FACTORS INFLUENCING BEHAVIOR AND SIGHTABILITY OF MOOSE IN DENALI NATIONAL PARK, ALASKA

A
Thesis

Master of Science

By
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Fairbanks, Alaska

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IN DENALI NATIONAL PARK, ALASKA

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Presented to the Faculty of the University of Alaska
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ABSTRACT

Moose in Denali National Park were studied in 1976-77 to assess aspects of moose behavior that might influence their sightability during aerial surveys. Interrelationships among diurnal activity, habitat use, and aggregation patterns were considered, and the relationship of season and weather to these aspects of behavior. Diurnal activity patterns changed markedly over short periods of time. Habitat use was strongly related to activity; moose tended to use denser cover when inactive. Aggregation sizes increased from late winter through fall and were larger in open habitats; moose in aggregations synchronized their activity. No relationship was found between aggregation size and weather; changes in activity and habitat use with weather appeared to be related primarily to diurnal weather patterns. Fall is the best time to conduct surveys, but sex-age composition biases will result; rapid changes in activity patterns over short periods of time make it important to replicate censuses.

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INTRODUCTION

Accurate assessment of population size and sex-age composition of moose (Alces alces) is essential if management of this species is to be effective. Demographic assessment has become an increasingly important task in Alaska because of increased consumptive use of moose by man, destruction of moose habitat by development, and maturation of seral forest habitats due to effective wildfire suppression.

Aerial survey from fixed-wing aircraft is the primary technique used in obtaining moose population data in Alaska. However, many animals are overlooked during these surveys (Timmermann, 1974). Survey technique, characteristics of observer and equipment, environmental conditions, and behavior of the animals influence the sightability of moose during aerial surveys; sightability is "the probability that an animal within an observer's field of search will be seen by that observer" (Caughley, 1974, p. 923).

Four aspects of moose behavior were considered in this study as potential influences on sightability of moose: seasonal patterns of diurnal activity, habitat use, the effects of weather on activity and habitat use, and characteristics of aggregations.

The potential importance of diurnal activity patterns of moose to aerial survey results has been suggested previously. Gasaway et al. (1980) found that standing moose had a much greater chance of being observed than lying moose during aerial transect surveys in May and June. Thus, diurnal variations in moose activity will affect the number of moose seen during surveys, depending on whether a survey is flown during a peak or low in activity. Sex and age composition counts will also vary if there are sex-age differences in activity patterns.

Habitat use by moose has previously been shown to be an important factor in their visibility (Timmermann, 1974). Gasaway et al. (1979), in a study of radio-collared moose, reported that habitat selection by moose was one of the most important variables affecting moose sightability from the air. Animals in open habitat types will be observed more easily than those in dense habitat types. Therefore, the precision and accuracy of population estimates will be affected if there is differential diurnal or seasonal habitat use. In addition, composition estimates will be unrepresentative if sex-age classes of moose make differential use of habitat types.

The influence of weather on pilots and observers during aerial surveys has been reported previously (e.g. LeResche and Rausch, 1974). However, the effect of weather on moose behavior has been investigated little. If moose alter either their activity patterns or habitat use in changing weather conditions, survey results may be affected. The set of conditions under which surveys may be flown is limited, but moose may alter their behavior within these limits.

Finally, aggregation characteristics of moose may influence their visibility. Size, composition, location of, and synchrony of activity within an aggregation are important factors influencing the accuracy of population and sex-age composition estimates.

The study objectives were:

1) to determine the influence of environmental factors, including season, time of day, and weather on moose activity, aggregation patterns, and habitat use,

2) to determine the variation in activity, habitat use, and aggregation characteristics among sex and age classes of moose;

3) to predict, qualitatively, optimum daily and seasonal timing of aerial surveys and predict biases in estimates of total numbers and sex-age composition of the population.

STUDY AREA

The study was conducted primarily in the eastern portion of Denali National Park, Alaska, formerly Mt. McKinley National Park (Fig. 1). Denali National Park was selected as the study area for this project for a number of reasons. At the time the study was undertaken, moose numbers in interior Alaska were generally very low, and the Park provided a large, relatively dense population which was habituated to humans. In addition, the presence of the Park road permitted easy access to areas with large numbers of moose. Observations of large areas from single vantage points were possible.

In the eastern portion of the Park, the "Outer Range" lies north of and parallel to the main mountain system. Between the two systems lies a broad valley, the floor of which is at elevations of 600-900 m. Most moose habitat in the eastern part of the Park lies either in this valley or along the river systems that transect it. The Park road runs through the valley, making moose habitat easily accessible to observation.

Moose were abundant in the study area. The approximate density of moose seen during November aerial surveys has been estimated at 0.3-0.6 moose per km^2 between 1974-1980 (Tankersley, 1981). Observed calf:cow ratios during November aerial surveys, 1974-78, have ranged from 8:100 to 19:100. Bull:cow ratios in the same period have ranged from 26:100 to 45:100 (Troyer, 1980).

Observations were made in March 1977 in the Reindeer Hills,

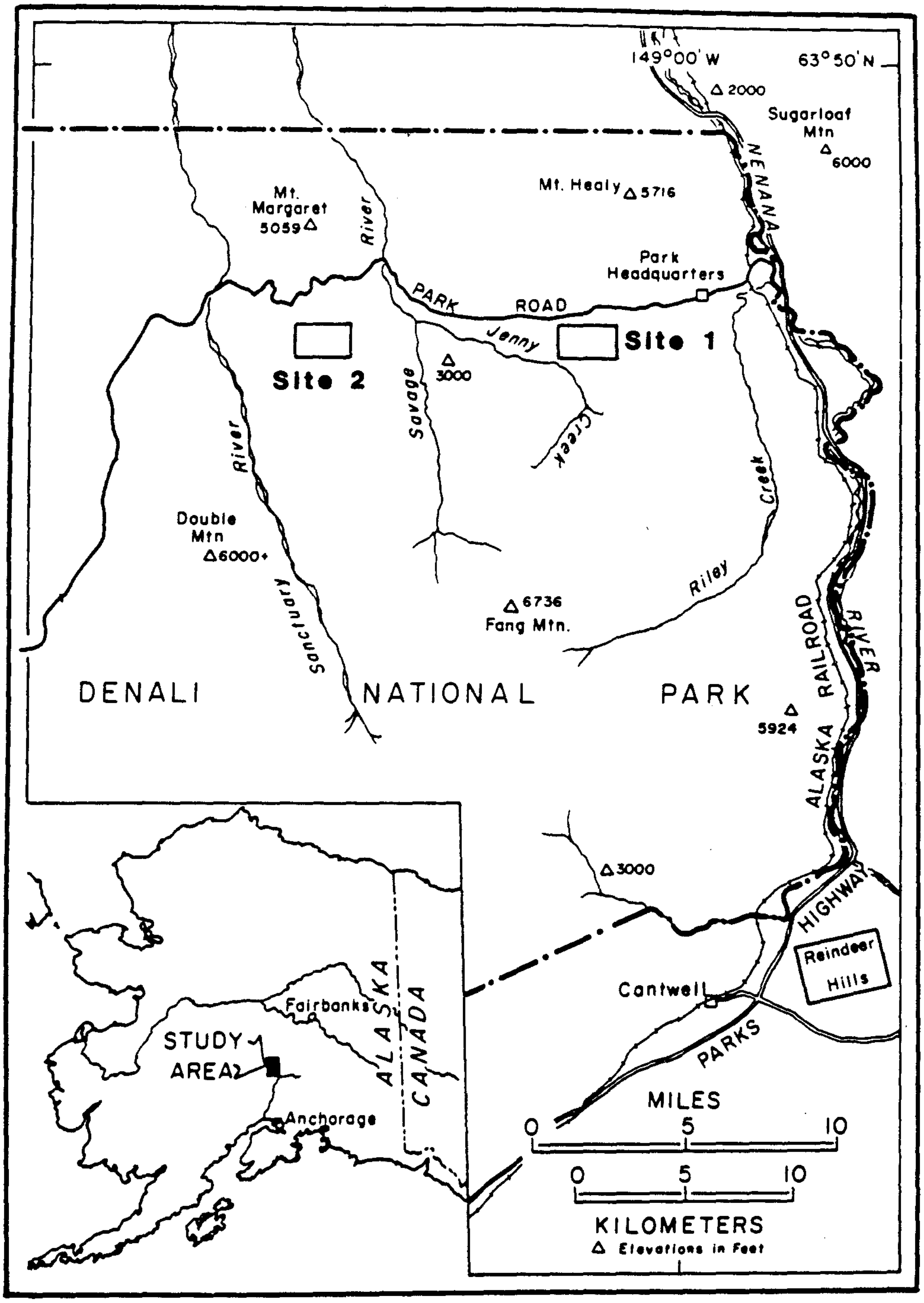

Figure 1. Map of the Denali National Park and Reindeer Hills study areas.

which lie approximately 50 km southeast of the Park study sites (Fig. 1). The vegetation and climate in this area are similar to those described below for the Park, but with increased precipitation.

VEGETATION

At the lowest elevations in the Park, vegetation consists primarily of boreal forest communities, with white spruce (*Picea glauca*) dominating, and black spruce (*Picea mariana*) in wetter sites. There are also large stands of aspen (*Populus tremuloides*) near the eastern boundary, and scattered balsam poplar (*P. balsamifera*) along major drainages.

At higher elevations, vegetation grades into the upland climax community described by LeResche et al.(1974), made up of the dominant shrub birch (*Betula nana* and *B. glandulosa*), willow (*Salix spp.*), and a variety of smaller shrubs and forbs. This vegetation is replaced by alpine tundra communities at higher elevations. Willows are most abundant on wet sites--along streams and on poorly drained north-facing slopes. Vegetative communities are more fully described in Viereck and Dyrness (1980).

Moose were found throughout the boreal forest and upland climax communities. I made most observations in the upland climax areas or in the transitional zones between forest and shrubland because moose were much more visible in the more open areas.

Two moist north-facing slopes within the upland climax community were heavily used by moose, particularly in summer (Sites 1 and 2 on

Fig. 1). Both provided a diversity of habitat types, including abundant willow growth and patches of spruce and herbaceous cover (Fig. 2). Moose were easier to observe at Site 2 because willows were shorter and spruce more scattered than at Site 1.

CLIMATE

The climate of Denali National Park has been described previously (Murie, 1944; U. S. Dept. Comm., 1970). Temperatures during the field portions of my study were generally above normal except in the fall of 1977; the winter of 1976-77 was one of the warmest on record (Fig 3a). Temperatures during the March-November study period ranged from 30.0°C to -28.9°C. Precipitation was variable (Fig. 3b); mid-summer was wet in 1976, but early summer and fall were dry. In 1977, spring and fall were wet, but the summer was very dry.

Photoperiod varies from a low of approximately 4 hours 10 minutes of sunlight on the winter solstice to a high of 21 hours 10 minutes on the summer solstice (Fig. 3c). Continuous sunlight or civil twilight, when the sun is six degrees or less below the horizon (see Selkregg, 1974), occurs from mid-May until late July.

Figure 2. Site No. 1, Denali National Park, showing diversity of habitat types present.

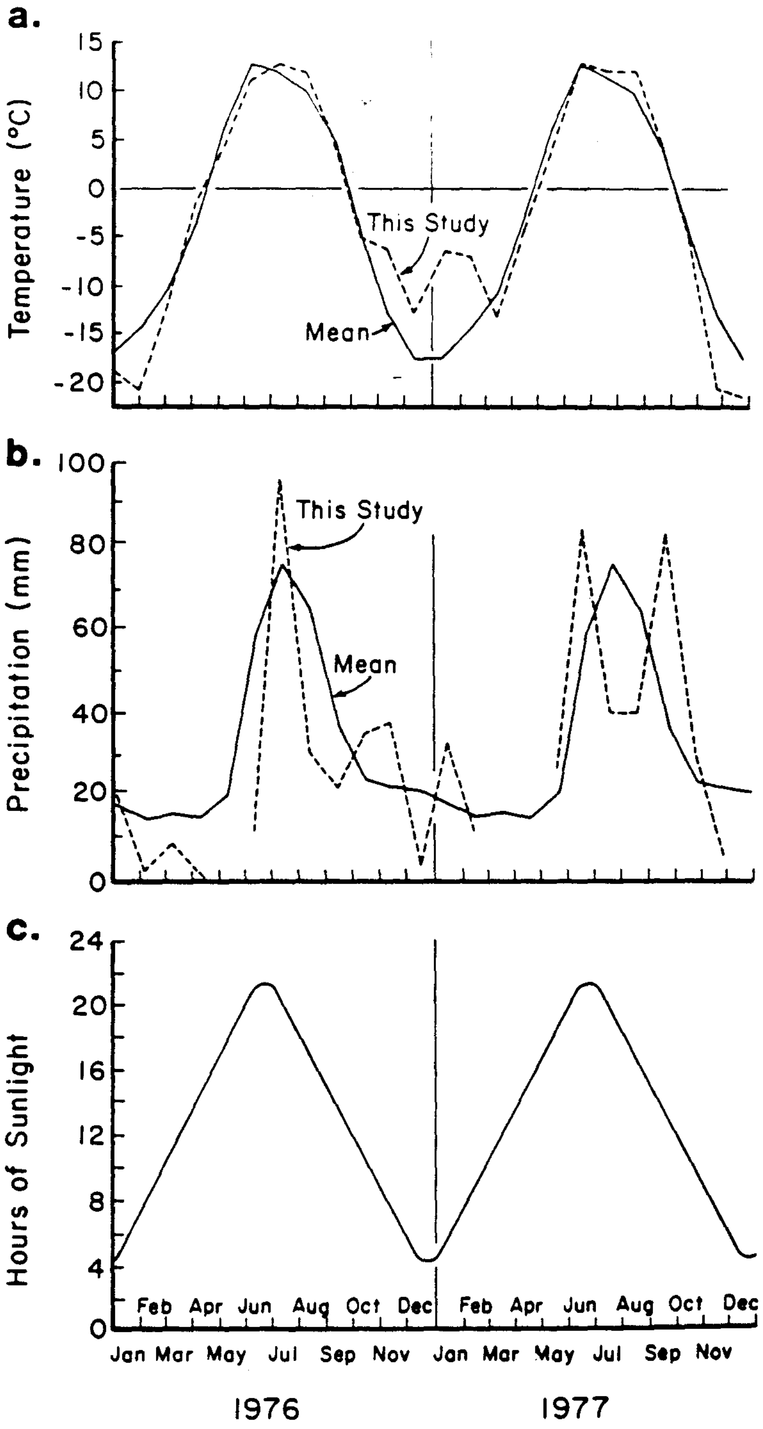

Figure 3. Mean monthly temperature (Nat. Oceanic Atmos. Admin.), precipitation (Nat. Oceanic Atmos. Admin.), and daylength (Univ. Alaska, Geophysical Institute), Denali National Park headquarters, 1976-77.

METHODS

DATA COLLECTION

Field work was conducted from 7 July through 6 November in 1976 and in March and 12 May through 8 November in 1977. I observed moose primarily at one of two sites (see Study Area). When no moose were visible in these two areas, I located moose by driving along the Park road and stopping every few hundred meters to scan the surrounding area with binoculars. I began observations when I located one or more moose. Observation periods lasted about 8 hours, unless disturbance or reduced visibility caused me to terminate observations earlier. Observation periods were staggered from day to day to adequately sample all hours with sufficient light for using a spotting scope. Disturbance was rarely a problem because most moose under observation were 1 km or more from my observation point and the Park road. However, some observations have been included of moose close to humans if they did not appear to be disturbed; most of these observations were made during the fall when rutting groups commonly aggregated near the road.

Identification and activity data were recorded every 15 minutes using the instantaneous scan method (Altmann, 1974). The following information was recorded for each moose observed:

1) Daily individual identification number. Each animal was assigned a number for the day.

2) Long term individual identification number. These

numbers were assigned to animals seen on two or more days; most identifications were of bulls, whose antler configurations made them identifiable at a distance.

3) Daily group identification number. Each group (also referred to as "aggregation" when consisting of more than one animal) was assigned a number for the day. My working definition of an aggregation was similar to Sigman´s (1977, p. 48): "a group [of two or more animals] which fed and travelled together...often staying together for several days." Moose in an aggregation usually remained within several meters (2-20 m) of some other member throughout an observation period, and showed similar direction and timing of movements.

4) Long term group identification number. These numbers were assigned to groups seen on two or more days.

5) Number of animals in the group.

6) Sex-age category of individuals. I recorded six categories: bull, cow without calf, cow with calf(s), yearling, unknown cow, and unknown sex and/or age.

7) Activity. A moose was defined as active when it was on its feet and as inactive when lying down. Activity was recorded on individuals except when large group sizes made it impossible to keep track of individuals; in those instances I recorded the number of moose involved in each activity.

8) Habitat type. The habitat type each moose was in at the time of a scan was short open (herbaceous or shrub

vegetation less than 2 m tall), tall shrub (shrub more than 2 m tall) or forest (scattered or dense spruce, or rarely, deciduous).

9) Time of Day (Alaska Daylight Time).

10) Date.

Twelve environmental parameters were recorded every 30 minutes:

1) Temperature ($^{\circ}C$) was measured in the shade 0.5-1.0 m above the ground.

2) Wind speed (km/hr) was measured with a Dwyer wind meter.

3) Wind direction was recorded as one of the compass octants.

4) Relative humidity was measured with a Weksler sling psychrometer.

5) Barometric pressure (mm Hg) was measured at the observation site and later standardized for 2000 feet (610 m) elevation.

6) Level of insect harassment was estimated from behavior of the animals (such as frequency of ear twitching) and scaled 0-3: 0=none, 3=heavy.

7) Precipitation type was recorded as: none, rain, snow, mixed rain and snow, or sleet and hail.

8) Precipitation intensity was recorded on a scale of 0-3: 0=none, 3=heavy.

9) Cloud cover was estimated to the nearest 10%.

10) Local cloud height was estimated by relationship to the height of mountains in the area.

11) Sunniness at the location of the observed animals was recorded as sunny, partly sunny, or shaded.

12) Incident lumens/m of light were measured with a Gossen Luna-Pro light meter at my observation site.

DATA ANALYSIS

The study period was divided differently in Section I than in Sections II, III, and IV. In Section I, the study period was divided into nine seasons: late winter (10-12 March), pre-calving/calving (12-31 May), post-calving (1-15 June), early summer (16-30 June), mid-summer (1-31 July), late summer (1-31 August), pre-rut (1-21 September), rut (26 September - 30 October), and post-rut (5-8 November). In Sections II, III, and IV, several of these time periods were combined for simplicity, and four seasons were considered: late winter (10-12 March), spring (1-31 May), summer (1 June-31 August), and fall (1 September-30 October); November data were not included because of small sample sizes.

Data were summarized and analyzed by season in each section with the aid of the Statistical Package for the Social Sciences (Nie et al., 1975) computer programs.

Diurnal Activity Data

The mean number of active moose per scan was calculated by dividing the total number of observations of active moose in a given hourly period (e.g. 0900-0959) within each season by the total number of scans made in that hour through the season. Since there were four scans in each hourly period each day, one moose could contribute four times to the activity count for that hour, if it were active at, for example, 0900, 0915, 0930, and 0945. If it were active at 0900 and 0915 and then bedded down, it would contribute twice to the activity count. Portions of the diurnal curves which were generated from fewer than four scans have not been included.

Approximate times of sunrise and sunset are indicated on the relevant figures; these figures are only approximate because daylength was changing rapidly (± 6-8 minutes per day) (Fig 3c.) during much of the study period. The actual hours of insolation on the study area were generally much less than these figures indicate, because the surrounding mountains blocked the sun early and late in the day.

Chi square analysis was used to test the significance of diurnal changes in the proportions observed of bulls, cows without calves, and cows with calves.

Habitat Use Data

Two- and 3-way chi-square analyses were used to test differences in habitat use among different sex-age classes, activities, and times of day. Late winter data were excluded because of small or zero expected values.

Weather Data

Correlation analyses were performed to determine zero-order correlations among continuously distributed weather factors.

The relationship between activity and weather was examined using 2-way chi-square analysis; weather data were grouped into several categories for each weather factor. Sex-age differences in activity with weather were tested with chi-square analysis. Correlation of mean percentage of moose active per day with rate of change of barometric pressure was tested using linear regression; data were selected from several periods of rapidly increasing or decreasing barometric pressure throughout the study period.

Interdependence of activity and weather factors with habitat use was tested with 3-way chi-square analysis. Means of each weather factor were determined for active and inactive moose in each habitat type; analyses of variance were used to test the significance of differences among these means.

Aggregation Data

Because I was sometimes not aware of all moose within an aggregation until I had been observing the aggregation for an hour or more, new data files were used when analyzing the aggregation data; these files consisted of either all records for each group after it reached its maximum size for the day, or a subsample of this file consisting of one record per group per day. In this way an aggregation of six moose, for example, will not appear in the analyses as an aggregation of four or five just because one or more moose were initially invisible (usually because they were inactive in dense cover).

The independence of aggregation size and activity was tested using 2-way chi-square analysis.

Multiple regression was used to determine which weather factors, excluding wind direction, best explained variation in aggregation size. Chi square analysis was used to test the independence of wind direction and aggregation size.

SECTION I

SEASONAL PATTERNS OF DIURNAL ACTIVITY

RESULTS

Diurnal activity patterns changed dramatically through the study period (Fig. 4). Activity levels were most uniform through the day in mid- and late summer, and showed the largest peaks and troughs in the following period, pre-rut.

The diurnal ratios of bulls to cows without calves to cows with calves during each season were highly variable (Table 1, Appendix 1). Although these differences were statistically significant, no diurnal pattern of differences was apparent.

DISCUSSION

Direct comparisons of my results with those of other moose activity studies are difficult for three reasons. First, most other studies pooled data for the entire summer, thereby masking any changes in activity patterns such as I observed in my study. Second, several of the other studies involved moose use of aquatics (e.g. Murie, 1934), which were not available to moose on my study area. Heavy summer use of aquatics may be related to mineral supplementation of the diet (Jordan et al., 1973). If so, activity patterns in aquatic areas may be similar to activity patterns at mineral licks. These activity patterns may be quite different than those of moose not in the vicinity of a lick. Activity patterns of

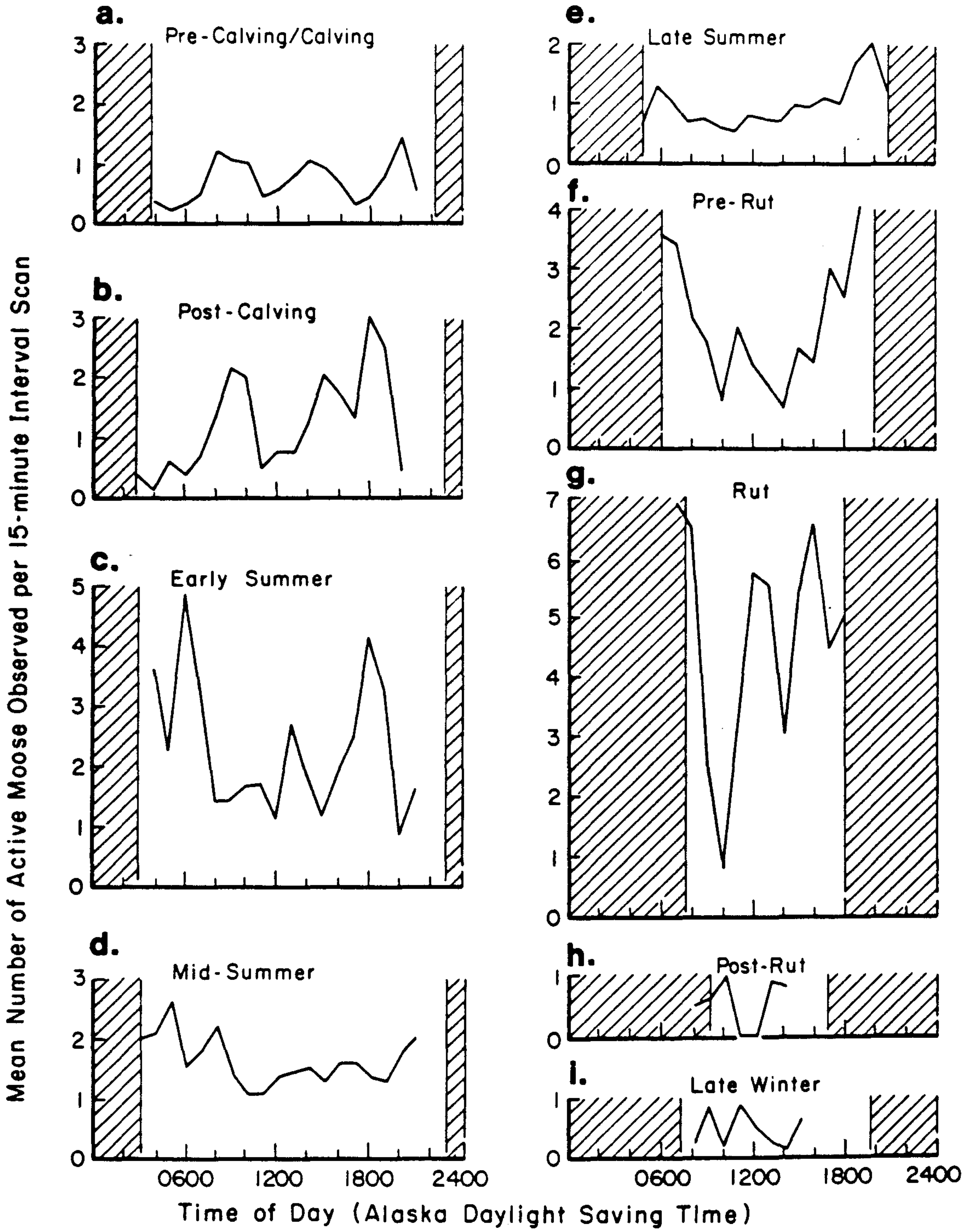

Figure 4. Diurnal activity patterns of moose, Denali National Park, 1976-77. Hours of twilight or darkness are shaded. Samples based on less than four scans have been excluded.

Table 1. Diurnal changes in observed sex ratios, Denali National Park 1976-77. Results of chi-square analysis testing the independence of observed sex composition and time of day are indicated (*p < 0.01, **p < 0.001). B = bulls, C = cows without calves, CC = cows with calves; sample size of cows without calves is indicated in parentheses following each ratio.

	B:C:CC						
Time	Pre-calving/ Calving	Post-calving	Early Summer	Mid-summer	Late Summer	Pre-rut	Rut
	χ^2=72.713(15)**	χ^2=38.819(15)**	χ^2=35.653(15)*	χ^2=54.702(15)**	χ^2=39.371(15)**	χ^2=62.381(15)**	χ^2=3.599(12)
0300-0645	467:100:67(3)	140:100:0(5)	62:100:15(52)	113:100:50(46)	27:100:9(33)	38:100:8(39)	-
0700-1045	95:100:63(41)	29:100:37(41)	37:100:29(62)	164:100:29(76)	61:100:15(105)	52:100:26(91)	15:100:2(334)
1100-1445	80:100:63(30)	42:100:22(36)	102:100:51(49)	104:100:15(204)	66:100:23(167)	24:100:43(70)	15:100:2(364)
1500-1845	14:100:145(22)	32:100:17(66)	54:100:32(91)	98:100:45(247)	66:100:26(182)	10:100:9(157)	16:100:1(444)
1900-2245	0:100:51(35)	300:100:0(5)	212:100:41(17)	134:100:60(86)	20:100:18(147)	42:100:0(24)	20:100:0(5)

moose at mineral licks in the Park 20 km from my study area were very different from what I observed (Tankersley, 1981). Third, the light regime at high latitudes is very different than at lower latitudes, and may function differently as a Zeitgeber (photoperiodic indicator). Geist (1963) hypothesized that light synchronized the morning and evening activity peaks of moose in British Columbia. In Denali, there is one continuous dusk to dawn twilight period each night in the summer (see Study Area), and photoperiod fluctuates radically through the year; activity was not as closely linked to light levels (Fig. 4) during most seasons as in some other studies.

Given these limitations, it still may be useful to compare observed moose activity in Denali with results of other studies.

In spring and early summer (pre-calving/calving, post-calving, and early summer), moose in my study exhibited three peaks in activity, although the timing and intensity of these peaks changed markedly through the period (Fig. 4a-c). Four activity peaks were observed by Geist (1963) in May and June; he suggested light synchronized the dawn and dusk peaks and an endogenous feeding rhythm synchronized the peaks in between. My data showed a suggestion of a fourth peak early in the morning during pre-calving/calving, which is not included in the figure because of a small sample size. If this fourth peak was real, then a series of evenly spaced, approximately equal-sized peaks (Fig. 4a) exists during pre-calving/calving, and does suggest a regular feeding rhythm. In the next two periods, however, only three peaks were seen (Fig. 4b-c).

From early to late summer, there was a flattening of the activity curves of moose in the Park. Early summer activity patterns closely resemble those reported in summer studies by Belovsky and Jordan (1978) and Joyal and Scherrer (1978). Moose in those studies showed three peaks in activity: morning and evening peaks, and an afternoon peak related to aquatic feeding. Moose in my study were also active in the afternoon, despite the absence of licks or aquatics (Fig. 4c). Later in the summer, activity was higher in the afternoon than in late morning, but no distinct peak was apparent (Fig. 4d-e). Activity levels were highest morning and evening as in other studies (e.g. Best et al., 1978), but sharp peaks were not apparent after early summer.

Moose activity in the Park was more crepuscular in the fall than at any other time during the study period (Fig. 4f-g). During pre-rut, activity levels were much higher around dawn and dusk than at other times of the day; during rut, activity was generally high in the afternoon, but was at maximum levels around dawn and dusk. In contrast, Best et al. (1978) found activity was greater during the day than around dawn and dusk in the fall; they suggested greater daytime activity in fall reflected greater social contact in relation to the rut. In my study, however, most rut-related behaviors were crepuscular, which has been observed elsewhere as well (Rykovskii, 1965). Activity during this time appeared to be strongly linked to light cues. Intensification of activity peaks and troughs was also a consequence of large aggregation sizes (see Section IV); to the extent that moose in an aggregation synchronize their activity with other members, peaks and troughs will be more sharply delineated than when animals are more uniformly dispersed.

Winter data (post-rut and late winter) from this study suggest activity differed in early and late winter. Post-rut observations suggested similar dawn and dusk peaks in activity (Fig. 4h) to those reported elsewhere (Best et al., 1978; Geist, 1960). In late winter, however, there were multiple peaks during daylight hours; moose activity has been found to be extremely variable in timing and duration from day to day in late winter on the Kenai Peninsula, Alaska (Sigman, 1977).

The one consistency in this pattern of changing diurnal activity is that activity always approached its lowest levels late in the morning, near midday. This was true throughout the study period (Fig. 4). Occasionally (e.g. pre-rut) activity was equally low at some time in the afternoon; generally late morning represented the time of minimum moose activity.

IMPLICATIONS FOR MANAGEMENT

The ideal moose activity pattern for aerial survey purposes would be an extended peak of three or four hours during which all animals are active. The number of moose counted would thus be maximized. Because all sex-age categories would be standing, all would be counted in proportion to their occurrence in the population (barring other differences in behavior, such as differential habitat use).

Unfortunately, this ideal situation does not occur. At no time during the day were all moose active. In addition, activity curves rose and fell sharply over short periods of time except in mid- to late summer, when vegetation density greatly reduces visibility of moose. At other times of the year, one may expect a variation of 3- to 7-fold in the number of moose active throughout the day (Fig. 4).

Conditions for aerial surveys were relatively good during pre-calving/calving when two fairly broad peaks in activity occurred during hours with good lighting (Fig. 4). From 0800-1000 and 1300-1600, approximately equal numbers of moose appeared to be active. One could expect to see only 1/4 to 1/3 as many active animals during the intervening low. These two periods meet the conditions of two 3-hour search periods recommended by Timmermann (1974) for aerial surveys. Bull:cow ratios were lower in the afternoon than in the morning, but I believe this was due to a sampling anomaly.

In the fall, the best time to conduct surveys appears to be in the afternoon during rut. Then activity was high and increasing in the afternoon except for a brief period around 1400 h. Low light levels around dawn and dusk preclude surveys at these times, although activity was highest then, and there were no 3- or 4-hour periods when relatively stable numbers of moose were active.

During post-rut, surveys must be conducted during midday because of low light intensity; this period coincides with low activity of moose. However, good snow cover increases the sightability of inactive moose relative to that of inactive moose during snow-free periods (Gasaway et al., 1979, 1980).

Since activity appears to be low during late morning throughout much of the year, survey work during this period should be avoided. If surveys are conducted during these hours, it should be with the awareness that the number of moose seen will probably be low.

The difference in photoperiod due to the high latitude and the absence of aquatics or mineral licks on the study area probably limit the applicability of these results to many other areas. Results from this study will be most useful for other high-latitude moose populations, and in habitats where aquatics or mineral licks are not common, or at those times when lick and aquatic use is not heavy. Variability in results of other studies is probably due in part to differences in these factors.

SECTION II

HABITAT USE

RESULTS

A strong bias existed in this study toward sighting moose in open habitats. Because these moose were much easier to observe, they are overrepresented relative to those using tall shrub or forest. While observed habitat use is not, therefore, an accurate representation of habitat use *per se*, it should provide a useful relative index of differences in habitat use under various conditions. These include differences by season, sex-age category, activity, and time of day.

Habitat Use in Relation to Activity

A strong interdependence existed among habitat use, activity, and sex-age category. The null hypothesis that these factors were mutually independent, and independence of each factor from the others, was rejected in every case ($p<0.001$) except one--activity was independent of habitat or sex-age category in fall (Appendix 2).

Observed habitat use varied between active and inactive moose of the same sex-age category in most seasons (Fig. 5, Appendix 3). In spring, bulls used short open habitat types more when they were active than when bedded down; conversely, tall shrub and forest were used more by inactive bulls. Cows without calves showed no significant differences in habitat use in relation to whether they

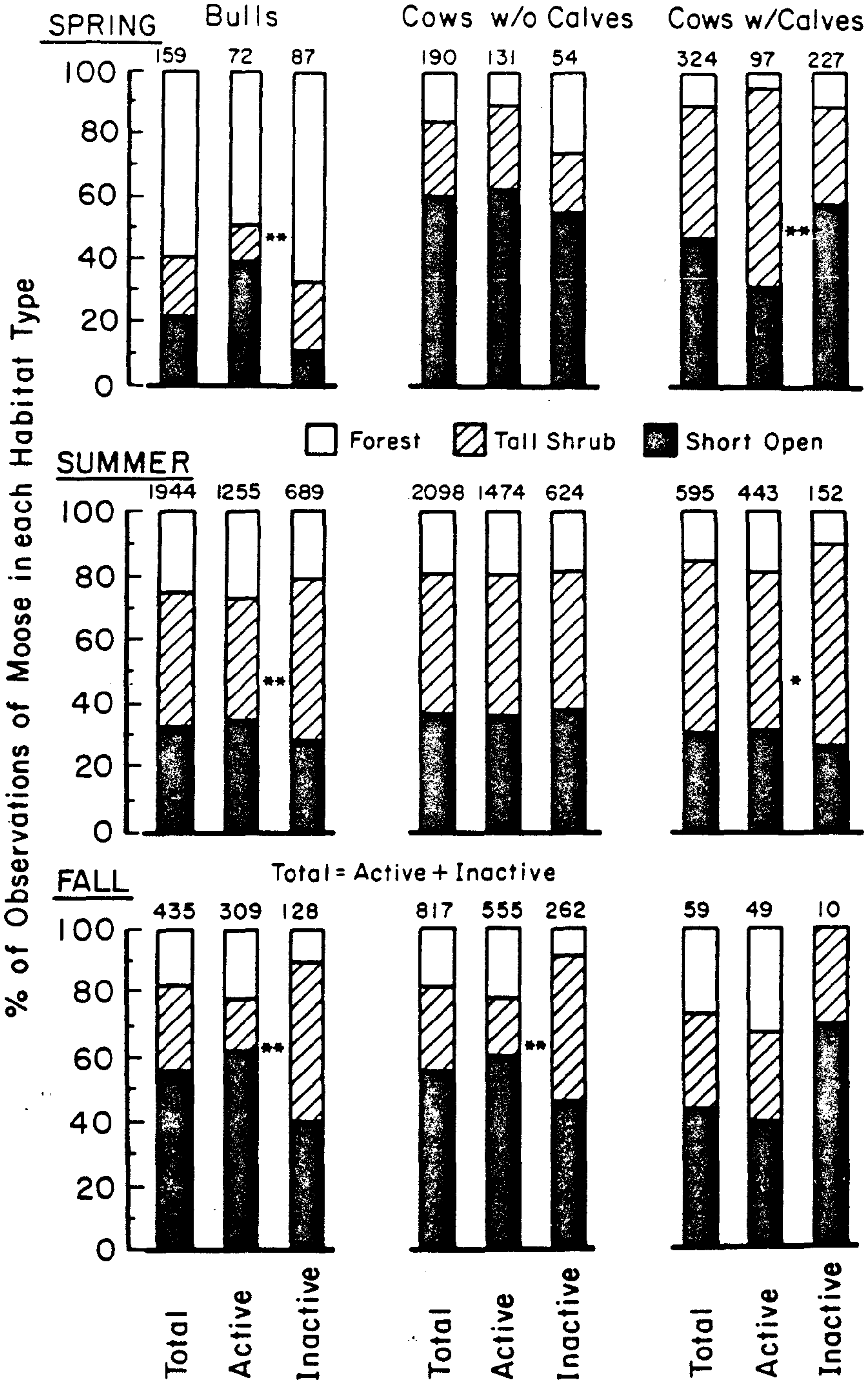

Figure 5. Habitat use by moose, Denali National Park, 1976-77. Sample sizes are indicated above each bar. Results of chi square analysis testing independence of habitat use and activity are indicated where significant (* $p < 0.01$, ** $p < 0.001$).

were active or inactive, although inactive cows used forest more than active ones. Cows with calves, exhibiting a very different use pattern, used tall shrub habitat types when they were active and short open habitats when inactive.

In summer, active bulls used short open habitats more than inactive bulls; conversely, tall shrub was used more by inactive bulls. Active and inactive cows without calves displayed a habitat use pattern similar to that I observed for bulls. Short open habitat types were used more by active, and tall shrub more by inactive cows with calves.

In fall, bulls and cows without calves used short open habitat types much more when active and tall shrub more when inactive. There was no significant difference between habitat use by active and inactive cows with calves, although the former were seen more in forest and the latter in short open habitat types.

Habitat Use in Relation to Season and Sex-Age Category

Observed habitat use patterns changed seasonally within each sex-age category (Fig. 5), and among sex-age categories as well in spring ($X^2=123.328$, df=4, $p<0.001$) and summer ($X^2=34.812$, df=4, $p<0.001$) but not as much in fall ($X^2=12.825$, df=4, $p<0.05$).

Only active moose were considered in the statistical testing of sex-age differences in activity for two reasons. First, earlier analyses demonstrated that activity was dependent on habitat use and sex-age category; these interrelationships are not a problem when only active moose are considered. Second, active moose are much more likely to be seen during aerial surveys than bedded moose (Gasaway et al., 1980); therefore, examination of habitat use by active animals can be used to predict which sex-age categories of moose will be most easily seen.

In spring, observed habitat use varied significantly among bulls, cows without calves, and cows with calves. Bulls were seen in forest more than any other habitat type; in contrast, cows without calves were most often observed in short open habitat types. Cows with calves were observed almost equally often in tall shrub and short open habitats in spring.

Observed habitat use patterns were much different in summer than in spring. All sex-age categories were most often seen in tall shrub habitat types. Bulls, however, still used forest more than cows; cows with calves made greater use of tall shrub areas than bulls or cows without calves.

In fall, observed habitat use was similar among all sex-age categories. All made greater use of short open habitat types than in summer. Cows with calves continued to make greater use of tall shrub than bulls or cows without calves.

In late winter (March), most cows with calves were observed in tall shrub, and most other moose were in forest; the data were not statistically analyzed because of small sample sizes.

Diurnal Patterns of Habitat Use

There was a strong interdependence among habitat use, time of day moose were seen, and sex-age category. The null hypotheses of mutual independence and independence of each of these factors from the others were rejected in every case ($p<0.001$) (Appendix 4).

Habitat use by moose was linked to time of day in spring, summer, and fall for each sex-age category ($p<0.001$) (Fig. 6, Appendix 5). In late winter, habitat use was independent of time of day.

In spring, diurnal patterns of habitat use varied among bulls, cows without calves, and cows with calves. Bulls primarily used forest early in the morning; use of forest declined later in the day, and use of tall shrub increased. No bulls were observed in late afternoon or evening. Cows without calves, in contrast, were observed in short open areas early in the morning; they made greatest relative use of forest around midday. Use of tall shrub was greatest in the evening. Cows with calves also used short open areas the most in the morning, while tall shrub use increased steadily with highest use levels in late evening.

In summer, diurnal patterns of habitat use were similar among bulls, cows without calves, and cows with calves. All moose used forest primarily around midday and short open areas primarily early in the morning and late in the evening.

All three categories of moose made heavy use of short open habitat types early in the morning in the fall. Bulls and cows

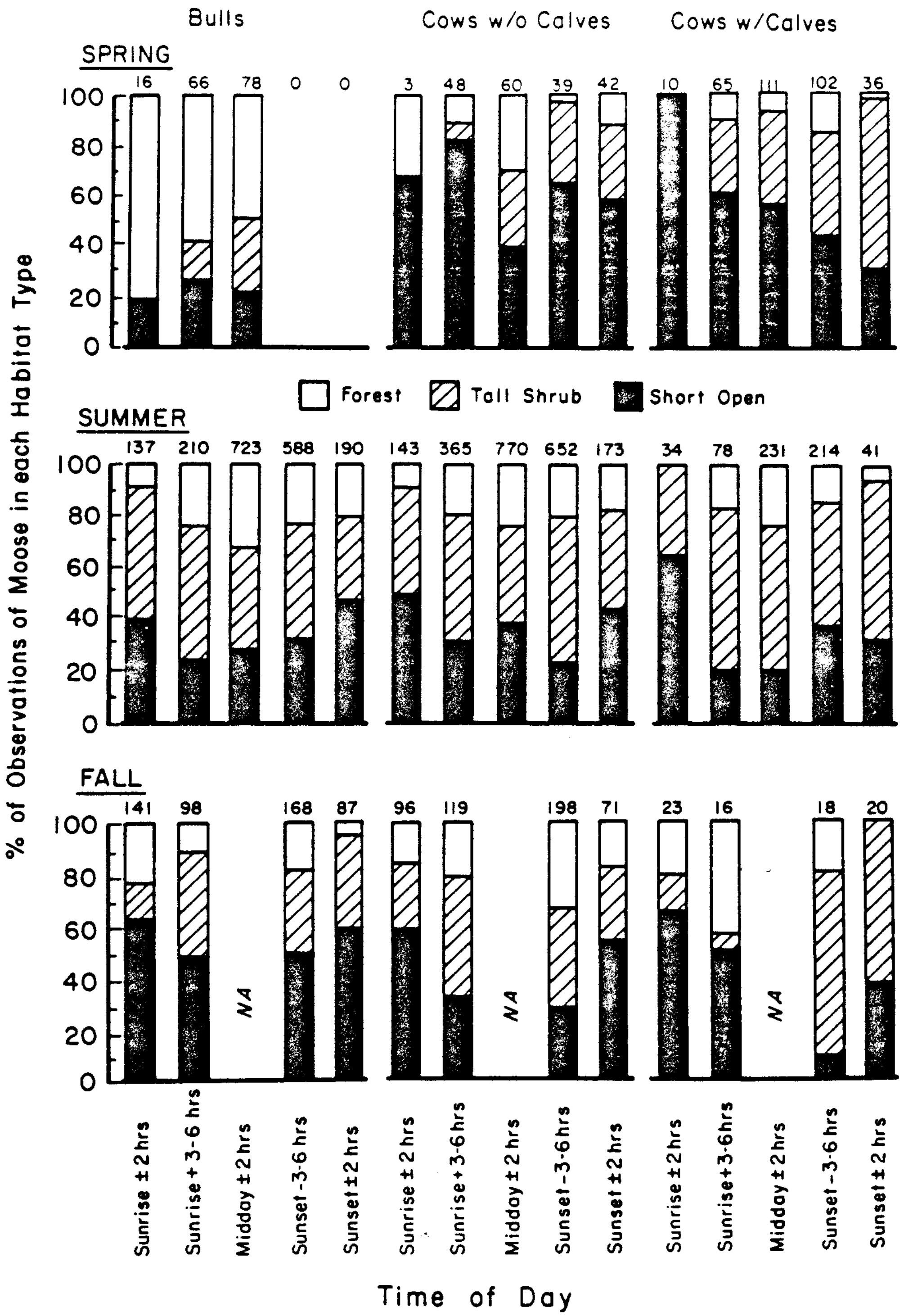

Figure 6. Diurnal habitat use by moose, Denali National Park, 1976-77. Sample sizes are indicated above each bar. The midday period has been incorporated in the adjacent periods because of shorter daylength.

without calves also used these areas heavily in the evening. Cows with calves, on the other hand, used tall shrub areas in the afternoon and evening.

DISCUSSION

Habitat Use in Relation to Activity

Visibility of moose is dependent on their choice of habitat as well as their activity. Gasaway et al. (1979) found that, during aerial survey work in winter, trees acted as visual barriers to the observer in the case of both standing and lying moose, while shrubs were a visual barrier mainly for lying moose. In addition, tall shrubs are effective visual barriers for all moose when vegetation is leafed out in summer. Thus visibility of moose is affected not only by activity and habitat use considered separately, but by the interactions of these two aspects of moose behavior as well.

Moose in the present study did select different habitat types for certain activities. Moose tended to feed in more open areas and move into denser cover for bedding. Commonly, a moose in an open area slowly made its way toward a patch of taller, denser vegetation in the last few minutes of a feeding period and bedded down there. Cows with calves in spring were the major exception to this pattern, but I believe this represents a sampling artifact. The many observations were of only a few cows, visible because they bedded in small islands of open habitat and moved into nearby tall shrub to feed. Of other moose, not all moved into denser cover to lie down; in many instances a moose feeding in the open bedded down in the same area. Murie (1934) and McMillan (1954) found no difference in lying in short open or dense habitat types.

Habitat Use in Relation to Season and Sex-Age Category

Sex-age differences in habitat use were observed in spring in the present study; results from other studies have varied. While I observed bulls in the spring using forested areas more and open areas less than expected values, Berg (1971) reported bulls used open areas the same as expected values in Minnesota. Gasaway et al. (1980) found bulls selected aquatic-herbaceous habitats and avoided tall canopies. Gasaway (pers. commun.) has suggested that the opposite behavior he and I have observed in bulls in two interior Alaska study areas may be a consequence of the different forest types in these areas. Forest patches on my study area are widely spaced white spruce with an abundant willow understory. In Gasaway's study area, however, very dense black spruce may discourage use by bull moose because of possible injury to velvet-covered antlers. I found cows without calves making greatest use of open habitats, while Berg (1971) and Gasaway et al. (1980) both found cows without calves avoided open areas. Cows with calves used tall shrub areas more than expected in the present study; Gasaway et al. (1980) also found that cows with calves selected tall canopies. In Minnesota, however, cows with calves used open areas (Berg, 1971), which suggests the high use levels of open habitat types by cows with calves that I observed during spring (Fig. 5) may be a real phenomenon and not the sampling artifact I suspected. Cows with calves I observed in open areas were usually bedded in a small opening surrounded by tall shrub. Such a position still provides the benefits of cover in tall shrub, but the opening might aid the cow in active defense of her calf.

Variation in habitat use by sex-age category was similar in summer to spring despite the overall greater use of tall shrub, i.e. proportionately greater use of forest by bulls, short open areas by cows without calves, and tall shrub areas by cows with calves. LeResche (1966) believed bulls used mature deciduous cover disproportionately in his study area, but Knowlton (1960) and Coady (1976) reported greater use of short open habitats by bulls in summer.

All types of moose showed similar habitat use patterns in fall in the present study, with use of short open habitat types predominating. Similarly, Coady (1976) and Lent (1974) found moose preferred open habitat types in fall. Cows with calves used tall shrub slightly more than other sex-age categories. In Minnesota, Berg (1971) found that cows with calves used tall mature habitats four times as much as short open habitats during rut, while bulls and cows used the two equally. Identical habitat use patterns by bulls and cows without calves during the present study probably resulted from their close association in large aggregations at this time.

In late winter, moose in this study and others used tall dense habitat types (e.g. Coady, 1976; Gasaway et al., 1977; Berg, 1971). Use of dense habitat types has been associated with less snow than in open areas (e.g. Krefting, 1974) and may also be a reflection of reduced feeding at this time (Gasaway and Coady, 1974).

Cows with calves showed a consistent difference in habitat use throughout the study period relative to bulls and cows without calves; they made greater use of tall shrub. This habitat type offers excellent cover from predators, and may facilitate avoidance of other moose as well. LeResche (1966) reported cows with calves used a dense area of scrub birch and aspen not used by any other sex-age category, and Peek (1962) reported more cows with calves than cows without calves using dense cover in summer.

Diurnal Patterns of Habitat Use

In broad terms, patterns of diurnal habitat use followed diurnal activity. This is what one would expect, given that habitat use was dependent on activity for most sex-age categories in most seasons. Use of short open habitats tended to be highest (Fig. 6) when activity levels were highest (Fig. 4), and use of forest and tall shrub combined was highest when activity levels were low. This was most evident in summer; I always thought I saw more moose early and late in the day, despite the absence of sharp activity peaks (Fig. 4d-e). Diurnal habitat use patterns help explain this phenomenon. In fall, high levels of use of open habitats also coincided with activity peaks (Fig. 4f-g). In spring, ther was not a clear coincidence of habitat use and diurnal activity, probably because the activity pattern in spring (Fig. 4a) was characterized by three evenly spaced, moderate, and equal-sized activity peaks, rather than crepuscular peaks.

IMPLICATIONS FOR MANAGEMENT

The dependence of habitat use on activity, season, sex-age category, and time of day indicates that bias will occur whenever surveys are flown.

The tendency of moose to use open habitats when active means active moose are easier to see than if no activity-habitat interaction occurred. Inactive moose will be very difficult to see because of their tendency to lie down in dense vegetation, as well as because of their inactivity. Diurnal habitat use patterns reinforce the activity-habitat interaction; therefore, an attempt should be made to conduct surveys during activity peaks, when the greatest number of moose will be active and in the open. Timing in terms of activity peaks has been discussed previously (see Section I).

Bias occurs as a result of differential habitat use by various sex-age categories of moose. Cows without calves will tend to be overrepresented in composition counts except in fall, because of their greater use of short open habitats. Bulls, in contrast, will tend to be underrepresented except in fall surveys; their greater use of forested habitat types in spring and summer makes a greater proportion of them very difficult to see. Cows with calves will probably be underrepresented during surveys flown in spring, summer, or fall, because of their greater use of tall shrub areas.

Applicability of results of the present study to those in other areas will be variable, depending on how closely moose habitats and activity patterns parallel those on the Denali study sites. Wide variation has existed in past studies, probably due in part to variability in habitats and activity patterns.

SECTION III

ACTIVITY AND HABITAT USE IN RELATION TO WEATHER

RESULTS

Activity and Weather

Moose activity levels under different weather conditions were highly variable (Fig. 7, Appendix 6).

In spring, activity of moose was generally independent of weather conditions, although activity was greater at low wind speeds (Fig. 7, Appendix 6, Table 2) and high temperatures (Fig. 7, Appendix 6). Wind speed and temperature both tended to increase diurnally (Appendix 8a). The diurnal activity pattern probably accounts for greater activity at higher temperatures; no activity peak was observed early in the morning when temperatures were low, but there was an activity peak in the afternoon when temperatures were near maximum (Fig. 4a). Activity was lower at high wind speeds despite the diurnal pattern of increasing winds; this suggests that moose modified their activity as a direct response to wind speed.

In summer, statistically significant relationships existed between moose activity and virtually all weather factors measured (Fig. 7, Appendix 6), but it is questionable whether these relationships are all biologically significant. Activity was highest in conditions of northerly or westerly winds at low to moderate speeds, low cloud cover, low light intensity, moderate humidity (which, along with insect harassment, was considered only in summer,

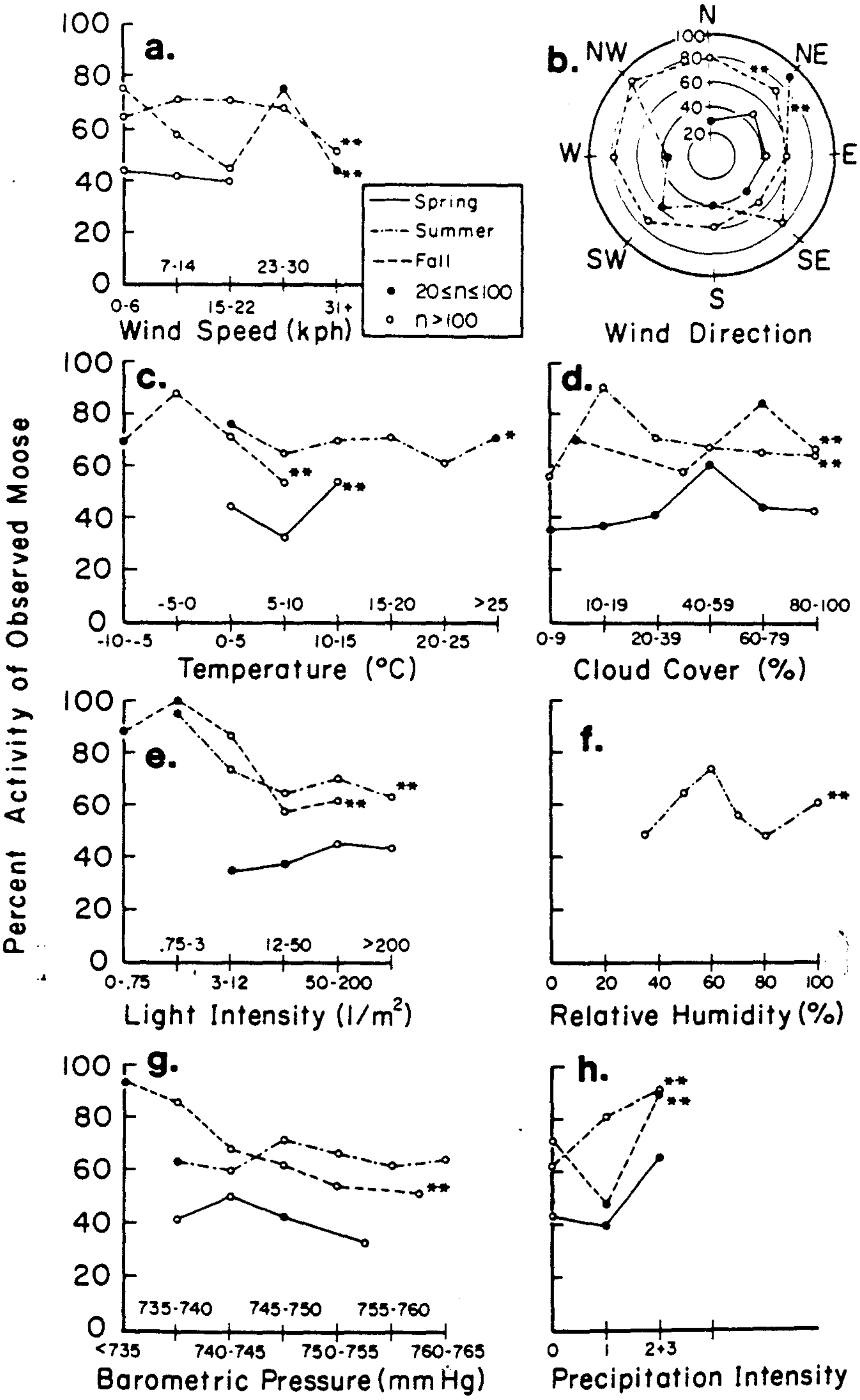

Figure 7. Activity of moose under various weather conditions, Denali National Park, 1976–77. When two weather categories were combined because of small sample size, the data point has been located between the two categories. Results of chi square analysis testing independence of activity and weather are indicated where significant (*p < 0.01, **p < 0.001).

Table 2. F-statistics from analysis separating active and inactive moose on the basis of continuously distributed weather variables, Denali National Park, 1976-77 (*p < 0.01, **p < 0.001). Sample sizes in each season are indicated in parentheses.

Weather Variable	Spring (695)	Summer (2317)	Fall (1635)
Wind speed	7.175*	0.5058	32.58**
Temperature	2.589	3.172	20.33**
Barometric pressure	2.796	0.6055	50.99**
Light intensity	0.9359	4.206	42.39**
Cloud cover	2.485	1.140	9.028**
Precipitation intensity	1.593	13.17**	1.407
Day of year		57.25**	
Humidity		0.9603	
Insect harassment		0.9119	

because of small or zero sample sizes in spring and fall), and moderate levels of precipitation. It should be noted that sample sizes for periods of precipitation were small; in rainy weather I generally could not see the study sites. Clear patterns of change in activity levels were not apparent in relation to temperature or barometric pressure. Day of year, which was included with weather factors in summer because the summer study period was much longer than spring or fall, provided the best separation between active and inactive moose (Table 2). Moose were less active as the summer progressed. Correlations among weather factors showed a diurnal pattern similar to spring, and also a seasonal pattern (Appendix 8b).

In fall, significant differences existed in activity levels of moose in relation to all weather factors (Fig. 7, Table 2) except precipitation intensity which, as in summer, was represented by small sample sizes. High levels of activity were associated with low wind speed, northerly winds, low temperatures, high cloud cover, and low barometric pressure. Results are more difficult to interpret, because correlations among weather factors were weaker than in spring and summer, and did not show a clear diurnal pattern (Appendix 8c). I believe this is because weather conditions were very different in the fall during the two years of the study; in 1976 weather tended to be clear and dry, with cold nights and warm days, while 1977 was cloudy and wet with little temperature fluctuation (Fig. 3a-b). Moose were less active at high wind speeds, high temperatures, and high light intensity, and at high barometric pressures. This pattern of correlations corresponds in part with diurnal and seasonal changes in activity I noted during the two years: activity tended to be highly crepuscular in fall (Fig. 4f-g), when light levels, temperatures, and wind speeds were low. However, activity also appeared to be less intense in fall of 1977, when many low pressure systems moved through the Park.

No significant correlation was found between rate of change of barometric pressure and activity levels throughout the study period ($r=0.231$, $n=19$, $p>0.05$).

Differences in activity levels of moose in different sex-age categories under different weather conditions were also highly variable; these differences were usually statistically highly significant, but seldom showed a clear pattern of activity differences among different sex-age categories (Fig. 8, Appendix 7). Such was the case with activity levels with changes in light intensity, cloud cover, precipitation intensity, and wind speed.

However, clear patterns of sex-age differences in activity were seen with some weather factors (Fig. 8). In terms of the chi-square analyses, both bulls and cows were more active than expected when winds were northerly or easterly, and cows with calves were more active when winds were southerly in spring, summer, and fall. In summer and fall, bulls remained active at higher temperatures than cows with or without calves, although all sex-age categories tended to be most active at low to moderate temperatures. Bulls were also

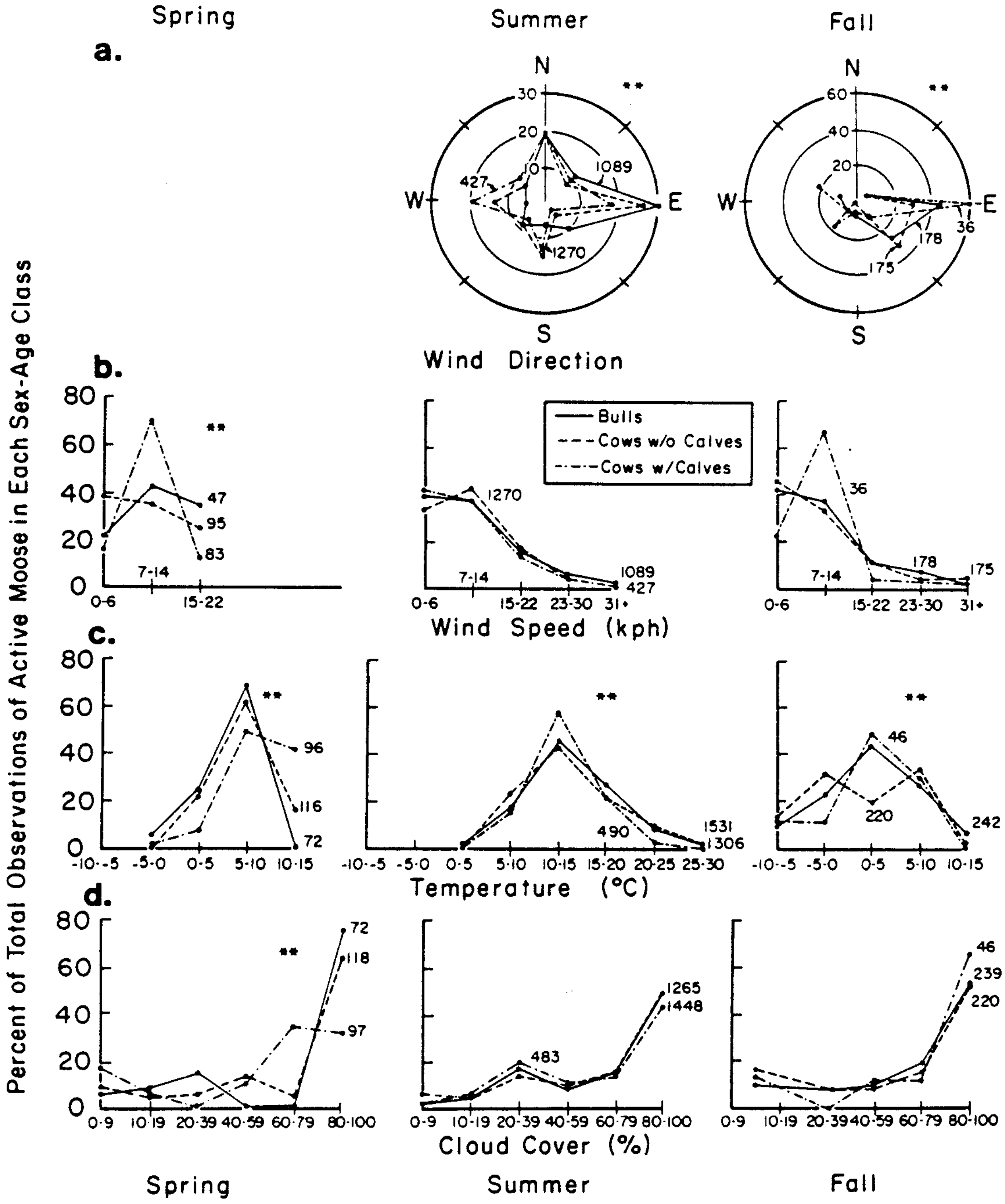

Figure 8. Activity of bulls, cows without calves, and cows with calves under various weather conditions, Denali National Park, 1976-77. Sample sizes are indicated near each graph. Results of chi square analysis testing independence of number of active versus inactive moose in each sex-age category and weather are indicated where significant (*p < 0.01, **p < 0.001).

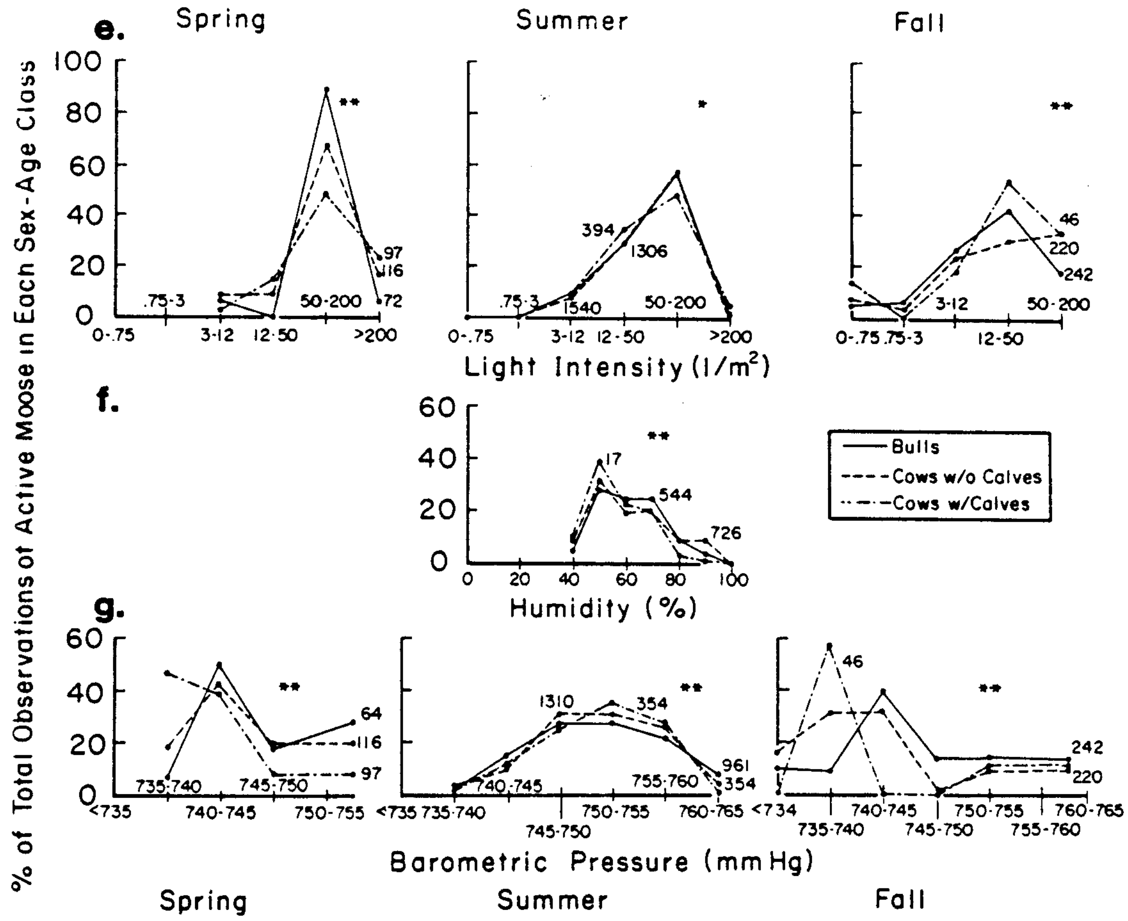

Figure 8. Activity of bulls, cows without calves, and cows with calves under various weather conditions, Denali National Park, 1976-77. Sample sizes are indicated near each graph. Results of chi square analysis testing independence of number of active versus inactive moose in each sex-age category and weather are indicated where significant (*$p < 0.01$, ** $p < 0.001$).

more active than cows when humidity was high in summer. A higher proportion of bulls than cows tended to be active at high barometric pressures.

Habitat Use and Weather

Moose showed differential habitat use in different weather conditions (Tables 3-4) throughout the study period. In spring, moose used short open and forest habitat types at lower temperatures and light intensities than tall shrub. In summer, moose used short open habitats when wind speed, temperature, and light levels were low, and cloud cover, precipitation intensity, and humidity were high. In fall, moose used short open habitats when wind speed, temperature, barometric pressure, and cloud cover were low.

DISCUSSION

The intent of the present study was to determine what variation in weather conditions influences moose behavior. The response of moose to virtually all weather conditions measured was statistically significant in one or more seasons; however, I think there is good reason to doubt that statistical significance is an accurate reflection of biological significance in all these instances. Results of other studies of moose have been ambiguous. It appears that moose do respond to changing weather conditions with altered activity or habitat use, but these responses are not as strong nor as

Table 3. Means and standard deviations of weather factors for active and inactive moose in various habitat types, Denali National Park, 1976-77. Figures in parentheses are mean values for ordinal variables. F-statistics for those data are given in Table 4.

Weather Factor	Active			Inactive		
	Short Open	Tall Shrub	Forest	Short Open	Tall Shrub	Forest
Spring						
Wind Speed Index	(1.39) ± 1.14	(1.67) ± 0.93	(1.71) ± 0.97	(1.73) ± 1.23	(1.89) ± 0.747	(1.71) ± 1.08
Temperature	7.1 ± 2.5	9.1 ± 2.79	7.1 ± 3.1	6.6 ± 2.5	8.9 ± 2.5	7.4 ± 3.4
Barometric Pressure	775.3 ± 4.0	771.2 ± 4.5	778.0 ± 5.6	774.4 ± 4.9	775.6 ± 7.1	776.1 ± 5.2
Light Intensity	1199.51 ± 819.65	1643.57 ± 900.40	1523.29 ± 841.22	1502.99 ± 938.00	1567.84 ± 1105.95	1366.78 ± 747.11
Cloud Cover	4.96 ± 1.57	4.72 ± 1.79	4.55 ± 1.96	4.62 ± 1.77	4.77 ± 1.93	4.36 ± 2.03
Precipitation Intensity Index	(0.364) ± 0.741	(0.087) ± 0.284	(0.290) ± 0.710	(0.195) ± 0.594	(0.059) ± 0.238	(0.346) ± 0.679
Summer						
Wind Speed Index	(1.41) ± 1.31	(1.85) ± 1.13	(1.83) ± 1.16	(1.43) ± 1.27	(1.68) ± 1.19	(2.04) ± 1.09
Temperature	13.31 ± 4.17	14.40 ± 4.67	13.77 ± 3.78	13.01 ± 5.12	14.50 ± 4.43	14.55 ± 2.86
Barometric Pressure	780.4 ± 5.4	781.3 ± 5.2	781.9 ± 4.4	780.7 ± 6.4	781.0 ± 5.7	781.8 ± 5.4
Light Intensity	508.54 ± 86.74	937.03 ± 674.48	964.61 ± 633.76	613.20 ± 156.19	919.98 ± 677.24	992.98 ± 558.28
Cloud Cover	4.746 ± 1.616	4.32 ± 1.89	4.65 ± 1.69	4.86 ± 1.78	4.45 ± 1.97	4.93 ± 1.12
Precipitation Intensity Index	(0.152) ± 0.437	(0.135) ± 0.448	(0.188) ± 0.544	(0.104) ± 0.396	(0.033) ± 0.180	(0.068) ± 0.279
Humidity	62.0 ± 14.0	53.0 ± 13.0	60.0 ± 13.0	61.0 ± 18.0	56.0 ± 14.0	60.0 ± 9.0
Insect Harassment Index	(0.784) ± 0.814	(0.712) ± 0.716	(0.725) ± 0.690	(0.589) ± 0.753	(0.859) ± 1.01	(0.543) ± 0.609
Day of Year	206.7 ± 22.2	198.8 ± 23.9	198.5 ± 24.5	214.7 ± 22.7	204.5 ± 23.0	20[illegible].9 ± 22.7
Fall						
Wind Speed Index	(1.40) ± 1.16	(1.69) ± 1.11	(1.41) ± 1.33	(1.53) ± 1.16	(2.09) ± 0.826	(2.55) ± 1.74
Temperature	0.972 ± 5.093	4.95 ± 3.92	2.27 ± 5.24	1.34 ± 5.15	4.95 ± 4.34	6.88 ± 1.97
Barometric Pressure	776.2 ± 7.4	779.2 ± 4.9	773.7 ± 7.2	778.8 ± 6.0	778.9 ± 5.5	776.9 ± 6.1
Light Intensity	375.50 ± 354.12	508.40 ± 325.91	400.57 ± 358.64	578.81 ± 436.48	504.59 ± 282.75	414.31 ± 148.12
Cloud Cover	4.24 ± 2.13	4.16 ± 1.91	4.95 ± 1.55	3.92 ± 2.03	4.21 ± 1.80	5.00 ± 2.24
Precipitation Intensity Index	(0.221) ± 0.585	(0.242) ± 0.614	(0.223) ± 0.596	(0.219) ± 0.533	(0.230) ± 0.483	(0.636) ± 0.778

Table 4. F-statistics from analysis separating active and inactive moose in various habitat types on the basis of weather variables, Denali National Park, 1976-77. Sample sizes are indicated in parentheses (*p < 0.01, **p < 0.001).

Weather Factor	Spring (770)			Summer (6061)			Fall (1750)		
	F_{Activity}	F_{Habitat}	F_{HabxAct}	F_{Activity}	F_{Habitat}	F_{HabxAct}	F_{Activity}	F_{Habitat}	F_{HabxAct}
Wind speed	7.828*	2.707	0.259	0.661	68.146**	8.746**	27.557**	17.224**	29.102**
Temperature	1.041	35.866**	1.201	3.698	32.017**	1.964	7.643*	90.686**	13.962**
Barometric Pressure	1.362	18.912**	21.687**	0.913	15.209	0.849	25.716**	31.514**	7.316**
Light Intensity	1.464	4.786*	4.526	2.425	6.650*	2.326	38.341**	3.082	13.520**
Cloud Cover	2.101	2.101	0.851	1.602	78.320**	4.743*	4.785	25.031**	10.414**
Precipitation Intensity	2.966	10.904**	2.282	44.016**	5.674*	2.493	2.212	2.745	10.138**
Humidity				0.552	57.642**	1.483			
Insect Intensity					2.145	4.036	24.951**		
Day of Year				54.449**	18.052**	3.610			

predictable as with some other ungulates (e.g. Christie, 1967; Darling, 1937; Fox, 1978).

The effect of wind speed on moose behavior is clear; moose in this study showed reduced activity or use of denser habitat types or both in high winds. In other studies as well, moose have been observed to reduce their activity (Joyal and Scherrer, 1978; Glushkov, 1976) or avoid open areas (Peterson, 1955) or both (Skunke, cited in DeVos, 1958) in windy weather. This behavior has been attributed to the greater difficulty in detecting scents and hearing in windy weather (Skunke, cited in DeVos, 1958). In the present study, activity levels remained high in the summer except at the highest wind speeds (Fig. 7), but use of tall dense habitats was associated with high wind speeds. This suggests moose remained active, but moved into denser cover to feed. Moderately windy weather in summer may alleviate insect harassment, which might also be a factor in activity levels remaining high.

Response to temperature is less clear. In this study, moose tended to be more active at high temperatures in spring, but less active in fall, with no clear pattern in summer. DeVos (1958) and Geist (1963) found no difference in the number of moose they observed on warm or cool days; in contrast, feeding by moose has been negatively correlated with temperature in some summer studies (Belovsky and Jordan, 1978; McMillan, 1954). Habitat use varied consistently throughout the study period, with moose tending to use short open habitat types at low temperatures and taller, denser habitat types at high temperatures; this may well be part of the diurnal pattern of habitat use (Fig. 6) rather than a response to temperature _per se_.

Responses to cloud cover, precipitation, and humidity are not clear. Activity levels tended to be highest in partly cloudy weather in spring, clear weather in summer, and mostly cloudy weather in fall (Fig. 7) in the present study. Activity also tended to be greater when precipitation was present. Most other observers, in contrast, have noticed higher activity levels in clear weather (Mould, 1977; Joyal and Scherrer, 1978) and reduced activity in rain (Markgren, 1966; Skunke, cited in DeVos, 1958; Joyal and Scherrer, 1978). There was a clear bias in this study toward periods of light precipitation when visibility remained high, so what I observed during periods of light precipitation may not be representative of times of moderate to heavy rainfall. It may be that periods of light precipitation, with their lower light intensities and cooler temperatures, are used by moose to extend activity periods. Mean cloud cover values tended to be highest for moose observed in short open habitats (Table 3), suggesting that clouds are performing a shading function performed by vegetation in tall shrub or forest habitat types.

The stimulating effect of clear weather on ungulate rutting behavior has been described by Fraser (1968). Rykovskii (1965) noted bull moose stopped calling in rainy weather, and rutting behavior was less intense when weather was warm or cloudy. Roby (1978) and Curatolo (1975) both reported a negative correlation between cloud cover and rutting behavior in caribou. I observed the same pattern of behavior in the present study; activity levels in relation to temperature and light intensity support my subjective impression, but those in relation to barometric pressure and cloud cover do not (Fig. 7).

Barometric pressure appeared to be an important factor in relation to moose behavior in the fall, but not summer, and only in relation to habitat use in spring (Fig. 7, Tables 2-4). Evidence from studies of several other mammals has suggested that brown bears (Craighead and Craighead, 1972), Dall sheep (Heimer, 1973), and caribou (Henshaw, 1968) may be able to detect and respond to changes in barometric pressure. No differences in moose activity with changing barometric pressure have been detected in previous studies, however (Glushkov, 1976; Geist, 1963). There was no correlation between rate of change of barometric pressure and moose activity, but a strong relationship between absolute barometric pressure and activity, which I am unable to explain.

Sex-age differences in activity, even when consistent, seem inexplicable, and I tend to doubt their validity. Bulls remaining active at higher temperatures and humidities than cows may be evidence for somewhat different physiological mechanisms at work in the two sexes; possibly bulls are able to dissipate heat from their antlers prior to shedding of velvet. Without further evidence, however, I am more inclined to attribute the results to sampling artifacts, rather than true behavioral differences.

IMPLICATIONS FOR MANAGEMENT

Variability in moose activity and habitat use in different weather conditions limits predictability for aerial survey purposes. It appears that once diurnal patterns of change in weather conditions are taken into account, other weather conditions tested probably played a relatively minor role in directly and immediately influencing moose behavior in this study.

The exception is moose activity and behavior in relation to wind speed. When winds were strong, moose were less active and/or used taller, denser habitat types than when there was little wind. Either behavior would make them more difficult to observe during an aerial survey. Aerial surveys are not normally conducted in very windy weather because of viewing difficulties associated with pilot and observer; evidence from the present study indicates moose behavior will lead to a further underestimation if surveys are conducted in these conditions.

Applicability of the results of this study to other areas is limited because of the absence of clearly delineated changes in behavior. In areas where changes in weather are more clearly defined, such as Southeast Alaska, it might be important to consider weather conditions for their influence on moose behavior. However, in this study, I would say weather is important primarily for its influence on pilot and observer, and not for its influence on moose.

SECTION IV

CHARACTERISTICS OF AGGREGATIONS

RESULTS

Seasonal and Sex-Age Differences in Aggregation Size

Mean aggregation size increased through the year. Mean aggregation size was 1.0 (SD=0, n=14) in late winter, 1.1 (SD=0.91, n=59) in spring, 1.5 (SD=1.6, n=404) in summer, and 3.3 (SD=3.3, n=101) in fall. As mean aggregation size increased seasonally, the proportion of single animals observed declined (Fig. 9).

Aggregation size was influenced by sex-age composition. Aggregations of bulls only and cows without calves only were similar in size in spring and summer (Table 5), but the cow without calf groups were much larger in fall. Mean size of mixed groups was much larger than bull or cow without calf group size throughout spring, summer, and fall. Differences in group sizes by sex-age category were not significant in spring, but were in summer ($X^2=99.418$, df=4, $p<0.001$) and fall ($X^2=49.023$, df=4, $p<0.001$). Cows with calves were rarely seen in association with other moose, and their mean group size did not change seasonally.

Aggregation Size in Relation to Habitat Use

There was a strong interrelationship between aggregation size and location in spring ($X^2=78.01$, df=6, $p<0.001$), summer ($X^2=237.73$, df=14, $p<0.001$), and fall ($X^2=191.22$, df=16, $p<0.001$). In spring,

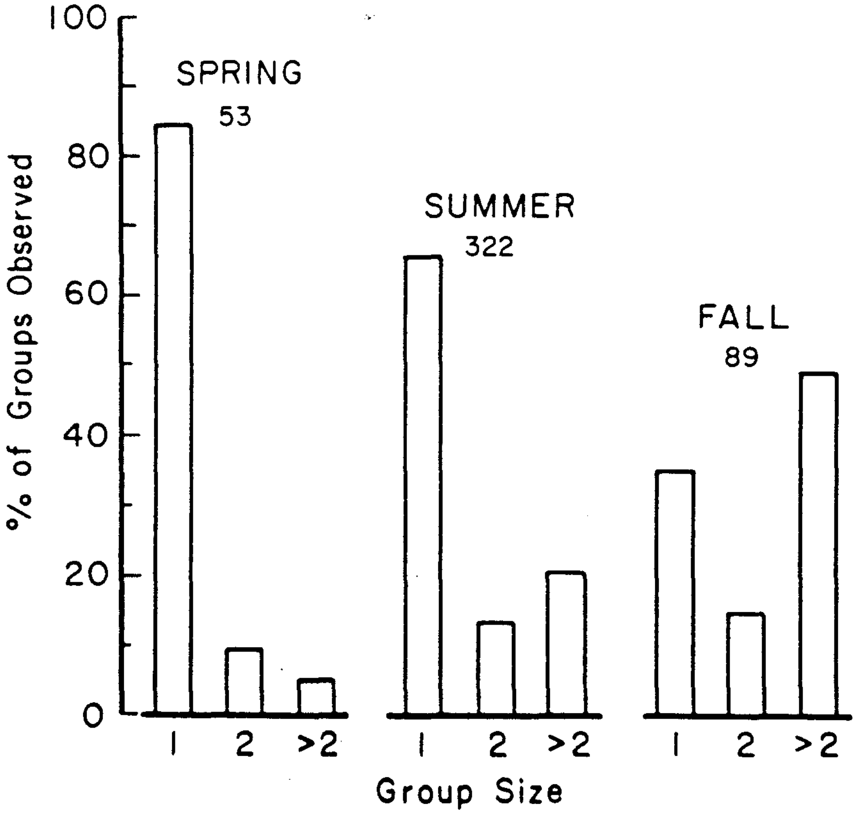

Figure 9. Group sizes of moose, Denali National Park, 1976-77. The number of groups observed in each season is indicated.

Table 5. Mean sizes and standard deviations of bull and cow without calf aggregations in Denali National Park, 1976-77. The number of groups observed in each season is indicated in parentheses.

	Bulls Only	Mixed	Cows Only
Spring	1.33 ± 0.58 (3)	4.00 ± 2.83 (2)	1.28 ± 0.74 (25)
Summer	1.54 ± 1.00 (6)	4.11 ± 1.77 (52)	1.58 ± 1.33 (113)
Fall	1.13 ± 0.34 (16)	5.56 ± 4.93 (39)	3.61 ± 3.84 (26)

groups of one or two moose were observed in tall dense habitat types (tall shrub and forest) more than expected. Groups of three or more, however, were observed more than expected in short open habitats. The same pattern was observed in summer, except in the case of large groups of six or more moose; they were observed most often in tall shrub or forest. In fall, smaller groups (≤ 5) again preferred tall dense habitat types, and large groups preferred short open habitats.

Synchrony of Activity within Aggregations

A high degree of synchrony of activity occurred among moose within aggregations (Table 6). Synchrony, when all moose in an aggregation were either standing or lying, occurred in 97, 83, and 57% of groups observed in spring, summer, and fall, respectively.

Aggregations showed a higher level of activity than single moose, spending more time active or partially active, and less time inactive, than single animals (Table 6).

Weather and Aggregation Size

No relationship between weather and aggregation size was identified. Precipitation intensity best explained differences in aggregation size in spring (Appendix 10), accounting for 18% of the variation. In summer and fall, the best variables explained only 1 and 2%, respectively, of the variation in aggregation size. Wind direction, considered separately, had no significant impact on group size.

Table 6. Synchrony of activity of aggregated versus single moose, Denali National Park, 1976-77. The number of observations is indicated in parentheses.

	Group Size	All Inactive	Part Active	All active
Spring	1	70% (120)	-	30% (52)
	≥ 2	46% (17)	3% (1)	51% (19)
Summer	1	34% (152)	-	66% (299)
	≥ 2	17% (26)	17% (26)	66% (102)
Fall	1	9% (2)	-	91% (20)
	≥ 2	20% (20)	43% (43)	38% (38)

DISCUSSION

Social groups of a temporary nature have long been noted to exist among moose, despite their solitary nature compared with other cervids (e.g. Peterson, 1955). These groups vary in size; the variation is related to "breeding activities, mother-young relations, male social system, sex ratio of the population, and external influences of forage, topography, and cover" (Peek et al., 1974; p. 135).

Although moose commonly occurred in aggregations of two or more, most groups contained one animal (or cow with calf). I observed about the same proportion of lone moose and a higher proportion of groups consisting of more than two moose as in other studies (Table 7).

Seasonal and Sex-Age Differences in Aggregation Size

Seasonal patterns of aggregation size vary greatly among populations. On the Kenai Peninsula, seasonal patterns of aggregation size were similar to what I observed in Denali National Park (Peek et al., 1974). Mean aggregation sizes were small in late winter, somewhat larger in summer, and increased through the rut to the largest values in late October on the Kenai Peninsula. Great variability in group size there in spring also suggested a tendency for moose to be aggregated then, although mean group sizes were still small. While I did not observe these large spring aggregations when I began field work 12 May, other researchers in the Park have noticed

Table 7. Frequencies of group sizes observed in the present study and other moose aggregation studies. Sample sizes are included in parentheses whenever possible, as well as the portion of year included in the study period.

	Group Size		
	1	2	> 2
Houston (1973) (Jan-Dec, 3249)	58%	26%	16%
Geist (1963) (May-Sep)	~60-85%	~10-30%	~3-15%
Dzieciolowski (1979) (Jan-Dec, 345)	48%	33%	19%
Present study (May-Nov, 595)	62%	13%	25%

them earlier in the month (VanBallenberghe, pers. commun.) In other studies, moose have shown different seasonal agggregation patterns. Berg and Phillips (1972) observed the smallest groups in March and April and the largest in October, as I did in the present study, but aggregations continued to be very small in summer in Minnesota, whereas I found aggregations larger then than in late winter, based on a small late winter sample size. Group sizes in some other populations have been largest in winter and smallest in summer, with intermediate values in spring and fall (Geist, 1963; Peek et. al, 1974). In all studies, aggregation sizes tended to be largest in late fall or early winter. In other seasons, the tendency to aggregate is highly dependent on characteristics of a given population.

Sex-age category of moose is also a factor in aggregation size. Cows with calves were seldom observed associated with other moose in the present study; the same pattern of avoidance of other moose has been observed elsewhere (e.g. Houston, 1974) and has been attributed to the cow´s defense of the calf against any object construed as threatening (Geist, 1963). Bulls and cows without calves were more sociable and were commonly observed in association with other moose. Group sizes of cows without calves, which reached maximum size in fall, approximated those observed on the Kenai Peninsula. Peek et al. (1974) postulated that large cow groups there were a consequence of a lower bull:cow ratio there than in other areas in that study. The bull:cow ratio in Denali National Park, estimated at 31 to 45 bulls per 100 cows during this study (Troyer, 1980), is also lower than in some other studies (e.g. Peek et al., 1974). In addition, calf survival was extremely low during the study (Troyer, 1980); as a result, there was a high proportion of cows without calves on the study area by early summer. Bulls, too, were commonly observed in association with other bulls or in mixed-sex groups. Studies in Alaska (Peek et. al, 1974), Ontario (Cobus, 1972) and Montana (Knowlton, 1960) have also reported bull associations are common. In other studies (Altmann, 1959; Geist, 1963), however, bulls were solitary in summer.

Aggregation Size in Relation to Habitat

Moose (Peek et al., 1974) and other ungulates (e.g. Hirth, 1977) tend to form larger aggregations in open habitats. I observed this pattern of behavior in spring, and in summer for small and moderate-sized groups. The use of dense cover by very large groups in summer in the Park is not easily explicable; it may be a consequence of a large number of moose concentrating in a small area of excellent habitat, and aggregating because of proximity. The large aggregations that formed in the fall moved into open shrub or tundra portions of the study area as a part of reproductive activities (Lent, 1974).

Crook (1970) suggested that larger group sizes in open habitats have a psychological basis, that the greater number of group members in these habitats is a substitute for cover provided by vegetation in denser habitats. Invoking such a hypothesis for large group sizes of moose in open areas in fall does not seem necessary, but it may provide the best explanation for the same tendency at other times of the year. Smaller group sizes in dense cover may also be a consequence of the difficulty of visual communication between animals in those habitat types.

Synchrony within Aggregations

The degree of synchrony of activity of moose within an aggregation influences sightability of moose during aerial surveys. Because a lying moose is more difficult to see than a standing one, aggregations with one or more moose standing will be easier to detect than one in which all moose are bedded.

Results indicate that moose within an aggregation do in fact tend to synchronize their activity with other group members. Gasaway et al. (1980) observed a high level of synchrony within moose aggregations; furthermore, this synchrony expressed itself in a generally higher level of activity within aggregations than among single moose. Of the aggregations they observed, 88% showed synchronous activity and 60% of those were standing groups. In the present study, 97%, 83%, and 57% of aggregations observed in spring, summer, and fall, respectively, showed synchronous activity (Table 6). In one half to three quarters of these groups, all moose were standing. The proportion of aggregations with all animals lying was much lower than for single moose throughout the spring and summer.

This suggests, as Gasaway et al. (1980) observed, that the amount of time spent active is greater when a moose is associated with other moose. From spring through fall, there was a decline in the degree of synchrony observed. I believe this is because mean group sizes were increasing through this period (Fig. 10). This increase in group size, especially in fall, made it increasingly likely that one or more moose would remain feeding after the first bedded down. Bedding down or resumption of activity by the entire group was often spread out over an hour or more within very large groups.

Weather and Aggregation Size

Weather does not appear to influence aggregation size of moose. Because moose form very temporary aggregations, the potential exists for them to respond to short term changes in weather conditions with altered aggregation sizes. This was not the case in the present study, despite other changes in moose behavior with changing weather (Section III).

IMPLICATIONS FOR MANAGEMENT

Aggregation behavior of moose has a potentially great effect on results of aerial surveys. Moose in aggregations have a greater chance of being observed on aerial surveys than lone moose because aggregated moose show a high degree of synchrony of activity and an increased level of activity. To achieve an accurate total count of moose, therefore, surveys should be conducted when moose are the most aggregated--in late fall and early winter. Most moose surveys in interior Alaska are conducted in early winter, as soon as snow cover is complete. Smaller aggregations during the remainder of the year will make it more difficult to assess total numbers of moose.

Sex-age differences in aggregation sizes suggest that biased composition estimates will result whenever surveys are conducted. Cows with calves will be underestimated because of their isolation from the larger and more easily seen aggregations.

Mixed-sex aggregations have the largest mean size in spring, summer, and fall, which will tend to reduce the bias toward either bulls or cows without calves. Cows without calves will be easier to see in the fall, because of their large mean aggregation size, but this may be offset by the high visibility of bull moose antlers when velvet has been shed.

SUMMARY AND CONCLUSIONS

Season appeared to be the most important influence on diurnal activity patterns in this study. Activity showed the least variation through the day in mid- and late summer, and showed the largest peaks and troughs during pre-rut. Sizable peaks in activity levels, suitable for aerial surveys, occurred twice a day during pre-calving/calving, and in the afternoon during rut. Throughout the study period, activity levels were lowest in late morning, and survey work should be avoided at that time. Predictable composition biases will not occur on the basis of activity alone.

Habitat use and activity were interrelated; moose tended to use more open areas for feeding and move into denser cover for bedding. This means that inactive moose will be extremely difficult to see during surveys, and emphasizes the importance of conducting surveys during diurnal activity peaks to achieve as accurate a count as possible. Bias in composition counts will occur whenever surveys are flown as a result of differential habitat use by various sex-age classes. Cows with calves will tend to be underrepresented because of their greater use of tall shrub habitat types; bulls will also tend to be underrepresented in spring and summer because of their greater use of forest. Fall is the best time for aerial survey work because all sex-age classes use open habitat types more than in spring or summer.

Weather did not appear to be as strongly interrelated wih activity and habitat use. Moose were less active or were in taller, denser habitats when winds were strong. Otherwise, most significant changes in activity or habitat use with changing weather conditions appeared to be part of a diurnal pattern, and can be most effectively considered by considering those diurnal activity patterns in themselves.

Aggregation characteristics play an important role in aerial visibility of moose. Mean aggregation sizes increased from late winter through fall, and varied by sex-age category. Composition bias will result from the isolation of cows without calves from other moose. Moose in an aggregation showed a high degree of synchrony of activity and spent more time active than single moose; the latter behavior pattern will make moose in an aggregation easier to spot from an aircraft. Aggregation size and habitat use were interrelated; aggregations tended to be larger in open habitat types, but aggregation size appeared to be unrelated to weather.

Fall is the season when most aerial surveys are conducted at the present time. Findings in the present study confirm that this is the optimum time for conducting such surveys because moose spend more time in open habitats and are more aggregated than at other times of the year. Since surveys cannot be conducted around dawn and dusk, when activity levels are at a maximum, they should be conducted in the afternoon when activity is fairly high. Activity levels of moose are very low in late morning in the fall.

The importance of doing replicate censuses must be emphasized.

Because diurnal activity patterns changed so rapidly over fairly short periods of time, they might be expected to vary at the same time from year to year, depending on phenology. Repeated censuses will permit the calculation of means and variances.

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PERSONAL COMMUNICATION

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Appendix 1. Mean number of active moose in each sex-age category observed per 15-minute interval scan in each season, Denali National Park, 1976-77.
n - number of observations in that time interval for all n ≥ 4. Post-rut and late winter data were excluded because of small sample sizes.

	Pre-calving Calving				Post-calving				Early Summer				Mid-summer				Late Summer				Pre-rut				Rut			
Time	B	C	CC	n	B	C	CC	n	B	C	CC	n	B	C	CC	n	B	C	CC	n	B	C	CC	n	B	C	CC	n
0000-0045																												
0100-0145																												
0200-0245																												
0300-0345					0.37	0.00	0.00	8					1.50	0.50	0.00	8												
0400-0445	0.33	0.00	0.00	6	0.00	0.13	0.00	8	1.14	2.29	0.14	7	1.00	0.50	0.42	12												
0500-0545	0.00	0.21	0.00	14	0.25	0.37	0.00	8	0.75	1.00	0.50	8	0.67	1.28	0.61	18	0.18	1.06	0.00	17								
0600-0645	0.15	0.00	0.15	13	0.25	0.13	0.00	8	1.75	2.87	0.25	8	0.61	0.50	0.27	26	0.31	0.68	0.16	19	0.94	2.44	0.19	16				
0700-0745	0.50	0.00	0.00	16	0.44	0.22	0.00	9	1.63	1.37	0.25	8	1.00	0.42	0.23	26	0.21	0.68	0.15	34	1.21	2.08	0.13	24	1.00	5.57	0.29	14
0800-0845	0.33	0.67	0.19	27	0.33	0.67	0.33	9	0.14	0.79	0.50	14	1.14	0.62	0.34	29	0.23	0.33	0.08	61	0.72	1.44	0.00	18	0.70	5.63	0.10	30
0900-0945	0.19	0.43	0.27	37	0.33	1.08	0.75	12	0.00	1.00	0.43	14	0.56	0.80	0.05	41	0.29	0.30	0.05	86	0.19	0.94	0.00	16	0.32	1.96	0.00	28
1000-1045	0.44	0.21	0.32	34	0.08	1.67	0.25	12	0.36	1.18	0.14	22	0.93	0.30	0.09	46	0.19	0.39	0.02	93	0.12	0.00	0.00	17	0.25	0.92	0.00	24
1100-1145	0.00	0.11	0.21	28	0.07	0.33	0.07	15	0.90	1.54	0.05	20	0.51	0.44	0.14	66	0.21	0.21	0.10	113	0.27	1.00	0.00	22	0.44	2.93	0.04	27
1200-1245	0.18	0.07	0.21	28	0.13	0.50	0.13	16	0.23	0.71	0.18	17	0.60	0.56	0.02	75	0.29	0.43	0.03	123	0.24	0.81	0.00	21	0.43	5.19	0.09	21
1300-1345	0.29	0.32	0.18	28	0.19	0.56	0.00	16	0.77	0.92	0.54	13	0.67	0.66	0.09	94	0.32	0.32	0.09	119	0.13	0.83	0.00	24	0.67	4.90	0.05	21
1400-1445	0.37	0.53	0.07	30	0.20	0.56	0.20	25	0.69	0.46	0.54	26	0.73	0.73	0.06	97	0.18	0.43	0.10	122	0.14	0.50	0.00	22	0.60	2.43	0.10	30
1500-1545	0.09	0.33	0.33	33	0.52	1.24	0.14	21	0.22	0.55	0.19	27	0.42	0.70	0.16	108	0.28	0.56	0.14	110	0.00	1.37	0.00	19	0.47	4.19	0.06	32
1600-1645	0.00	0.23	0.46	26	0.05	1.26	0.31	19	0.48	0.96	0.44	25	0.69	0.61	0.34	112	0.33	0.44	0.16	95	0.19	1.23	0.00	26	0.74	5.80	0.00	35
1700-1745	0.00	0.04	0.22	23	0.50	0.60	0.20	10	0.71	1.65	0.12	17	0.68	0.62	0.29	105	0.37	0.72	0.13	79	0.46	2.42	0.00	24	0.69	3.39	0.00	23
1800-1845	0.00	0.20	0.20	20	1.75	1.25	0.00	8	1.46	1.85	0.85	13	0.55	0.44	0.30	87	0.41	0.44	0.11	71	0.00	2.28	0.00	18	1.27	2.64	0.09	11
1900-1945	0.00	0.52	0.24	21	1.63	0.63	0.00	8	1.83	0.92	0.50	12	0.38	0.46	0.31	71	0.26	1.03	0.18	62	0.71	1.71	0.00	14				
2000-2045	0.00	0.90	0.50	20	0.40	0.00	0.00	5	0.18	0.45	0.09	11	0.79	0.56	0.19	57	0.29	1.45	0.24	49								
2100-2145	0.00	0.37	0.19	16					1.50	0.13	0.00	8	0.88	0.38	0.33	42	0.00	0.90	0.30	10								
2200-2245													0.67	0.55	0.55	9												
2300-2345																												

Appendix 2. Three-way chi-square analysis of habitat use, activity, and sex-age class of moose, Denali National Park, 1976-77 (**$p < 0.001$).

	χ^2(df)		
H_o	Spring	Summer	Fall
Habitat use, activity, and sex-age class are mutually independent	325.480(12)**	105.010(12)**	151.597(12**)
Habitat use is independent of activity and sex-age class	253.538(10)**	81.908(10)**	143.802(10)**
Activity is independent of habitat and sex-age class	319.255(10)**	87.655(10)**	23.136(10)
Sex-age class is independent of activity and habitat use	170.898(8)**	69.692(8)**	144.525(8)**

Appendix 3. Two-way chi-square analysis testing the hypothesis habitat use is independent of activity among bull, cow, and cow with calf moose in Denali National Park, 1976-77 (*p < 0.01, **p < 0.001).

		χ^2(df)	
	Spring	Summer	Fall
Bulls	27.365(2)**	30.681(2)	62.769(2)**
Cows without calves	6.141(2)	0.958(2)	71.322(2)**
Cows with calves	32.783(2)**	9.651(2)*	5.109(2)

Appendix 4. Three-way chi-square analysis of time of day moose were seen, habitat use, and sex-age class in Denali National Park, 1976-77 (**$p < 0.001$).

H_o	Spring	Summer	Fall
Time, habitat use, and sex-age class are mutually independent	373.389(28)**	268.196(36)**	575.222(28)**
Time is independent of habitat use and sex-age class	215.375(24)**	231.956(32)**	477.309(24)**
Habitat use is independent of time and sex-age class	223.618(22)**	252.496(28)**	436.896(22)**
Sex-age class is independent of habitat use and time	246.910(22)**	134.178(28)**	234.728(22)**

Appendix 5. Two-way chi-square analysis testing the hypothesis habitat use by moose is independent of time of day among bulls, cows without calves, and cows with calves in Denali National Park, 1976-77 (**p < 0.001).

	χ^2(df)			
	Spring	Summer	Fall	Late Winter[1]
Bulls	88.092(18)**	196.622(38)**	59.517(26)**	
Cows without calves	69.906(30)**	270.584(38)**	105.850(26)**	6.532(8)
Cows with calves	68.408(30)**	71.447(30)**	32.395(6)**	

[1] All sex-age classes combined.

Appendix 6. Two-way chi-square analysis testing the hypothesis moose activity is independent of weather for specified weather variables in Denali National Park, 1976-77 (*p < 0.01, **p < 0.001).

	χ^2(df)		
Weather Variable	Spring	Summer	Fall
Wind speed	6.687(3)	36.751(4)**	33.748(4)**
Wind direction	8.993(5)	205.877(7)**	60.357(6)**
Temperature	18.371(3)**	20.015(5)*	46.459(4)**
Barometric pressure	10.137(3)	39.720(5)	55.395(5)**
Light intensity	2.733(3)	35.995(4)**	60.342(4)**
Cloud cover	7.994(5)	66.532(5)**	19.073(3)**
Precipitation intensity	8.716(2)	107.762(2)**	20.373(2)**
Humidity		78.077(5)**	

Appendix 7. Two-way chi-square analysis testing the hypothesis that the number of active bulls, cows without calves, and cows with calves observed is independent of weather for specified weather variables in Denali National Park, 1976-77 (*p < 0.01, **p < 0.001).

	χ^2(df)		
Weather Variable	Spring	Summer	Fall
Wind speed	28.486(4)**	17.572(8)	17.902(8)
Wind direction	72.085(4)**	153.816(14)**	37.647(10)**
Temperature	54.861(6)**	70.586(10)**	61.138(8)**
Barometric pressure	44.641(6)**	52.826(10)**	106.208(10)**
Light intensity	25.225(6)**	29.455(10)*	28.325(8)**
Cloud cover	91.214(10)**	22.307(10)	10.537(8)
Precipitation intensity	32.458(4)**	1.467(4)	6.433(4)

Appendix 8a. Correlation coefficients among weather variables in spring, Denali National Park, 1977 (n=395) (*p < 0.01, **p < 0.001).

	Wind Speed	Temperature	Barometric Pressure	Light Intensity	Cloud Cover	Precipitation Intensity
Wind Speed						
Temperature	0.4163**					
Barometric Pressure	-0.1193	-0.4088**				
Light Intensity	0.3025**	0.4499**	-0.0072			
Cloud Cover	0.2243**	0.1583*	-0.2507**	0.0735		
Precipitation Intensity	0.1667*	-0.0411	0.0241	-0.1609	0.2556**	
Time of Day	0.2675**	0.4099**	-0.2938**	-0.0910	0.3057**	0.1276

Appendix 8b. Correlation coefficients among weather variables in summer, Denali National Park, 1976-77 (n=890) (*p < 0.01, **p < 0.001).

	Wind Speed	Temperature	Barometric Pressure	Light Intensity	Cloud Cover	Precipitation Intensity	Humidity	Day of Year	Insect Harassment
Wind Speed									
Temperature	0.3898**								
Barometric Pressure	0.1871**	0.2325**							
Light Intensity	0.4359**	0.4278**	0.2209**						
Cloud Cover	0.0748	-0.3000*	-0.1590**	-0.0747					
Precipitation Intensity	-0.2034**	-0.2214**	0.0189	-0.2028**	0.1921**				
Humidity	-0.4057**	-0.6408**	-0.0761	-0.4283**	0.4619**	0.3553**			
Day of Year	-0.2607**	0.0018	-0.3589**	-0.4881**	0.0136	0.0554	0.1608**		
Insect Harassment	-0.1707**	0.1486**	0.2415**	0.1974	-0.2845**	-0.0703	-0.1053*	-0.5133**	
Time of Day	0.0739	0.1075**	-0.3589**	-0.1745**	0.0853	-0.0028	-0.1477	0.0812	0.0559

Appendix 8c. Correlation coefficients among weather variables in fall, Denali National Park, 1976-77 (n=523) (*p < 0.01, **p < 0.001).

	Wind Speed	Temperature	Barometric Pressure	Light Intensity	Cloud Cover	Precipitation Intensity
Wind Speed						
Temperature	-0.1926**					
Barometric Pressure	0.1230*	-0.7881**				
Light Intensity	0.1983**	-0.1973**	0.2292**			
Cloud Cover	0.2106**	-0.3286**	0.1615**	-0.2415**		
Precipitation Intensity	-0.0443	-0.0916	0.0109	-0.2042**	0.3508**	
Time of Day	0.1974**	0.0256	-0.0854	-0.1973**	0.0323	0.0031

Appendix 9. Three-way chi-square analysis testing independence of weather factors, activity and habitat use of moose in Denali National Park, 1976-77. H_{o_1}: the weather factor, activity, and habitat use are mutually independent.

H_{o_2}: the weather factor is independent of activity and habitat use.

H_{o_3}: activity is independent of weather and habitat use.

H_{o_4}: habitat use is independent of weather and activity.

*p < 0.01, **p < 0.001.

Season	Factor	Wind Speed	Wind Direction	Temperature	Barometric Pressure	Light Intensity	Cloud Cover	Precipitation Intensity	Humidity	Insect Harassment
Spring	H_{o_1}	65.758(17)**	124.475(17)**	143.616(12)**	184.438(17)**	57.562(17)**	81.306(22)**	49.439(12)**		
	H_{o_2}	60.509(15)**	122.289(15)**	131.543(10)**	178.192(15)**	54.248(15)**	74.331(20)**	42.506(10)**		
	H_{o_3}	25.830(11)*	34.141(11)**	20.612(18)*	79.178(11)**	24.393(11)	24.863(14)	20.880(8)*		
	H_{o_4}	61.182(14)**	118.882(14)**	130.453(10)**	181.585(14)**	56.309(14)**	78.961(18)**	46.026(10)**		
Summer	H_{o_1}	387.719(27)**	500.426(37)**	237.325(22)**	384.089(27)**	248.719(17)**	162.189(22)**	104.973(12)**	417.929(27)**	277.739(17)**
	H_{o_2}	377.484(25)**	471.677(35)**	229.532(20)**	381.762(25)**	236.302(15)**	154.429(20)**	85.507(10)**	410.779(25)**	250.092(15)**
	H_{o_3}	152.467(17)**	278.330(23)**	108.942(14)**	130.384(17)**	65.058(11)**	123.004(14)**	75.371(8)**	167.110(17)**	205.653(11)**
	H_{o_4}	348.606(22)**	345.637(30)**	221.537(18)**	328.322(22)**	204.240(14)**	154.059(18)**	57.998(10)**	319.899(22)**	143.946(14)**
Fall	H_{o_1}	427.203(22)**	236.365(22)**	246.852(12)**	256.907(12)**	279.022(17)**	229.437(22)**	169.669(12)**		
	H_{o_2}	315.892(20)**	142.903(20)**	129.895(10)**	153.156(10)**	168.484(15)**	113.121(20)**	119.500(10)**		
	H_{o_3}	215.222(14)**	132.722(14)**	142.124(8)**	131.062(8)**	188.928(11)**	169.823(14)**	83.698(8)**		
	H_{o_4}	312.195(18)**	188.535(18)**	182.345(10)**	202.254(10)**	168.657(14)**	169.881(18)**	88.453(10)**		

Appendix 10. Regression analyses of weather variables in relation to aggregation size in Denali National Park, 1976-77. Sample sizes for each analysis are indicated in parentheses.

	Spring (51)			Summer (147)			Fall (89)	
Weather Variable	R^2	Simple R	Weather Variable	R^2	Simple R	Weather Variable	R^2	Simple R
Precipitation Intensity	0.17802	0.42193	Barometric Pressure	0.01347	0.11608	Cloud Cover	0.02367	-0.15383
Time of Day	0.20069	-0.12542	Light Intensity	0.02417	-0.07196	Light Intensity	0.04230	0.14942
Cloud Height	0.21537	-0.18515	Cloud Cover	0.03039	-0.09702	Temperature	0.05424	0.10356
Barometric Pressure	0.23292	0.06677	Cloud Height	0.03662	-0.08322	Cloud Height	0.06132	-0.09606
Cloud Cover	0.23646	0.14448	Insect Harassment	0.04109	-0.04746	Precipitation Intensity	0.06621	-0.08576
Temperature	0.23747	-0.13747	Temperature	0.04469	-0.04214	Time of Day	0.06794	0.06753
Wind Speed	0.23807	0.07970	Time of Day	0.05256	0.02927	Barometric Pressure	0.06825	-0.10491
			Wind Speed	0.05491	0.01377			
			Day of Year	0.05524	0.00737			
			Humidity	0.05532	0.01908			