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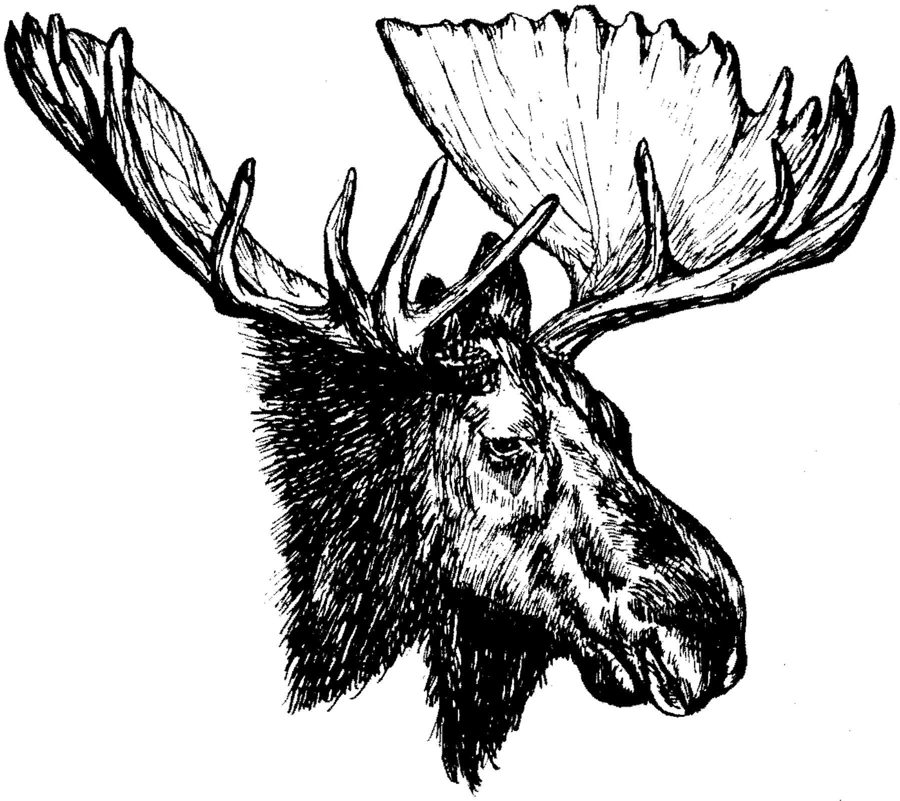
ALASKA DEPARTMENT OF FISH AND GAME
JUNEAU, ALASKA

MOOSE BEHAVIOR STUDIES

By Marilyn J. Sigman and Albert W. Franzmann



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Final Report
Federal Aid in Wildlife Restoration
Projects W-17-7, W-17-8 and W-17-9
Job 1.13R

(Printed July 1977)

FINAL REPORT (RESEARCH)

State: Alaska

Cooperators: Marilyn J. Sigman and Albert W. Franzmann

Project Nos.: W-17-7, W-17-8 and W-17-9 Project Title: Big Game Investigations

Job No.: 1.13R Job Title: Moose Behavior

Period Covered: July 1, 1974 through June 30, 1977.

SUMMARY

Behaviorial studies under this job were conducted by Marilyn J. Sigman, a graduate student at the University of Alaska-Fairbanks. Her thesis entitled "The importance of the cow-calf bond to overwinter moose calf survival" was presented and accepted for the Degree of Master of Science (May 1977). An abstract of the thesis follows:

> Observations 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 wind-thrown aspen trees is described. In 1975, aggregations occurred apparently in response to a concentrated food source resulting from mechanical habitat manipulation. Extremely high moose densities with considerable turnover resulted. 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 was attributed primarily to declining habitat quality in combination with conditions of colder winter temperatures and deeper and more persistent snow cover.

From her thesis material Sigman wrote a paper entitled "A hypothesis concerning the nature and importance of the overwinter cow-calf bond in moose." The paper, presented at the 13th North American Moose Conference and Workshop at Jasper Park, Alberta, Canada, was well accepted. The body of this final report is the paper as written by Marilyn J. Sigman.

CONTENTS

BACKGROUND

Because the nature and importance of the winter cow-calf bond are not well understood, public controversy over the desirability of hunting cow moose (*Alces alces*) with calves poses an unanswerable management problem. The mother-infant bond, described as the social relationship of the two and the associated range of mutual benefits, usually continues through the calf's first year. Actual behavioral observation of cows and calves during the winter is an obvious approach to an understanding of the importance of caretaking patterns during this period, but one with considerable logistic problems. Several researchers have observed moose during winter (Altmann 1958, 1960; Geist 1960, 1963; Timofeeva 1967, Houston 1968), but one aspect of moose behavior which has not been emphasized is the flexibility of behavioral response to different conditions which might be expected from a species adapted to the use of seral habitat.

The Moose Research Center and surrounding Kenai National Moose Range in southcentral Alaska have been the site of a study of the winter cow-calf bond since 1971. Measurement and description of concurrent conditions of range quality, weather and snow conditions, and predator concentrations allow some generalization about the nature of the cow-calf bond and of the factors influencing the importance of the bond in overwinter calf survival.

STUDY AREA

Behavioral observations were conducted during the winters of 1971-72, 1972-73, and 1974-75, primarily within the four 2.6 km^2 pens of the Moose Research Center (MRC) and nearby areas within the Kenai National Moose Range (KNMR) (Fig. 1). In addition to observations in the MRC, Johnson (1975) observed moose in the Lobe River Valley on the west side of Cook Inlet during 1972 and around the town of Soldotna in 1973. During the winter of 1974-75, the KNMR staff carried out a vegetation rehabilitation project in the Willow Lakes area. The vegetation was crushed with LeTourneau tree crushers (method described in Hakala et al. 1971). During February and March 1975, I observed concentrations of moose in the 23 km^2 Willow Lakes Rehabilitation Area (WLRA). I also observed cows and yearlings during spring 1975 in Mount McKinley National Park, Alaska (Fig 1).

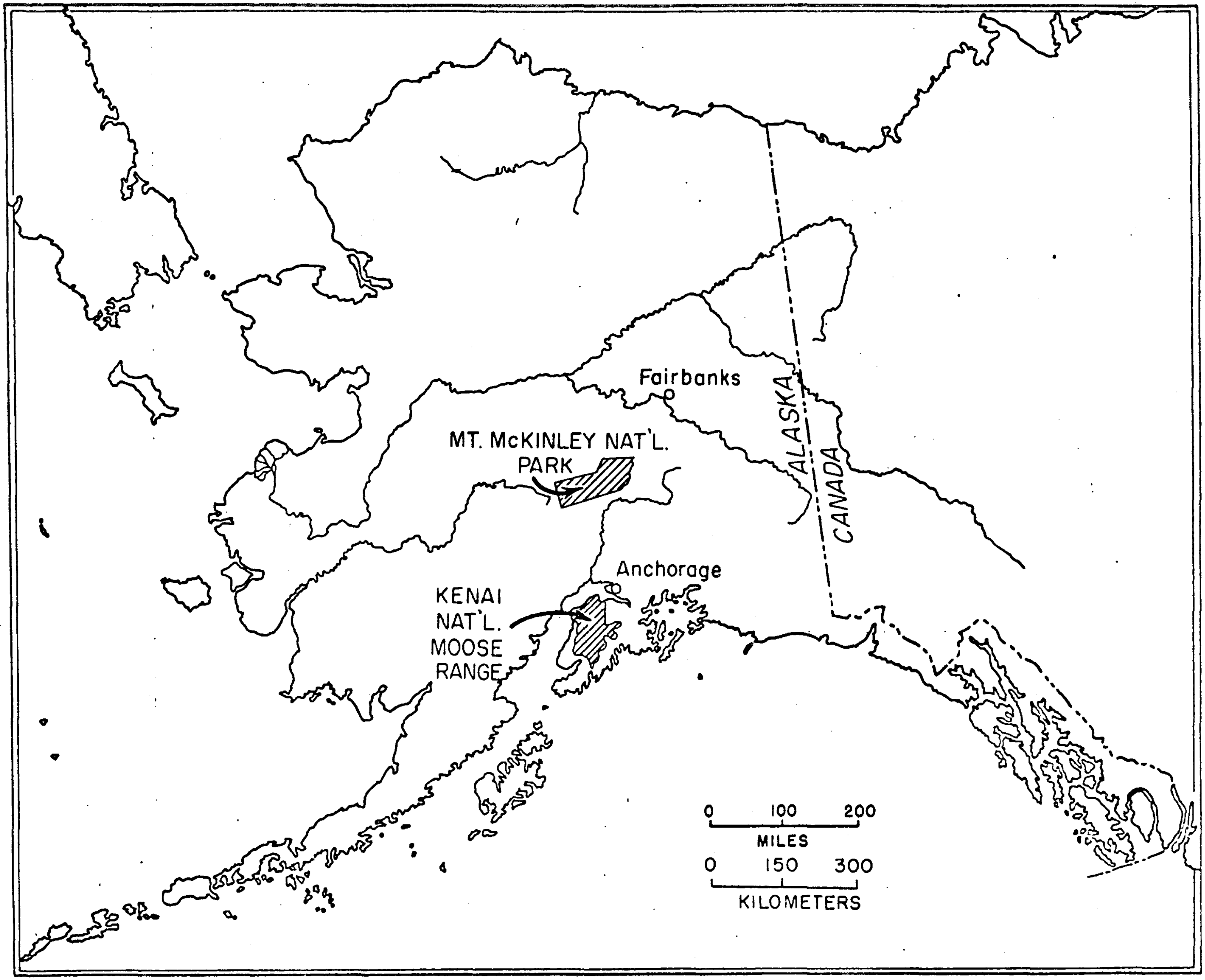

Figure 1. Map of Alaska with study areas indicated.

Spencer and Hakala (1964) and Bishop and Rausch (1974) have described the topography, climate, and fire history of the Kenai Peninsula in detail, as well as the population dynamics of resident moose. The MRC, a cooperative research project of the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service, and the WLRA are both located in an area extensively burned in 1947. Both areas contain vegetation representative of the 1947 Burn; regrowth areas with paper birch and white and black spruce predominating and remnant stands with mixed birch, spruce, and aspen. The Burn typically contains a great deal of interspersed habitat types and, thus, has a large "edge" effect (LeResche et al. 1974a).

Range conditions in this area have generally declined in recent years. Bishop and Rausch (1974) considered the range to be chronically deficient. Oldemeyer et al. (in Franzmann and Arneson 1975) stated that the major range change on the northwestern Kenai Peninsula was modified species composition. The area was formerly a multispecies range and was not dominated by paper birch, a relatively poor winter forage.

During this study, snow cover on the Peninsula was deeper and more persistent than that reported previously. Bishop and Rausch (1974) noted these changes for the years 1971-72 and 1972-73. Winter 1973-74 was somewhat milder, but winter 1974-75 followed the same general pattern of the other two years. Based on a comparison of monthly means to a previous 10-year average (1961-71), most winter months were colder during the three years of this study. Wolves (*Canis lupus*), virtually absent from the Peninsula in the early to mid 1900's, built up to significant numbers in the early 70's. Conservative estimates of the number of wolves on the Peninsula in early 1976 ranged from 60 to 70 (A. Franzmann, R. Ritchey, pers. comms.).

The moose population on the Peninsula declined concurrent with these changes (Bishop and Rausch 1974. Winter mortality of calves on the northern Kenai Peninsula was especially high during the three winters in which the study was conducted, and calf mortality within the Pens was 100 percent for these winters. Bishop and Rausch (1974) noted that mortality was highest among calves and that mortality commenced at relatively low snow depths on the Kenai compared to other parts of Alaska. They suggested that previous mild winters had supported very high populations and encouraged the persistence of densities capable of altering plant species composition. Recently, Oldemeyer et al. (in Franzmann and Arneson 1975) demonstrated the importance of variety in the diet of moose. LeResche and Davis (1973) stressed the importance of nonbrowse, low-growing species during the winter, and they later suggested that the unavailability of non-moose forage because of excessive snow was the cause of nearly total calf mortality on the Kenai Peninsula (LeResche et al. 1974b).

METHODS

Table 1 summarizes the areas where moose were observed and the types of animals observed during this study. At the MRC, attempts were made to trap cows and calves, both inside and outside the pens, in fenceline traps during fall and winter. During late summer 1971, Johnson (Johnson et al 1973) "created" orphan calves by trapping cows and calves

Table 1. Summary of behavioral observations conducted on the Kenai Peninsula and other areas of Alaska during winters 1971-1975.

Winter	Study Area	Type of Moose Observed	Observer
1971-72	Moose Research Center	Introduced orphans, penned cows and calves	
	Lobe River Valley	Free-ranging	Johnson
1972-73	Moose Research Center	Penned cows and calves Introduced orphan	
	Vicinity of town of Soldotna	Free-ranging	Johnson
1973-74	No Observations		
1974-75	Moose Research Center	Penned cows and calves	
	Willow Lakes Rehabilitation Area, 1947 Burn	Free-ranging, in aggregations or solitary	
	Mt. McKinley National Park	Free-ranging cows, yearlings, and newborn calves	Sigman

outside the MRC and releasing the calves into a pen. He "created" 11 such orphans this way and also collared one orphan that had been born in the pen. In 1972-73, he introduced four cow-calf pairs, two "orphans," and two lone calves into the pens. In fall 1974, one orphan, one cow and two cow-calf pairs were trapped and marked inside the pens.

All animals were marked with ear flagging and/or collars. Orphan calves were radio-collared, as were one or both members of a cow-calf pair trapped inside the pens or intended for the pens. During all winters, some calves that had been born inside the pens remained unmarked.

Methods for locating both penned and free-ranging moose included tracking with a radio receiver, tracking in snow cover, accidental sightings from the ground, or aerial sightings.

The types of observations emphasized included those of activity patterns (duration and frequency of feeding and resting periods and movements), social interactions ("helping" behavior on the part of the cow, "following" behavior on the part of the calf or yearling), and use of specific habitat types and food plants.

RESULTS AND DISCUSSION

FACTORS INFLUENCING CALF MORTALITY

Factors which might be expected to result in calf mortality or increase calf mortality rates include: 1) severe snow conditions, 2) severe combinations of low temperatures, winds, or snow storms, 3) a rapidly increasing wolf population, and 4) a decline in winter range quality. An examination of these factors on the Kenai Peninsula during the study can help to determine the role of observed caretaking patterns.

Snow Conditions

Snow conditions during winter 1974-75 were similar to those of 1971-72 and 1972-73. Fig. 2 illustrates the relative severity of four winters and the timing of known calf deaths in the pens of the MRC. The very early loss of calves after snow had accumulated to moderate depths is obvious. Only qualitative descriptions of various layers in the snow pack were recorded at the MRC, so the possible interaction of variable snow hardness with increasing depths cannot be determined.

Weather Conditions

Although air temperature is one of the most easily measured components of weather, it can vary considerably with micro-climate. Accurate records of maximum and minimum temperatures at the MRC are not available; however, the fairly complete records of the Kenai FAA weather station can be used to indicate general trends. All winter months were colder than the previous 10-year monthly average during some of the years of the study, and January, in particular, was much colder during all four years (Fig. 3).

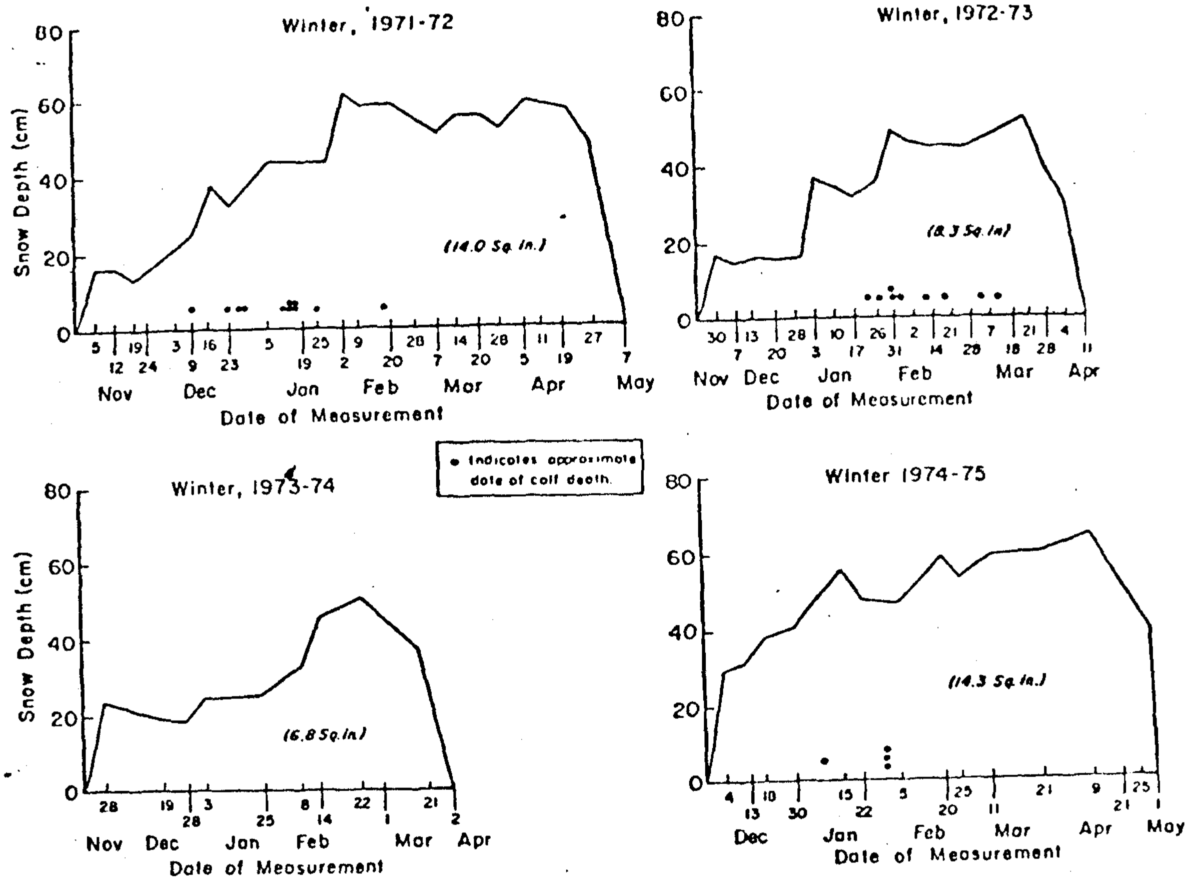

Figure 2. Snow depths measured in thin birch-spruce regrowth habitat at the Moose Research Center from 1972 through 1975 (Adapted from Moose Research Center Progress Reports 1973, 1974, 1975).

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.

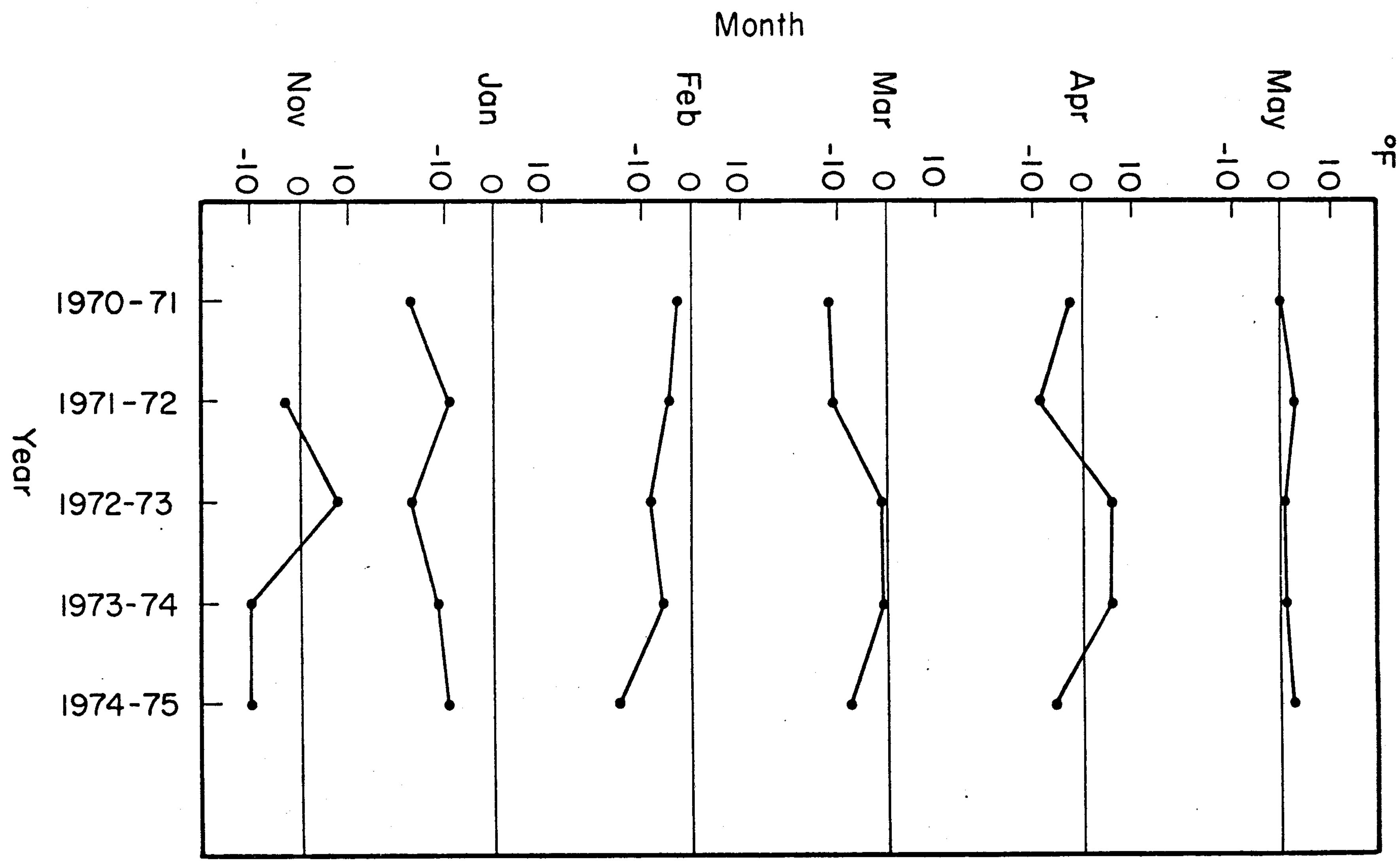

Figure 3. Departure from 10-year averages (1961-71) of monthly average temperatures at Kenai FAA weather station during the winters 1971-75.

The actual capacity of moose to thermoregulate has never been measured, but Gasaway and Coady (1974) suggested that thermoregulatory metabolism may be a negligible cost of the overall energy budget of moose. A calf, however, would have a disadvantage at extremely cold temperatures because it has a higher surface area to volume ratio than an adult and loses more heat per unit of weight to the environment. At any rate, it is likely that colder temperatures and specific combinations of cold, snow, and wind conditions did affect the timing and extent of calf mortality.

Wolf Predation

Wolf populations in this area were increasing in the early 70's and a number of wolf-killed calves and adults were located. Wolves did not enter the pens of the MRC and a study of wolf populations, movements, and impacts on the moose population was begun only this year. It is possible to speculate that the extremely high calf mortality in the early 70's was probably not significantly increased by wolf predation. In fact, wolf numbers may have built up because of the large supplies of calf carcasses during those winters. The situation may now have changed; examination of recent wolf-killed moose indicated that wolves were not selecting calves or adults with low marrow fat content (Franzmann and Arneson 1976).

Nutrition

Deficiencies of the present winter range in this area have been described. In general, a major consequence of a persistent snow cover is prenatal nutritional stress, which affects viability of the fetus, calf size at birth, and vigor of the calf (Knorre 1959, Houston 1968, Peterson 1974). The cow must recover from winter weight losses, lactate, and put on fat reserves on the summer and fall ranges, and the calf must grow and put on fat reserves. On the Kenai, vulnerability of calves to nutritional stress is demonstrated by the calf deaths early in the winter. Nonbrowse forage is an important alternate food during the winter (LeResche and Davis 1973), and it seems that even moderate early snow cover results in nutritional stress because additional energy must be expended to crater for the ground vegetation.

Bond Disruption

Table 2 characterizes the bond status of various cow-calf pairs observed on the Kenai Peninsula. A few pairs exhibited close association until the death of the calf; one cow displayed searching behavior near the carcass; and another cow defended her dead calf from an observer for several days. Several pairs maintained a loose association with observed separations. Most of these pairs separated permanently. Finally, agression by cow #79 towards her previously abandoned calf was observed. In a final report on Johnson's observations, LeResche et al. (1974b) concluded that:

> 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.

Table 2. 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 calf's death	Johnson
#89/#90	Continuous	Cow seen searching and vocalizing in area of calf carcass	Johnson
#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
#79/#117	Separation	Cow seen alone several times Active chase of calf by cow 2 days before death of calf	Sigman

Accumulated evidence since 1971 indicates that bond disruption is a common occurence on the northern Kenai. Many lone calves were sighted outside the MRC 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 were substantial during the winters of 1971-72, 1972-73, and 1974-75 (P. Arneson, J. Davis, A. Franzmann, D. Johnson, and R. LeResche, pers. comms.).

Behavior of cows toward calves from which they had separated differed from that of cows toward yearlings at the time of parturition. In Mt. McKinley National Park, I observed instances of intolerance of yearlings by precalving cows. Later, cows accompanied by newborn calves made sustained, repeated aggressive charges toward yearlings. These yearlings appeared reluctant to leave the cow when disturbed or to leave the vicinity of the cow. On the other hand, Johnson (1975) observed fairly indifferent separations and reunions of cows and calves. The aggression toward a previously separated calf that I observed was particularly brief and effective. It is possible that part of the mechanism of bond disruption is the cow's failure to "recognize" or tolerate a calf whose weakened condition changes its physical appearance. The weakness of the calf would then lessen its ability to pursue the cow, which must move to satisfy its own maintenance needs. Thus, bond disruption would in most cases be a fairly passive process for the cow, and bond maintenance would require persistence from the calf.

Regardless of the mechanism of bond disruption, the question still remains whether or not a sustained over-winter bond is advantageous to calf survival. Johnson (Johnson et al. 1973) could discern no pattern with respect to the time of mortality of orphans and calves with cows during the two winters with 100 percent calf mortality. During my own observations, all radio-collared calves died. In fact, although Table 2 shows an observed variety of cow-calf behavior patterns, survival of the cow and death of the calf were often the case on the northern Kenai during the period 1971-75. Disruption of the cow-calf bond no doubt reduced the ability of the calf to exploit available resources. Even if calves had stayed with cows, however, they probably would have died sometime during these severe winters. Furthermore, their presence might have stressed the cows, affecting their chances of survival and the viability of fetuses.

HYPOTHESIS CONCERNING THE NATURE OF THE WINTER COW-CALF BOND

Patterns of winter range use include migration, use of a traditional home range, and local movements within the home range. However, within these general patterns, it appears that moose do not occupy the 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. 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. Because moose are likely to be in negative energy balance throughout the winter (Gasaway and Coady 1974), survival depends upon maintaining a rate of fat and protein utilization within a range that does not result in death from undernutrition before the winter period ends.

Evidence of selection for certain habitat types or forage species would demonstrate that use of winter range is not random. Several studies have shown that moose select specific winter habitats (Telfer 1970, Krefting 1974, Peek et al. 1976) and that moose are often found in a single habitat type for several days or months (Timofeeva 1967, Loisa and Pullainen 1968, Van Ballenberghe and Peek 1971). Within general habitat types, moose exhibit feeding selection for various forage species (Milke 1969, LeResche and Davis 1971). I observed a form of forage selection during cratering activity. Moose often sniffed or extended their tongue into the snow prior to cratering.

Apart from direct evidence of selection of forage species in Alaska, it is theorized that moose, as large generalist herbivores, must necessarily be selective feeders, particularly during winter. The optimum model for such an animal is to possess feeding preferences which it learns through trial-and-error throughout its lifetime (Westoby 1974). It can then adjust its diet to a variety of food sources that change in location, quantity, or quality. By this process, the large herbivore could obtain sufficient energy by obtaining an optimum nutrient mix within the fixed bulk of its rumen.

Habitat use by moose within the MRC pens differed from that reported in the literature; they utilized or travelled through several small areas of different habitat types in a few hours or a single day. This behavior was probably due to the nature of the 1947 Burn area with its considerable interspersion of habitat types. Overall, a preference for regrowth areas and mature hardwood stands can be demonstrated, where advantages of increased food availability must outweigh disadvantages of deeper snow (LeResche and Davis 1971). The consequence of a poor winter range such as the birch-dominated 1947 Burn area is that when the availability of the major alternate food source becomes limited by snow conditions, forage selection becomes crucial to survival. However, because willow species make up such a small percentage of the winter range (LeResche and Davis 1971), moose apparently cannot at present select browse species more palatable than birch. With a limited range, exploitation of food sources to obtain that "optimum nutrient mix" as often as possible may be particularly crucial for successful overwintering.

The importance of habitat and of range selection suggests a role for the cow-calf bond. 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 for survival. A certain range of strategies of habitat occupation will insure successful overwintering, depending upon the underlying nutritional status of cows in the population and the actual winter conditions.

Many features of moose life history make learning by the calf likely, although little evidence exists that ungulates, in general, actively teach their young (Lent 1974). Mayr (1975) discussed the concept of noncommunicative behavior, behavior directed at objects that do not respond, such as food or habitat. Under certain conditions selection favors open programs for noncommunicative behavior, wherein the content of a behavioral sequence is supplied by experience rather than determined by genetics. These conditions include dynamic habitat and food sources, 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. Thus, if moose calves do have open behavioral programs, a calf on the Kenai could learn to select cranberry, the major nonbrowse plant, by trial-and-error, or it could learn by associating with a cow and imitating her feeding selections. Open programs, as opposed to genetic programs, allow for additional input during the animal's ontogeny. According to Mayr (1975), the object of an open program (e.g., cranberry as food source) is acquired through experience, although the motor patterns elicited (e.g., cratering and ingestion) are rigidly determined.

Learning specific objects of open programs does not necessitate active teaching on the part of the cow. The extent to which the calf follows the cow, feeds and beds in the same area, and selects the same foods could constitute an imprinting process. To apply the concept further to moose feeding behavior, the strategy of selecting food in a particular sequence to obtain optimum rumen fill would be learned in association with the cow, although high palatability of certain plant species that have long been moose food is likely innate (Markgren 1966).

The capacity represented by innate palatabilities would thus be complemented by trial-and-error learning and would result in use of a great variety of foods. The cow would serve as a model to increase the efficiency for sampling the environment. The calf could then feed by imitating the cow's food selection, the cow could directly provide foods to the calf, or the cow could yield her feeding site to the calf. All three behaviors were observed during this study, although a wide range of feeding patterns occurred. Such behavior demonstrates the type of benefits that the cow can provide to her associated calf.

Another aspect of following behavior would result in the use of the same habitat by the cow and calf. The calf could then imitate and learn from the cow and benefit from her choices of food and habitat type. Markgren (1975), on the basis of his orphan calf studies in Sweden, believed 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. Lone calves that I observed did stay in very small areas for long periods of time and were less wary of my approach, compared to cow-calf pairs and solitary adult moose.

During the winters 1971-75, synchrony of activity and rest within cow-calf pairs was marked, but several times the cow and calf rested or fed at different times. A lack of synchrony may be an important indicator of the fate of the calf. Bubenik (1965) has hypothesized that ungulate calves out of synchrony with their dams may be displaying atypical activity patterns which could disrupt digestive efficiency so that a calf would become increasingly weak and lose resistance to decimating factors.

Following the cow can also decrease the vulnerability of the calf to predators. Mech (1966) observed that most calves killed by wolves were seperated from cows. Active defense of the calf is apparently usually successful.

Finally, a calf may follow a cow to new habitat or 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 surrounding Game Management Units (KNMR files). 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 in which flexibility towards environmental components is at a premium. Thus, the animal can expand its range temporarily or occupy new areas on a permanent bases. 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 are of primary importance, while factors such as winter conditions and predators are of secondary importance.

It is possible that under optimum conditions 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 the moose, if food supplies are optimal, a calf needs less help foraging strategically and even "poor mothers" (i.e., inexperienced, young, or primiparous cows) can raise calves to yearling age. The fact that moose calves are indeed able to survive without cows under some conditions has been demonstrated by the successful transplants of calves in Alaska (Burris and McKnight 1973).

Geist (1974) has related twinning rates to habitat conditions by suggesting that high twinning rates are an adaptation to the abundant, highly-nutritious food supplies available soon after a burn and that the birth of single calves is favored as habitat conditions decline. It follows that maternal behavior and the survival of calves to yearling age are similarly adaptive. Both processes will be favored under good habitat conditions, with the opposite situations - abandonment of calves and high calf mortality - being favored under declining habitat conditions. Certainly, however, predator densities and snow conditions have an impact on successful reproduction.

Under the conditions on 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, successful reproduction in the sense of raising young to sexual maturity was relatively infrequent during the study period. Active or passive separation of pairs was a common occurrence early in "severe" winters. The successful long-term strategy for cows is apparently one that allows them to survive stressful periods at the expense of offspring survival. This form of mother-infant relationship, favoring survival of the proven reproductive, is obviously adaptive in a species that frequently expands its range and colonizes local areas of newly-created seral habitat.

On the whole, behavioral research provides insights for management, though often of a subtle nature. The present study indicates that caution is in order before generalizing from moose behavioral studies that may describe responses by a single population to a unique set of conditions.

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