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MOOSE BEHAVIOR STUDIES

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SUMMARY

Previously reported studies concerning feeding habits, the influence of snow on feeding, ontogeny of cow-calf behavior, survival of orphaned calves, habitat use, local movements, aggregations and mechanisms initiating migration in moose are summarized and findings discussed.

CONTENTS

BACKGROUND

Moose *(Alces alces)* management requires knowledge of moose behavior patterns as well as of demographic facts. Feeding habits, the cow/calf bond and movements and social behavior are three categories of behavioral information directly applicable to management. Studies at the Moose Research Center over the past five years have concerned these aspects of moose behavior as it occurs on the Kenai Peninsula. Results of these studies have been presented in four Project Progress Reports (LeResche 1970, LeResche and Davis 1971, LeResche et al. 1973 and Franzmann and Arneson 1973), one Final Report (Johnson et al. 1973), several publications (LeResche 1972, 1974; LeResche and Davis 1973; Peek et al. 1974) and a M.S. Thesis (Stringham 1974a). This Final Report summarizes important findings reported in greater detail in these other publications.

Feeding Behavior

Biomass and species of plants eaten by moose are important factors in the species' ecology. Traditional studies of relationships between wild ungulate consumers and plant producers have stressed abundance, production and use of large woody shrubs (cf. Spencer and Chatelain 1953, Spencer and Hakala 1964, Houston 1968).

Utilization estimates from analyses of plants are very difficult (LeResche and Davis 1971) with current techniques, therefore, many studies have examined animals and their behavior to discover patterns of use. Most of these studies (e.g. Bassett 1951, McMillan 1953, Harry 1957, Knowlton 1960, McMahan 1964, Houston 1968, Bell 1970, Nicholson et al. 1970) are concerned primarily with the kinds of food eaten, but many also attempt to estimate quantity of food consumed (cf. Van Dyne 1968). Common techniques range from feeding trials of captive or domesticated animals (Palmer 1944, Bilby 1968, Reid 1968, Marsh et al. 1971, Ulrey et al. 1971) to micro- and macro-analyses of stomach contents or feces from killed or living animals (Mulkern and Anderson 1959, Brusven and Mulkern 1960, Storr 1961, Bear and Hansen 1966, Stewart 1967, Field 1968, Gaare 1968, Sparks 1968, Sparks and Malechek 1968, Galt et al. 1969, Hansen and Flinders 1969, Nellis and Ross 1969, Williams 1969, Medin 1970, Rice 1970, Ward 1970), chemical methods (Theurer 1970) and observations of wild (Harper et al. 1967, Miller 1968, Houston 1968) or tame (Bjugstad et al. 1970, Bergerud and Nolan 1970, Hungerford 1970, Laycock and Price 1970, Martin and Korschgen 1963, Nixon et al. 1970, Short 1970, Wallmo and Neff 1970, LeResche et al. 1971) animals.

Tame animal studies solve most of the problems associated with measuring use from what is left behind and demonstrate food habits not obvious when browsed plants are observed (LeResche et al. 1971). However, other variables are introduced when tame animals are dealt with. Feeding behavior of tamed animals may be altered by taming or by supplementary feeding necessary to tame the animals. Little objective evidence is available to dispute these problems, but much empirical data (Buechner 1950, Wallmo 1951, McMahan 1964, Wallmo and Neff 1970) suggest these are minimal, especially if supplemental feeding ceases when observations begin. Problems of individual variation and quantification are more serious (cf. Wallmo and Neff 1970).

In moose food studies, emphasis on woody shrubs has persisted despite an impressive array of evidence that moose are extremely catholic in their tastes. Especially in spring and summer, they consume forbs, grasses, mushrooms, lichens and practically all other floral components of their environment. Murie (1934) reported a great variety of foods taken on Isle Royale. Peterson (1955) listed more than 100 species or groups of plants taken at least occasionally by moose. Houston (1968), although stressing that browse was the most important food class during all seasons in Wyoming, demonstrated that moose ate significant quantities of grasses, sedges, rushes and forbs in spring and summer. Peek (1974) has reviewed all moose food studies to date.

Effects of Snow on Moose Feeding Behavior

The potential effects of snow on moose distribution, behavior and survival have been well documented in several reviews (Formozov 1946, Nasimovich 1955, Coady 1974). Until now, most research has considered the effects of snow on ungulate movements (Des Meules 1964, Kelsall 1969, Kelsall and Prescott 1971, Coady 1974, LeResche 1974).

Snow depth is considered the most important variable for moose (Coady 1974), because migration from summer to winter range and daily activity may be influenced, and because food becomes less accessible as snow depth increases. Little mention has been made of moose pawing through snow for food, as do elk (*Cervus canadensis*) (Murie 1951), muskoxen (*Ovibos moschatus*) (Lent and Knutson 1971 and Tener 1965) and caribou (*Rangifer tarandus*) (Pruitt 1959 and Henshaw 1968). Des Meules (1964) stated, "Moose do not appear to have learned to use their feet to dig for food beneath or within the layer of snow...On two instances only, we have seen evidence of moose nuzzling through 8 or 10 inches of soft snow to reach underlying browse."

However, "cratering," or pawing through snow for food, is a common phenomenon on the Kenai Peninsula. Here moose often crater above timberline for dwarf willows (*Salix* sp.), in sedge meadows for *Carex* and in mature forests for a variety of understory plants. Feeding studies also reported here have discovered significant winter utilization of decumbent forage species (especially lowbush cranberry--*Vaccinium vitis-idaea*--and lichens), and have indicated that cratering for food is an important behavioral pattern. Therefore, a study was designed to measure the frequency and location of crater digging and its relation to snow parameters, and to estimate the energetic cost of this behavior.

The Cow-Calf Bond as a Factor In Calf Mortality

Moose calf production, measured as a calf:cow ratio in early June, rarely approaches either the biotic potential of the species or even the pregnancy rate of the preceding autumn (LeResche and Davis 1971). In addition, calf loss sometimes exceeds 25 percent during the first two weeks of life, and may exceed 50 percent in the first five months (LeResche 1968). Some causes of early calf mortality have been documented (LeResche 1968), but are still poorly understood. Very likely, the mother-young relationship is an important mediator of early calf survival, and two separate studies at the MRC considered the causes of early calf mortality (Davis in LeResche and Davis 1971) and the ontogeny of cow-calf behavior during summer (Stringham 1974a).

The role of the cow in calf survival may be also very important during the calf's first winter, when food becomes difficult to find or secure, locomotion is hampered and predators gain a new advantage. Although legend has it that the cow increases the calf's chances of survival by leading it to food, "breaking trail" through snow, bending shrubs to within the calf's reach and defending it from wolves, the cow may in fact hinder the calf's survival--by competing for food or using the calf as a "sacrifice" to escape wolves (*Canis lupus*). Whether a calf's chances for survival are altered by the presence of the cow, and if so, whether they are increased or decreased, is an important theoretical and practical question, especially where management involves hunting cows in autumn. A study of orphaned calves within the MRC and in nearby areas was designed to explore this question (LeResche et al. 1973, Franzmann and Arneson 1973).

Local Movements, Habitat Use and Social Behavior

Seasonal relationships between moose and habitat and social relationships among individual moose are important mediators of ecological and population dynamics. Associated studies have defined seasonal movements (migrations) and population identity of moose on the Kenai Peninsula and elsewhere (LeResche and Davis 1971, LeResche 1972, LeResche et al. 1973, Franzmann and Arneson 1973, LeResche 1974).

Because the 2.6 km^2 enclosures at the MRC are smaller than the normal home range of moose, and because moose within them are forced to remain within 2-3.5 km of other individuals enclosed in the same pen, social relationships are undoubtedly altered within the pens. Four studies were designed to evaluate aspects of this problem. One considered home ranges of animals within MRC enclosures (LeResche and Davis 1971), and an associated study investigated habitats used by enclosed moose during different seasons. A third study analyzed social associations and aggregations of moose within the pens (LeResche and Davis 1971) and in several areas outside the pens (Peek et al. 1974). The fourth study considered "migratory tendency" of enclosed moose by observing seasonal differences in fenceline pacing and correlating these with known migrations outside the pens (LeResche 1974). This study was designed to indicate whether any "internal" migratory urge might be present in moose confined in a location removed from some of the apparent external stimuli for migration.

OBJECTIVES

To determine what species of browsed and grazed plants are taken in what pattern by moose and to qualitatively estimate consumption of all plant material by moose.

To evaluate the effects of snow conditions on moose feeding patterns and the related snow cratering behavior of moose.

To locate parturient cows during the calving period and post-partum cows during succeeding weeks, to ascertain time and cause of early calf mortality.

To investigate the development of behavior of moose calves.

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

To determine patterns of moose habitat use within the enclosures.

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

To analyze "migratory tendency" of enclosed moose and determine whether internal factors may mediate migratory movements.

PROCEDURES

Moose Feeding Habits

Tame moose were obtained as calves in October 1969 (two males) and May 1970 (one female). All were born in spring, 1969. They were raised on natural moose range, with calf starter feed (Alaska Mill Feed Co., Anchorage) fed supplementally until July 1970. The three were confined together in a 10-acre pen (containing a 4-acre lake) through November 1970. Summer observations were made within this pen. In

November the males were released into a one-square-mile enclosure with 14 other moose. "Normal range" winter observations were made of these animals. "Depleted range" winter observations were made of the female within the 10-acre pen, which had supported the equivalent of 213 moose per square mile during the previous winter and was supporting 107 moose equivalents per square mile during the winter of observations.

Tame moose were located by radio-telemetry and food intake was recorded by an observer standing 1-2 m from the moose and recording species and size of each bite eaten. The observer used pencil on an IBM optical page reader sheet or spoke into a tape recorder. Hours of observation were distributed throughout daylight hours. Bite size in summer was recorded by estimating number of leaves ingested. Bites were classified into four categories: less than 5 leaves, 6 to 10 leaves, 11-20 leaves and more than 20 leaves. Mean number of leaves per bite in each category was taken as 2.5, 7.5, 15, and 25, respectively. Mean weight of each bite by category was then calculated as 2.5, 7.5, 15, and 25 times the mean weight of 500 randomly selected leaves from 100 separate plants. Bite size in winter was recorded by estimating length of stem ingested. Bites were classified in 4 categories: less than 3 inches (7.6 cm), 3 to 6 inches (15.2 cm), 6 to 12 inches (30.5 cm) and more than 12 inches. Mean length of stem in each bite category was taken to be 3.8 cm, 11.4 cm, 22.8 cm and 38.1 cm, respectively. Thirty terminal stems of each of these lengths were then randomly clipped from six plants of each species considered. Mean weight per bite was calculated using the mean weight of the appropriate 30 stems. Biomass of food ingested per day was estimated by applying these weight/bite estimates to estimated bites/day. Plants were collected for chemical analyses during the first week in May. Analyses were done by WARF Institute (Madison, Wisconsin).

Effects of Snow on Feeding Behavior

Snow quantity and quality were monitored in Pens 1 and 2 using one permanent plot in each of the following habitat types: dense mature hardwoods, thin mature hardwoods, sedge meadow, spruce regrowth, birch-spruce regrowth (thin), birch-spruce regrowth (dense), spruce-*Ledum* and mature spruce. At weekly intervals a trench was dug in each plot and the total depth, thickness and consistency of each snow layer were recorded. Depth of "sink" in the snow of man's foot was also measured. Presence of lowbush cranberry and the ground vegetation was recorded.

During the first winter of observations (1971-72) feeding crater concentrations were searched for and when found the habitat type was identified and the area of the concentration measured. Each crater was then measured in length, width and depth. Species of plants eaten and present in each crater and their relative abundance were recorded. Also, the location of the craters within the plot was noted to determine if moose used keying characteristics before digging a crater. Snow profiles were taken at each crater concentration area.

In the second winter (1972-73) cratering activity by moose was studied and evaluated by observing both adults and calves, inside and outside the MRC enclosures. Observations noted were; number of digging "paws" per crater, time spent digging per crater, time spent feeding per crater, total time per crater, number of craters dug per digging period and forage utilized in each crater.

Early Calf Mortality

Eight adult females were marked with radio-collars and located daily during the parturition period in late May and early June 1970 and at irregular intervals of about one week thereafter.

The Cow-Calf Bond

This study was carried out intermittently during summer 1970, and with more regularity during summer and autumn 1971, by S. F. Stringham, Alaska Cooperative Wildlife Research Unit. His study method involved observing cows and calves from close range (at least two cows apparently were acclimated to his presence) and recording whatever behavior he noticed.

Orphan Calf Survival

The study was conducted at the Kenai Moose Research Center during the winters of 1971-72 and 1972-73. During the first winter emphasis was placed on orphan calves. David C. Johnson, graduate student (MS) at the Alaska Cooperative Wildlife Research Unit, was responsible for the work.

Between September 21 and November 23, 1971, 11 calves were trapped from the area outside the MRC. These calves were released in Pen 4. When the mothers were also trapped, they were released outside the pens. One calf that was born in Pen 4 was orphaned when its mother died from a drug overdose. This calf was also used in the orphan project. Seven of the calves were equipped with radio-collars and all were ear tagged for identification. Most observations were made in Pen 4. One lone calf was observed in Pen 3 for several days in February 1972.

During the winter of 1972-73 emphasis was on non-orphan calf behavior and Mr. Johnson was hired as a temporary game biologist to conduct the work (Johnson et al. 1973). On September 18, 1972 trapping of cows with calves from the area outside the pens began and by November 11, 1972, four cows with calves were introduced into Pen 4. Both mother and calf were equipped with radio-collars in two cases. One of the other cows had a radio as did one other calf. All mothers and calves were marked.

Six calves were born inside the moose pens in the spring of 1972. One calf was born in Pen 1, four calves were born in Pen 2, and one calf was born in Pen 4. On October 12, 1972, one of the Pen 2 calves escaped into Pen 1 with its mother. The Pen 4 calf was not seen after October 20, 1972, and was assumed to have died. Before winter, two of the cows were equipped with radios. All of the cows and two of the calves were marked.

Prior to the winter months, Pen 1 had two cow/calf pairs, Pen 2 had three cow/calf pairs and Pen 4 had the four cow/calf pairs that had been introduced from outside the pens.

During both winters of the studies, field procedures were almost identical. They were as follows:

A. Survival and Physical Condition

Calves and cow/calf pairs were observed on a daily basis dependent upon availability of each. Consequently some individuals were observed more frequently than others. Activity, behavior and condition of observed moose were noted, locations plotted on a map and dates of separation and mortality were recorded. The moose were located by one of the following methods:

1) Tracking with radio-receivers;
2) Sighting from ground and tracking in snow cover;
3) Aerial sightings.

B. Mortality Factors

When a dead calf was located, the following procedure was used:

1) Investigate events prior to death;
2) Autopsy the calf when possible;
3) Collect hair and femur samples.

C. Behavior Patterns

Types of observations that were emphasized were:

1. Social Interactions
   a. frequency of contact
   b. type of contact
   c. description of animal or group contacted

2. Activity Patterns
   a. feeding
   b. resting
   c. movements

D. Feeding

An attempt was made to determine what vegetation was used by the calves:

1) Rumen analysis on dead calves;
2) Identification of plants after observed feeding by calf;
3) Locating calf and back tracking in snow to determine what plants had been used.

E. Comparative Analysis

Survival and behavior of orphaned calves were compared to:

1) Survival and behavior of all calves at MRC;
2) Survival of calves outside enclosures;
3) Survival and behavior of calves at MRC with mothers.

Local Movements, Habitat Use and Migratory Tendency

Relocation of all moose radio-collared for the 1970 spring calf study was continued at irregular intervals (approximately one week) until the radios failed or until April 1971. Each observation was plotted on a 1:10,105 scale vegetation-type map. Habitat type, time of day, activity, date and other moose present were recorded.

All observations of enclosed moose along fencelines from May 1969 through March 1972 were analyzed, and correlations were drawn between fenceline location (e.g. north side, northeast corner), season and known movements of unenclosed moose (cf. LeResche 1972, LeResche and Davis 1971). For the purposes of this analysis, a sighting along a given fenceline (i.e. north) indicated an attempt (or urge) to migrate in that direction (i.e. northward).

Moose Aggregations

Following are the methods used as described in Peek et al. (1974):

> We follow Bergerud and Manuel (1969) in defining an aggregation as any group of animals that occur within reasonable proximity to each other. The problem of determining whether these aggregations were dictated by external factors such as topography or forage supplies, or whether they are in fact social groups wherein individuals interact among each other (Etkin 1964) will be discussed.
>
> Most aggregations were located by aerial search using a Piper Super-Cub, Aeronca Champ or Bell G3B helicopter. In addition, summer observations in southwestern Montana were made from vantage points where moose could be readily located from the ground due to the open nature of the area. In Minnesota, summer observations included moose using lakes, streams and ponds, as investigated from a canoe and also by air. All Alaska data were obtained by aerial search. Information from southwestern Montana was obtained from 1958 to 1960 and from 1965 to 1967, from Alaska between 1970 and 1972 and from Minnesota between 1967 and 1970. Aggregations have been grouped according to different periods representative of moose phenological patterns as follows: calving

period; summer; prerut; rut; postrut; early winter; midwinter; late winter; spring. These periods seemed most likely times when group sizes may vary for one reason or another.

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

FINDINGS

Feeding Habits

Results of this study were reported fully in LeResche and Davis 1971, 1973, and LeResche et al. 1973. These results are summarized by the following abstract from LeResche and Davis 1973.

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

species during part of the winter is probably an important factor in supporting the very high moose densities found on this range.

These results called attention to several aspects of moose ecology that were previously unknown or largely ignored. It was confirmed that Alaskan moose consume a far greater variety of plant material than is usually realized, and that factors other than browse production and availability are involved in determining overwinter carrying capacity of the habitat. Once again it was demonstrated that snow is important to moose population dynamics and behavior; however, this study showed that even a relatively light snow pack can have serious consequences for a moose population, when it depends upon non-browse foods. Whereas 70-100 cm is normally considered the threshold snow depth for serious effects on moose (cf. Coady 1974), this study showed that 20-40 cm of snow, if persistent, can cause significant mortality in very dense moose populations. It suggested that unavailability of understory plants may be a limiting factor in many moose populations, and that populations with nonbrowse foods available during a part of the winter are the ones that achieve spectacularly high densities of 4-6 moose per km^2 (10-15 per mi^2). The study pointed out the probable cause (snow over non-browse forage) for nearly total calf mortality during two recent winters on the Kenai lowlands.

The springtime predilection of moose for the foliose lichen (*Peltigera*) suggested the possibility of competition between moose and caribou re-established on the western slopes of the Kenai Mountains and on the Kenai lowlands. We have insufficient knowledge regarding food habits of upland moose, and no information regarding the importance of lichens to caribou on the Kenai Peninsula, but the possibility of competition should be investigated.

Influence of Snow on Feeding of Moose

Snow-feeding relationships suggested by the above study were further investigated in subsequent years. Emphasis was placed on quantifying digging (or "cratering") behavior. This is a behavior pattern not previously associated with moose, but one that is quite common for much of the winter in the 1947 Kenai burn and during autumn and early winter in sedge meadows throughout Alaska.

General conclusions were reported in LeResche et al. (1973) and Franzmann and Arneson (1973), and may be summarized as follows:

1. Cratering (digging with feet) does not become important until snow depths exceed about 20 cm. Until then, understory forage is eaten by nuzzling through the snow with the nose.

2. Cratering occurred throughout the period of total snow cover, but was less intense as spring approached.

3. Approximately 40 percent of foraging time may be spent cratering--the rest of the time being used to eat above-snow forage.

4. Snow depth thresholds, beyond which cratering does not sustain life, were 50-60 cm for calves and 60 cm for adults.

5. Snow density or hardness thresholds were not detected, but granular conditions caused difficulty in cratering. Digging strokes per crater varied between 5 and 208 and mean number of strokes per crater varied with conditions between 31 and 82.

6. Cratering concentrations varied from 19 to 58 craters per hectare.

Causes of Early Calf Mortality

No calf mortalities occurred, with the exception of twins lost during a breech birth. Their 9-year-old mother also died from the breech presentation.

Ontogeny of Moose Calf Behavior

Little reliable, new information resulted from this study, but Stringham (1974a,b) prepared an excellent review on the subject, drawing in part from his experiences at the MRC. An abstract (Stringham 1974a) follows:

Abstract

> The literature is reviewed and original observations are presented on birth sites, protection of infants, activity patterns, nursing, weaning, and breakdown of the cow-calf bond in moose. Unlike other ungulates, moose depend primarily on active defense to protect their infants from large predators. Hence, they are called "defenders" or "Verteidiger Type." Young infants are not usually isolated from their mothers and siblings. Calves were active only three-quarters as much as their dams and were rarely active more than a few minutes while their dams were resting. A cow's ventral outline, accentuated by color-shading patterns of teats, udder and pelage, probably releases and orients suckling attempts. Neonates first suckle while their dams are bedded. They solicit nursing by tongue-flicking, vocalizing, making mouth-movements which produce sucking sounds, and expose the bright pink gums and tongue in flashes; and by nuzzling the mother. Between their first and ninth weeks of life, two calves decreased proportion of time nursing more than 100-fold.

Overwinter Survival of Orphan Calves

The results of this study were partially reported in a Job Final Report (Johnson et al.) in 1973, as well as being partially reported in LeResche et al. 1973. Both sources should be consulted for exact details of the study.

Death of all orphaned and unorphaned calves during both winters 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. All calves apparently died of malnutrition due to unavailability of understory forage. Eight orphaned calves weighed lost a mean of 35 kg from autumn until their deaths in December or January, or 20 percent of their original body weight.

Probably the most important knowledge gained from the study was 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. Calves separated from their mothers often associated with other moose (associations with other cows, cows with calves, bulls, and other calves were all observed). Large aggregations of "lone" calves were observed in winter, and probably contained many calves with live (but not present) mothers. The fact that such separations occurred suggests that maternal care may not be available to some wintering calves due to natural behavioral traits, and that it might thus be beyond the power of game managers to provide such care during harsh winters.

Local Movements and Habitat Use

Results of this study are reported in detail in LeResche and Davis (1971). Home ranges (after Mohr and Stumpf 1966) varied from 38-121 acres, or only 15 to 47 percent of the available areas within each 2.56 km^2 pen. Overlap of home ranges was considerable (36-47 percent), and activity centers were closer together than expected by chance, suggesting non-random habitat selection. Immature birch-spruce habitats were used most frequently throughout the year, and no hourly preference for habitat types was demonstrated. Animals' daily movements were shortest in September, October and January ($\bar{x}$ 350-450m) and longest in July, November and December ($\bar{x}$ 700-850m).

Patterns of Aggregations

These results are reported in detail in LeResche and Davis (1971) and Peek et al. (1974). Within the MRC enclosures, degree of association was highest during rut and in February and lowest in December and January and just before parturition. Nonpregnant cows showed reduced sociality during the precalving period similar to pregnant animals.

Peek et al. not only summarized monthly differences in group size and composition in Alaska and other areas, but correlated differences with habitat (vegetation and terrain) and population composition. The following is an abstract of this paper:

> Distributions of annual aggregation patterns in three populations of moose occupying different habitats are evaluated. Aggregation sizes were related to breeding activities, mother-young relationships, the male social system, sex ratio of the

population, and habitat characteristics including forage sources, topography, and cover distribution. Group sizes were highest and most variable in the population of Kenai, Alaska, which was most dense of the three, and lowest and least variable in southwestern Montana, the least dense population. The highest group sizes occurred in fall and winter, and were lowest in summer. Cows were most gregarious in the Kenai population where the sex ratio favored females. Bulls appeared to aggregate following the rut, perhaps for establishment or reaffirmation of a rank order. Largest group sizes occurred when moose were primarily on the most open parts of their habitat: alpine tundra on the Kenai; recent cutover areas in northeastern Minnesota; and willow bottoms in Montana. This tendency may have a psychological basis, wherein the larger group replaces the role of cover in providing security for the individual, but in mountainous terrain animals were concentrated on forage sources at low elevations where snows were least likely to hinder movement and foraging. In contrast, on the relatively even terrain in northeastern Minnesota, successful occupation of late winter cover where forage was sparse was facilitated by dispersal of the population. The highly solitary and aggressive nature of the cow which escorts a calf may serve as a strategy for defense against predation.

Migratory Tendency in Enclosed Moose

Detailed results were presented in LeResche et al. (1973) and LeResche (1974). The conclusion was that enclosed moose (many of which had been first enclosed as adults) had migratory tendencies consistent with actual movements of unenclosed moose. This suggested that "internal" mechanisms, (probably responding to day length or solar angle) as well as climatic and phenological factors (e.g. snow, leaf fall) at the point of migration play a role in stimulating seasonal movements. The role of learning (e.g. as demonstrated by behavior of moose born within the enclosures) remains to be clarified.

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