowshoes that invariably "crunched" with each step. However, if I was able to get into a good position for observation without causing the moose to run away, the poor sight of the moose often allowed me to remain as long as I was reasonably still. Loud noises or sudden movements resulted in attention by the moose and undisturbed observation was possible more often when I was downwind.

Observation of a wild animal always entails the possibility of influencing the behavior, resulting in an obvious reaction to the observer's presence or a less obvious modification. As an observer, I was always faced with making a subjective judgment as to whether or not the animal had been disturbed.

Obvious reactions included getting up from a bed when I approached, running away quickly, moving slowly but constantly without stopping to eat for fairly long periods of time (30 minutes or more) while I was following, and aggressive behaviors such as threats, vocalizations and charges directed at me. After such behavior, I terminated observation. The less obvious modifications that may have resulted from my presence were difficult to define, although they may have involved avoidance of areas or routes of travel, restricted movement, or intensive feeding.

In most cases in MRC pens, I located and approached moose without any of the obvious disturbed reactions other than the assumption of an alert posture. If I did not approach too closely (less than 30 m) and was as still as possible after seeing them, these moose would begin feeding in the same place or continue lying down within a few minutes. Such moose would attend briefly if I made sudden movements or noise. Individual moose, after having been observed several times for fairly long periods, became less wary with each observation period, attending only briefly and at shorter approach distances (approximately 15 m).

The WLRA contained "outside" moose who had never been confined, although several had been trapped and handled at the MRC. They were not accustomed to observation by humans, although they had most likely encountered humans during the summer or fall because the Kenai National Moose Range is a popular recreation and sport hunting area. When I first visited the WLRA, most groups of moose would disperse as I came within 300 m of them. The majority of long-term observations were made from a distance of about 200 m from a "blind"- type situation. Although a few moose would leave the area as I approached the small stand of trees that I used as a blind, and several would attend, I assumed that behavior was undisturbed after allowing a 30-minute period for adjustment. Closer approach, up to 20 m, was possible when strong winds drowned out the crunching noise of approaching snowshoes and blew human scent downwind from the moose.

RESULTS

Descriptions of Categories of Behavior Observed :

Geist (1963) has provided the only detailed descriptions of moose behavior. The following categories of behavior were observed during this study and are the ones referred to in the Results and Discussion of Time/Activity Patterns.

Feed Birch - consisted of feeding on woody browse (twigs and branches). Feeding on paper birch accounted for nearly all observations. The breaking off of twigs and branches and the "riding down" of saplings has been described in Geist (1963). Feeding on birch was a fairly continuous activity; the moose would usuallly move slowly through a stand of birch regrowth, feeding on several trees from one position before moving to a different area of the same stand (Photo 2).

Feed Aspen - Although aspen bark consumption has been noted by several workers (Kellum 1941, Kaletsky 1965, Timofeeva 1965, Krefting 1974a), no detailed description of the method of feeding is contained in the literature. This feeding behavior consisted of the moose stripping the bark and cambium layer from down mature trees. The moose gnawed

Photo 2. Moose #79 feeding on birch in a thin birch-spruce regrowth area

bark off the trunk and branches of such trees, pawing to remove snow from buried branches. This feeding behavior was also a continuous one. The moose often bedded down and stayed in an area with several down trees for several days. When aspens were first felled during the crushing operations, moose consumed the upper twigs and branches that were usually out of reach, and then began to feed on the bark (Photo 3).

Crater - Cratering is another feeding behavior that has not been described. Moose seemed to search for a suitable location to crater, sniffing or extending their tongue into the snow periodically. They then pawed and removed snow from an oval or rectangular area by repeatedly extending a foreleg, then bending the leg and moving it back in a scooping motion. They often pawed several times with one leg, then several times with the other. They would feed briefly on uncovered ground vegetation between bouts of pawing. Lowbush cranberry was the major plant in the ground cover in most cases (Figure 4).

Travel and Browse - consisted of moving through an area, pausing only to nibble small plants, sniff and paw a few times, or take a few bites of birch or aspen. In the spring, browsing included brief bouts of feedinon g ground

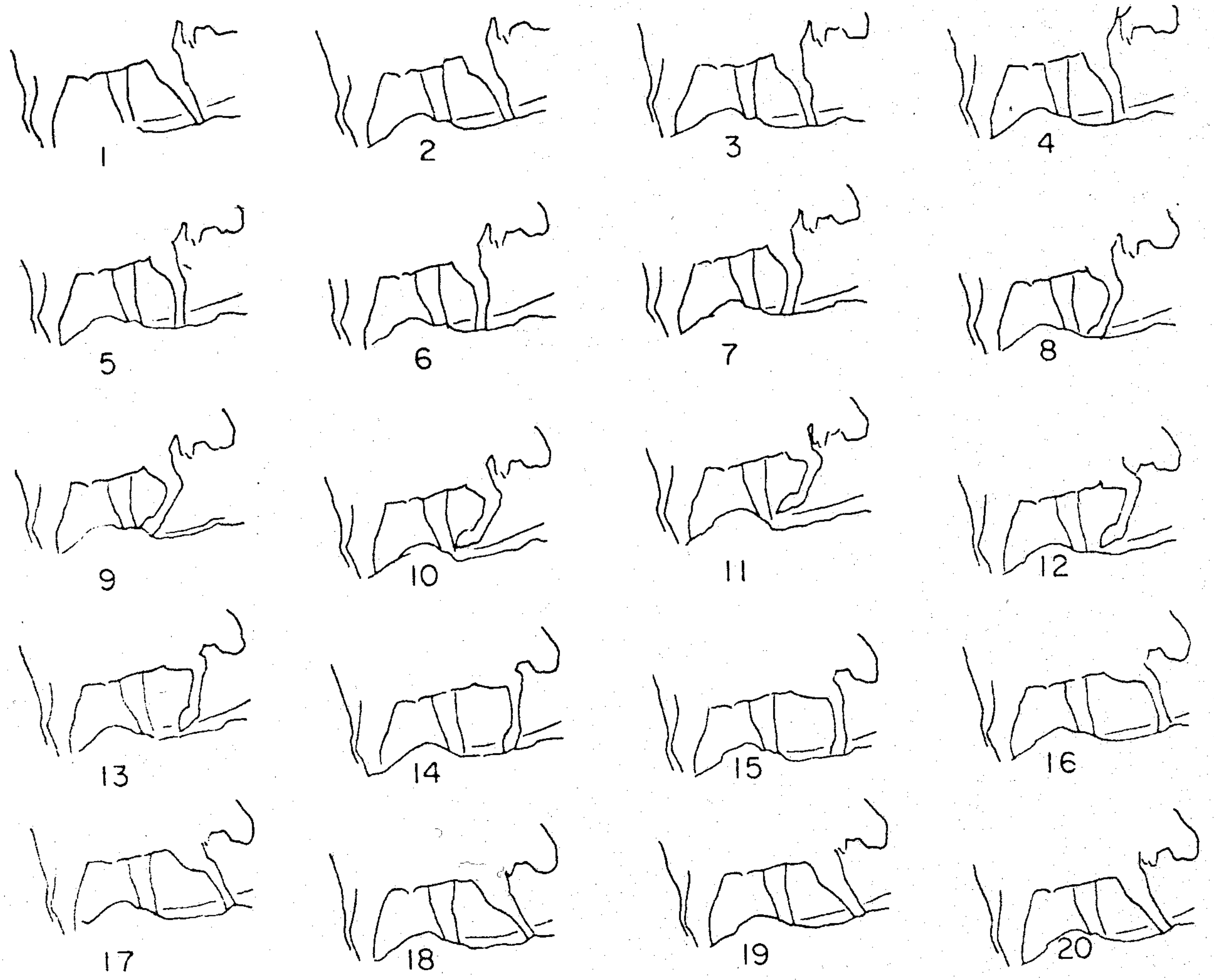


Figure 4. Selected frames from filmed cratering sequence.

vegetation uncovered by snow melt.

Travel - a steady movement between feeding bouts

Lying - consisted of lying down. The motions of lying down, getting up, and various lying postures have been described by Geist (1963). Moose ruminated while lying and sometimes closed their eyes. They attended to sounds frequently, swivelling their ears in the direction of the noise.

Comfort Movements - included stretching, position changes, yawning, shaking, and scratching on a branch. These occurred intermittently and have been described by Geist (1963).

Agonistic behavior - Very few instances of agonistic behavior were observed. Geist (1963) has described threat postures, vocalizations, and attack sequences. I observed both brief charges, which might be considered threats, and more prolonged chases of fleeing moose. Contact between two moose was never observed. The animal being attacked moved a short distance from the agressor when threatened and left the feeding area after repeated charges or a chase.

Feeding displacement - This interaction did not follow

Geist's descriptions of agonistic behavior. On a few occaisons, one moose approached another moose slowly from the rear, while uttering short, low moans. The response of the other moose was to move away a short distance and yield its feeding site. This approach did not appear to be aggressive. Cows sometimes yielded feeding sites to calves when calves either approached from the rear or began feeding very close to where the cow was feeding.

Time/Activity Records

All observations assigned to categories previously described are included in Appendix C. The percentages of total observation time devoted to each category is shown graphically in Figure 5. The percent of time spent by cow #79 in each activity is presented separately because observation of her accounted for 53 percent of total observation time. Eight other moose were observed; eleven moose, including three semi-tame moose, were sighted incidental to long-term observations of the nine. Lying predominated over any activity and feeding on aspen and birch were the major activities.

The fairly continuous time/activity record of moose #79 throughout the winter is presented in an actogram in Figure 6. This actogram represents a series of daylight observation periods. Table 2 presents complete bouts of activity and rest and the mean length of each type of bout. The length of rest and feeding periods varies considerably. Mean values for Moose #79 and moose in the WLRA are compared in Table 3. Both mean length of activity and rest bouts are greater for Moose #79.

In Figures 7-17, the percentage of animals seen active (of total number of animals seen) has been plotted for each fifteen-minute interval from 0800 to 1500 AST for each

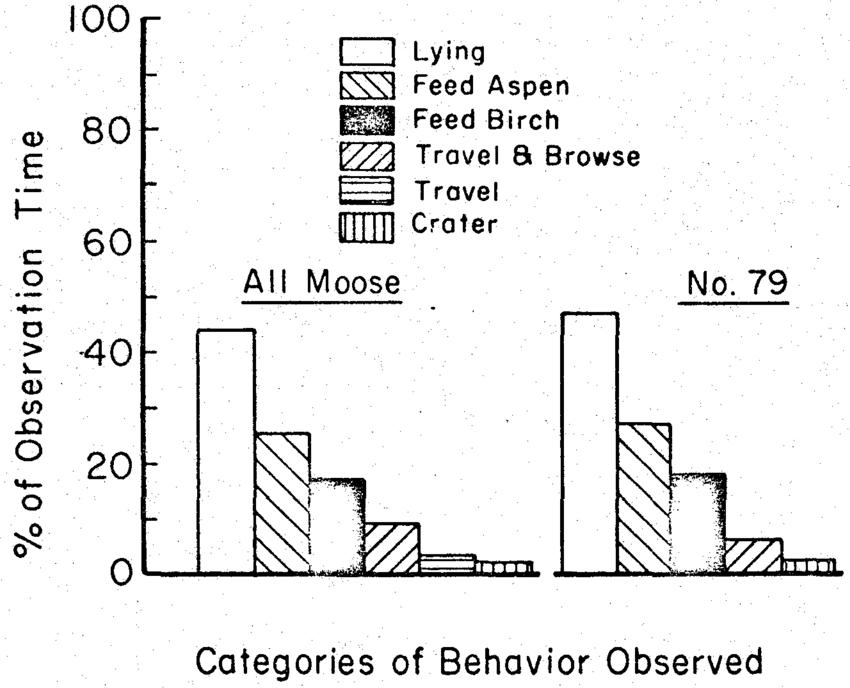


Figure 5. Percentage of total observation time (n = 7609 minutes) that moose in the Moose Research Center were engaged in various behavior patterns during the period of study. The behavior patterns of #79 are presented separately because observation of her accounted for 53% of total observation time.

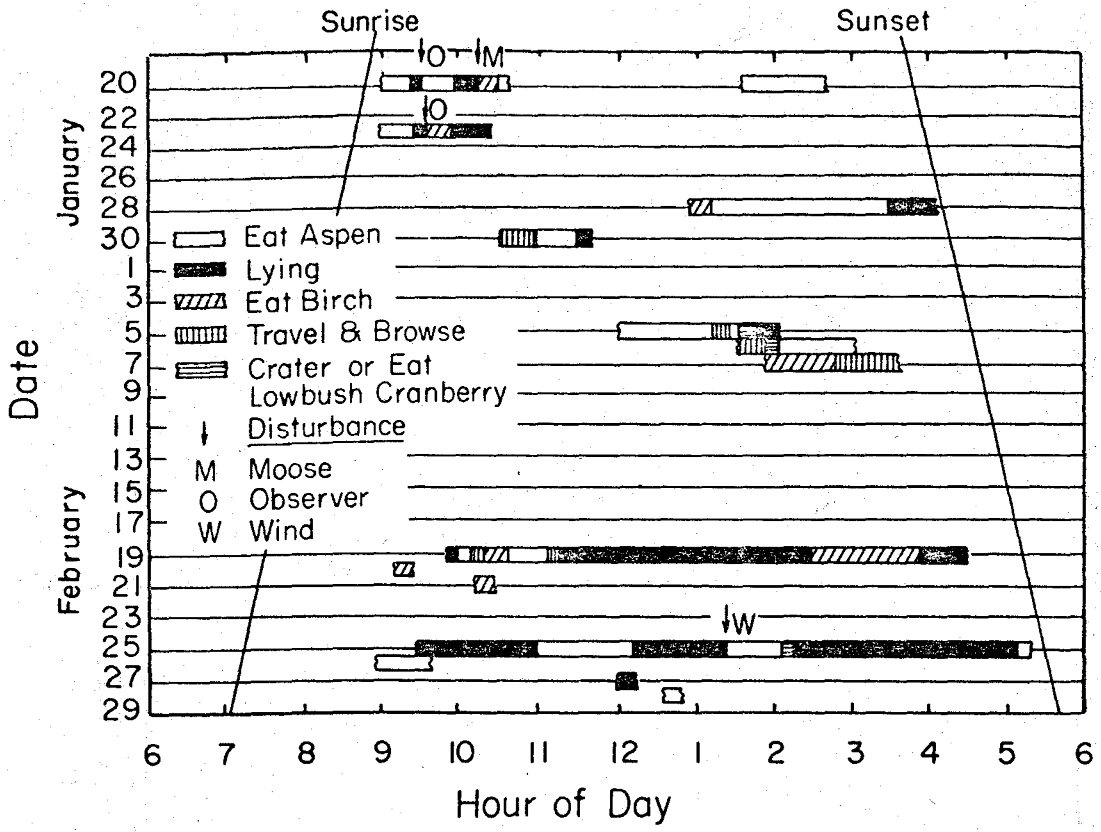


Figure 6a. Actogram of penned female moose #79 showing activity patterns during the period 20 January through 28 February, 1975.

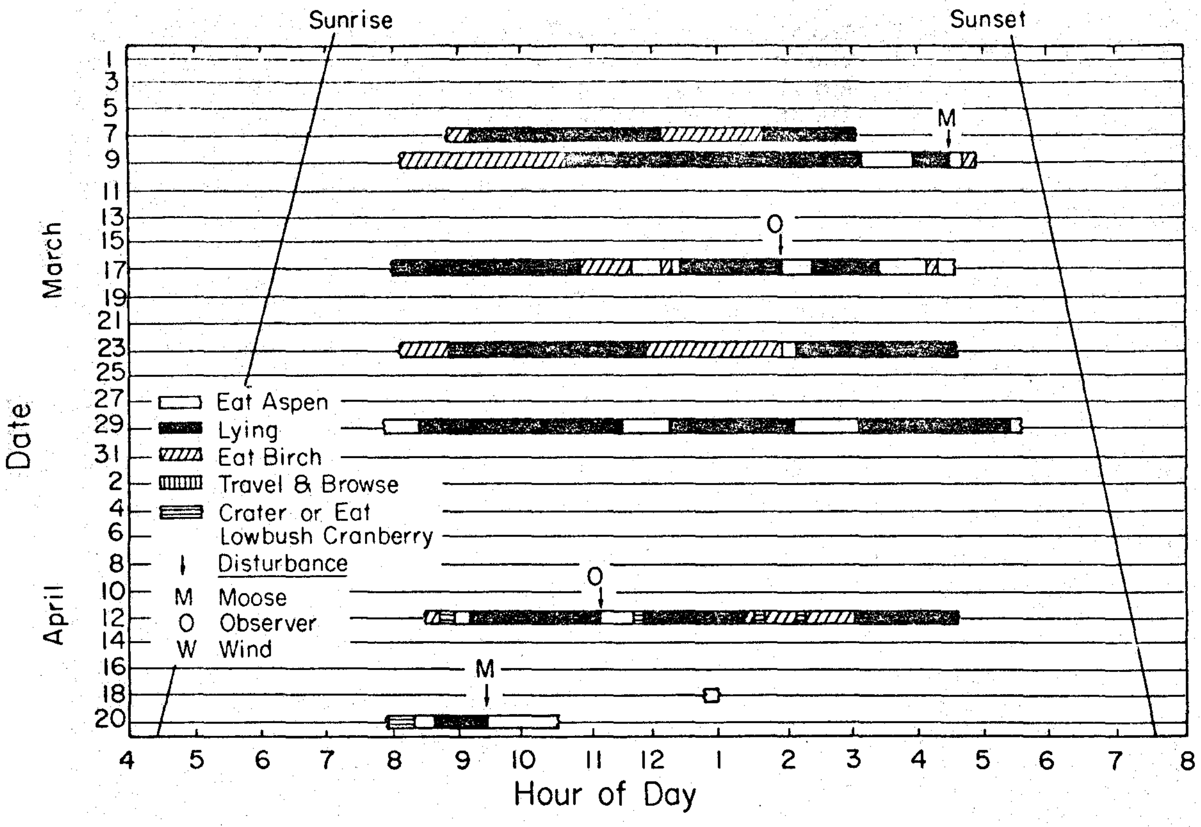


Figure 6b. Actogram of penned female moose #79 showing activity patterns during the period 1 March through 20 April, 1975.

Table 2. Completed bouts of rest and activity observed at the Moose Research Center from January through April, 1975. Mean length of bout is also shown. (Dist.) indicates a bout terminated by disturbance.

Date	Moose #	Type of Activity	Active (min.)	Lying (min.)
24 Jan.	670	Feed Aspen	75	97
	Calf	Feed Aspen	65	95
2 Feb.	670	Feed Birch	73	182
19 Feb.	79	Feed Aspen,		
		Feed Birch	75	195
		Feed Birch	91	
20 Feb.	40	Feed Birch	36	165
25 Feb.	79	Feed Aspen	75	75
		Crater,		
		Feed Aspen	50	140
7 March	79	Feed Birch	73	167
9 March	79	Feed Aspen	50	270
			30(Dist.)	
17 March	79	Feed Birch,		
		Feed Aspen	86	91(Dist.)

Table 2, continued.

Date	Moose #	Type of Activity	Active (min.)	Lying (min.)
17 March	79	Feed Aspen	24(Dist.)	70(Dist.)
23 March	79	Feed Birch, Feed Aspen	141	173
29 March	79	Feed Aspen	70	145
		Feed Aspen	73	100
			132	
10 April	36	Feed Aspen	83	107
11 April	36	Feed Aspen	25(Dist.)	
12 April	36	Feed Aspen	77	95
		Feed Aspen, Travel and Browse	113	
13 April	79	Feed Aspen, Travel and Browse	36(Dist.)	122(Dist.)
		Feed Birch, Travel and Browse	100	90(Dist.)
Number of undisturbed bouts			18	16
Mean length of bout (min.)			78	142

Table 3. Comparison of mean length of activity bout and rest bout in daily activity of penned moose #79, Moose Research Center, and moose in the Willow Lakes Rehabilitation Area during the study period.

Type of Bout	#79		KNMR Moose	
	Number Bouts	Mean Length	Number Bouts	Mean Length
Activity	11	80	13	67
Rest	9	155	16	87

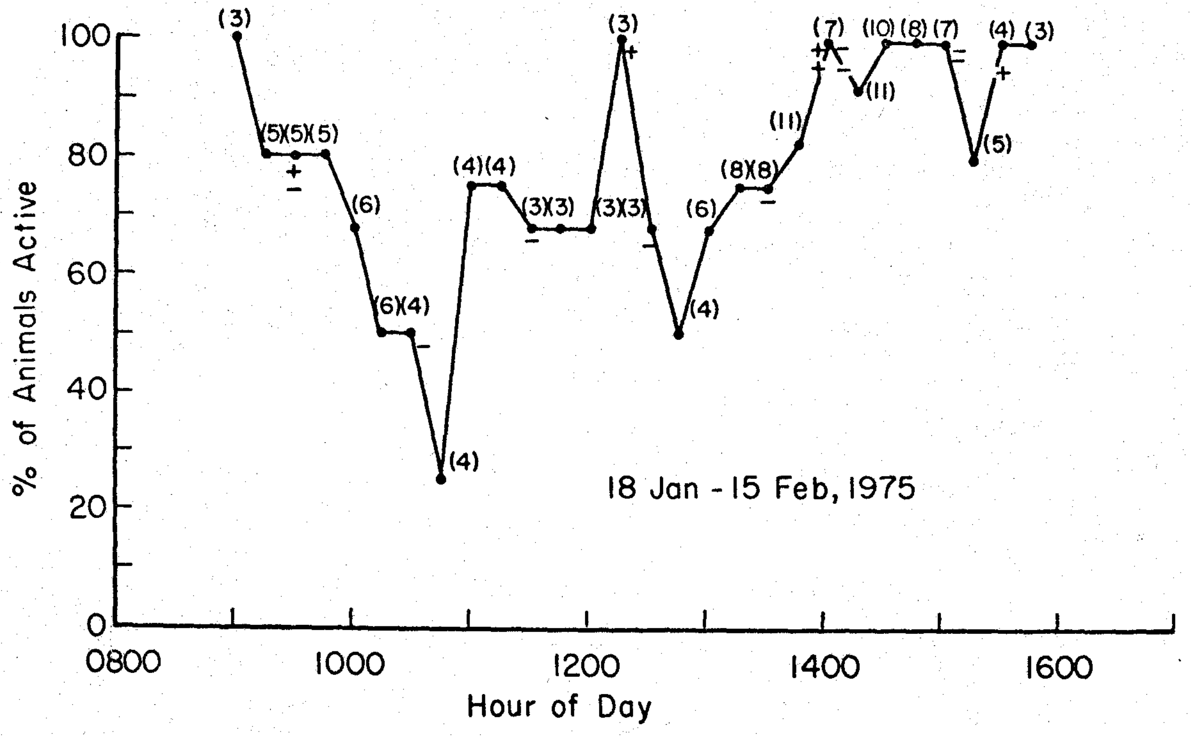


Figure 7. The percentage of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). Sightings occurred during the period indicated. (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. The sample size for each point is given in parentheses.

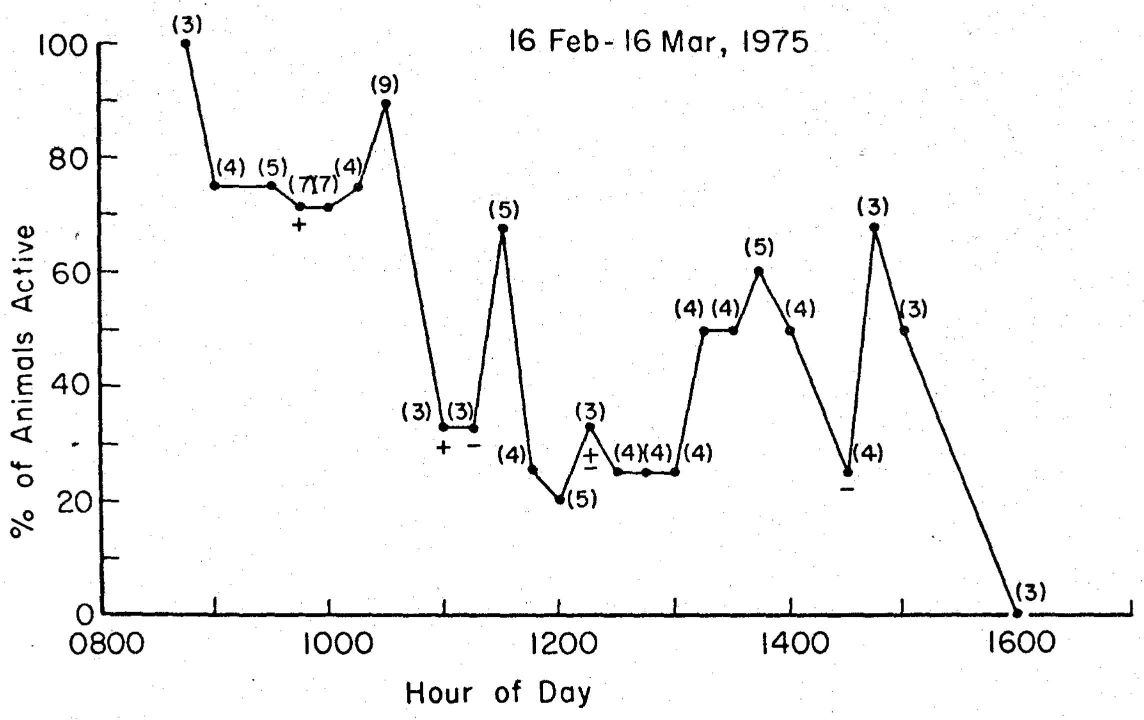


Figure 8. The percentage of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. The sample size for each point is given in parentheses.

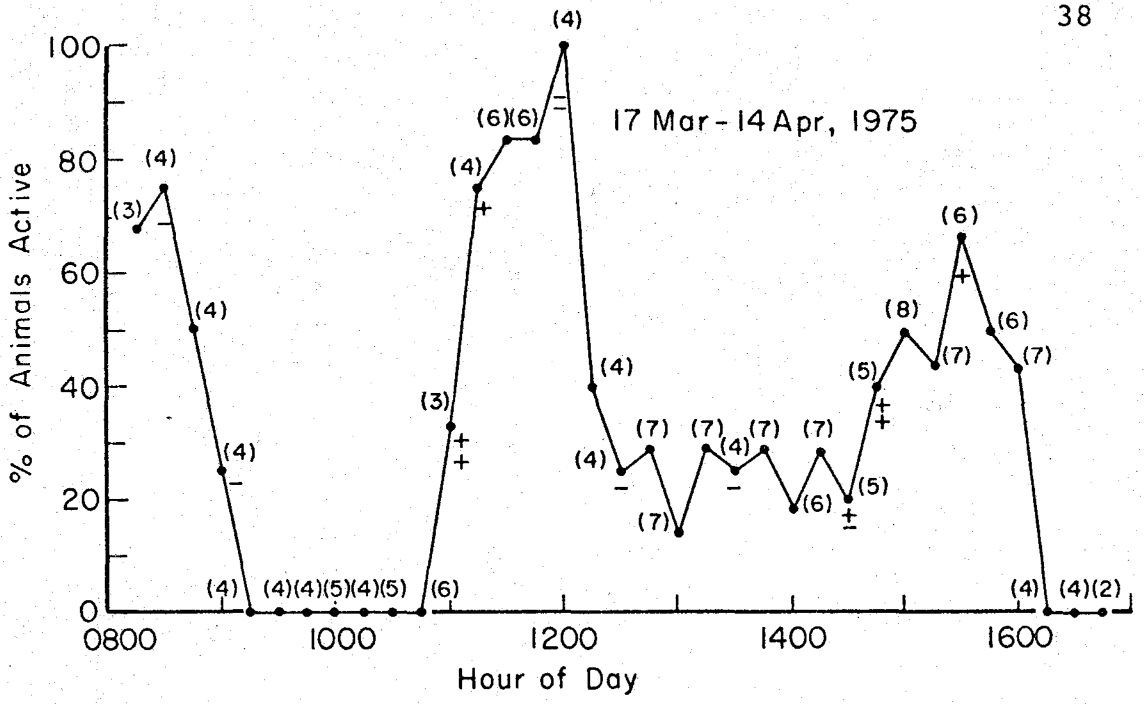


Figure 9. The percentage of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. Sample size for each point is given in parentheses. Note peak from 1100-1200.

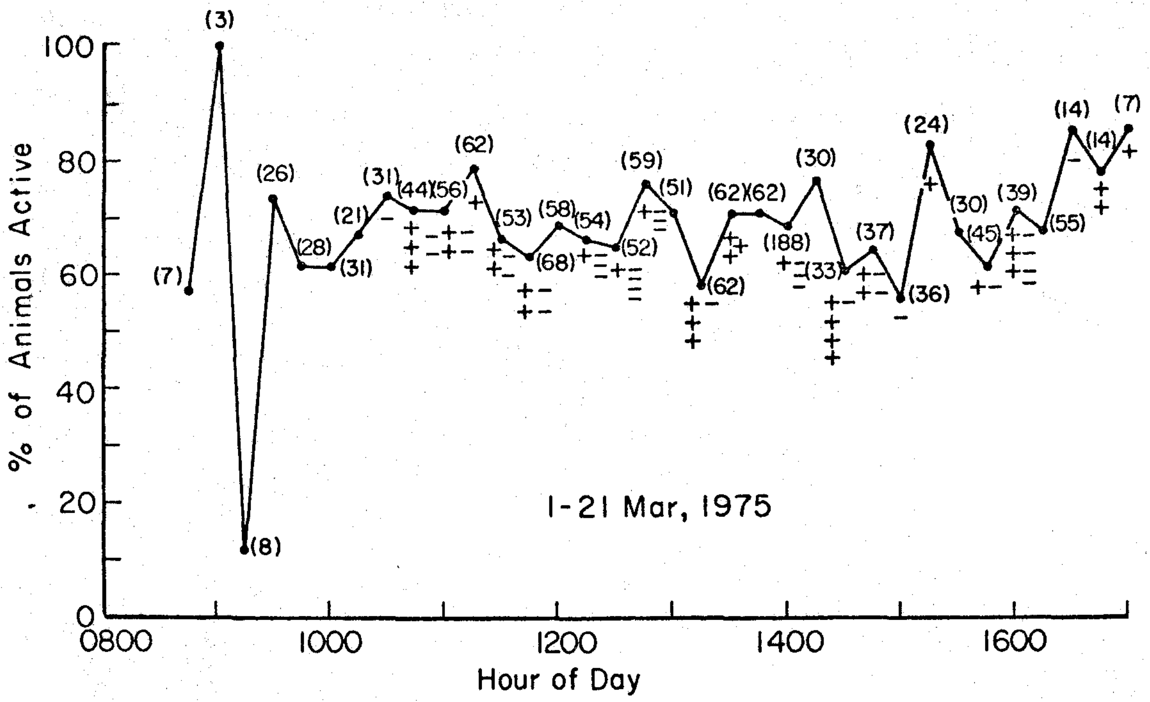


Figure 10. The percentage of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. The sample size for each point is given in parentheses. Note the high level of activity throughout the day.

Figures 11-12. The percentages of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). Sightings occurred during the periods indicated. (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. The sample size for each point is given in parentheses. In Figure 11, note peak from 1000-1100. In Figure 12, note peak from 1430-1600.

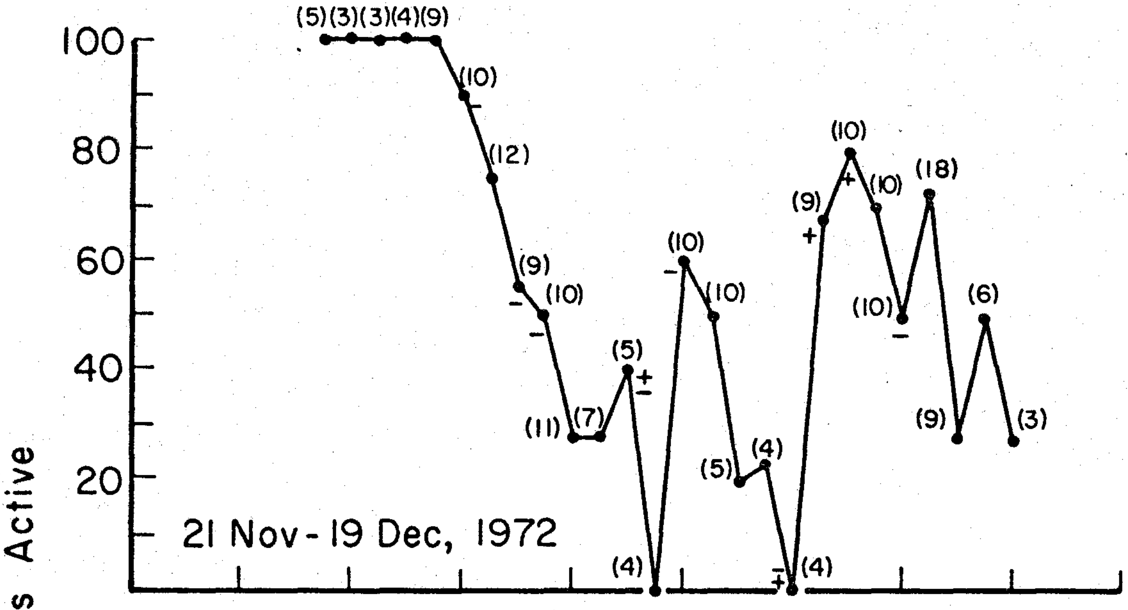


Figure 11

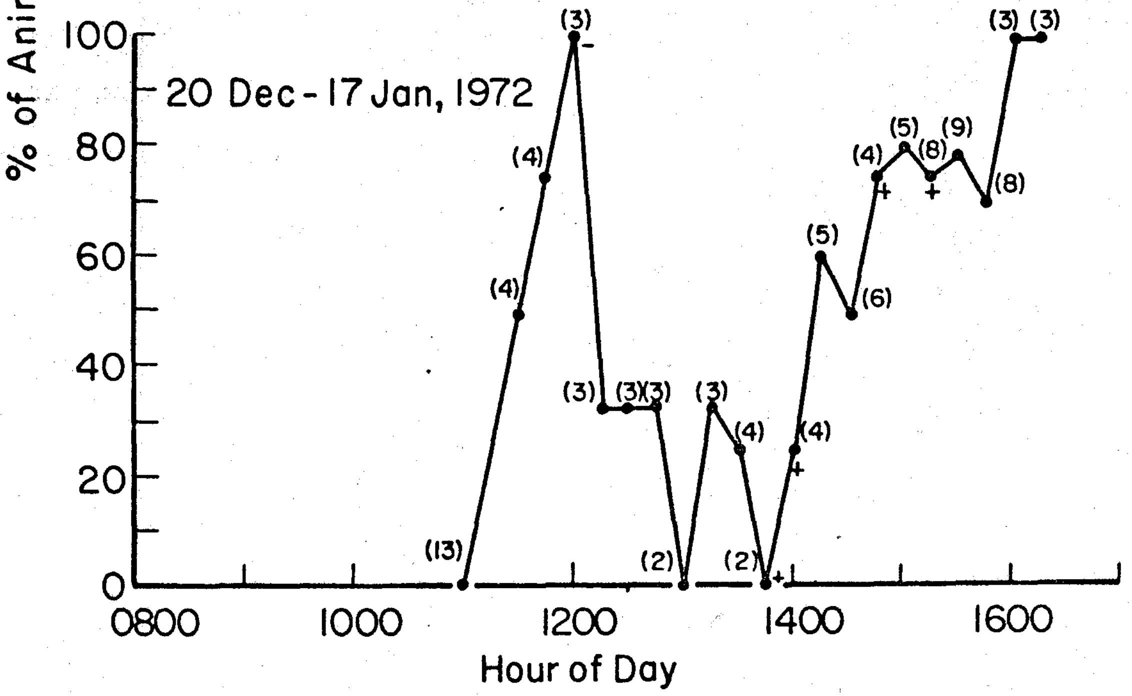


Figure 12

Figures 13-14. The percentage of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). Sightings occurred during the periods indicated. (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. The sample size for each point is given in parentheses. In Figure 13, note peak from 1200-1300 and depression from 1530-1700. In Figure 14, note peak from 1230-1300.

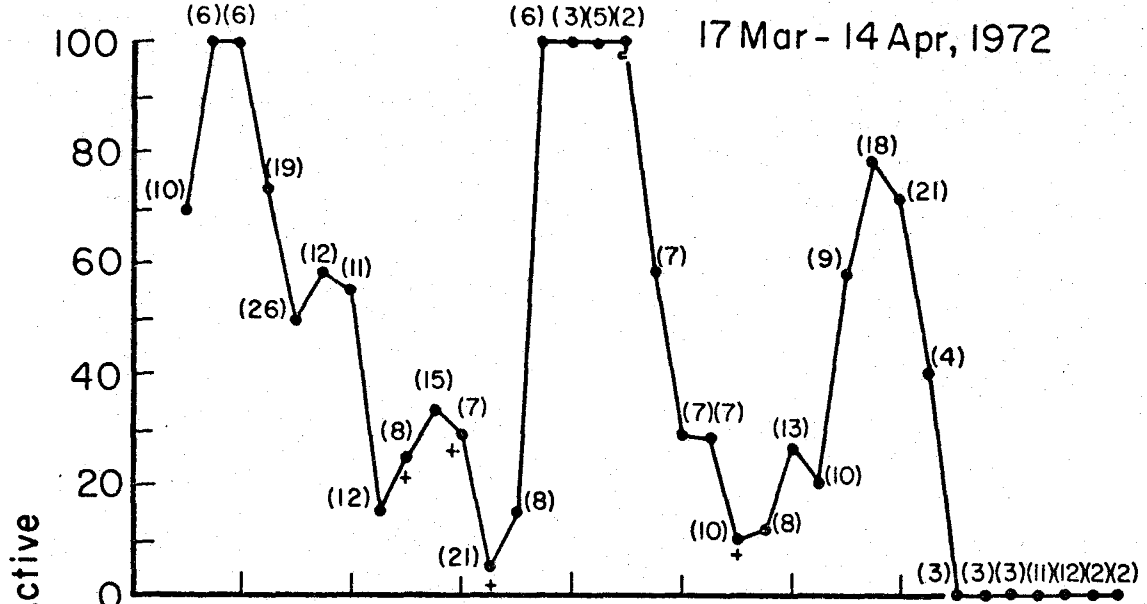


Figure 13

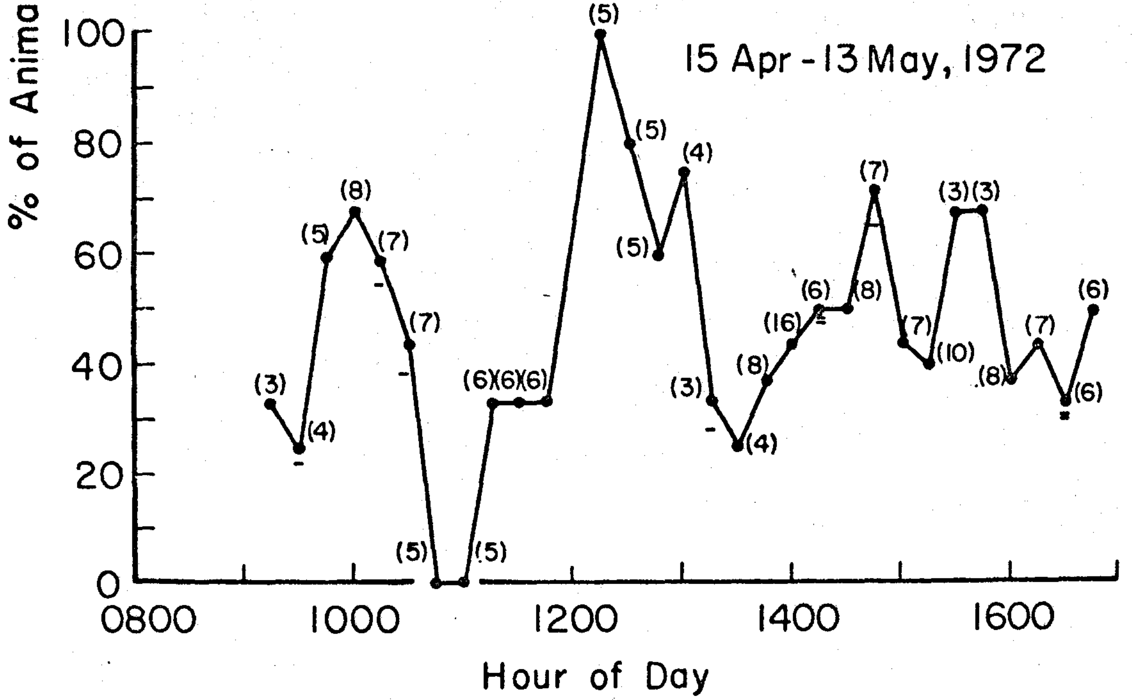


Figure 14

Figures 15-16. The percentage of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). Sightings occurred during the periods indicated. (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. The sample size for each point is given in parentheses. In Figure 15, note peak from 0900-1000 and widely fluctuating values. In Figure 16, note peak from 1530-1630 and intermediate values throughout most of the day.

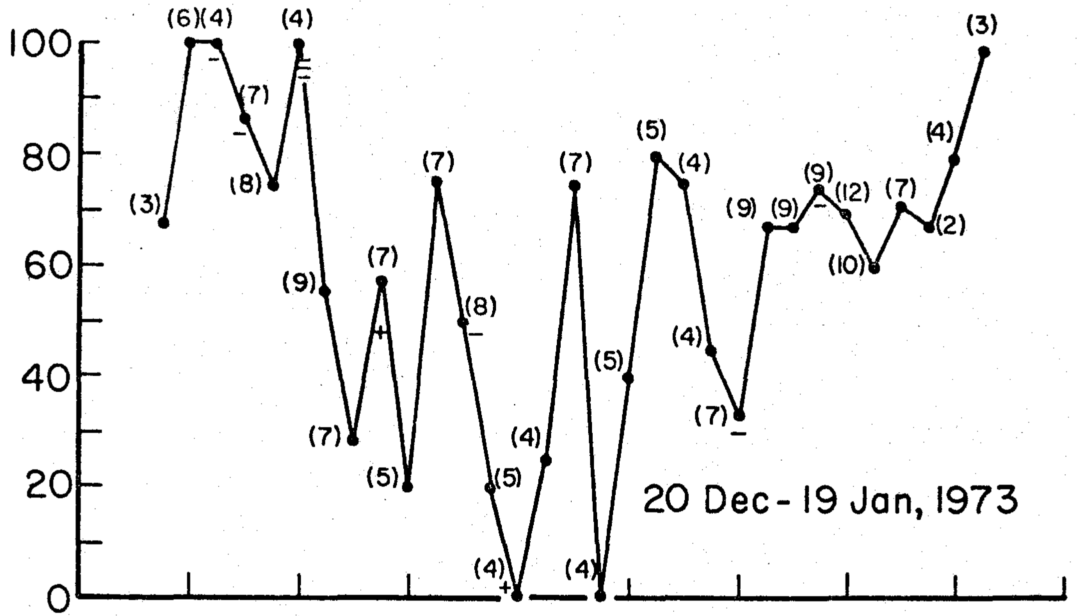


Figure 15

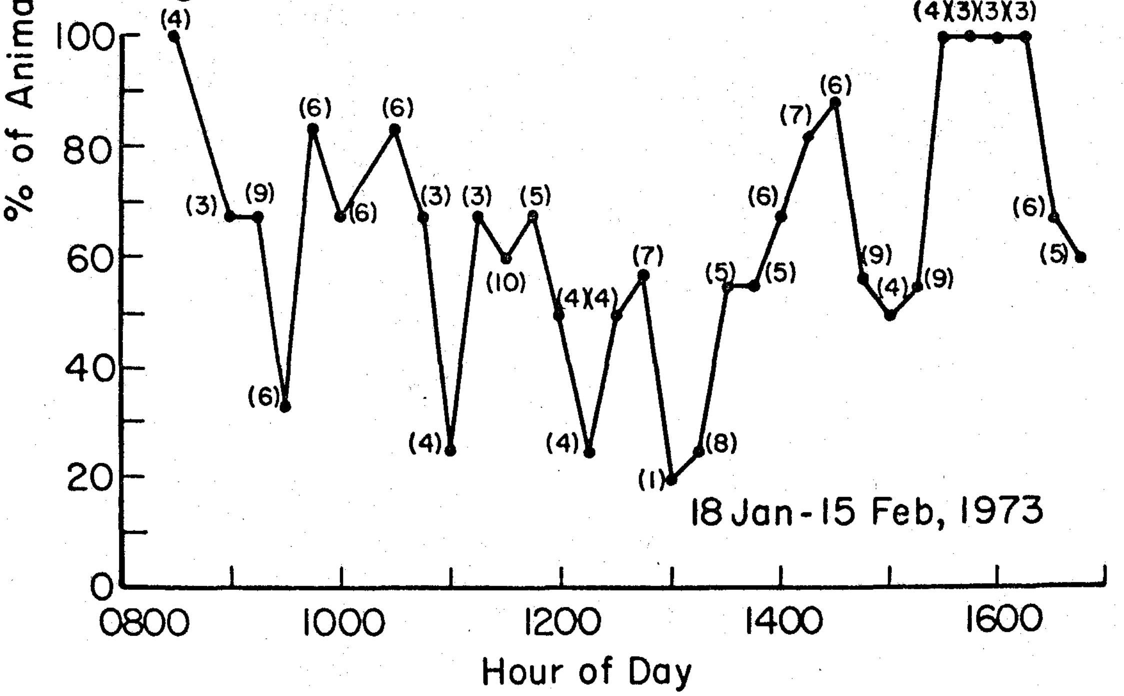


Figure 16

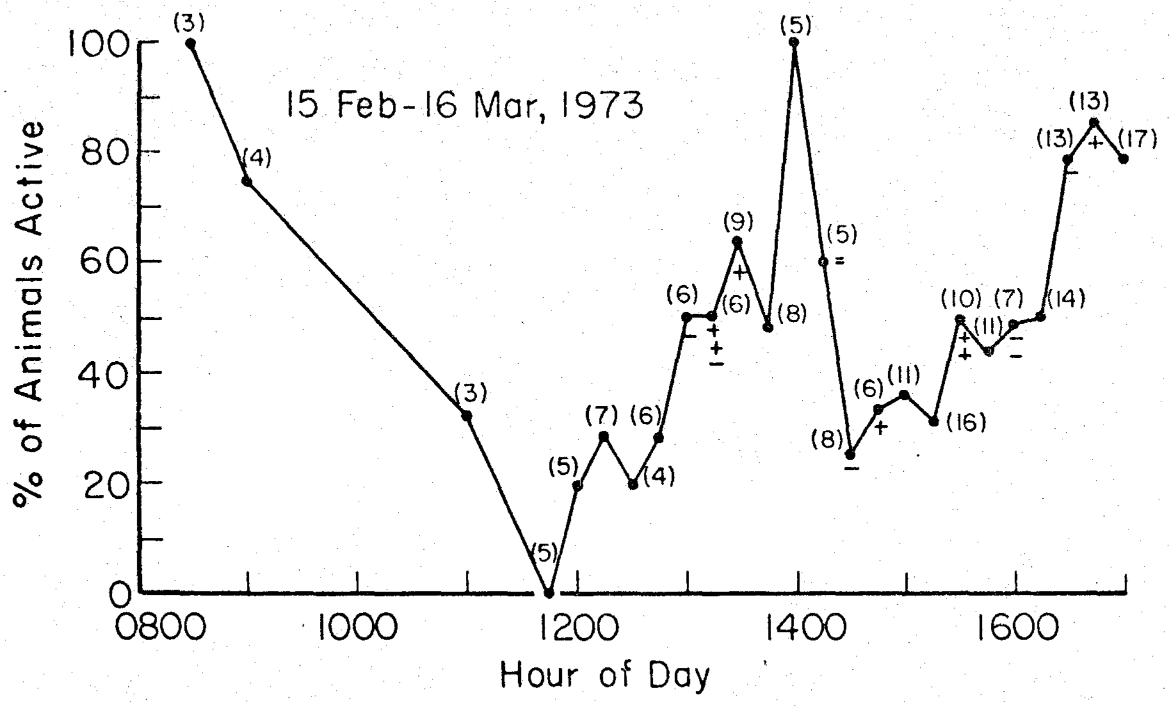


Figure 17. The percentage of animals that were active (i.e., of all animals observed during an interval) is plotted for each 15-minute period (0900-1600). (+) indicates that an animal stood up during the preceding interval; (-) indicates that an animal laid down during the preceding interval. The sample size for each point is given in parentheses. Note peak from 1615-1700 and depression from 1100-1245.

28-day period after the winter solstice during which data was collected. Records from 1971-72 and 1972-73 are included for comparative purposes. A great deal of variability in peaks and minima of activity can be seen.

Daily Movements

Table 4 contains observed movements, the period of time during which the movement occurred, and snow depths at the time of the movement.

Table 4. Records of timed movements by penned moose at the Moose Research Center from January through April, 1975. Snow depths are shown for each recorded movement.

Date	Animal #	Time (hrs.)	Snow Depth (cm.)	Distance Moved (m.)
2/16-17	73	24.75	40-45	390
2/19	79	6.0	40-45	266
2/19-20	79	17.5	40-45	190
2/20-21	79	25.0	40-45	286
2/20-21	40	6.0	40-45	400
2/26	79	24.0	40-50	115
2/26-27	40	24.0	40-50	961
2/27-28	40	24.0	40-50	392
3/7	79	5.5	50	67
3/23	79	7.0	50-55	230
4/12*	36	8.0	50-55	310
4/13	36	8.0	50-55	420
4/18	36	24.0	50-55	545

*Vaccinium emergent

Social behavior

Definitions

Observation of aggregations and associations was complicated by the difficulty of defining each behavior. In one study of moose aggregation, Peek et al. (1974) utilized a definition of "reasonable proximity" in counting aggregations during aerial surveys. Houston (1974) distinguished a single moose as being at least 150 feet away from groups or by exhibiting independent actions or movements . Berg and Phillips (1972) conducted telemetry studies of winter spacing of moose in northeastern Minnesota and defined an "association" as "two or more adult moose which inhabited the same general area and occasionally came in contact with each other.

None of these definitions fit the situation in the WLRA. Rather, the nature of vegetation types crushed provided a definition on the basis of occupation and movement through spaces of aggregation. That is, stands of mature timber were crushed and they became areas where a concentrated food supply was located since moose spent relatively long periods feeding on the bark of downed mature aspen trees. These areas were defined by natural features such as lakes, open space, or uncrushed regrowth stands. Moose were obviously outside the areas defined by these natural features or "in aggregation" by virtue of their presence in the defined area.

I defined an association of moose as a more cohesive group which fed and travelled together in and out of these areas, often staying together for several days. Finally, an interaction was defined as a brief encounter between two or more moose which resulted in behavior by one or more moose that appeared to be in response to the behavior or presence of the other moose (excluding cow-calf pairs).

These definitions are the basis for the following results. The numbered areas where aggregations were observed appear on the map in Figure 3. Table 5 summarizes observed aggregations. These results are not comparable to those of other studies of aggregation because the definition of aggregation was so different. Thus, the range of the number of animals seen in each area of aggregation has been converted into a relative density (per km), so more meaningful comparisons can be made (Table 6). Figure 18 illustrates the dates on which individual moose were observed aerially or from the ground in or near the WLRA. Descriptions of collared moose observed in the WLRA can be found in Appendix E.

My own field notes and those of David Johnson, describing interactions in detail, are on file in the office of the Alaska Cooperative Wildlife Research Unit,

Table 5. Summary of aggregations seen in the Willow Lakes Rehabilitation Area from February through April, 1975. All sightings are ground sightings.

Number Moose in Aggregation	Type of Aggregation	Number of Sightings
2	Cow-calf pairs	9
	Other pairing	6
	Total	15
3	Mixed	7
4	Mixed	6
5-9	Mixed	11
10-15	Mixed	6
16-20	Mixed	0
21-25	Mixed	2

Table 6. Summary of densities observed on areas of aggregation in the Willow Lakes Rehabilitation Area during the period February through April, 1975. See Figure 3 for location of areas.

Area	Area (sq. km.)	Range of relative densities(/sq. km.)	Mean relativ density(/sq. km.)	n
1	0.5	14-24	18	2
2a	4.0	0.25-5	2.6	18
2b	0.5	6-28	9.0	4
3	0.5	4-14	8.0	3
4	0.5	14	7.8	1
5	0.5	9-18	10.8	2
6	0.5	12-30	22	2
7	0.75	12.5	12.5	2

Maximum density = 30/ sq. km.

Mean relative density + 2.57 moose/sq. km.

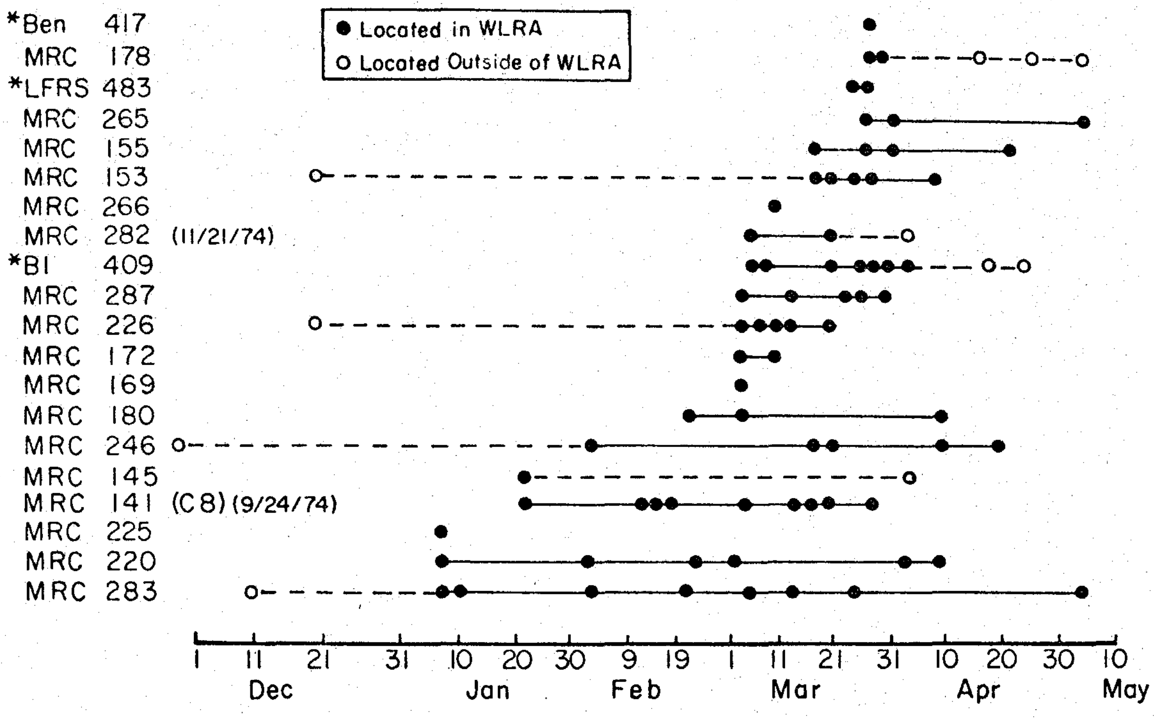


Figure 18. Sightings (aerial and ground) of collared moose in or near the Willow Lakes Rehabilitation Area from 1 December, 1974 through 1 May, 1975. Aerial sightings are by Bob Ritchey, Kenai National Moose Range staff, and Paul Arneson, Alaska Department of Fish and Game. Ground sightings are by Arneson or Sigman.

Fairbanks, Alaska. The observed associations are included in Appendix D.

Cow-calf Behavior

The following is a summary of observed cow-calf behavior during the winter of 1974-75. My field notes and those of David Johnson, detailing cow-calf behavior observed during the winters of 1971-72, 1972-73, and 1974-75, are on file in the office of the Alaska Cooperative Wildlife Research Unit, Fairbanks, Alaska.

Total calf mortality within the pens early in the winter of 1974-75 precluded a long-term study of individual cow-calf pairs. The moose involved in the cow-calf portion of this study are listed in Table 1, along with the approximate time of death of the calves and one cow.

Calf #119 was never observed alive. Cow #79 was observed alone several times between 20 January and 28 January. On 28 January, her calf #117 was radio-tracked and found with her. The pair travelled and fed together for fifteen minutes. Then the calf approached the cow. The cow vocalized and charged the calf. After this display, the cow proceeded to a downed aspen feeding site, and the calf moved off in another direction. The calf was found dead two days later.

Attempts to observe lone calf #116 and cow #R-70-8 were not successful. In early February, only a faint signal from the radio of #116 could be heard and the calf may already have been dead and buried under the snow. Cow

#R-70-8 was located a few times in February, but always in dense regrowth where disturbance and poor visibility precluded long-term observations.

Cow #670 and her calf, both of whom were not radio-collared, were located and observed together three times, including two days (24 January and 25 January) at a downed aspen site. The pair exhibited synchrony in their feeding and bedding activities although the calf moved off to feed alone on two occasions, as did the cow on one occasion. #670 was observed alone on 3 February and several times after this date. The calf was not seen after 25 January, nor was a carcass found.

An uncollared calf, tentatively identified as one orphaned in July, 1974, was seen in Pen 2 on an aerial survey on 24 January (P. Arneson, pers. comm.). I observed the calf on 27 January. The calf appeared to be in poor condition then and exhibited wandering and intermittent browsing on a variety of foods.

Cow #138, a moose collared outside the Pens, was observed with her calf on 16 January and 17 January. The calf's behavior on the latter date indicated that she was in poor condition. The cow moved along the north fenceline of Pen 2 and crossed through a hardwood stand travelling west. The calf moved slowly and was very reluctant to enter the hardwoods. The cow stopped within the stand and vocalized three different times. After five minutes, the cow moved on to another hillside. The calf walked back and forth past the cow's trail through the hardwoods, at one point moving back 100 m in the direction that she had come as if to go around the stand. She finally moved past the cow's trail and entered the hardwoods farther north, 20 minutes after the cow had moved on, the calf laid down in the hardwoods as the cow continued travelling and browsing 300 m away. The calf was not seen again. A well-scavenged carcass was found on the shore of Coyote Lake on 2 February. This carcass was tentatively identified as that of this calf because #138 was sighted near the carcass soon after it was discovered.

Some observations of cows with calves were made in the WLRA. The increase of moose in the area occurred at the same time as MRC calf mortality and aerial sightings of lone calf groups (P. Arneson, pers. comm.). Two of the "outside" cows collared at the MRC in the fall but observed in the WLRA still had calves in late March. MRC #141(C-8) had lost twin calves by mid-February, one MRC cow lost a calf between late December and mid- March, and MRC #220 apparently lost a calf in early March. Seven calf carcasses were found in the area.

Cow-calf pairs were often seen in aggregation with other moose. However, they tended to flee immediately when disturbed by the observer or aerial counts. The cow and calf fled together, unless they were widely separated at the time of the disturbance, and they often fled with other cow-calf pairs. In comparison, approaches to penned calves never resulted in flight; even the response of a calf with a cow was to freeze with its rear to the observer.

Nursing attempts were observed both in the Pens and the rehabilitation area. These attempts followed a disturbance of some kind and were immediately refused by the cow, who moved away several steps. On 24 January, the calf of #670 made such an attempt. Another attempt was seen in the WLRA on 4 March. On 21 March, a cow and calf were browsing about 300 m apart on a hillside above Willow Lake. The calf reacted to my presence first and ran three-quarters of the way across the lake, then stopped. The cow did not move until she saw me five minutes later. She then ran across the lake towards the calf. The two met and the calf appeared disturbed and then made an unsuccessful nursing attempt.

Observations were made in Mount McKinley National Park from 15 May to 15 June, 1975. Four instances of chasing behavior in cow-yearling pairs were seen. On 22 May, a cow was lying down and her male yearling was feeding nearby. The sounds of someone pitching a tent, striking metal against metal, apparently caused the cow to get up and move in the direction of the sound. The yearling approached the cow while she was attending. The cow wheeled and threatened the yearling. This behavior was repeated a few minutes later when the cow threatened and then charged the yearling. On 25 May, a male yearling was observed running to keep up with the cow even though they were obviously feeding and travelling together. The behavior of chasing by the cow and frequent running to keep up by the yearling were observed the next day also.

On 28 May, A cow and female yearling were seen feeding in the same area. The cow charged the yearling and small twin calves followed her. The cow repeatedly charged the yearling, who would run off 20-30 m, stop, and begin to feed. The cow would charge again. This sequence occurred five times until finally, the yearling moved off to a distance of 150 m. The cow approached to within 80 m of the yearling, then both cow and yearling began to feed. The next day, cow, calves, and yearling were seen feeding in the same area, with the yearling approximatedly 20 m from the cow. In response to my approach on both days, the cow moved into cover with the calves and the yearling moved off in another direction.

Measurements of Environmental Factors

Snow Conditions

The derived properties of snow which have most commonly been measured and correlated with moose behavior include depth, temperature, density, and hardness (Coady 1974). Neither snow temperatures nor densities were measured in this study and no values are available for the Kenai Peninsula. Total snow depths were monitored by MRC staff in each of seven different habitats throughout the winters of 1970-75 (LeResche et al. 1973, Franzmann and Arneson 1973, 1974, 1975). Qualitative descriptions of the appearance and consistency of snow within the various layers were noted, e.g., medium granules. Such descriptions were subjective an observers varied in their use of descriptive terms.

Table 7 describes observed effects of measured snow depths on moose in the MRC. Table 8 summarizes the effects of snow conditions on habitat use.

Based on subjective descriptions of snow layer consistency, the typical snow pack could be described very generally as composed of 2-4 distinct layers with increasingly coarse textures toward the base. Snow within

Table 7. Observed effects on moose of measured snow depths at the Moose Research Center, 1971-75.

Effect on moose	Snow Depths (cm)	Source
Calf mortality 1971-72	20-44	Johnson, unpub.
1972-73	30-50	Johnson, unpub.
1974-75	45-55	Personal observations
Beginning of cratering activity	20	LeResche et al. 1974
Detrimental to calves foraging for ground vegetation	50-60	Franzmann and Arneson 1973
Detrimental to adults foraging for ground vegetation	>60	Franzmann and Arneson 1973
Cessation of cratering	50-60	Personal observations

Table 8. Summary of habitat use by moose in relation to snow conditions in the Moose Research Center from January through April, 1975. Days of habitat use refers to the number of days that that moose were observed using the habitat.

	Habitat use (in days) Mature Hardwoods	Regrowth Types	Both
Frequent snowfalls	0	3	1
Melt	16	11	4
Cold - no snow	3	4	2
Total	19	18	7

the pack was sometimes in powder or crystal form, but more often wet and compacted into granules of various sizes or dense lumps. Thin ice crusts (0.3-3.8 cm) sometimes separated the layers that composed the top layer. These descriptions are typical of th snow maturation process described by Klein et al. (1950).

The duration of medium to excessive depths may actually determine the impact of the snow conditions on the population. A method which takes into account both snow depth and duration is that of measuring the total area under the plotted snow depths by a planimeter. The numbers enclosed by the resultant polygons in Figure 19 are the values obtained by this method. The timing of observed calf mortality is also shown.

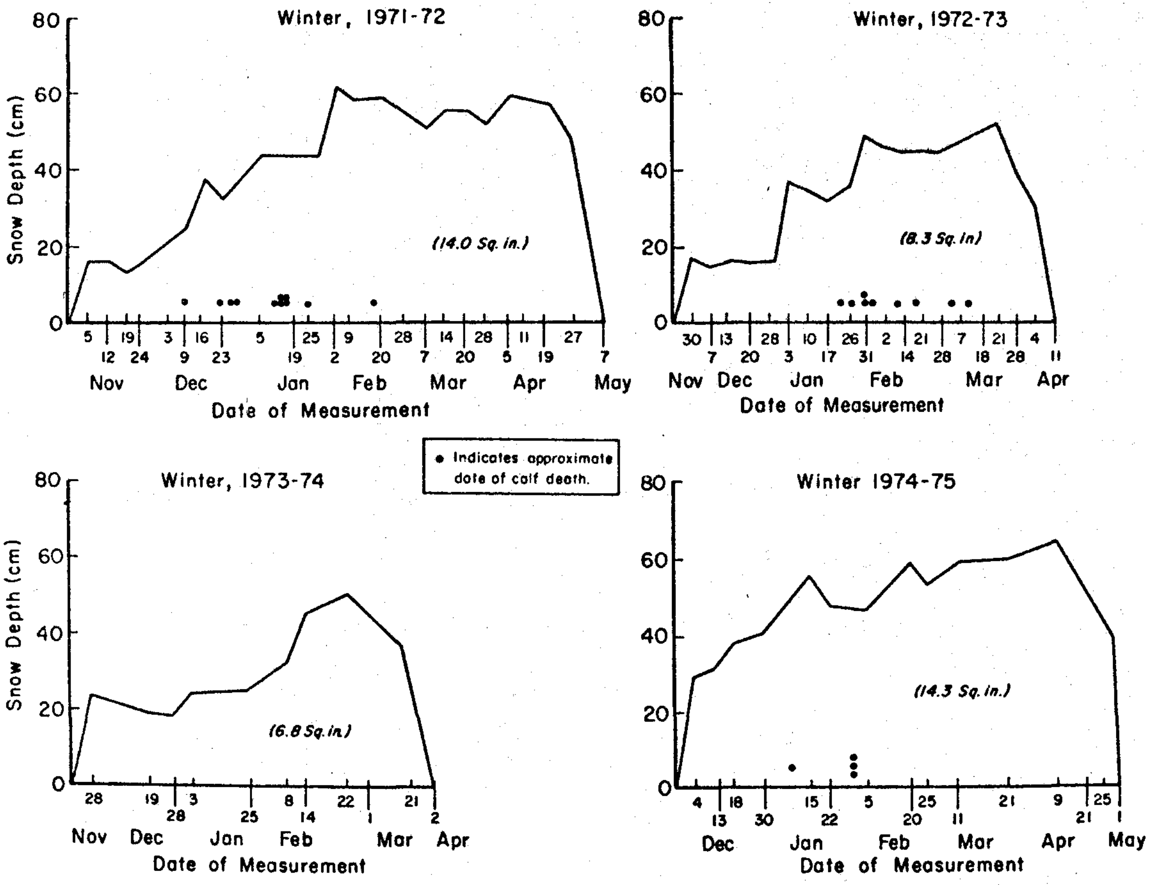


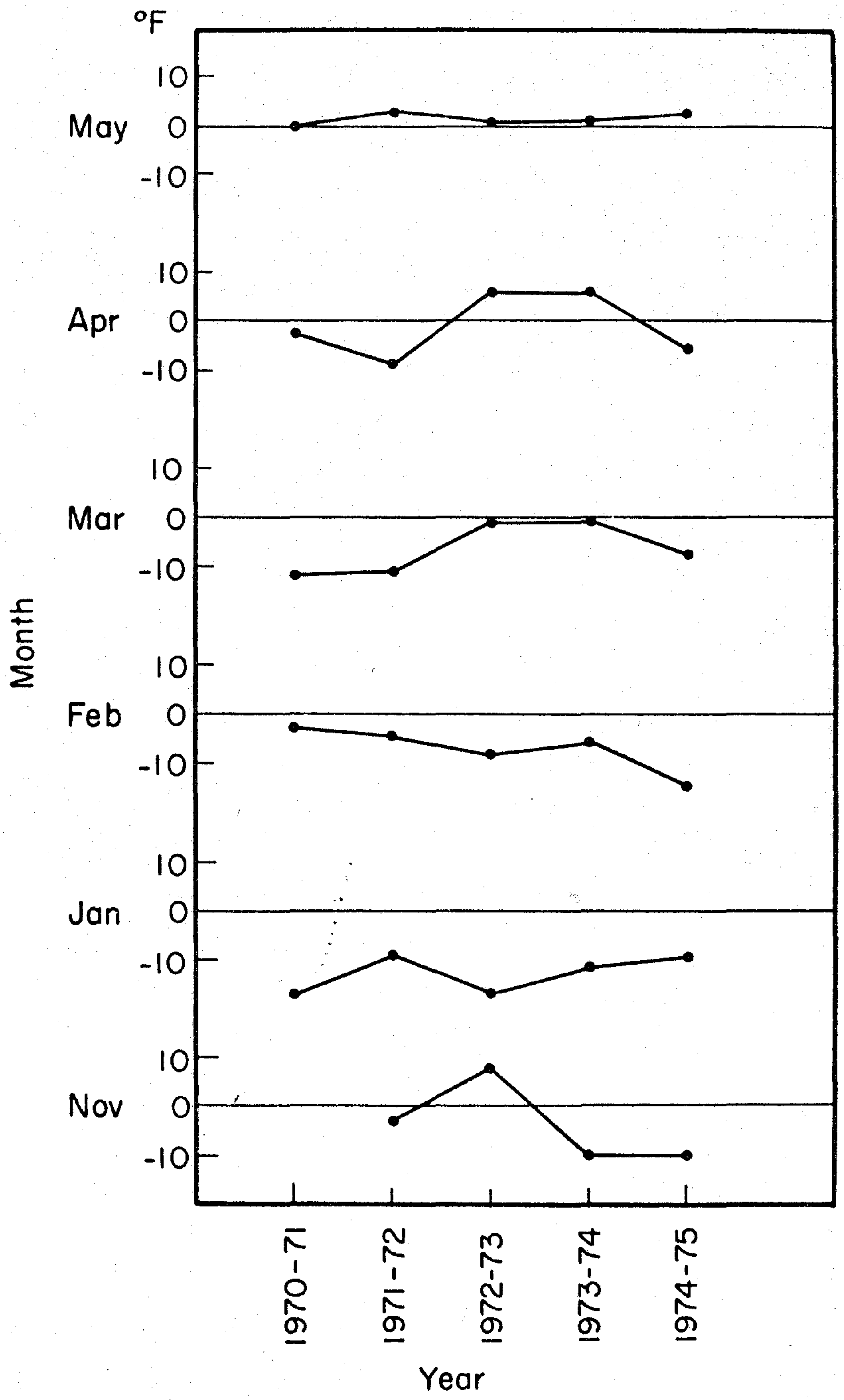
Figure 19. Snow depths measured in thin birch-spruce regrowth habitat at the Moose Research Center from 1972 through 1975 (Adapted from LeResche et al., 1973, Franzmann and Arneson 1973, 1974, 1975). Measurements inside the polygons are the results of planimeter calculations of the enclosed areas and are an indicator of the relative severity of each winter.

Weather Conditions

Temperatures were measured at the MRC once or twice daily, usually in early morning and late afternoon or night. These measurements are not maxima or minima, but at least indicative of the daily range. Official weather stations in the area exist at Kenai airport, Kasilof, and Soldotna. However, only Kenai has reported complete data for the 1971-75 period.

The departure of the mean monthly temperatures from the 10-year averages (1961-1971) for each month are shown for each winter in Figure 20. Kenai temperatures tend to be more moderate than those in the 1947 Burn, but they can be used to indicate general trends.

Figure 20. Departure from 10-year averages (1961-71) of monthly average temperatures at Kenai FAA weather station during the winters 1971-75.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May 0
-10
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Apr 0
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Mar 0
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Feb 0
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10
Jan 0
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10
Nov 0
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Month
1970-71
1971-72
1972-73
1973-74
1974-75
Year

Figure 20.

Predators

Coyotes (*Canis latrans*)

Coyotes are common on the Kenai Peninsula. During the course of my study, I frequently heard singing by two different packs near the Moose Pens. Coyotes could pass through the fences of the Pens easily and I often saw their tracks along trails. In February, they were present in the WLRA, where I heard them singing and observed their tracks on packed surfaces and around moose calf carcasses.

On 13 March, I sighted three coyotes on Portage Lake and on 14 March, I sighted a single coyote 400 m east of Duckling Lake.

Timber wolf (*Canis lupus*)

No wolves were observed in the Pens during the winter of 1974-75, although tracks of a single wolf were seen on Coyote Lake in late April.

On the basis of observations of tracks, wolves were present in the WLRA, although no accurate estimate of the numbers involved is possible. Tracks of packs of wolves were observed after snowfalls throughout late March in various areas where moose had been seen in aggregation. On 18 March, 6-7 sets of very large tracks were observed on

Duckling Lake. The dimensions of the largest set measured 15.2 cm by 11.4 cm. Several calf carcasses were in the same areas as the tracks, but I discovered the carcasses late after the death of the calves so tracks near the carcasses could only be related to scavenging by wolves. Wolf predation as the cause of death could not be inferred in any of the cases.

DISCUSSION

Activity Patterns

From Figure 5, it can be seen that moose were engaged in feeding behavior for 53 percent of the time during which they were observed. Laying down and movement, including travelling and browsing, accounted, respectively, for 44 and 12 percent of observation time. Other activities took up a small portion of observation time. Gaare et al. (1970) reported values of 41-48 percent of time spent grazing, 30-40 percent spent lying, 2-11 percent spent standing, and 9-12 percent spent walking for wild reindeer on winter range. Trotting or running took up less than one percent of observation time. These values were reported for animals on range that the authors characterized as overgrazed. Thomson (1973) pointed out the effect of food quality on different parts of the range in altering the proportion of time spent feeding and moving. Animals on poor range could be expected to spend less time standing or idle. The low percentage of standing and other activities (less than one percent) observed during the winter of 1974-75 may have been influenced by range quality. On the other hand, LeResche and Davis (1971) reported a concentration of feeding activity into the daylight hours during winter, which could have accounted for the reduction of other activities.

No comparable values for mean length of feeding or activity bouts exist in the literature.

Numerous biasses are involved in the methods used to obtain the data presented in Figures 7-17. These include variations in the methods by which moose were located and the usually greater probability of observing an active animal than a lying one. A bias occurred in the MRC Pens depending on whether moose were located by telemetry, snow-tracking, or accidentally. A different type of bias existed for observation in the WLRA. As stated earlier, most observations were made from a blind-type situation. However, the defined "area of aggregation" included the top and part of a hill that was not visible from the blind. To give an estimate of the actual percentage of animals seen of those in the area, the percentage of the maximum number of animals seen per day to the total number of animals in the WLRA (as determined by aerial surveys) ranged from 3 to 48 percent. During the course of observation, many animals disappeared from sight by walking over the hill. Others lay down or were laying down among the large downed trees and were difficult to see. This bias in recorded observations may have been similar from day-to-day, but the graph (Figure 10) probably overestimates the percentage of animals active in each 15-minute interval. The data was lumped regardless of age and sex of the animals observed and divided into 28-day periods, although changes in the light/dark cycle were continuous. The data includes observations in the MRC by two different observers, observations in the Soldotna area (February-March and March-April, 1972), and in the WLRA. Snow and weather conditions varied between years and between areas, but only incomplete records exist for these differences.

The analysis demonstrates certain trends in activity patterns. Bubenik (unpub. ms.) made the distinction between observing an animal's 24-hour program and its diurnal periodicity. The latter would result from long-term (at least 72 hrs) of identifiable individuals in their natural habitat and social situation (e.g. solitary or herded). The analysis of my data may contribute to an understanding of daylight "programs," but diurnal periodicity or its absence can only be inferred by comparisons with reported rhythmic features of moose activity patterns. Even then, as Thomson (1973) stated with respect to wild reindeer populations,

> The strength and combined effect of various influences on Hardangervidda (Norway) determine the particular pattern of activity of the wild reindeer which live there. For a population in a different area, the activity pattern would be similar only insofar as environmental influences afforded similar pressures.

With these qualifications in mind, the following features emerge from the analysis of Figures 7-17:

1) Activity programs include 3-5 peaks and 2-4 depressions of activity during the daylight period.

2) Peaks and depressions are not consistent in frequency or timing of occurrence over the observation periods.

3) Intermediate values (25-75 percent of the animals are active) occur frequently, indicating that synchrony of activity and rest is rare.

The first feature is common to all ruminant animals. Bubenik (unpub. ms.) characterized their general activity pattern as being polyphasic, with 4-11 peaks per day. In addition, the number and duration of peaks was sometimes species-specific. Thomson (1973) reported that the activity of "all ruminant populations in a natural environment" consisted of a long-term 24-hour rhythm which set activity to the time of day and a short-term polycyclic rhythm based on the physiology of feeding. Nighttime activity is also common to many species and a kind of "stupefied" sleep was observed in roe deer by Bubenik (1965). Both Thomson and Bubenik (unpub.) attempted to define the controlling and modifying factors of activity cycles. They agreed that a search for endogenous versus exogenous control was meaningless because no evidence existed that large mammals in the north displayed a periodicity describable as endogenous rather than diurnal (Bubenik unpub. ms.), and because in Thomson's words: "In a natural environment, the question of exogenous or endogenous control is academic because the controlling effect on the activity pattern is identical." The major influence or synchronizer of cycles is light, usually the period of alternation of light and dark. Thomson mentioned factors of individual variations in age and sex, food availability changes, habitat type (open versus forest), weather (temperature, humidity, wind), and other animals, including those of the same species and predators, and those which harassed or disturbed the individual animal. Bubenik focussed upon differences in patterns due to age, month of the year, and weather factors such as air temperature, humidity, wind force, and precipitation. In ruminants, the factors of rumen capacity and turn-over time appears to affect the appetite of the animal. Thus, bulk and quality (digestibility) of food can determine the length of rest periods, just as food availability may determine the length of foraging activity which fills the rumen. All of these factors may affect a wild ruminant population and the activity patterns of individuals.

Generally, the energy balance of the animal determines its nutrient and energy requirements while its condition (good versus poor) determines the efficiency of obtaining and processing food. Although many factors modify the day-to-day activity patterns of an individual, abnormal or stress conditions totally disrupt the pattern. Such disruption is manifest in activity patterns that have surges of activity when depressions might be expected and an increased number of peaks or dislodged and obliterated peaks (Bubenik unpub. ms.).

Researchers have described several winter activity patterns of moose. Geist (1961) indicated that light initiated the first activity peak of the day and that two peaks during the day are caused by an "endogenous feeding rhythm." The evening peak was synchronized by a light-dark change, although the endogenous peak took precedence if it came before or after dusk. Denniston (1956), reporting on a Wyoming moose population, described initiation of a five-hour feeding period one hour before dawn, with feeding periods dispersed throughout the day, separated by two or three rest periods. He also noted pronounced activity at dawn and dusk, as did Peterson (1955). Timofeeva (1967) reviewed two Russian studies which described a significant decrease in moose activity during late morning and mid-day. Between 1000 and 1500, a majority of the animals were resting and 1500-1600 was the peak of afternoon activity. In her own research, Timofeeva found a large number of browsing moose between dawn and 1100. For the remainder of the day, during each hour some moose were seen feeding while others were seen lying. From November to December, moose fed in the dark before dawn and had an activity peak from 0900 to 1000. In times of short daylight (6-7 hours), the extended rest following a morning peak and the evening peak was absent. She reported that moose lay most of the night, but got up to feed several times. Altmann (1956) reported concentrated feeding at night during winter, and Murie (1934) reported that moose were active at all hours, including night. Peterson (1955) felt that moose were more active nocturnally and this might have been supported by the fact that 80 percent of the winter moose kill on the Alaska Railroad occurred at night (Rausch 1959). However, Van Ballenberghe and Peek's (1971) telemetric study of moose movements in northeastern Minnesota found that the average distance of daytime movement was approximately equal to that of nighttime.

The features of moose activity patterns that might be said to be typical include an alternation of rest and activity bouts throughout the 24-hour period, a morning feeding period, and dawn and dusk activity peaks, with a mid-day rest period a less common feature. Thomson stated that moose display a pattern typical of animals occupying forest habitat; a pattern characterized by lying during mid-day and activity at dawn and dusk. The evidences shows that many factors must modify this general pattern.

My own results support a view of great individual variability rather than adding up to a single general pattern. The variation among periods of observation may be due to differences in environmental factors such as food availability and quality, and snow and weather conditions. The peaks of activity in the 1200-1300 period in Figures 13 and 14 are interesting because they contradict the report of Denniston (1956) that the mid-day resting period lengthened as daylength increased. These late-winter observations, where a mid-day resting period was absent rather than long, occurred around the town of Soldotna where moose were often aggregated. The winter of 1972 was severe in terms of snowdepths so increased activity could have resulted from competition for limited food resources. Also, the animals were periodically disturbed by dogs, cats, snow machines, cars, and the observer (Johnson unpub.).

Moose displayed a fairly low level of activity in the winter of 1974-75, considering that 44 percent of all observation time consisted of watching resting moose. Moose #79 was the main animal observed for long periods of time so this pattern could have been particular to her. However, the poor quality of forage could have increased rumination time, thus duration of rest boats. Thomson's results may also explain why results are not those predicted. In his two-year study, reindeer exhibited fixed bouts of activity and rest only in early to mid-winter and not during other seasons. Possibly, species-specific patterns are only expresesed under certain conditions. Finally, the cow may have been exhibiting an overall strategy that resulted in energy conservation under severe winter conditions. Strategies of habitat occupation will be discussed in a later section. The amount of nighttime activity may have compensated for reduced daylight activity, but this amount is not known.

In contrast, the moose in the WLRA exhibited a high level of activity throughout the day. Both active and lying moose were observed during the same periods. Although the actual level of activity was undoubtedly somewhat lower than observed due to the bias of increased sightability of active animals, the continuous use of the food source by large numbers of moose during daylight hours and the low level of synchrony of rest and activity is still evident. This concentrated resource may then have resulted in the expression of an evolved opportunistic behavior to exploit the short-term resource, a behavior that overcame the influence of other environmental factors acting upon the activity pattern. Thomson (1973) stated that the pattern exhibited by species could vary with the nature of the habitat. He cited Geist's (1960) observations of moose in open mountain regions as fitting the pattern of other species in the open: frequent alternation of rest and activity. This flexibility of activity patterns may explain the activity in the WLRA.

In summary, any comparisons to be made on the basis of the analysis of data presented must be qualified. First, sample sizes are fairly small and vary for each interval when observations were made. No trends from early to late winter are consistent from year to year. Most observations of lone calves were not long enough to determine if their patterns differred from those of calves accompanied by cows. However, comparisons with other moose studies do show changes in the number and occurrence of activity peaks and an absence of the distinct patterns reported by other researchers. Either individual variability is greater than such studies have indicated or environmental influences varied irregularly during these observations and masked any endogenous activity pattern. To gain information on individual variability, more long-term observations of individuals are needed. Thompson stated that activity patterns remain stable when the influences of exogenous and endogenous factors remain constant. Conditions may have varied on the Kenai from month to month and year to year in an irregular fashion and the effects of various factors may have varied from individual to individual. Future investigators would do well to measure the magnitude of possible environmental influences while making observations.

Feeding Behavior

The importance of birch browse and ground species, particularly lowbush cranberry, in the diet of moose at the MRC reflects current conditions of the winter range in the 1947 Burn. It is a range deficient in variety. In the winter of 1974-75, aspen bark was also a major food with respect to the amount of time spent feeding upon it. Provision of this food supply was the result of a windstorm and rehabilitation efforts by humans, both fairly irregular agents.

The large percentage of total observation time (25 percent) that moose fed on downed aspen not been noted in previous winters at the MRC. Moose occupying the WLRA also fed on aspen bark for several days in the areas of downed mature vegetation. Aspen bark was obviously an important alternate food during the winter of 1974-75.

Other researchers have noted the favorable effect of windthrown trees on moose habitat (Peterson 1955, Krefting 1974a). The use of mechanical means to provide winter browse was first suggested on the Kenai Peninsula by Culver (1923) who proposed hiring men to chop down birch trees during the severe winter of 1922-23. Kellum (1941) noted that captive moose ate bark from fresh-cut trunks in their pens all winter and that they preferred the bark to other foods in the spring. Russian researchers have also observed the use of aspen bark as food. Kaletsky (1965) observed domesticated calves feeding on aspen bark in late fall. They began eating it in mid-October and fed intensively on it in early November. Timofeeva (1965) stated that moose began regularly to gnaw the bark of aspen trees at the time of spring thaws.

The significance of bark as winter food is complicated by the observed use of both standing and downed trees. Des Meules (1968) and Murie (1934) both cited the use of bark of standing trees as an indication of browse shortage in winter but as a preferred feeding activity in the spring. Peterson (1955) disagreed, noting a small amount of barking of standing trees in late winter and spring in Ontario which he did not consider indicative of food shortage. Timofeeva (1965) indicated that 8-19-year-old stands of deciduous trees were greatly damaged by moose in late winter when many willows and aspens were denuded of bark. The evidence from Isle Royale indicates that extensive barking of standing trees during winter may indicate browse shortages or extremely high moose densities although use of bark from downed trees is an irregular and opportunistic feeding behavior which takes the pressure off of other browse species (Murie 1934, Aldous and Krefting 1946, Krefting 1951, Krefting 1974a). In the MRC, the use of downed trees probably played a similar role. Although a few instances of debarking of standing trees was seen, most edible bark was above the reach of moose.

The observed cratering activities of individual moose in the WLRA does not accurately reflect the cratering activity taking place within the pens, considering the large number of craters seen. Although the reliance on aspen bark as a food source may have resulted in less time spent cratering compared to other winters, the observed cratering probably underestimates the relative importance of the activity in providing winter food. In comparison, Johnson spent 40 percent of his observation time observing cratering in the winter of 1972-73 (Johnson et al. 1973). Much activity may have taken place in early winter when observation periods were few. All signs of fresh cratering ceased around 10 March, when snow depths reached their maximum in the different vegetation types of 40-65 cm.

The overall contribution of ground vegetation to the winter diet is difficult to determine. Several researchers have considered food plants obtained by cratering to be an important component of the winter diet (Seemel in KNMR Narrative Report 1967, LeResche and Davis 1973, Franzmann and Arneson 1973, Johnson et al. 1973). Although it is difficult to tell what the moose is feeding on in a crater, in the winters of 1971-72 and 1972-73, lowbush cranberry has been the plant most often seen in the craters with evidence that plants were actually fed upon (Franzmann and Arneson 1973, Johnson et al. 1973).

LeResche and Davis (1973) stated that the degree of utilization of ground vegetation depended upon snow-determined availability, although lowbush cranberry was available without cratering during the winter that they observed use. During the winter of 1971-72 and 1972-73, lowbush cranberry was obtained by cratering through variable snowdepths (Figure 22). Moose did not begin cratering until the second major snowfall of 1972-73, nuzzling through 15-18 cm before snow depths increased. They cratered throughout the winter (maximum snow depths in the 40-55 cm range), although activity decreased towards the end of winter (Franzmann and Arneson 1973). My own study indicated that "availability" was restricted only at maximum snow depths in the range of 50-60 cm, a limit that may have reflected sensory limitation in detecting the presence of food plants.

LeResche and Davis (1973) summarized the importance of non-browse foods on the Kenai as follows: "non-browse plants not only increase biomass of forage available, but also provide higher protein, ash, carbohydrates, and digestibility levels, as well as enhanced variety." In fact, the use of non-browse food or ground vegetation, especially during mild winters, is thought to be an important element in supporting the high densities of moose wintering in the 1947 Burn which were capable of altering species composition of the range (Bishop and Rausch 1974). Cratering may not provide adequate nutrition during moderate or severe snow conditions.

Until recently, the feeding behavior of cratering was thought to be fairly unique to the conditions on the Kenai. Both Franzmann and Arneson (1974) and Oldemeyer and Seemel (in Franzmann and Arneson 1975) felt the behavior to be indicative of the current poor range conditions. Certainly, little mention of moose pawing through snow for food is contained in the literature. Des Meules (1964) stated:

> Moose do not appear to have learned to use their feet to dig for food beneath or within a layer ofsnow . . . on two instances only have we seen evidence of moose nuzzling through 8-10 inches of soft snow to reach underlying browse.

Markgren (1975) noted the rare behavior that orphan calves displayed by pawing through the snow to obtain dwarf shrubs, mainly Vaccinium myrtilus , Vaccinium vitis-ideae, and Calcuna vulgaris. He thought this feeding behavior to be an inability or slowness on the part of the orphans to switch to winter browse when no adult moose initiated the behavior. However, Kaletsky (1965) in Russia observed a rapid switch-over to a diet of woody browse in early November by calves feeding on their own without any adult to imitate.

As I began to investigate the occurrence of this behavior, several reports emerged from many different areas of Alaska. Cratering has been observed in the Colville River basin for dwarf willow, dwarf birch, and sedges (Renewable Resources Consulting Services Ltd. 1973, E. Mould, pers. obs.), on the Tanana Flats for herbaceous plants (J. Coady, pers. obs.), in Creamer's Fields, Fairbanks, for dead grasses, mainly Agropyron repens (pers. obs.), around Anchorage for ferns (ADFG personnel, pers. obs.), and in the Paxson area (A. Franzmann, pers. obs.). Many of the observers considered the behavior to be common.

What is not known is the impact of deeper snow and various crust conditions of energy expenditure during cratering. Oldemeyer and Seemel (in Franzmann and Arneson 1975) suggested that the energy expended in digging through deep snow might be greater than the nutritive value received. The changes in snow conditions occurring on the Kenai Peninsula will be discussed in later sections.

Earlier studies of feeding behavior confirm the small number of species which make up the bulk of the winter diet. LeResche and Davis (1973) found that feeding by three tame moose in February through May, 1971, differed significantly on the "normal" range of the Pens and the "depleted" range of a portion of the Pens that had been heavily stocked for 18 months. Moose on normal range consumed 72 percent birch stems, 21 percent cranberry, and 3 percent willow, with the remaining 4 percent made up of four species. Those of depleted range consumed 22 percent birch stems, 51 percent cranberry, 23 percent fruticose lichens, 1 percent willow and 4 percent of ten other species. Johnson et al. (1973) observed feeding primarily on birch and ground vegetation in the winters of 1971-72 and 1972-73 but Johnson (unpub.) also noted incidents of feeding upon aspen bark, young birch and aspen plants, alder, grasses, and sedges. Although determination of foods consumed in craters is difficult, Franzmann (unpub.), Arneson (unpub.), and Johnson (unpub.) noted possible feeding on wild rose, Labrador tea, and lichens in craters in addition to cranberry.

Data from analyses of rumen contents of dead animals on the Kenai are available, although such samples are often biassed by the small number of animals used in such studies (Peek 1974) and variability in digestibility and thus ease of identification of dietary components (Bergerud and Russell 1964). These analyses (LeResche and Davis 1971, Cushwa and Coady 1976, Johnson unpub.) support the observations of an increasing reliance on birch browse as a staple, the virtual absence of willow in later years, and the importance of cranberry in the winter diet. Cushwa and

Coady (1976) summarized differences in food habits of moose on the Kenai and in the Interior during the winter of 1971-72; moose at Fairbanks most frequently ate willow, birch, and aspen in decreasing order; but on the Kenai, they most frequently ate birch, aspen, and willow. These differences were attributed primarily to food availability.

The variety of palatable species on the Kenai Penninsula is initially limited by the absence of quantities of willow and a palatable conifer. The major alternative to birch browse, which dominates the winter range, is cranberry, but its availability during winter is greatly affected by snow conditions. Under these conditions, survival through the winter depends on strategic occupation of habitat and opportunistic use of short-term food supplies such as aspen bark. The capacity for opportunistic exploitation of food sources may be an example of the overall opportunistic character of moose behavior. Flexible behavior patterns may be necessary to successfully occupy habitat which changes in quantity and quality.

Daily Movements

Some of the values in Table 4 may be related to specific factors. Cow #40 was observed rarely and may have been moving in an attempt to escape from me, especially when she moved 961 m on 26 February. This movement was almost entirely through spruce regrowth and she fed very little. The distance of 392 m on 27 February may not have been caused by disturbance, but it should be viewed in light of the fact that #40 died a few days after this observation. Wind may have influenced the pattern depicted in the inset on Figure 18, because the movement occurred during a night when heavy winds and drifting of snow occurred. Bull #73 was first seen on 16 February when he arose from a bed when I approached. I saw him the next day in a bed next to the one he had left. This disturbance and return to a former bedding site may have brought about the circular pattern of travel, although he cratered and bedded down several times along the way.

Table 9 summarizes average daily movements found in the literature and the snow depths when the measurements were made. Snow conditions have been cited as a factor influencing daily movements by the authors who reported the snow depths during their studies. Snow depths were in the range of 40-50 cm during most of my observations of daily

Table 9. Literature review of observed mean daily movements by moose during winter. Snow depths and habitat are shown when reported. Sample sizes are noted in parentheses.

Sex or Age	Average Daily Movement (m)	Habitat	Snow Depths (cm)	Source
-	700-900	-	65-70	Semenov-Tian-Sanskij 1948
-	115	-	-	Saino 1955
F	42 (25)	Dense fir-birch	120	Van Ballenberghe and Peek 1971
	267 (6)	Logging road used	"	"
	204	Open fir-birch	"	"
F Yearling	30 (27)	Dense fir	"	"
	175	"	"	"
	286	"	"	"
F and M	400 (18)	Dense aspen-willow	"	Phillips, Berg, and Siniff 1973
F(cow) and calf	510 (26)	-	70-80	Loisa and Pullainen 1968

Table 9, continued.

Sex or Age	Average Daily Movement (m)	Habitat	Snow Depths (cm)	Source
F and M	1600	-	-	Timofeeva 1967
F (cow) and calf	1000 (6)	Cut-over	70-75	"
	(10)	Hardwood-conifer forest	40-65	"

movements, with snow deepest in regrowth habitat where much of the movement took place. The mean distance moved during a 24-hour period (n=5) (disregarding the value of 961 m for the reason mentioned above) is 328 m. This is an intermediate value in the range reported in the literature. One way that movements observed in the MRC were different from those reported in the literature was the use of different habitats in rapid succession in the pens, rather than remaining in one habitat type for several days or weeks. This behavior is probably due to the edge effect characteristic of the 1947 Burn.

Food availability is another factor cited as an important influence on daily movements (Loisa and Pullainen 1968). On 26 February, #79 divided her time between a downed aspen site and a nearby regrowth area. During the winter, she returned several times to the downed aspen site, where several trees were available in a small area. This site could be considered a "high use area" of her home range, a term defined by telemetry studies by Van Ballenberghe and Peek (1971). The availability of bark was related to weather conditions (Table 8). The rapid use of different habitat types made possible by the tremendous edge effect may have made it easier to obtain a variety of foods in a short distance.

Late winter has been reported as a time when travel is limited (Timofeeva 1967, Stevens 1970, Goddard 1970, Van Ballenberghe and Peek 1971). The measurements made in the pens are not sufficient to make a meaningful comparison. However, the increased travel distances in early spring when cranberry became emergent is obvious. The time spent travelling and browsing also increased during this period.

On the basis of my data, it is impossible to determine whether differences in distance moved per 24-hour period might be attributed to snow depths or factors other than the ones already mentioned. Differences that could be related to snow depth would be important because of the relationship of snow conditions to the animal's energy balance. Hopefully, future research will detail the movement patterns of moose in different age and sex categories and monitor the environmental variables that have been suggested as major influences.

In general, it appears that in the 1947 Burn, food availability is usually greater in regrowth areas, although supplies of downed aspen and higher mean percent cover of cranberry can increase the use of mature hardwood habitat when snow depths increase in the regrowth areas. Both habitats have some of the deepest snow of any of the seven habitat types in the MRC.

The use of trails by moose has not often been observed, even with deep snow. Johnson (unpub.) observed a well-packed trail system in the Big River Valley, west side of Cook Inlet, in early March, 1972. Snow depths were considerably deeper (173-183 cm) than the maximum measured at the MRC for the entire winter. Johnson observed a group of 33 moose walking single file down one of their trails, which was packed to a depth 1.8 m below the surface of surrounding snow. This area had high mortality during this winter but a large proportion of the animals surviving were calves (ADFG 1972). According to Mattfeld (1974), trails can greatly decrease the energy expenditure per individual for an equal increment of energy acquired by feeding activity.

On one occasion in the WLRA, I observed a bull following in the footsteps of a cow as they crossed a windswept lake covered by hard-packed snow. But for the most part, no trail-making behavior was observed on the Kenai Peninsula.

Social Behavior

Aggregations and Associations

Aggregations, as defined under results, were observed from January through April, 1975, in the WLRA. Because the definition of aggregation differs considerably from those used by other observers, the sizes of observed aggregations are not directly comparable. However, the frequency of observation of aggregations of various sizes in other areas of moose winter range may put the situation in perspective.

Aggregation size in winter in various areas in Russia were reported by Timofeeva (1967) to range from 7-12 rarely in one area and from 11-15 in another area. In her own studies in the Leningrad oblast, 92 percent of all sightings were of solitary moose or of a group of two which was invariably a cow and calf. In the entire oblast of Leningrad, 90.5 percent of all moose sightings were of one moose or of groups of two to four. The maximum group size reported in Russia was 18 (Nasimovitch 1955). Timofeeva reported increased aggregation size in late winter, and related small group size to a low density population and a relatively mild winter.

Houston (1974) reported that observations during the period 1963-69 in Teton National Park, Wyoming resulted in 58 percent single moose, 26 percent groups of two moose and

16 percent groups of three or more moose. Females with calves were the most solitary during all periods. He stated that moose showed preferences for certain areas rather than attachment to a group.

Peek et al. (1974) compared aggregating behavior in three sub-species of moose by the method of extensive aerial surveys. As noted earlier, the definition that they utilized was one of "reasonable proximity." They reported a mean aggregation size of 1.41 for March in below timberline habitat on the Kenai Peninsula. Based on their results, they assigned tendencies to aggregate to different segments of the Kenai moose population at different times of the year. The population as a whole tended to aggregate in March and April, and cows tended to aggregate in all months except February and March. Cows with calves showed a lesser tendency to aggregate than did lone cows in all months. Bulls associated with cows more frequently than with other bulls during winter, possibly due to the disparate sex ratio.

Although these observed tendencies to aggregate may have played a part in the occupation of the WLRA throughout the winter, the situation was a highly unusual one in terms of the densities reached and maintained by the small area. No selection for sex or age segment of the population was evident.

Based on semi-monthly aerial counts of the entire crushed area, densities ranged from 1.0 to 9.2 moose per square kilometer (KNMR files). The relative densities on areas of aggregation (Table 6) ranged from 0.25 to 30 moose per square kilometer. Peterson (1955) reviewed moose densities on winter range in North America. He cited three conditions which would give rise to abnormally high concentration: artificial or natural isolation where dispersal was impossible, such as an island; enforced seasonal concentrations on restricted winter range, such as that in mountain regions; and temporary responses to particularly favorable habitats, such as a salt lick. Under the second condition, he reported a value of 15 moose per square kilometer. Coady (1974) cited values of 10 moose per square kilometer in Montana and 19 per square kilometer in Jackson Hole, Wyoming. The densities reached in the WLRA, as well as the size of aggregations, were obviously much greater than under any other set of conditions reported in the literature.

The concentrated food supply was the main factor responsible for the observed densities. Aggregations ranging from 2-12 were common in the Soldotna area in March and April in areas where willow and birch browse were concentrated (Johnson, unpub.). Other researchers have observed aggregations occurring where preferred browse is clumped, on the North Slope of the Brooks range where groups of 6-12 moose often occur in willow stands (Renewable Res. Services Ltd. 1973) and in deer yards (Mattfeld 1974). Peek et al. (1974) concluded that aggregations from the middle of winter through spring were primarily related to extrinsic factors of forage location and cover. Since cover was negligible in the area where the food source was located, it appears safe to conclude that the aggregations were related to the short-term, concentrated and abundant food supply on a range where food availability and quality was generally low.

This study points out the problem of defining aggregating behavior in a mostly asocial species. Future research might include winter surveys of newly-burned areas and areas where habitat rehabilitation is being attempted to gain information on how moose occupy such "new" habitat singly or in groups.

LeResche (1974) argued that range extension was a rare phenomenon in moose and attributed the 400 percent increase tht occurred in the wintering population in the 1947 Burn within four years to reproduction by resident moose. However, data from the occupation of the WLRA indicate that redistribution on the wintering grounds can occur, that is, a large number of moose in a usually low-density population could heavily utilize a small area of optimal winter range.

This phenomenon again illustrates the opportunistic nature of moose behavior. Figure 18 illustrates that individuals stayed a variable length of time from a few days to several months. Numbers of moose in the total area increased steadily, so there must have been considerable turn-over of individuals. Based on trap records and aerial sightings of collared moose, the movement of some of the moose into the WLRA may have been part of a general westward movement through the area of the MRC. Yet, it seems that theories about how moose typically distribute themselves on winter range cannot adequately explain the initial movement and persistence of many cows, bulls, and lone calves into this area, although the picture of seasonal moose movements on the Kenai Peninsula is far from complete. Perhaps range and snow conditions on the Kenai in the early 70's brought about increased searching behavior by individuals and dispersal from traditional winter home ranges.

The associations observed in the WLRA are of interest. While having no ostensible social purpose in late winter, the group may have served as th psychological replacement for vegetative cover (Crook 1970). These associations are an approximation to a true social unit as defined as involving interactions beteen members (Etkin 1964). However, the sightings of individuals both in association and alone indicates that the group was fairly loose-knit.

Interactions

Interactions between individual moose must be viewed in light of the usual low probability of moose even meeting on winter range. The MRC, the WLRA, and the town of Soldotna each represent a certain set of conditions that increased this low probablility. Obviously, confinement results in a greater overlap of home ranges and more meetings in the pens. Many interactions were observed within a short period in the Soldotna area in 1972 (Johnson, pers. obs.), but this was probably a particularly stressful situation. Moose had come into an area with a fairly concentrated human population in response to harsh winter conditions and browse shortages. Most interactions took place when some identifiable disturbing factor was present so they could not be considered defense of territory or competition for food. The special conditions in the WLRA have already been described.

More interactions were observed in the pens than in the WLRA in 1975, even though many more moose were observed in the latter area and in high densities. In fact, more interactions were observed in the Soldotna area in 1972 than in the WLRA. These differences may be related to the nature of the short-term and evolutionary relationships of moose to their food supplies. In the short term, a downed aspen in the pens represented a concentrated food supply in a situation where overall food supply was low. This same relationship held true for willow clumps in the Soldotna area in late winter, but to a lesser extent since winter range was not limited by fences. Also, willow and birch browse was more dispersed than downed trees. But in both cases, agressive displays paid off in terms of feeding sites or dominance demonstrated. On the other hand, although downed aspens were the main food resource in the WLRA, the total area constituted an abundant food supply for many moose for a relatively long period. The few interactions may heve resulted from one individual violating another's "personal space," the limit to which the presence of any other animal is tolerated.

Geist (1974a) explored the question of the amount of competition for food that could be expected in a species that had evolved in the type of habitat that moose traditionally occupy. He stated that

> dispersed and diffused food of low density per unit area will lead to a selection against food competition by overt agression, as will highly localized food resources found at high density; overt agression will be selected for as a means of intra-specific competition where it will result in a significant return in food in short supply, compared to the cost of defending it.

Therefore, the best strategy of competition with widespread, diffuse supplies is to feed more intensely and save energy for growth and reproduction.

> Conversely, when food is localized and super-abundant, there will be selection against agression . . . The cost of defense now becomes prohibitively high and it becomes more adaptive to feed as much as possible (increasing rate of food intake) rather than wasting time and resources fighting.

These two possibilities cover most of the situations that moose would encounter. Therefore, neither the past situation of declining range quality nor the situation of abundance in the WLRA should result in displays of overt agression for food.

These evolutionary pressures are evident in the form that agression typically took. Displays were very brief and consisted of threats and short charges on the part of the agressor and short movements by the animal displaced, usually not to the extent of leaving the food source. Even in the high concentrations observed, individual moose usually seemed oblivious to the presence or movements of others. The exceptions to this were cows with calves and the associations already discussed. Several times, one moose would alert to my presence and flee, running past many other moose without any of them ceasing to feed. On two occasions, repeated low passes by an airplane caused many of the moose to flee a variable distance, but others did not even rise from lying positions. Although concentrations of moose repeatedly occurred in different parts of the crushed area, these aggregations appeared to be the result of individual movements. The behavior of moose in the areas of aggregation was similar to that observed by Peterson (1955) by moose using a salt lick during the summer. He described moose who "treated each other with tolerance and indifference and usually entered and departed wholly independently of other individuals."

Cow-calf Behavior

Although only one case of cow-calf separation was observed in the winter of 1974-75, evidence has been accumulating since 1971 that intermittent or permanent separation of cow-calf pairs has been rather common. During the winter of 1971-72, Johnson conducted a study at the MRC involving the creation of "orphans" by trapping cows and calves from outside the enclosures and placing the calves into Pen 4. He then made observations on orphans and calves with mothers. During the winter of 1972-73, he also made observations on cows and calves, although he did not create any orphans. Both years, calf mortality was 100 percent within the pens. One cow-calf pair definitely became separated during the first winter for a period of 21-64 days prior to the calf's death (LeResche et al. 1973). During the second winter, five calves were seen alone intermittently and finally permanently for a period ranging from five days to one month before death (Johnson et al. 1973). In a final report on the project, LeResche et al. (1974) concluded:

> cow-calf pairs separated naturally during harsh winters. Separations were usually permanent , but sometimes intermittent, and possibly a majority of non-orphan calves separated from their mothers before dying.

More evidence is provided by the incidence of lone calf sightings that have occurred each winter at the same time that calf mortality was occurring in the pens. Most of these reports have not been compiled, so no quantitative estimate is possible. However, the number of sightings have been substantial during the winters of 1971-72, 1972-73, and 1974-75 (P. Arneson, J. Davis, A. Franzmann, and R. LeResche, pers. comm.). Johnson et al. (1973) thought that the number of lone calves in winter was much greater than could be accounted for by loss of cows due to hunting.

No survey information on the occurrence of lone calves in late winter in other areas of Alaska is available for several reasons. Many fall surveys include a small number of lone calves, but fall composition counts and spring parturition counts are usually the only type of survey flown in each area (Bishop and Rausch 1974). Late winter or early spring survival counts are only flown if the winter is already suspected to be one in which a high winter kill occurred. Such counts were flown in Game Management Units 15A and 15B in 1972 and 1973 (Appendix A), but only after low calf numbers were noted. The counts were conducted well after the time that winter kill was an obvious fact, and lone calves may already have died. A review of Survey/Inventory reports published by the Alaska Department of Fish and Game for the years 1970-75 contains only one reference to a high incidence of lone calves in a spring survey conducted in May, 1968, in the area of Yakutat (ADFG 1972). Snow conditions were considered severe in the winter of 1967-68 and 16 lone calves were seen in 416 total moose counted. The reliability of aerial counts in assessing the incidence of lone calves might be questioned, however. Coady (unpub.), working with radio-collared animals during winter surveys on the Tanana Flats, recorded several instances when cows were seen aerially without their calves and later seen with them. Lone calf sightings may not always mean that a separation of cow and calf has occurred although most of those made on the ground by Johnson were of the cow and calf in distinctly different areas.

As has been noted, movement into the WLRA occurred at the same time as calf mortality within the pens. An aerial survey on 25 January by Arneson (ADFG files) identified a group of three lone calves in a small area near the MRC.

The literature contains variable information about the time that suckling is terminated. The observed late-winter suckling attempts may not have been unusual, although all were terminated abruptly which indicates that the cow was not lactating. Johnson et al. reported a successful brief (15 sec.) nursing attempt on 5 January, 1972. Given the circumstances of suckling attempts that I observed, the response was possibly one to the stress being imposed on the calf by my presence and not a genuine attempt to nurse.

The cow's rejection was probably based on her lack of milk, but the response by different cows to the close approach of their calves was highly variable and may have been a good indicator of the status of the bond between cow and calf.

The observations made in Mount McKinley National Park of cows and yearlings should be those of the natural break-up of the bond at the time of parturition. When agression was shown towards a yearling by a cow with calves, it was repeated several times with little effect on the permanent separation of the yearling. This behavior indicates to me that a bond still existed on the yearling's part in its continued following of the cow in feeding and movement. This reluctance of the yearling to leave the cow was noted by several other workers (Murie 1934, Altmann 1958). On the other hand, parturient cows and the one observed late in the season which did not calve displayed a lack of tolerance to their yearlings when approached closely while feeding or when disturbed. This behavior would indicate a weakening bond on the part of the cow, eventually becoming an intolerance at greater distances. The agression shown to the male yearling which had six-inch antler spikes may have been a response to another moose whose appearance was changing rapidly from that of the calf that had elicited caretaking behavior. This decreasing recognition of young is a factor common to the breakdown of maternal bonds in other species (Harper 1960). A similar mechanism may be at work on the Kenai where for reasons that will be discussed in detail later, calves may be smaller and weaker than normal. As the calves become weaker an approach death, the cow probably "recognizes" or feels less "bonded" to the calf that is following her. Certainly, the behavior of cow #79 towards her calf was not similar to that of cows and yearlings observed near or after parturition. The singular display and response of the calf to leave the area was similar to that of moose observed during interactions over food, although adult moose, when threatened or charged, usually only moved a few moose-lengths away from the agressor. I would conclude that no bond existed between cow #79 and her calf. This may also have been true for the separations observed by Johnson.

Environmental Factors

Snow Conditions

Table 10 summarizes observed effects on moose at increasing snow depths. When these values are compared to Table 7 and Figure 19, it can be seen that calf mortality occurred at depths considerably lower than those reported to have significant negative effects on moose populations. Bishop and Rausch (1974) also concluded that winter mortality on the Kenai Peninsula commenced at lower snow depths and/or after shorter durations of snow than in the Interior.

Increased snow depths on the Kenai in the winters of 1970-75 appear to be one of the changes in conditions concurrent with the decline of the moose population. Bishop and Rausch (1974) earlier characterized Kenai Peninsula winters as characteristically mild in terms of snow depth and duration compared to other areas of Alaska. Cushwa and Coady (1976) contrasted the Kenai with the Interior, citing snow depths of 40 cm for short periods of time and rare depths of 60 cm. The snow depths measured in the MRC in the winter of 1971-72, 1972-73, and 1974-75 are considerably higher than those described by these other authors. One of the most notable differences is the persistence of the snow cover which kept the ground vegetation covered completely,

Table 10. Literature review of effects of observed snow depths on moose.

Snow Depths (cm)	Effect on moose	Source
<30	Initiates downward migration	Kelsall 1969
30-40		
40-50	No effect	Nasimovitch 1955
	Movement restricted - 44 cm	Kelsall 1969
50-60	Movement to heavy cover	Phillips et al. 1973
60-70	Sufficient for bedding 61-100 cm	Des Meules 1964
	Movement definitely impeded	Nasimovitch 1955
	Calves follow in trail of adult	Ritcey 1967
	Restricted mobility	Prescott 1968

Table 10, continued.

Snow Depths (cm)	Effect on moose	Source
70-80	Increased use of conifer cover	Des Meules 1964, Telfer 1967
	Movement restricted	Kelsall and Prescott 1971
	Critical if long-lasting	
	Increase in percentage of calves in wolf kill - 76 cm	Peterson 1974
80-90	Movement severely restricted	Kelsall 1969
	Yarding behavior	Kelsall and Prescott 1971
90-100	Movement hindered	Telfer 1967
	Substantial winter mortality if several months duration	Coady 1973
	Critical - winter mortality substantially increases	Nasimovitch 1955
>100	Confinement to small areas	Kelsall and Prescott 1971
	Critical for moose unless of short duration	Kelsall 1969

in contrast to the thaw periods in 1970-71 and 1973-74 (MRC files).

Little data is available on the parameters of the snowpack that are related to support capacity. However, in his review of snow and moose behavior, Coady (1974) concluded: "throughout most of the circumboreal range of moose and within favorable habitat, snow conditions that provide support are apparently seldom extensive or persistent enough to significantly benefit moose." Kelsall and Prescott (1971) agreed and observed that litle effect was seen upon moose walking through snow when sinking depths were in the range of 20-35 cm.

Considering observed sinking depths of man in the snow pack and subjective descriptions of crusts in the MRC, crust conditions were probably rarely beneficial to moose and often exerted a neutral effect on movement most of the time during the four winters. However, the granular layer of snow nearest the ground which increased in thickness as winter progressed may have caused more caving in of craters, requiring more effort (Franzmann and Arneson 1973).

Although snow depths and persistence of cover may have increased during the 1971-75 period, the depths reached were still moderate, compared to other areas of Alaska. Importantly, winter mortality was more selective for calves on the Kenai than in other areas of Alaska (Bishop and Rausch 1974). Based on measurements around carcasses in the MRC, calves died in depths similar to those in nearby regrowth habitat (Johnson unpub.). Johnson (Johnson et al. 1973) concluded that snow depths of eighteen inches (45.7 cm) were sufficient to cause calf mortality at the MRC. Most deaths occurred after the first build-up of snow of the winter. This high calf mortality after the first build-up of snow indicates an apparent vulnerability to stress and rapid weight loss. Some factors that may have contributed to the poor condition of the calves early in the winter will be discussed in a final section.

Certainly the effects of snow depth is related to range. An explanation that Bishop and Rausch advanced was that the earlier mild winters had supported very high moose populations in the 1947 Burn encouraging a persistence of densities capable of altering plant composition by eliminating willows and aspen on the winter range. The importance of non-browse, i.e. low-growing plants, has already been discussed. LeResche et al. (1974) cited snow over non-browse forage as the probable cause for the nearly total calf mortality on the Kenai lowlands during some winters.

Weather Conditions

"Weather" is a term that covers many environmental variables that impact on wild animal populations. Air temperature is one of the most easily measured, but one that varies to the extent of constituting micro-climates in areas differing by a few inches of elevation. The effect of this variable and general pattern over the winter period depends on the thermoregulatory capabilities of the species and the existence of behavioral adaptations to extreme conditions. The actual capability of moose to thermoregulate has never been measured but Gasaway and Coady (1974) indicate that the lack of obvious behavioral adaptations such as restricted movements and postures that reduce the surface area exposed to the air during periods of extreme cold (-50 F.) mean that thermoregulatory metabolism is a negligible cost in the overall energy budget of moose. They commonly encounter low temperatures on winter range in Alaska.

A calf would have a disadvantage in extreme cold because it has a higher surface area to volume ratio than an adult and loses more heat per unit of weight to the environment. Calves are probably able to thermoregulate at adult capacity going into the winter; infant caribou are metabolically mature at nine weeks (Hart et al. 1961).

Little is known about the relative abilities of adults and calves to cope with extreme cold temperatures.

From Figure 20, it appears that January was considerably colder during all years. February was colder for four of the years. March was colder for three, April was colder for two, while December and May mean temperatures were fairly constant or slightly warmer than 10-year averages.

Wind has also been cited as affecting winter activity patterns (Bubenik unpub. ms., Thomson 1973). Twice, in the winter of 1975, moose appeared alarmed and terminated lying periods abruptly when strong winds were blowing and trees were creaking loudly. The indirect effect of wind storms in providing browse and affecting distribution on specific habitats have already been discussed.

Obviously, all the factors of temperature, humidity, cloud cover, snowfall, and wind interact in patterns that determine the relative "severity" of the winter and its impact on calf survival. Verme and Ozoga (1971) attempted to define the influence of winter weather on white-tailed deer and concluded that animals were able to stand intense mid-winter severity if it was of relatively short duration. Extensive mortality, rather, was due to a prolonged siege of environmental stress, with heavy snowfall and bitter cold weather as equally limiting factors on deer welfare.

These two variables may not have equal effects on moose because deer are much smaller and may have a narrower zone of thermoneutrality.

The known calf deaths in the pens in 1975 occurred after a cold spell with below-zero temperatures. Johnson (unpub.) noted that cold weather followed by wet, warm weather seemed to have a bad effect on calves. Perhaps as calves weakened, their ability to adapt to different conditions lessened. At any rate, weather conditions were most likely not the primary cause of calf deaths but may have affected the timing and extent of both calf and adult mortality.

Predators

Coyotes

Coyotes are commonly associated with moose in the greater part of moose range, but generally not considered an effective predator. Hatter (1945) recorded a low percentage of moose calf remains in summer scats of coyotes which he thought resulted from coyotes consuming carrion or an occasional newborn calf that had been hidden and left by the cow. Krefting (1974a) describes the abundance of coyotes on Isle Royale, but neither he nor Peterson (1955) considered the coyote to be an effective predator. In the case of Isle Royale, the coyote population decline was concurrent with the build-up of wolves, possibly as a result of competition in scavenging.

Wolves

Wolves apparently completely disappeared in the early 1900's on the Kenai Peninsula (Bishop and Rausch 1974). Incidental sightings occurred in the 1960's (B. Ritchey, pers. comm.), but the first substantiated sightings occurred in 1968. Wolf numbers evidently built up rapidly. LeRoux (1974) surveyed tracks of 61-76 wolves in 1974. Due to the difficulty of distinguishing tracks except in open areas, he thought the figures were a minimal estimate. His final estimate was that 75-100 wolves occupied the entire Kenai Peninsula. Conservative estimates in early 1976 placed the numbers in the 60-70 range (B. Ritchey, A. Franzmann, pers. comms.).

Franzmann and Arneson (1976) compared marrow-fat values of wolf-killed calves and adults to those of calves and adults dying of other causes in the MRC and areas of the Kenai Peninsula. Marrow fat values from calves killed were significantly different from those of calves dying accidentally; however, the values were significantly higher than those of suspected winter-killed calves. In other words, wolves were not selective for calves with very low marrow fat values that may have been close to death from starvation.

The timber wolf is considered by Peterson to be the "most serious natural predator" of moose, although he considered the overall effect of the wolf on moose populations to be a controversial one. Pimlott (1967) thought that the association of moose and wolves was long-term and that the two species co-evolved. He theorized that ungulates and predators, particularly moose and wolves, evolved together in a relatively stable environment and that because wolves were always present as effective predators, there was no pressure on ungulates to evolve mechanisms of self-regulation of their population numbers.

Several studies appeared to confirm the role of the wolf as regulator of abundance and vigor of the moose population. The selectivity by wolves for young and old moose has been established by several studies in North America (Burkholder 1969, Frenzel 1974). In a series of studies on Isle Royale, wolf predation on moose was shown to be selective for young, old and diseased animals, although the overall impact on the moose population was influenced by nutritional factors and snow conditions (Mech 1966, Shelton 1966, Peterson and Allen 1974). Mech thought that wolf and moose populations on Isle Royale had reached a state of dynamic equilibrium in the early 1960's. He concluded that each population was relatively stable so that any substantial fluctuations in each would be absorbed by the other. He further concluded that wolves were, indeed, controlling the Isle Royale moose population.

The Isle Royale studies seemed to confirm Pimlott's (1967) theory. However, studies after 1970 discounted early findings. Wolf predation accounted for most adult mortality primarily in winter and the percentage of kill in the 1-6 or prime age classes increased after 1970 (Peterson 1974). Even the suspected stability of moose numbers was disproved by more accurate census methods. Jordan et al. (1971) conducted more intensive surveys and found that the moose population had increased from 1950-1970, while the wolf population had remained stable. Eventually, Mech (1974) concurred that the moose herd had increased; that Isle Royale wolves, also increasing in number after 1970, were not regulating the moose herd and were only cropping part of the available surplus production.

Other researchers dispute the role of wolves as regulator. Cowan (1947) conducted a classic study of the composition of two moose populations in wolf-inhabited and wolf-free areas and concluded that wolves were a critical factor influencing the survival of young moose to yearling age. Moose may indeed be formidable prey for wolves under most circumstances (Stanwell-Fletcher 1942, Peterson 1955).

Long-term studies of the habitat on Isle Royale (Krefting 1974a) affirmed Schaller's (1972) analysis of the ultimate effects of predators: "while predators may be a major fctor limiting size of the populations, the primary factor which ultimately exercises control is the habitat." In 1970, the moose population peaked and subsequently declined. The percentage of wolf-killed calves with serious fat depletion increased after 1970, indicating that malnutrition had increased (Peterson 1974). The increased kill of prime-age moose mentioned earlier was attributed to nutritional handicaps in the first winter of their life which left them permanently vulnerable to wolf predation.

Particular snow conditions apparently increase moose vulnerability. Deep snow hinders moose movement. On Isle Royale, the percentage of calves in the wolf kill increased significantly when depths exceeded 76 cm (Peterson and Allen 1974). Increased snow depths had the effect of concentrating moose in conifer cover on lakeshores which were primary wolf travel routes. Deep snow can be critical in hampering calf movement ahead of the cow in a typical flight response or in slowing the return of a cow to an undefended calf. Peterson and Allen cited several instances of calf injury or predation in these types of situations. Stanwell-Fletcher (1942) suggested that while moose were commonly associated with wolves in early winter in British Columbia, that they seriously hunted them only after January when food supplies were low and moose were in deep snow.

In deep, soft snow, wolves are at a comparative disadvantage because of their shorter legs. But their much lower weight-load-on -track gives them an advantage on crusts that cannot support adult or calf moose. Peterson (1955) and Nasimovitch (1955) cited the increased vulnerability of moose under these conditions and Peterson and Allen observed it on Isle Royale.

In summary, the evidence from studies done in areas other than the Kenai Peninsula indicates that habitat conditions and snow conditions affect the vulnerability of different segments of the population during the winter period. Calves, in particular, are vulnerable to wolf predation under most conditions, although the presence of the cow and her active defense of the calf is usually successful. The relationship of the moose and wolf populations on the Kenai Peninsula has not yet been studied. It should be noted that the present situation is one of a declining moose population with calves particularly vulnerable to winter mortality and a large, increasing wolf population.

FACTORS INFLUENCING THE NATURE OF THE COW-CALF BOND

Previous sections have described a moose population that built up to extremely high densities on seral vegetation following a burn, and recently declined. The winters 1971-72, 1972-73, and 1974-75 can be characterized by declining range conditions involving obvious deficiencies in the variety of foods and possible deficiencies in energy and essential trace minerals. Further, colder winters with a more persistent snow cover affected the availability of browse and low-growing food sources.

The vulnerability of moose calves in this population, resulting in death after the first build-up of snow to moderate depths, has been discussed. The following discussion will evaluate seasonal stresses upon cows and calves that may influence the nature of the cow-calf bond and its importance to overwinter calf survival.

Extensive winterkill of calves occurred during the winters 1971-72, 1972-73. and 1974-75, Calf mortality within the MRC was 100 percent during these three winters and 80 percent in 1973-74. The moose population wintering in the 1947 Burn suffered similar losses as the results of survival counts flown in late winter, 1970-75, in Game Management Unit 15A illustrate (Appendix A). Random stratified counts of the KNMR flown each year in early spring show a decreasing percentage of calves in the population in successive years. In 1971, calves comprised 20 percent of the KNMR population as determined by a random stratified count flown in early spring. In 1974, 18.2 percent of observed animals were calves, and in 1975, only 12.3 percent were calves (KNMR files).

Franzmann and Arneson (1976) reported femur marrow fat values of adults and calves collected at the MRC and other areas of the Kenai (Appendix A). Four of six winter-killed calves had marrow fat values less than 10 percent and five wolf-killed calves had values less than 10 percent, indicating that malnutrition was probably a major mortality factors.

To determine the importance of various factors on calf mortality, it is necessary to trace the progression of possible stresses on the calf prior to death. During the prenatal period, nutrition of the cow is important to fetal growth. In most ungulates, fetal growth is relatively slow throughout the winter, and accelerates rapidly in the four-six week period before parturition. Verme (1962) found that this final period was the critical one for deer in terms of nutrition. He found that captive white-tails in good condition in mid-April had excellent reproductive success (10 percent fawn loss) if maintained on a high nutritional plane but poor success (90 percent fawn loss) if maintained on a poor diet. When deer in poor condition in mid-April were placed on a high nutritional plane, fawn loss was 35 percent. Thus, a late snow melt, such as that which occurred in 1972 and 1975 (Figure 19), could have had an important effect on fetal growth and viability.

Generally inadequate prenatal nutrition could have occurred on the poor winter range of the northern Kenai. In other ungulate species, results of such stress include resorption of the fetus, high incidence of stillbirth, and high mortality at parturition. These mortality mechanisms have not often been observed in Alaska moose (Rausch and Bratlie 1965), although resorption of the fetus has been reported by several workers in Russia, especially after severe winters (in Markgren 1969). Bishop (in Rausch 1967) observed incidents of stillbirth and calf loss during tagging operations of newborn calves on the Tanana Flats following a severe winter. Since Rausch and Bratlie were reporting after years when conditions for moose production were considered extremely favorable (Bishop and Rausch 1974), and since observation of prenatal and parturition loss is extremely difficult, it is possible that some fetus and calf loss occurs by these mechanisms under declining conditions.

Prenatal nutrition has also been shown to determine the size and physical condition of the young animal at birth in deer (Verme 1963) and moose (Knorre 1959, Houston 1968). Peterson (1974) assumed that bone growth during the period of nutritional stress would be most affected and measured metatarsal length of calves on Isle Royale as an index of calf size at birth. He found significant differences between years with calf size at birth being correlated with the severity of the previous winter.

A small or weak calf would be more vulnerable to mortality factors. Substantial mortality does occur during the period immediately after birth; a calf crop may be reduced by more than 50 percent during the period May to October (LeResche 1968). Also, since growth continues for many years or throughout life, residual effects of poor prenatal nutrition can occur. Peterson found retardation of epiphyseal union in some cohorts by 3-5 years. Growth rates of moose on the Kenai are generally slow compared to other areas of North America (LeResche and Davis 1971), and this may be a symptom of inadequate nutrition. Rausch (1965) reported the survival of cohorts was sometimes erratic, citing the current 9-year-old class on the Kenai as an extremely weak one because it was born in a spring following a severe winter. The possiblity of permanent vulnerability to wolf predation has already been mentioned.

The importance of summer/fall range conditions to successful reproduction has been documented in deer (Julander et al. 1961). Little information is available to indicate that summer range in the 1947 Burn is deficient in terms of energy or specific nutrients. Oldemeyer (pers. comm.) indicated that winter range quality was more critical than any possible differences in summer range.

Even if summer range was nutritionally adequate, a small or weak calf might be unable to grow and develop fat reserves to last the winter period. Similarly, a cow in poor condition at parturition would have difficulty recovering and putting on fat while nursing a calf during the summer. Fat reserves are critical because the cow and calf are most likely in negative energy balance throughout the winter (Gasaway and Coady 1974).

During the fall, residual effects of poor winter-spring or summer nutrition can affect a cow's participation in breeding. Pregnancy rates were much lower in 1973 and 1974 in the MRC than the average 85-95 percent reported for other areas of Alaska during the period 1950-1970 (Franzmann and Arneson 1973, 1974). It should be noted that decreased pregnancy rates can come about in several ways. Mature cows can fail to come ito estrus or yearling cows can fail to reach sexual maturity. Poor range conditions have been tied to unsuccessful breeding by yearlings (Markgren 1969, Pimlott 1959). However, another consideration is the bull:cow ratio. Depressed cow ratios can result in lowered conception rates (Bishop and Rausch 1974). Low ratios do, indeed, characterize the Kenai Peninsula population.

Another effect of depressed bull:cow ratios is that of prolonging conception so that cows become pregnant in a second or third estrus over a three-four month interval (Edwards and Ritcey 1958, Rausch 1959, Markgren 1969). The evidence that late conception may be occurring on the Kenai is meager. Rausch (1967) found a wide range of fetus sizes at one time on the northern peninsula in 1965 which he attributed to generally low bull:cow ratios and extremely low ratios in local areas.

However, if low bull:cow ratios did result in late pregnancies, parturition would be delayed and calves would have a shorter period for growth. The observed slow growth rates on the Kenai Peninsula may indicated that this is indeed happening.

Another factor affecting calf survival is cow survival. When cows are killed by hunters, this loss occurs in the fall when the calf is three or four months old. Because cow seasons are a management tool, the question of whether or not a calf with its dam has any advantage in over-winter survival is an important one. Unfortunately, it has not been answered adequately on the Kenai.

Several researchers have reported the inability of orphan moose calves to survive the winter (Murie 1934, Denniston 1956, Altmann 1958, Houston 1968), although they gave little evidence and did not specify winter conditions, range conditions, or predator concentrations. It is apparent that under some conditions orphan moose calves can survive. Markgren (1975) summarized Scandinavian studies as agreeing that orphan calves would perish in northern areas with severe winters or if the calves were born late or if they lost their mothers early in the autumn. He concluded from his own study of orphan calves in Sweden that many orphan calves did survive, although they had permanently retarded development. In Alaska, several populations of moose have been established by transplanting calves which were raised in captivity. Successful transplants have occurred in areas where no moose or low numbers of moose were present and habitat conditions were good (Burris 1971, Burris and McKnight 1973).

After his two year study at the MRC, Johnson (LeResche et al., 1974) concluded:

> death of all orphaned and unorphaned calves during both years of the study precluded any statements regarding the advantages of maternal care. Furthermore, no pattern of date of death relative to presence or absence of the cow was discernible.

My data does not change this conclusion. On the Kenai, the period 1971-75, the survival of the cow and death of the calf was often the end result of the association of the cow and calf, regardless of an observed variety of behavior patterns that constituted a "bonding" (Table 11). Even though some "helping" behavior by cows was noted, this was rare with respect to food-getting or trail-breaking which could have enhanced the energy balance of the calf.

It appears that most lone calves on the Kenai die eventually during severe winters unless, perhaps, they attach themselves to other lone calves or adults or find a concentrated food supply. Attachment to a group or another adult is probably rare, although brief associations of lone calves with adults were seen (Johnson, unpub.). In all events, many calves may not form an attachment that increases their chances of survival. Markgren (1975) noted all orphans that he studied remained solitary most of the time. He reported several instances of unsuccessful attempts by an orphan to join a cow and calf or groups of moose. The calf was attacked repeatedly in these cases.

In my study, lone calves, alone or in a group, tended to remain in small areas. It is possible that they stay in a small area until they deplete the food and become too weak to find another food source. Markgren observed one calf that had a decided inclination to remain in the area where it was originally found, while another calf travelled

Table 11. Characterization of the status of the bond of cow-calf pairs observed on the Kenai Peninsula, 1974-75

Cow and Calf	Bonding	Behavioral manifestations	Observer
R-70-7/R-70-8	Close, continuous until calf's death	Cow tolerant of close approach Calf seen lying in contact with cow Nursing attempt - 5 Jan., 15 sec. Calf fed on *Vaccinium* that cow uncovered	Johnson
#79/#82	Close, weakening before death of calf; separation	Calf fed in same crater as cow Pair several hundred m apart 2 weeks before calf's death	Johnson
#52/#83	Separation before calf's death	Calf alone at least 10 days before death	Johnson
#89/#90	Continuous	Cow seen searching and vocalizing in area of calf carcass	Johnson

Table 11, continued.

Cow and calf	Bonding	Behavioral manifestations	Observer
#87/#88	Loose, separation	Calf seen alone several times Calf alone one month before death	Johnson
#91/#92	Loose, separation	Cow and calf seen apart many times Separation 15-20 days before calf's death	Johnson
Uncoll./Uncoll. (Big River Valley)	Continuous	Cow defended dead carcass from observer (3 days)	Johnson
#138/Uncoll.	Strong, continuous	Cow waited for weak calf to catch up Cow persisted in area of calf carcass	Sigman
#670/Uncoll.	Close	Synchrony of bedding feeding Nursing attempt, 25 Jan.	Sigman

Table 11, continued.

Cow and calf	Bonding	Behavioral manifestations	Observer
#79/#117	Separation	Cow seen alone several times Active chase of calf by cow 2 days before death of calf	Sigman

considerable distances. All calves that he observed had a tendency to return to the center of an activity range. He thought that under conditions of deep snow and food shortages, migration by orphans would probably not be successful.

Markgren (1975) concluded that the loss of a cow in the autumn was a serious disadvantage to the calf, although the final fate of the orphan depended primarily on food supply and winter climate. It also depended on the relations of the lone calf to other moose, and the calf's behavior patterns of feeding and reacting to environmental phenomena. In the case of the Kenai Peninsula, disruption of the cow-calf bond through death of the cow or abandonment no doubt reduced the ability of the calf to exploit available resources. However, most calves would probably have died sometime during a severe winter even if they remained with the cow while perhaps stressing her, affecting her chances of survival, and affecting the viability of a fetus she might be carrying.

Thus, it seems that any combination of the following factors, all of which are likely to be affecting moose wintering in the 1947 Burn, would seriously reduce a calf's probability of surviving to yearling age:

1) Winter range deficient in variety or essential minerals affecting prenatal nutrition;

2) Prolonged or severe snow conditions affecting prenatal nutrition;

3) Low bull:cow ratios resulting in delayed conception and calving;

4) Poor summer/fall nutrition of the cow and/or the calf;

5) Separation from the cow during fall or winter

6) The winter conditions of 1) and 2) above during the calf's first winter.

Although studies of orphans and cow-calf pairs on the Kenai have not contributed to an understanding of the general nature of the cow-calf bond, theoretical considerations may define what that relationship may be in terms of the limiting conditions for overwinter survival of cow and/or calf. For background, it is necessary to discuss how moose are distributed on winter range.

Distribution of moose on winter range is determined by traditional occupation of particular areas of winter range (Loisa and Pullainen 1968, Houston 1968, Van Ballenberghe and Peek 1971). LeResche (1974) reviewed studies of winter home ranges in North America and found that they rarely exceeded 5-10 square kilometers. He also found that all studies agreed that the same areas were used by the same individuals. Although traditional use of areas by individuals has been observed in Alaska, there is evidence that winter home ranges are much larger than those reported in the literature (Coady, unpub.).

The second factor influencing distribution is the observed traditional migrations over long distances in response to environmental factors (Edwards and Ritcey 1956, LeResche 1972, 1974; Pullainen 1974). Snow, forage, and internal stimuli have been cited as factors "mediating" seasonal movements. Coady (1974) concluded that the evidence pointed to snow as a major influence on migration, not as an ultimate cause; the chief effect of varying snow conditions being exerted on the timing of traditional movements. Migratory tendencies interact with other factors affecting winter habitat selection.

However, some populations winter in the same general area that they occupy year-round and other populations migrate long distances to rutting and calving grounds and also occupy distinct winter and summer range. Such populations may mingle in the winter as they do in the 1947 Burn (LeResche et al. 1974).

The fact that deep snow has the effect of limiting movements has already been discussed. It thus has the effect of decreasing the area of range occupied. Within its range, where food availability is physically restricted by deep snow, the moose moves to preserve the most favorable, i.e. least negative, ratio of energy intake to expenditure (Coady 1974). These traditional patterns of range occupation and variable responses to environmental stimuli interact and bring about the distribution of the population over its winter range in a manner that is far from clear.

A third group of stimuli to movement is that which results in colonization of new areas or exploitation of food sources and cover outside the traditional home range. The occupation of the WLRA is a unique illustration that massive redistribution on winter range can occur.

Within these patterns of range occupation, moose do not occupy winter range randomly. Rather, their behavior can be termed a "strategy," which implies that individual animals exhibit consistent choices or preferences for habitat and food type. These preferences are influenced by environmental conditions. The net effect of the day-to-day behavior expressed by the timing and extent of movement, the duration of feeding, and the amount and type of food consumed is overwinter survival or death. The importance of these decisions resides in the fact that the moose is in negative energy balance through out the winter period (Gasaway and Coady 1974). To meet energy needs for maintenance, fat reserves must be used. Thus, survival depends upon maintaining a rate of stored fat and protein utilization and weight loss that does not result in death before the winter is over.

Several studies have shown that habitat selection does take place. Krefting (1974b) reviewed studies in north-central North America and presented the evidence for selection of denser cover in late winter where moose have an advantage in sinking depths and crust conditions. Telfer (1970) indicated that the majority of tracks were found in areas where sinking depths were below maximum, which means that moose may be able to select advantageous routes of travel. Most accounts of moose winter behavior involve restriction to a single habitat type for several days or months (Timofeeva 1967, Loisa and Pullainen 1968, van Ballenberghe and Peek 1971).

The use of habitat types was somewhat different on the Kenai. Individuals often passed through several habitat types during the course of a day or a single feeding bout. Table 8 summarized habitat use by moose in Pen 2 in relation to snow pack conditions. Moose were located in mature hardwood stands as frequently as in regrowth and often used both habitat types on the same day. When snow depth measurements in the different habitat types in the MRC are compared, both mature hardwood stands and regrowth habitat have some of the deepest snow recorded in each period (LeResche et al. 1973, Franzmann and Arneson 1973, 1974, 1975). Moose are probably selecting for food availability as the relationship of occupation of hardwoods and snow melt indicates, rather than cover or energetic advantages. LeResche and Davis (1971) found that regrowth habitat types were preferred year-round. During 1975, the supply of downed aspen probably accounted for the equal use of hardwood types. The use of dense conifer stands, which are preferred in other parts of North America, is not really an option in Alaska because there is no palatable conifer.

Theoretically, moose must be selective feeders. Westoby (1974) constructed a model for the diet of large generalist herbivores. The rationale for the necessity of selection was as follows: food processing is proportional to gut size and metabolic requirements are proportional to body weight. Thus, as the size of the animal increases, its energy requirements increase and the limitation in the system is the rate of processing of food into energy. The optimum model for a large herbivore is to possess feeding preferences provided by long-delay learning so that it can obtain the optimum nutrient mix within a fixed bulk. Long-delay learning means that the animal will continue sampling the environment and have the possibility of greater variety. A consequence of selection is that certain less abundant plants are more intensively used than the more abundant, less preferred ones. Selection also means that food quality is more important than availability. Low levels of preferred species constitute a constraint on the system.

Studies have shown that selection for various plant species does take place in moose (Milke 1969) and in deer species (Klein 1970), and in domestic selective grazers like sheep (Arnold 1964). LeResche and Davis (1971) demonstrated a marked selection for willow on birch seral range on the Kenai.

Some selection may occur with respect to cratering sites. A sequence of cratering that I filmed included the moose extending its tongue into the snow before cratering. Moose were often seen sniffing the snow as well. The stimuli for cratering may be aromatic substances given off by the ground cover foods. Snow depths and crusts could affect the intensity of the cues and account for the lack of cratering activity at maximum depths.

It is relatively easy to determine that certain foods are being selected over others; it is extremely difficult to determine what is being selected for. The question emerges: what is food quality? The basis for differences in palatability is poorly understood. After reviewing a number of studies attempting to correlate various chemical and physical parameters of plant species with observed feeding behavior, Arnold (1964) concluded "what can be said is that there are certain characteristics that increase the chances of a species being liked and others that have the reverse effect." Loisa and Pullainen (1968) provided evidence that variety was important. They observed a cow and calf that periodically switched winter foods even when several types of foods were readily available. They concluded that moose needed more than one food item. Peek (1974) reviewed all food studies of moose in North America and found that most winter diets included a number of major foods. However, a productive and relatively dense moose population could be maintained on two major species, paper birch and balsam fir, even while other preferred species were being eliminated from the range. On the Kenai where no palatable conifer exists, Oldemeyer et al. (in Franzmann and Arneson 1975) concluded that five different species in sufficient quantities would more adequately meet the nutritional needs of moose than any one species, no matter how abundant.

The factors affecting species composition and relative abundance of individual species ultimately limits the range of choices available to the animal, and thus, variety in the diet. Determinations of relative palatibilities of different species often fails to take this into account. In the case of the Kenai, the variety of foods is extremely limited and food habits reflect the plant composition of the range. Moose are apparently unable to exert much selection on their poor range. Low levels of willow or other palatable species may thus be the constraint on the system proposed by Westoby (1974). Because the range is so limited, the strategy of exploiting food source to obtain the "optimum nutrient mix within a fixed bulk" as often as possible may determine successful overwintering.

With these descriptions of moose winter behavior as background, it may be possible to determine the role of the cow-calf bond during the winter period. Lent (1974), in his review of mother-infant relations in ungulates, reported that while the importance of the mother-infant bond that extended through the winter was suggested by many authors, no statistics were available to provide concrete support for the importance of the bond. He concluded that there was little evidence that chances for survival of ungulate young were increased by maternal instruction; learning through imitation was difficult to establish although the possibility of imprinting in feeding preferences was suggested. Concrete evidence of transmission of tradition was lacking. One major theory is that the purpose of the cow is to protect the calf from predators (Murie 1934, Geist 1971). Cows have been observed putting up a vigorous fight, as Murie recounted an account of a cow driving away two large Husky dogs in Mount McKinley National Park. Mech (1966, 1970) described maternal behavior of active defense of the calf from wolves, with the cow standing behind the calf or fleeing behind it, protecting the calf's rear. This strategy appeared to be successful as long as the calf did not become separated from the cow. On four occasions, when the calf was separated, it was killed by the wolves. Bubenik (unpub. ms.) hypothesized that the dam had the psycho-physiological role of synchronizing the young animal's activity for efficient utilization of the environment.

The difficulty of surviving on winter range increases as range quality decreases, so that non-random use or selection, of food and habitat, becomes increasingly important. The degree to which selection must be learned by the calf may determine the importance of the cow-calf bond in increasing the calf's chances of survival. It is likely that such learning does occur. Mayr (1975) discussed the concept of noncommunicative behavior, behavior directed at objects that do not respond, such as food and habitat. Under certain conditions, selection favors non-communicative behavior which consists of open programs as opposed to genetic programs. An open program allows for additional input during the animal's ontogeny. According to Mayr, the object of an open program (e.g. cranberry as food source) is acquired through experience although the locomotion elicited (e.g. cratering and ingestion) is rigidly determined. The conditions that favor selection for open programs of non-communicative behavior include habitat and food sources that are dynamic, a long life with time for learning, and a long period of parental care with time for filling in open programs with information on enemies, food, shelter, and other immediate components of the environment.

Little evidence exists to support a conclusion that moose cows actively teach calves, although the extent to which the calf follows the cow, feeds and beds in the same area, and selects the same foods could constitute the imprinting that would give open behavior programs specific objects. During my observations and those of Johnson, calves sometimes followed and sometimes led the cow without a discernible pattern as to snow conditions or disturbance. On several occasions, cows were seen waiting for a calf to catch up with her after both fled from a disturbance. On the other hand, calves were seen trotting to keep up with cows during undistubed movements both during severe winter conditions and in the spring prior to calving.

To expand Mayr's concept of open programs, in the case of moose feeding behavior, although high palatability of certain plant species that have long been moose food is likely innate (Markgren 1966), the strategy of selecting particular foods in a particular sequence to obtain optimum rumen fill might be learned by association with the cow. The capacity represented by innate palatabilities is probably complemented by trial-and-error learning which results in the use of the greatest possible variety of foods. The cow increases the efficiency of sampling the environment. The calf could feed by imitating the cow's choice of food, the cow could provide foods to the calf, or she could yield her feeding site to the calf.

All three of these behavior patterns were observed. A wide range of feeding patterns occurred. Pairs sometimes fed on the same food type and sometimes on different food types in the same area. Markgren (1975) made some observations that suggested that food choice of calves was by imitation of cows. However, he also observed that the diet of orphan calves was largely the same as that of other moose, although they exhibited a one-sided choice periodically and pawed through the snow for dwarf shrubs, which adults did not do. In the MRC, orphan calves exhibited the same feeding behavior that adults did, although they could have imitated other adult moose. Orphans in the pens may also have had a problem with selecting the variety of foods necessary; most died from malnutrition with stomachs largely filled with birch browse.

Provision of food by the cow was seen on a few occasions. On two occasions, calves were seen feeding on birch and willow saplings that the cow had bent over and a few times the calf fed in a crater dug by the cow or enlarged a crater that the cow had started (Johnson unpub.)

During my observations of a cow and calf in an area with several downed aspen trees, the calf approached and displaced the cow several times and she moved off. This same behavioral sequence was seen in an interaction between Rastus, an 18-month-old semi-tame male, and cow #670 (pers. obs.). This interaction differed markedly from the agressive display by Rastus during the fall towards a cow of similar size. He thrashed his antlers and moved toward the cow, causing her to leave the feeding area. The non-agressive displacement which he displayed in late winter is probably a submissive approach that, in winter, usually results in cows yielding to their calves. Calves often approach the cow when they are disturbed by the presence of an observer. The cow's response is either toleration or protection of the calf or the aggression displayed by cow #79 towards her separated calf and by cows in the spring towards their yearlings.

Cratering is a likely behavior for an open program. The moose must "decide" to crater or select another site once it receives the stimulus of a certain intensity. This decision-making process could be filled in during parental care. A lone calf evidently knows how to crater or perform other feeding behaviors efficiently, but he must know where to crater so that expenditure of energy is compensated by the food ingested.

Synchrony of cow and calf has important consequences. Synchrony of movement means that the cow and calf will be in the same habitat where the calf can imitate and learn from the cow and benefit from her choices of food and habitat type. Markgren (1975) thought that the moose calf learned winter feeding localities as it travelled with the cow and that poor local knowledge was one of the factors increasing orphan mortality.There were considerable differences in the number of times that each cow-calf pair was seen in the same area ranging from constant association to infrequent association, and finally, separation. There was also a range in the proximity of bedding sites. In early March, 1972, the calf of R-70-7 lay nestled up and touching her mother, an occurrence that Timofeeva (1967) cited as common. For the most part in the MRC, if cows and calves were seen lying the same area, bedding distances varied from 10 to 50 m. Timofeeva stated that cow and calf beds were separated by 1-6 m. Distances between cow and calf beds appeared to be somewhat greater in the WLRA, but this was open habitat. Following the cow can decrease the vulnerability of the calf to predators. Mech (1966) observed the most kills of calves by wolves occurred in the open when the calves were separated from the cows.

Synchrony of activity and rest may also be important.During the winters 1971-75, marked synchrony of cow-calf pairs was seen, but many times, the cow and calf lay and fed at different times. If Bubenik's (unpub. ms.) hypothesis is correct, calves out of synchrony with their cows may have been displaying atypical activity patterns which could disrupt digestive efficiency so that the calf would become increasingly weak and lose resistance to decimating factors.

Lone calves tended to stay in areas of aggregation after the time most adults had moved away. On two occasions, a group of three lone calves stayed in an area after other moose had fled in reaction to my approach. I was able to approach them to within 30 m. This lack of wariness and tendency to stay in areas which may no longer be optimal habitat may affect their chances of survival. On the other hand, Markgren (1975) noted a considerably longer flight distance in the orphans that he observed.

Finally, a calf may follow a cow to new habitat or to a concentrated food source such as that in the WLRA. Winter calf survival was better in the WLRA than in other parts of the Kenai National Moose Range and Game Mangement Unit 15A. The number of calves per 100 adults ranged from 31 to 62, the upper value being recorded on 18 April. In contrast, the number of calves per 100 adults in a nearby control area decreased steadily with a maximum of 35 in December and a low of zero in 31 moose counted in April (KNMR files). The KNMR random stratified population count, conducted March 12-14, 1975, revealed 13 percent calves in high density moose areas (including the WLRA) and nine percent calves in medium density areas.

The capacity to move and locate irregularly-provided food sources is also a feature of open programs. The conditions that favor open programs include a dynamic habitat wherein flexibility towards environmental components is at a premium. Thus, the animal can expand his niche or occupy new ones. In the 1947 Burn, moose calves that could and did follow dams to the WLRA increased their chances of surviving the winter, possibly regardless of any bond with a cow while they occupied the area.

A general conclusion might be that the importance of the cow-calf bond depends on environmental factors that affect the nutritional status of cows and calves and, in particular, pregnant cows. The quality and distribution of the forage supporting the moose population is of primary importance, while other factors such as winter conditions and predators, are of secondary importance.

Trivers (1974) has proposed a model for

parent-offspring conflict which puts bond termination in perspective. According to his theory, conflict is the outcome of natural selection acting in opposite directions on two generations. At most, the cow has the potential to double her genetic representation in the next generation if she both raises a calf to the point where it can survive independently and carries a fetus to term. The calf benefits by association with the cow as long as it increases its own "inclusive genetic fitness." Trivers ' theory goes on to state that if the female's inclusive genetic fitness suffers first, conflict will result. In Trivers terms, the cow will try to reject the calf as soon as the costs in units of fitness exceeds the benefits in the same units which will happen at the point after her probability of doubling her genetic representation in the next generation is reduced, but probably well before her chances of replacing herself in the next generation are reduced. In energetic terms, at a point when the calf necessitates energy expenditure or reduces intake by the cow that is also needed for her own maintenance and fetal growth, caretaking behavior and finally, tolerance of the calf may be sacrificed for fetal growth. Even if the cow is not pregnant, her survival ought to be favored by evolutionary considerations because she is the proven reproductive. Under the same conditions, and in the spring, the calf has something to gain by staying with the cow and thus, must either be chased away when the cow is willing to break the bond or, through weakness, fail to keep up with the cow.

It is possible that under optimum conditons, both cows and calves have an adequate energy balance throughout the year, and that the expression of caretaking behavior by the cow actually contributes to increased calf survival. On the other hand, it is more likely that in an asocial species such as moose that if food supplies are optimal, the calf needs less help foraging strategically so that even "poor mothers" can raise calves to yearling age. This follows Geist's (1974b) theory that the reproductive potential of ungulates is a function of the ecological variables that individual species are adapted to. He shows that the reproductive potential of moose is a function of rapidly expanding but slowly contracting habitat that moose colonize after forest fires. He applies the theory to twinning rates which are high when forage is abundant and the growth and birth of twins is favored and lower as the burn habitat is reinvaded by conifers, and the birth of a single, well-developed young is favored because limited resources must be concentrated. The hypothesis that is being advanced is that maternal behavior and the survival of calves to yearling age is similarly adaptive, both processes being favored under good habitat conditions and their opposites -

abandonment of calves and high mortality - favored under declining conditions. Certainly, however, predator densities and snow conditions have an impact of successful reproduction.

Trivers' (1974) theory may explain the selective pressures that result in active and passive bond termination. Given the conditions in the 1947 Burn where nutritional inadequacies of winter range available to pregnant cows may result in the birth of small and weak calves following severe winters, it appears that successful reproduction, in the sense of raising young to sexual maturity, is rare. The successful long-term strategy of the species may be one that allows the cow to survive stressful periods.

Range conditions, winter conditions, and wolf predation often interact in their effects on moose population dynamics. Isle Royale, Michigan, is the best documented long-term study of the impact of these factors on a moose population. Unusually deep snows in certain years on Isle Royale have resulted in the birth of calves which are permanently vulnerable to wolf predation. Peterson (1974) stated that generations of calves born after severe winters accounted for almst all of prime age wolf kills of the early 1970's. He summarized the factors contributing to the decline of the Isle Royale moose population as

> nutritional stress from a combination of plant successional trends which reduced browse supply, increased winter severity because of deep snow, and an increasing moose population during the 60's (resulting in over-browsing).

In north-eastern Minnesota, Van Ballenberghe (1972 in Frenzel 1974) suggested that herd debilitation from winter stress was related to increased wolf predation on moose, particularly calves. Wetzel (1972 in Frenzel 1974) implicated declining range conditions in the same area. In the Nelchina Basin in Alaska, habitat deficiencies were considered a "possible contributing factor" while wolf numbers were probably most important in causing substantially reduced production and survival (Bishop and Rausch 1974). They conclude that "deep snow was clearly the factor precipitating population decline in the Nelchina" with predation and hunting appearing to have "impeded population recovery." One theory of predator-prey cycles, based on long-term observation of a hare cycle (Keith 1974) postulates that increased predator numbers follow increased prey abundance with, a significant time lag. Depletion of the food supply coupled with self-regulatory mechanisms initiates the decline of the herbivore population while the subsequent high density predator population acts to depress the prey and prolong periods of low density while the vegetation is recovering. Managers of Alaska moose herds concur with the depressive effect of large predator populations: "where severe winters result in moose population decreases, wolf populations may accelerate the decrease through intensive use of the youngest age classes and random use of older age classes." This picture is complicated where hunting pressure is sufficient to use the annual surplus; then wolves are directly competing for this resource (Rausch et al. 1974).

These facts point to a grim future for the Kenai Peninsula moose population. High density wintering populations were maintained for many years in the 1947 Burn due to abundant browse supplies, the tremendous edge effect, and mild winters during a period when effective predators were virtually absent from the area. As the Burn began to lose its value as winter forage, winter severity increased, initiating a decline in the population. Adequate information is not available on the rate of wolf population build-up, but it is possible that the winters of 1970-75 provided enough winter-killed calves to support a rapid build-up of wolves living off scavenged food supplies alone. The large wolf population that has been estimated to exist on the Kenai presently has the potential for accelerating the decline of the population and keeping it depressed at a low level especially if no large-scale habitat improvement occurs. The feasibility of large-scale mechanical rehabilitation is questionable and the ability of crushing to bring about rapid secondary succession of preferred species is in doubt because nutrients in downed vegetation are not made readily available in quantity for new growth as they are in the process of fire. Given the present range conditions, the effect of wolves in the winter of 1974-75 was similar to that of wolves on Isle Royale in the early 1970's; calf survival would probably not have increased greatly, if at all, in the absence of wolves (Peterson 1974). The effect of wolves on calf and adult mortality may increase, depending on range conditions, and winter severity.

IMPLICATIONS FOR MANAGEMENT

This particular behavioral study was rather broad in scope with a number of aspects of moose winter behavior being reported on for a few seasons of observations. The fact that the reported behavior reflects a particular set of environmental conditions is emphasized throughout the interpretation of data. Thus, while the type of information that such methods can provide to wildlife managers has been demonstrated, extrapolation of findings to other moose populations, or even to the Kenai Peninsula moose populations under a different set of conditions, is limited.

The major generalizations that have been drawn from observations of specific feeding, activity, and caretaking patterns are that moose winter behavior is both flexible and opportunistic in response to changes in the environment. Managers could utilize observed changes in behavior, particularly that of cow-calf pairs, to assess the status of the herd and its habitat, and should develop techniques that take advantage of this inherent adaptability of the species. Habitat use by relatively stable populations of moose and some land uses by humans are thus compatible, as long as an adequate amount of habitat for seasonal use and cover are maintained on a long-term basis. Within limits, the location of suitable habitat is seemingly not as important as it is for species such as caribou whose use of areas of range and migration routes is less flexible. Managers should continue efforts to develop effective methods of habitat manipulation.

Traditionally, wildlife managers in Alaska have managed areas for maximum sustained yield of the most abundant or sought after game species. The Kenai National Moose Range, in particular, was charged with the mission of "protecting the natural breeding and feeding range of the giant Kenai moose of the Kenai Peninsula" (KNMR Executive Order). However, a number of recent considerations indicate that management of the ecosystem as a whole is preferable to single-species management. Given the present range conditions on the Kenai, the expense of mechanical habitat rehabilitation, and public response to wolf reduction programs, the managers of the Kenai National Moose Range must soon make the decision whether management of the area for large or maximum numbers of moose is a feasible goal. The following is a series of options for management of the moose population and specific recommendations.

Options for management of the Kenai Peninsula moose population

1. Management for sustained maximum yield of moose of either sex to hunters.
2. Management for quality hunting - either in terms of quality of the animal taken, i.e. trophy bull, or in terms of quality of the hunting experience.
3. Management for maximum wildlife/wildlands recreational use of the area with maximum opportunity for the public to view moose.
4. Management for the goal of a balanced (not necessarily static) system of habitat, moose, wolves, human use, and informed human attitudes.

The past history of management on the Kenai has indicated that the first three options are not completely compatible. The final option may appear idealistic and unrealistic, but, if achieved, it would accomplish a noble compromise of human desires and the long-term integrity of the ecosystem.

Specific recommendations for management of the Kenai Peninsula moose population

1. It is likely that an initial reduction of the large wolf population on the Kenai Peninsula would increase the chances of winter calf survival. This reduction should be considered a short-term measure. If recruitment into the herd increases substantially, management of wolves should then be directed towards maintaining viable populations of wolves and moose.

2. Reduction of hunter take to a minimum will have the effect of increasing the recruitment of yearling bulls into the population, thus the possibility of maintaining pregnancy rates. This is particularly true because hunters in the area are averse to cow seasons and the adult bull segment of the population is quite low. One way to achieve a minimal hunter take is to establish quality hunting in areas where moose density is relatively high by restricting access and methods of taking moose. Maximum sustained yield harvest could be allowed in areas where access cannot be limited effectively and moose densities are relatively low. Monitoring the harvest would provide valuable

information, as well as discouraging poaching.

3. Other factors affecting the dynamics of the moose population should be monitored annually. These include wolf densities, snow depths and structure of the snowpack, and weather conditions. Range conditions and behavior patterns should be monitored on a periodic basis.

4. Future management must be based on a primary consideration of habitat quality as the limiting factor to a sustained population size. If moose numbers are to be maintained or increase from present levels, recent burns must begin to produce more browse naturally or areas with unsuitable vegetation must be manipulated. The best way to manipulate habitat to produce desired browse, whether it be mechanical crushing, logging, or controlled burning, must be determined. Maintenance of a certain amount of moose habitat should be a long-range goal, although location of habitat could probably be shifted over several years without decreasing use by moose. Permitted human land uses should be compatible with this long-range goal.

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APPENDIX A.
SELECTED STATISTICS OF KENAI PENINSULA MOOSE POPULATIONS

Moose population levels of the Kenai National Moose Range as determined by random stratified sampling techniques.

Year	Population Estimate
1971	7904 ± 1461
1972	5692 ± 1348
1974	4850 ± 1045
1975	3375 ± 1920

Taken from KNMR files

Survival Counts from Game Management Units on the Kenai Peninsula, 1973.

Unit or Subunit	Date of Count	Sample Size	Calf (%) in Herd
15A[1]	26 Feb	202	5.4
15A[1]	27 Feb	77	5.2
15A	24 Apr	304	7.9
15A	10 May	142	6.5
15A	16 May	149	10.1
15B	11 May	92	16.3
15C	22 Feb	289	16.3
15C	30 Mar	37	16.2
15C	11 May	149	16.2
7	8 May	56	7.1

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[1] Taken from report by Franzmann and Arneson (1973)

[1] Counts made in the immediate area of Moose Research Center

Productivity (Spring-Fall survival), Game Management Units
15A and 15B, taken from ADFG aerial surveys

Date	Subunit	% Calf Winter Mortality
4/14-5/4/70	15A	44.8
5/14/71	15A	50.2
5/15/72	15A	80.6
Spring, 1972	15B	>95
5/10/73	15A	75.3
Spring, 1973	15B	95.9
5/7/74	15A	74.4

Mean percent dry weight of calf femur marrow at the
Kenai Moose Research Center and other parts of the Kenai
Peninsula (Sample sizes in parentheses)

	Winter Kills		
Winter	Kenai Peninsula	Outside MRC	Inside MRC
1971-72	6.9 (45)	7.1 (2)	8.1 (8)
1972-73	7.3 (1)	7.6 (2)	7.3 (9)

Taken from Franzmann and Arneson (1973)

APPENDIX B.

POPULATIONS WITHIN MOOSE RESEARCH CENTER ENCLOSURES, 1971-75

Pen No.	Month/Year	No. of Females	No. of Calves	No. of Yearlings	No. of Males	Total Moose
1	Jun. 1971	6	7	4	2	19
	Jul. 1972	7	1	0	5	13
	Nov. 1972	7	2	0	4	13
	Apr. 1973	7	0	0	4	11
	Jun. 1973	6	4	0	3	13
	Dec. 1974	2	1	0	3	6
	May 1975	4	0	0	5	9
2	Jun. 1971	9	9	3	4	25
	Jul. 1972	7	4	0	5	16
	Nov. 1972	8	3	0	6	17
	Apr. 1973	6	0	0	2	8
	Jun. 1973	4	1	0	2	7
	Dec. 1974	6	4	0	4	14
	May 1975	7	0	0	4	11
3	Jun. 1971	6	3	2	2	13
	Jul. 1972	7	0	0	1	8

Populations within MRC enclosures, continued.

Pen No.	Month/Year	No. of Females	No. of Calves	No. of Yearlings	No. of Males	Total Moose
3	Nov. 1972	6	0	0	1	7
	Apr. 1973	6	0	0	1	7
	Jun. 1973	6	2	0	1	9
	Dec. 1974	5	2	0	1	8
	May 1975	6	0	0	1	7
4	Jun. 1971	8	6	5-7	3	22-24
	Dec. 1971	14	17	5-7	4	40-42
	Jul. 1972	11	1	0	2	14
	Dec. 1972	15	6	0	3	24
	Apr. 1973	14	0	0	2	16
	Jun. 1973	8	2	0	2	12
	Dec. 1974	12	2	0	3	17
	May 1975	12	0	0	3	15

Adapted from LeResche et al. 1973, Franzmann and Arneson 1973, 1974, 1975.

Chronological observations, continued.

	Animal #	Feed Birch		Feed Aspen		Crater		Travel Browse		Travel		Stand		Lay		Total Time
		(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)
1/23/75	79	53	66											32*	34	85
1/24/75	670			126**	51			25	10					96	39	247
	Calf			140**	54			25	10					95	36	260
1/25/75	670			55												
				125										x		
	Calf			41						x						41
				95	76			35	24							130
1/27/75	Unmarked Calf	x		x				95								95
1/28/75	79			134	90			15	10							149
	117							15								15
1/20/75	79			30*,**	55	20	45							x		55
2/4/75	670	73	27											192	73	265
2/5/76	79			25	32	20	26	32	42					x		77

Chronological observations, continued.

	Animal #	Feed Birch		Feed Aspen		Crater		Travel Browse		Travel		Stand		Lay		Total Time
		(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	&	(MIN.)
2/6/75	79			60	60	12	10	30	30							102
2/7/75	40	120								x						120
	79	65	68			30	32									95
2/10/75	R-70-8	x														
	670	40	29			30	21			70	49					140
2/16/75	73	x		x		x										
	1	x														
2/19/75	79	91	25	20	6	5	1	65	18			195	50	376		
2/20/75	40	74	26					15	5	x				196	69	235
	79	x														
2/21/75	79	x		x												
2/25/75	79			120	28			10	2					295	69	425

Chronological observations, continued.

	Animal #	Feed Birch		Feed Aspen		Crater		Travel Browse		Travel		Stand		Lay		Total Time
		(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)
2/26/75	40	x														
2/27/75	79			x												
	40	x														
2/28/75	79			x												
3/7/75	79	88	27											242	73	330
	120	x														
3/9/75	79	130	25	55	11					30	6			300	58	515
	120	x														
	3	x														
3/15/75	120	x														
	36	x														
	79	x														
3/16/75	670			x**												

Chronological observations, continued.

	Animal #	Feed Birch		Feed Aspen		Crater		Travel Browse		Travel		Stand		Lay		Total Time
		(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)	%	(MIN.)
3/17/75	79	45	10	72	16			10	2	14	3	4	1	300	67	445
	670			x												
	1	x														
3/23/75	79	172	34	12	2					2	1	5	1	314	62	505
3/29/75	79			377	70									158	30	535
4/10/75	36			35	19			41	22	4	2	3	2	107	56	190

Appendix D.

DETAILED OBSERVATIONS OF ASSOCIATIONS OF MOOSE, 1985

14 Feb. - Cow and bull travel together, fleeing observer as she approaches an area of aggregation in DLA. Bull waits for cow, who vocalizes as she approaches.

1 March - Cow and bull cross Duckling Lake, bull follows in cow's trail.

11 March - Two calves and yearling feed in close proximity (often 1-3 m apart) for three hours of observation, east of Duckling Lake.

12 March - Observer approaches hill, east of Duckling Lake, where no moose are visible. Two calves, a female and a male, are lying down with a male yearling in a small area among the down trees in the area of aggregation. The group is observed lying together until observer presence causes them to flee as a group.

13 March - Two calves feeding together east of Duckling Lake. Two are seen feeding

on the same downed aspen tree.

14 March - Aerial survey of area of aggregation causes all moose east of Duckling to get up, flee, or attend. One group of seven appears to be feeding and travelling together. Th e group consists of one bull (MRC #246), three bulls, two calves, and one yearling. Two hours later, Moose #245 6 has moved across a hillside and over the hill out of sight. The other six moose follow much the smae path, at varied rates, and all move over the hill within ten minutes. One aggregation of moose has been observed several days before this, one-half mile south of the hillside. The group includes #246 and #141 (C-8) The latter moose is on the hillside on 14 March, apparently alone. Moose #246 appeared on the same hillside alone on 13 March.

After all moose on hillside flee, observer approaches hilltop. Two calves, male and female, are lying down. The pair flee together.

18 March - Two calves seen, on hill one-fourth mile south of site east of Duckling Lake.

23 March - Two calves feeding north of Swan Lake Road, south of Nest Lake. Both run into road at car approach. They run down road, one climbs over berm; the other tries, finally runs down road another one-fourth mile, gets over berm on opposite side of road.

APPENDIX E.

COLLARED MOOSE OBSERVED IN WILLOW LAKES REHABILITATION AREA, KENAI PENINSULA, 1974-75

MRC - Moose Research Center, Kenai Peninsula, Alaska
LFRS - Lower Funny River Strip, Kenai Peninsula, Alaska
Ben - Benchlands, Kenai Peninsula, Alaska
BI - Big Indian Drainage, Kenai Peninsula, Kenai Peninsula, Alaska
Fr W/W
Rr Y/P - Refers to a four-color collar, with two front panels white, and two rear panels yellow and pink. Colors used in the collars are Blue, Yellow, Pink, White, and Red.

Moose #	Collar	Sex	Area Tagged	Date Tagged
MRC #129	Fr W/W Rr Y/Y	F	MRC	9 Feb., 1972
MRC #141 (C-8)	W with Blue #12	F	5 mi. SE of Moose L.	7 May, 1972
MRC #145	Fr B/W Rr R/R	F	MRC	3 Oct., 1972
MRC #153	Fr W/W Rr Y/P	F	MRC	7 Dec., 1972
MRC #155	Fr B/P Rr Y/P	F	MRC	3 Jan., 1973
MRC #169	Fr B/P Rr R/P	F	MRC	1 March, 1973

Collared Moose Observations, continued.

Moose #	Collar	Sex	Area Tagged	Date Tagged
MRC #172	Fr R/R Rr Y/W	F	MRC	6 March. 1973
MRC #178	W with Blue #89	F	MRC	21 March, 1973
MRC#180	Fr B/B Rr W/Y	F	MRC	11 April, 1973
MRC# 220	W with Blue #26	F	MRC	4 June, 1974
MRC #225	W with Blue #25	F	MRC	16 Jan., 1974
MRC #226	W with Blue #20	F	MRC	17 Jan., 1974
MRC #246	W with Blue #98	M	MRC	11 June, 1974
MRC #265	W with Blue #70	F	MRC	1 Oct., 1974
MRC #266	W with Blue #10	F	MRC	1 Oct., 1974
MRC #282	W with Blue #14	F	MRC	21 Nov., 1974
MRC #283	W with Blue #38	F	MRC	11 Dec., 1974
MRC #287	W with Blue #6	F	MRC	17 Dec., 1974
LFRS #483	Fr Y/B Rr P/B	F	LFRS	Oct. 1973

Collared Moose Observations,, continued.

Moose #	Collar	Sex	Area Tagged	Date Tagged
Ben #417	Fr B/Y Rr R/R	F	Ben	Oct. 1973
BI #409	Fr Y/Y Rr W/W	F	BI	?

Taken from MRC files