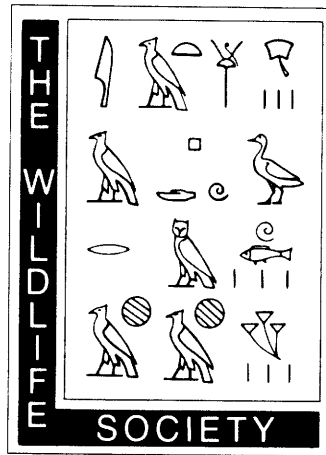


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POPULATION DYNAMICS OF MOOSE IN SOUTH-CENTRAL ALASKA

by

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FRONTISPIECE. Warren B. Ballard equips a neonate moose calf with a radio collar to aid in determining causes of mortality in south-central Alaska. (Photo by R. Dixon)

POPULATION DYNAMICS OF MOOSE IN SOUTH-CENTRAL ALASKA

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Abstract: Demography, movements, and habitat use of moose (*Alces alces*) were studied in south-central Alaska from 1976 through early 1986 and historical data were reviewed. Initially this study tested the hypothesis that predation by wolves (*Canis lupus*) was limiting moose population growth. When reductions in wolf densities failed to greatly increase calf moose survival, we attempted to directly identify and quantify causes of calf and adult moose mortality. Concurrently, we sought to quantify movements, habitat use, productivity, and the effects of severe winters. Lastly, we tested the hypothesis that predation by brown bears (*Ursus arctos*) was limiting moose population growth.

During 1976 through 1985, 218 neonates, 61 calves 5–10 months of age, and 184 adults were captured and either radio collared or equipped with visual collars. The moose population was estimated at 710 moose/1,000 km² in 1980, and at 844 moose/1,000 km² in 1983 ($\lambda = 1.06$). Average age of adult cow moose was 7.7 years. Pregnancy rates averaged 81%. Twinning rates averaged 38%. Parturition occurred between 18 May and mid-June. Overall, calf sex ratios were not different from 1:1 except in 1977 when males predominated.

Survival through 5 months of age averaged 39% with twin and single calves having similar survival rates. Predation accounted for 83% of total mortality among neonates. Ninety-six percent of natural mortality occurred during the first 6 weeks of life with brown bears accounting for 73% of the mortality. During severe winters, males 6–12 months of age had lower survival rates than females of similar ages. Annual calf survival rates averaged 34% and 31% for females and males, respectively. Yearling and adult female annual survival rates averaged 94 and 95%, respectively. Bulls >2 years of age had low rates of natural (excluding hunting) mortality.

Average size of moose groups containing radio-collared individuals was greatest in October and lowest in August. Major periods of moose movement occurred during autumn and spring migration and during rut (late Sep–Oct). Total home range sizes for migratory moose averaged 505 km², whereas those for resident moose averaged 290 km². Nine of 15 radio-collared offspring (mean age = 14 months) partially or fully dispersed from the cow's home range. Males dispersed more frequently and had larger home ranges than females.

Spruce (*Picea* spp.) and willow (*Salix* spp.) vegetation types were used disproportionately more than their availability. During winter, areas with relatively low browse biomass were heavily used by moose, because browse was more available due to shallow snow depths.

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INTRODUCTION

Historically, Game Management Unit (GMU) 13 in south-central Alaska has been one of the most important moose (*Alces alces*) hunting and viewing areas in Alaska. Estimates of sex-age composition were initiated in 1952, and annual surveys have been conducted since 1955. Between 1963 and 1975, about 18% of the documented statewide harvest came from the area. According to Bishop and Rausch (1974), the moose herd increased during the 1940's and 1950's in response to favorable range conditions, low numbers of predators, and relatively low harvests. Bishop and Rausch (1974) also concluded that harvests only slightly affected sex and age ratios during that time period.

The moose population reportedly peaked in 1960 (Bishop and Rausch 1974). There appeared to be an inverse relationship between numbers of wolves and moose. Wolf (*Canis lupus*) numbers were reduced to about 12 by 1953 through predator control and aerial hunting activities (Rausch 1967a, 1969). Termination of those activities in 1952 resulted in a large increase in the wolf

population, which peaked in 1965, and an apparent decline in the moose population (Bishop and Rausch 1974). Use of poison during predator control activities also reduced brown (*Ursus arctos*) and black (*U. americanus*) bear numbers, which may have contributed to the moose population increase.

Severe winters apparently caused the moose population to decline (Bishop and Rausch 1974). With the exception of the winter of 1955-56, moose productivity was high and mortality low until the winter of 1961-62 when the population began declining. A severe winter also occurred in 1965-66, but its effects were not well documented. When a severe winter with record snowfall occurred in 1971-72, mortality was high and subsequent production and survival of calves were low.

Between 1962 and 1974, hunters became more efficient at harvesting moose because of increased use of aircraft and all-terrain vehicles. Consequently, while the moose population was declining, harvests remained "almost constant" (Bishop and Rausch 1974:577). After severe winters, the combined effects of human-, wolf-,

and perhaps bear-induced mortality precluded moose population growth and, in fact, may have contributed to further declines.

Another severe winter (i.e., 1974–75) further reduced calf survival, and the moose population appeared to continue its decline. Wildlife managers expected the moose population to recover during periods of mild winter conditions; however, it continued to decline during the 1960's and 1970's, and managers were faced with the problem of reversing the trend.

While the moose population in GMU 13 was undergoing these changes, feasibility studies for hydroelectric development were conducted along the Susitna River in GMU 13, an area that provided habitat for large numbers of moose. In 1948, Kaiser Aluminum Co. first examined the feasibility of hydroelectric development of the Susitna River. Subsequent development proposals have ranged from a 2-dam to a 12-dam system (Taylor and Ballard 1979). The Devil Canyon–Watana Creek 2-dam system was selected by the U.S. Army Corps of Engineers as the most viable of several development alternatives.

The present study was originally initiated to test the hypothesis that wolf predation was limiting moose population growth. At that time, range conditions appeared adequate to support greater numbers of moose, and the existing herd appeared in good physiological condition based upon available evidence (Franzmann and LeResche 1978). While the first hypothesis was being tested, we attempted to quantify recruitment and mortality within the moose population. When reduced wolf densities failed to greatly improve moose recruitment (Ballard *et al.* 1981*a*, 1987), we attempted to determine and quantify the causes of calf and adult moose mortality directly. Moose movements, habitat use, and distribution also were examined to aid the population assessment and to provide base-line data for evaluating the effects of hydroelectric development on the moose herd. Lastly, we tested the hypothesis that predation by brown bears was limiting moose popula-

tion growth. Based upon this and other studies, we examined several management strategies available to wildlife managers to deal with similar problems elsewhere. Studies of wolves and brown bears were conducted concurrently and have been summarized by Ballard *et al.* (1980*a,b*, 1981*a,b*, 1982, 1986, 1987, 1990), Miller and Ballard (1982*a,b*), Miller (1985), Miller *et al.* (1987), Ballard and Whitman (1988), and Ballard and Miller (1990).

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STUDY AREA

The study area included most tributaries that drain into the Susitna River upstream of the mouth of Portage Creek and other peripheral areas (Fig. 1). During 1976 through 1979, wolf and brown bear densities were reduced within all or portions of a 7,262-km² area (i.e., Susitna River Study Area [SRSA]) to determine the effects on moose calf survival (Ballard et al. 1987, Ballard and Miller 1990). Vegetation, topography, and general climate of the study area were described by Skoog (1968), Bishop and Rausch (1974), Ballard and Taylor (1980), Ballard (1982), and Ballard et al. (1987). Specific vegetation descriptions along the Susitna River were provided by Becker and Steigers (1987).

METHODS

Tagging and Relocating Moose

All moose were darted from a Bell 206-B (Jet Ranger) helicopter, except neonates, which were captured on foot (Ballard et al. 1979). Three combinations of drugs were used to immobilize adult and calf moose: (1) succinylcholine chloride (Anectine, Burroughs-Wellcome Co., Research Triangle Park, N.C.) with hyaluronidase (Wydase, Wyeth Laboratories, Philadelphia, Pa.), (2) etorphine hydrochloride (M-99, Lemmon Co., Sellersville, Pa.) with or without xylazine hydrochloride (Rompun, Haver-Lockhart, Shawnee, Kans.), and (3) carfentanil (Wildnil, Wildlife Laboratories, Fort Collins, Colo.) (Franzmann et al. 1984).

Radio collars were allocated within the moose population study area based upon relative numbers and distribution of moose counted during autumn or spring surveys. Within these allocation areas, adults were randomly selected for capture. Neonate

study areas were searched daily and cow-calf groups were mapped. An effort was made to distribute neonate collars in proportion to density and distribution of moose at parturition.

Captured moose were marked with a radio collar, a visual-numbered canvas collar (Franzmann et al. 1974), or both. Sixty-one 5–10-month-old calves, 115 adults (>1 yr of age), and 218 neonates (<1 month of age) were radio collared, and 69 other adults were equipped with numbered canvas collars. All adults were aged by counting cementum annuli of lower incisor teeth (usually I₁ or I₂) (Sergeant and Pimlott 1959). Each moose was ear tagged with numbered Monel metal tags. During spring, all female yearling (13–24 months of age) and adult (>2 yr of age) moose were rectally palpated (Roberts 1971) to determine pregnancy status.

Radio-collared moose were located from either a Piper PA-18 (Supercub) or STOL-equipped Cessna 180 or 185 fixed-wing aircraft. Each aircraft strut was equipped with a 3-element yagi antenna. We normally performed a series of broad, slow turns until the animal was close, at which time the search pattern developed into steep, sharp turns to visually observe the animal.

Moose relocations were plotted on 1:63,360-scale USGS maps. Time, behavior, and numbers of moose by sex and age class (within approximately 400 m of instrumented individuals) and vegetation type (Vioreck and Dyrness 1980) were recorded on standardized forms.

Sixty-five moose originally captured as 5–10-month-old calves and 115 adults (>1 yr of age) were located on 5,421 occasions (\bar{x} = 30 relocations/moose, range 2–104) from October 1976 through January 1986. Neonates were relocated and visually observed or their signals monitored on thousands of occasions (Ballard et al. 1979). Because all observations were made from fixed-wing aircraft, they were biased toward daylight hours between 0700 and 1800 hours, particularly during late autumn and winter (Fig. 2).

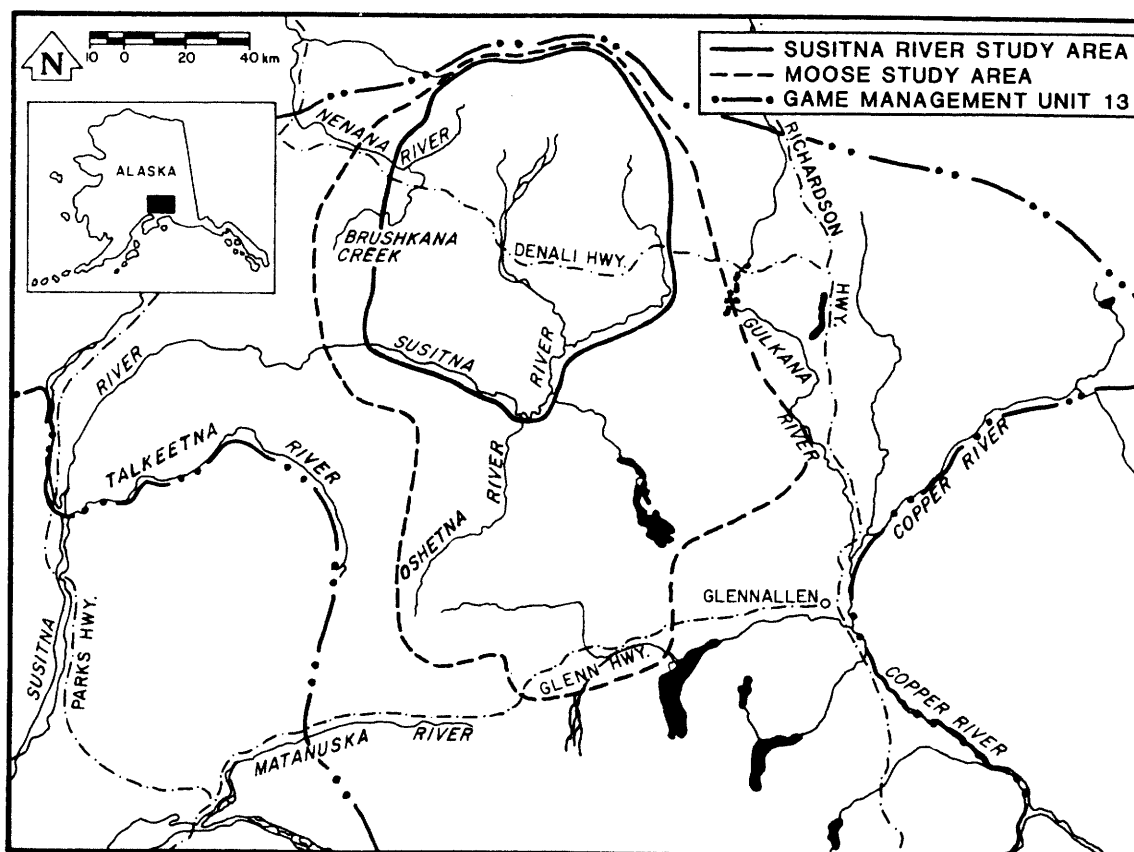


Fig. 1. Boundaries of GMU 13, the Susitna River Study Area, and the moose study area during 1976–86 in south-central Alaska.

Population Trends and Density

Autumn moose sex-age composition surveys have been conducted annually since 1955 in 15 different count areas (CA's) in GMU 13, ranging in size from 264 to 2,191 km² (Fig. 3). Search effort during these low-intensity surveys was usually about 0.4 minute/km². Flights were made along linear transects at 0.8–1.2-km-interval widths at 90–150 m altitude on flat terrain or along contours at similar widths in hilly and mountainous regions. Such surveys were conducted after the first major autumn storm that provided complete snow cover, usually late October through early December. Surveys usually were completed before bulls shed their antlers. Moose were classified into discrete sex and age classes according to relative size, presence and configuration of antlers, and presence

or absence of vulva patch. Bulls with spiked, forked, or small palmated antlers generally ≤ 76 cm wide were classified as yearlings based on comparisons of antler growth with age (Gasaway *et al.* 1987). Total moose observed per hour, bulls:100 cows ratios, calves:100 cows ratios, and percentage of herd represented by yearling bulls were routinely determined and used by managers as indicators of population trend and sex and age composition. Such surveys were not used to estimate population size or density, except when minimum estimates were desired.

Stratified random sampling (Gasaway *et al.* 1986) was used to estimate moose population size and density during autumns of 1980 and 1983. Quadrats were stratified on the basis of observed moose and tracks. Stratified quadrats were searched in the same pattern as those described for sex-

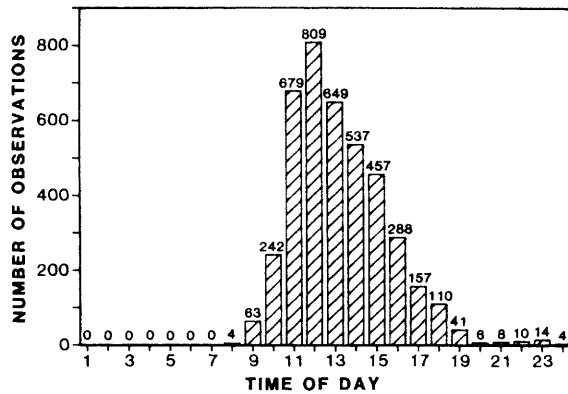


Fig. 2. Distribution of radio-collared moose relocations by time of day in GMU 13 of south-central Alaska, 1976-86.

age surveys, but transect widths were narrower and search intensity usually averaged about 1.5 minutes/km². Sampling intensity was not proportional to area. Density estimates for strata with wide confidence intervals (CI's) received additional

survey effort until CI's were about $\pm 15\%$ of the estimate. Total counts at search intensities ≥ 1.5 minutes/km² were conducted in selected small areas for calculation of sightability correction factors (Gasaway et al. 1986) and where documentation of winter moose densities in selected habitats was desired. Moose densities were calculated based on useable moose habitat only (excludes lakes, glaciers, and areas $> 1,220$ m elevation).

Survival and Mortality Rates

Survival rates of radio-collared calf (< 12 months of age), yearling (13-24 months of age), and adult (> 2 yr of age) moose were calculated using methods described by Pollock et al. (1989a). Survival rates were estimated on a monthly basis. Animals with which radio contact was lost were censored (eliminated from analysis) the month that

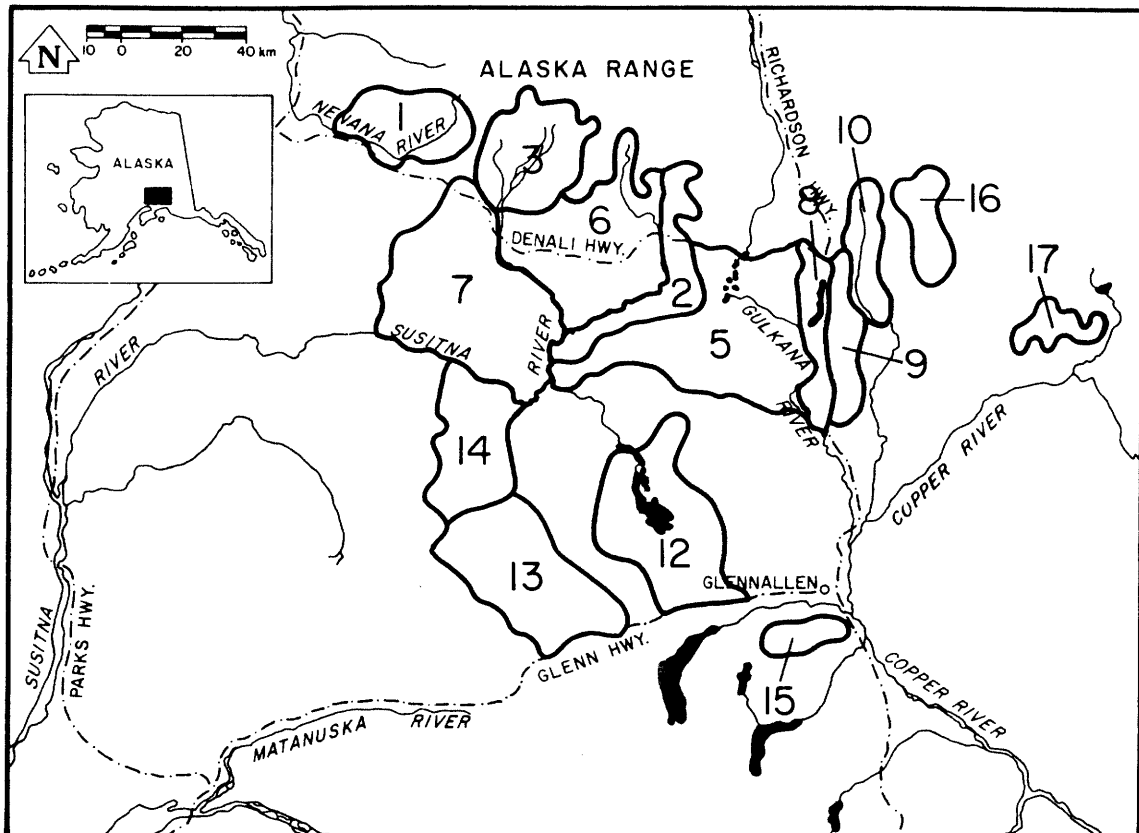


Fig. 3. Boundaries of autumn moose sex-age composition count areas that were surveyed annually and census areas surveyed in 1980 and 1983 within GMU 13.

radio contact was lost. Censoring was due to any 1 of 3 possible causes (Pollock *et al.* 1989*b*): (1) an animal had a transmitter that failed before the animal died, (2) an animal emigrated out of the study area, or (3) an animal survived past the end of the study period. When dates of last observation and documented death spanned several months, the median date was used.

Causes of mortality were determined according to methods described by Ballard *et al.* (1979) and Stephenson and Johnson (1972, 1973). Intensity of telemetry flights was not sufficient to allow cause of death to be determined for all adult moose. When monitoring intensity was frequent (*i.e.*, 1–2/week), it often was possible to classify cause of death based on ground examination at the site or actual observation of a predator on the carcass. Causes of death were classified as unknown, brown or black bear predation, wolf predation, hunting, miscellaneous (*e.g.*, stepped on by cow, pneumonia, auto collisions, *etc.*), starvation, or other winter-related conditions.

Hunting Mortality

Annual hunting mortality, which affected only bulls during the years of our study, was determined from harvest reports and highway check-station records. Although the submission of harvest reports by successful and unsuccessful hunters was required by regulation, compliance was always <90%, but nonresponse bias was not measured. To encourage hunters to report their results, reminder letters were sent each year except 1977 and 1979. Moose hunting seasons and bag limits from 1960 through 1986 are summarized in Appendix A.

Antler measurements recorded on harvest reports since 1978 provided an estimate of number of yearlings killed. Bulls with antler measurements ≤ 76 cm were considered to be yearlings or younger (Gasaway *et al.* 1987). Prior to 1980, bull calves could be legally harvested, but they always composed <0.05% of the annual harvest of bulls (R. W. Tobey, Alaska Dep. Fish and Game, unpubl. data). Beginning

in 1980, only bulls with antler spreads ≥ 91 cm or at least 3 brow tines on 1 antler could be legally harvested in GMU 13. Beginning in 1983, rural resident subsistence hunters were allowed to take any bull by permit; however, there was a 1 animal per household restriction. Beginning in 1984, only bulls with a spike or fork on 1 antler could be harvested within some portions of GMU 13. We did not measure crippling or poaching mortalities. Collisions with vehicles annually account for ≤ 30 mortalities (R. W. Tobey, Alaska Dep. Fish and Game, unpubl. data).

Home Ranges, Distribution, and Vegetation Use

Yearling and adult home range sizes were calculated using the minimum home range method (Mohr 1947). The method may be adequate for estimating home range sizes of animals occupying flat terrain and homogeneous habitat, but it may not be appropriate when large blocks of unused habitats or nonhabitats (*e.g.*, mountains, areas >1,220 m elevation, or lakes) are included within polygons. These latter unused areas are referred to as null habitats (Krausman *et al.* 1989). Home ranges that include null habitats are referred to herein as “home ranges,” whereas those excluding null habitats are referred to as “adjusted home ranges.” To compare home range sizes with and without null habitats, we modified Mohr’s (1947) method as follows:

1. Seasonal (*i.e.*, summer [May–Aug], autumn [Sep–Dec], and winter [Jan–Apr]) home ranges were calculated. Total and seasonal home range sizes were not calculated when numbers of relocations were <24 and <4, respectively, and we considered home ranges to be adequately defined only when numbers of relocations were ≥ 40 and ≥ 14 , respectively. In several cases, selected relocations from different seasons were included in another season’s home range calculations if the relocations were

- clearly grouped with a clump of relocations from a different season.
2. Straight lines connecting outermost relocations were used except in the following cases: (1) when elevations >1,097 m (excluded 3% of relocations) were involved, the boundary followed the contour line; (2) areas containing slopes >30 degrees were excluded; (3) for outlying relocations, the polygon was drawn from the 2 closest points to the outlier; and (4) when all relocations occurred on 1 side of a major drainage immediately adjacent to it, the boundary followed the drainage without crossing it.

Dates and timing of migrations and movements were determined by examining sequential observations of individual radio-collared moose. When sequential moose relocations deviated from a cluster of points, we assumed migration or movement to another range had occurred. Moose were considered to have arrived at a seasonal range when a relocation fell within the home range.

Seasonal and total home ranges between resident (overlapping seasonal ranges) and migratory (nonoverlapping) home ranges were compared. Distances between winter and summer home range of migratory moose were determined by measuring the closest points between seasonal home range polygons.

Availability of overstory vegetation types as well as elevations, slopes, and aspects were assessed by measuring these variables at points of a grid randomly overlaid on 1:63,360-scale topographic and vegetation maps. Use of these variables by moose was determined from radio relocations plotted on the maps. Elevations were determined by extrapolating between contour lines to the nearest 15-m interval. Slopes were classified into 3 categories: (1) flat, ≤ 10 degrees, (2) gentle, 11–30 degrees, and (3) moderate, >30 degrees. Aspect was classified as 1 of 8 compass directions from a line perpendicular to the contour lines through the moose location point.

Methods used to quantify and map browse and other vegetation were de-

scribed by Becker and Steigers (1987). Areas along the Susitna River were mapped to level IV of the vegetation classification system of Viereck et al. (1982) using 16 hectares as the minimum polygon size. Understory vegetative cover composed of willows (*Salix* spp.), alder (*Alnus* spp.), and birch (*Betula* spp.) were classified into 5 groups based upon ground surveys and photointerpretation of color infrared photographs. Browse biomass was sampled, based upon biomass averages and cover classifications, and then stratified into 7 categories ranging from high to zero biomass (see Becker and Steigers 1987). Point locations of radio-collared moose ($n = 2,930$) also were classified into 1 of the browse categories based on season of use. Selectivity (preference or avoidance) of habitat types was determined by chi-square analyses similar to Neu et al. (1974).

Relative distribution of moose was determined in 1980 and 1985. Aerial distribution surveys differed from other types of counts and censuses because less search effort was expended per unit area and no precise population estimates could be derived. A range of 0.4–0.8 minute/km² was expended searching for moose. Moose distribution was recorded on 1:63,360-scale USGS topographical maps. Similar to autumn censuses, winter distribution data were used to stratify areas into relative density strata (i.e., high, medium, low, and zero density). Total moose counts (no variance estimate) were conducted from fixed-wing aircraft in selected areas in late March to estimate moose densities on winter range.

Statistical Tests

Differences between mean age and home range sizes were compared by Mann-Whitney *U* tests or Kruskal-Wallis 1-way ANOVA corrected for ties (Snedecor and Cochran 1973). Count and proportion data were analyzed with chi-square tests and Bonferroni-*Z* test. Moose sex, age, and trend data were analyzed with Spearman's rank correlations by computing Pearson *r*'s on ranks (Conover 1971). Relationships between independent variables were exam-

ined by correlation analyses. Differences in survival rates of neonate twins versus singles as well as between sexes were tested with *t* tests. Differences in sex ratios were compared with a Logit model (Agresti 1984). Unless specifically stated, $P < 0.05$ was required for statistical significance.

DYNAMICS OF THE MOOSE POPULATION

Population Trends, Density, and Recruitment

Prior to 1963, numbers of moose counted per survey hour were variable and not correlated with survey year. From 1964 through autumn 1975, numbers of moose observed per hour of survey declined annually (Fig. 4). Sex and age composition indices (such as bulls:100 cows and calves:100 cows ratios, and percentage of yearling bulls in the herd) began exhibiting declines in the 1950's and declined through autumn 1975 (Fig. 4). In addition to the severe winters described by Bishop and Rausch (1974), severe winters also occurred in 1974–75 and 1978–79 (*see* Effects of Snow on Moose Distribution). Apparently Bishop and Rausch's (1974)

assessment that the moose population peaked in 1960 was subjective, because numbers of moose observed per hour during surveys suggest the population peaked in 1963. Sex and age population indices suggest the population may have begun declining prior to 1960.

Moose counted per hour of survey, bulls:100 cows and calves:100 cows ratios, and percentage of yearling bulls in the herd all reached their lowest levels about 1975 (Fig. 4). After 1975, sex, age, and abundance indices suggested an increase in the moose population ($P < 0.12$ to $P < 0.001$).

The moose population within the SRSA exhibited virtually the same trend as the remainder of GMU 13 (Fig. 5), except that the recruitment index (calves:100 cows) was more variable, but with a detectable downward trend ($P = 0.07$) within the SRSA prior to 1976. The moose population reached its lowest level in 1975 and increased thereafter, although mortality (reflected by calves:100 cows and percentage of yearling bulls) increased during the severe winter of 1978–79. Based upon total counts of cows and calves, proportionately more calves were produced and survived from 1976 to 1984 than from 1963 to 1975 ($\chi^2 = 18.3$, 1 df, $P < 0.005$). Reduced wolf

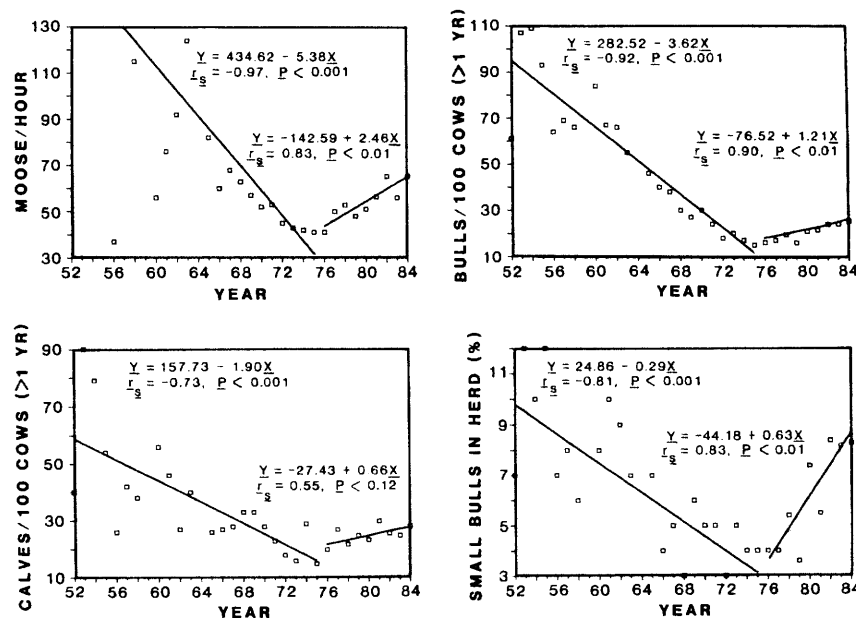


Fig. 4. Indices of moose density and sex-age composition as determined during aerial surveys conducted in 15 count areas within GMU 13 of south-central Alaska, 1952–84.

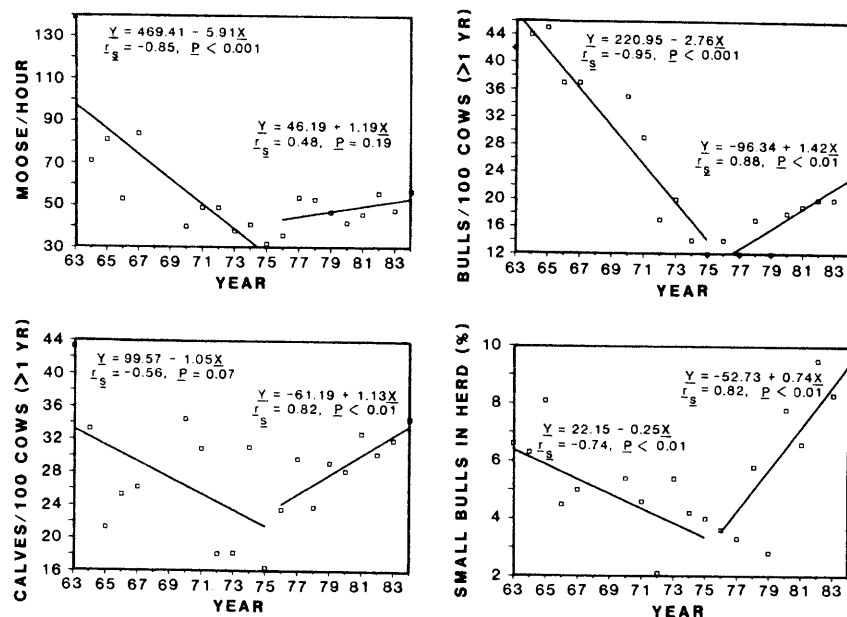


Fig. 5. Indices of moose density and sex-age composition as determined from aerial surveys conducted in the Susitna River Study Area of south-central Alaska, 1963-84.

and brown bear densities, mild winter conditions, and reduced harvests apparently contributed to an increase in the moose population (Ballard et al. 1986, 1987, 1990; Ballard and Miller 1990) (Figs. 4, 5).

Moose population censuses were conducted from fixed-wing aircraft in autumn in several portions of GMU 13 using survey methods described by Gasaway et al. (1986). Although census area (CA) bound-

aries varied between years because of different project objectives and funding restraints, CA's 3 and 7 were counted in both censuses. Census results indicated that moose densities increased by a factor of 1.02 to 1.23 from 1980 through 1983 (Table 1). Similarly, results from low-intensity autumn composition surveys (Fig. 5) and population modeling (Ballard et al. 1986) indicated the moose population was in-

Table 1. Range of moose population and density estimates within selected count areas within GMU 13 and SRSA in south-central Alaska during 1980 and 1983.

Year	Count area	Population estimate	±90% CI	Area censused (km ²)	Density (no./1,000 km ²)
1980 ^a	3	487	39	708	688
	7	1,513	358	1,726	877
	14	589	183	722	816
	3 & 7 ^b	1,728	182	2,435	710
	Subtotal	2,337	237	3,156	741
1983 ^a	3	600	62	708	848
	6	669	93	1,218	549
	7	1,539	278	1,726	892
	12	442	65	1,636	270
	3 & 7 ^b	2,056	215	2,435	844
	7 & impoundment zone	2,836	301	4,030	704
	SRSA	2,795	306	3,735	748
Subtotal	4,573	335	7,588	603	

^a Population estimates include sightability correction factor of 1.03 and 1.19 for 1980 and 1983, respectively.

^b Portion of SRSA.

creasing at a rate of approximately 1.03 to 1.06 times annually.

Autumn moose densities within GMU 13 were variable, ranging from no moose in a 51-km² sample unit to 4,354 moose/1,000 km² in an 18.6-km² sample unit. Over larger areas, densities were relatively high and less variable (Table 1). Greatest densities in GMU 13 occurred in portions of SRSA in 1983 and more recently in Sub-unit 13A west, whereas the lowest density occurred in CA 12 (Fig. 3). Recent autumn moose densities in GMU 13 were compared with those reported elsewhere in Alaska during 1980 through 1987 using similar census methods (Appendix B). Reported moose densities ranged from 50 moose/1,000 km² on the western Yukon Flats in GMU 25D to a high of 1,236 moose/1,000 km² along the lower Yentna and Kahiltna rivers in GMU 16B. Moose densities in GMU 13 were within the upper 25% of reported densities.

During the winters of 1981–83 and 1985, total counts of moose were conducted within the same areas along the Susitna River at an average survey intensity of 1.5 minutes/km². The purpose of these counts was to estimate winter density in areas that appeared to be important winter habitat based on relocation data of radio-collared adults. Comparison of annual counts suggested that late-winter use of habitats along the Susitna River during winters of moderate severity was highly variable, ranging from 42 moose in 1981 to 580 in 1983 (Table 2). Moose densities during these years ranged from 154 to 1,930 moose/1,000 km² with a mean of 1,091 moose/1,000 km². Observability of moose during these counts was low because of large topographical variation, dense vegetation canopy, and relatively poor snow and lighting conditions. Counts were conducted in spite of poor conditions because telemetry studies indicated that the largest numbers of moose occurred in the areas during those time periods. Calculated correction factors (Gasaway et al. 1986) often were high because of low observability. Telemetry data supported the use of high sightability correction factors during these

Table 2. Comparison among years of moose counts conducted within the same selected moose wintering areas along the Susitna River of south-central Alaska, 1981–85.

Year	Search intensity (min/km ²)	No. moose observed	Sightability correction factor ^a	Estimated no. moose ^b	Estimated density (no./1,000 km ²)
1981	2.0	42	1.00	42	154
1982	1.4	174	1.67	290	1,120
1983	2.1	161	3.60	580	1,930
1985	2.3	173	1.70	295	1,158

^a See Gasaway et al. (1986) for method of calculation.

^b No estimate of precision available.

seasons. For example, only 2 of 7 and 2 of 8 radio-collared moose in 1983 and 1985, respectively, were observed during the counts.

Age Structure

Average age of adult (>2 yr of age) cow moose, adjusted to spring season of capture, was 7.7 years ($n = 154$, $SE = 0.3$) during 1976–82 (Fig. 6). Average ages ($n > 10$) among years were different ($Z = 5.8$, 3 df, $P < 0.05$). Average ages of cow moose by year of capture were 7.5 years in 1976 ($n = 39$, $SE = 0.5$), 7.0 years in 1977 ($n = 49$, $SE = 1.0$), 9.4 years in 1980 ($n = 34$, $SE = 0.7$), and 7.6 years in 1981 ($n = 12$, $SE = 0.9$). Cows captured in 1976 ($Z = -1.6$, $P = 0.12$), 1977 ($Z = 2.2$, $P = 0.03$) and 1981 ($Z = 1.5$, $P = 0.14$) were younger than those captured in 1980. Cows ≥ 10 years of age composed 25% of the sample in 1976 and 1977, whereas they composed 62% in 1980; this suggests that age structure of the moose population shifted towards older individuals during this period. The exact opposite was expected, based on autumn calf:cow ratios; 1976–77 age structure was expected to be relatively old following several years of low recruitment, whereas a relatively young age structure was expected in 1980 following several years of improved recruitment because of predator control and mild winters. The former type of age structure was observed in the eastern portion of GMU 13 in 1975 where Van Balenberghe (1978) reported 49% of tagged moose were ≥ 10 years old. Although calves

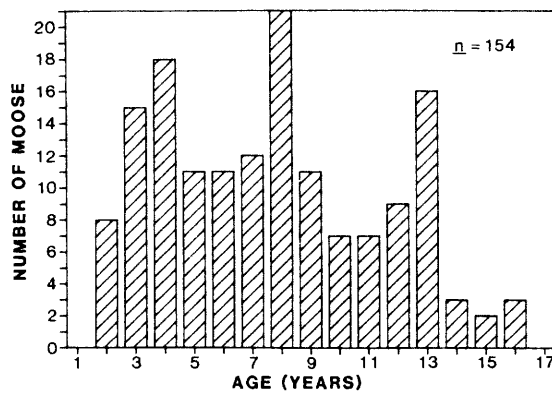


Fig. 6. Age structure of adult cow moose captured within GMU 13 of south-central Alaska, 1976-84.

and yearlings were avoided during capture, no attempt was made to avoid other age classes and no biases should have been expected. Data from 1981 did not fit the expected pattern. We attributed this difference to differences among subpopulations, as well as small sample size.

Productivity

Although pregnancy rates of adults (>2 yr of age) among years were variable, they were relatively high during the study: 88% in 1977 ($n = 59$), 73% in 1980 ($n = 37$), 79% in 1981 ($n = 14$), 82% in 1984 ($n = 11$), and 72% in 1985 ($n = 19$). Lower pregnancy rates after 1977 probably were due to inaccurate diagnoses and lower productivity of older recaptured moose. For example, 4 cows diagnosed as not pregnant in 1980 subsequently had calves. Of 8 biologists participating in the tagging effort that year, only 2 were experienced (i.e., had palpated >10 moose within previous 2 yr) at assessing pregnancy rates. Also, many of the cows examined in latter years were recaptures from previous years. Because older moose may be generally less productive than younger individuals (Markgren 1969), the rates reported here should be considered minimal. Overall, pregnancy rates averaged 81%. Pregnancy rates in GMU 13 were similar to those reported elsewhere for adults in Alaska and North America: 88% for eastern portion of GMU 13 (Van Ballenberghe 1978), 90% for GMU 9 on the Alaska Peninsula (Faro

and Franzmann 1978), 90% in GMU 5 near Yakutat (Smith and Franzmann 1979), 88% in GMU 20 of interior Alaska (Gasaway et al. 1983), and 71-90% for other North American moose populations (Blood 1974). Yearling productivity was less than that of adults; 2 of 5 yearlings physically examined actually produced calves.

Earliest observations of moose parturition were 18 May in 1979 and 24 May in both 1977 and 1978 for uncollared cows. During 1977, 1978, and 1980, timing of parturition and subsequent calf loss were determined by visually observing radio-collared cows and their calves at 3-5-day intervals from 24 May through June each year. After June, median dates between observations were used to calculate dates of apparent mortality. No attempt was made to determine causes of calf mortality for these animals. The earliest date at which radio-collared cows were observed with calves was 25 May, whereas the latest dates for newborn calves were between 7 July and 17 August 1978. Sixty percent of all calves were born between 29 May and 3 June of each year; 96% of births occurred by 10 June each year. The timing of parturition was similar to that reported in Alberta (Hauge and Keith 1981).

Sex ratios and twinning rates at parturition (Table 3) were determined by examining neonates during calf mortality studies conducted in 1977-79, 1980, and 1984 (Fig. 7) and by frequent monitoring of radio-collared cows in 1977-78 and 1980. Observed twinning rates were variable by area, year, and possibly method of collection, ranging from 17 to 63%. Pooled and individual area twinning rates may have increased each year of study, but because rates were not consistently collected in each area the apparent increases could not be statistically tested. Overall, observed twinning rates averaged 38%. Twinning rates of intensively monitored cows grouped into 3 age classes (2-6 yr, 7-11 yr, and 12-17 yr) did not differ by age of cow ($n = 59$, $\chi^2 = 2.7$, 2 df, $P > 0.25$). However, all cows but 1 within this sample were ≤ 14 years of age. Consequently, no differences were expected

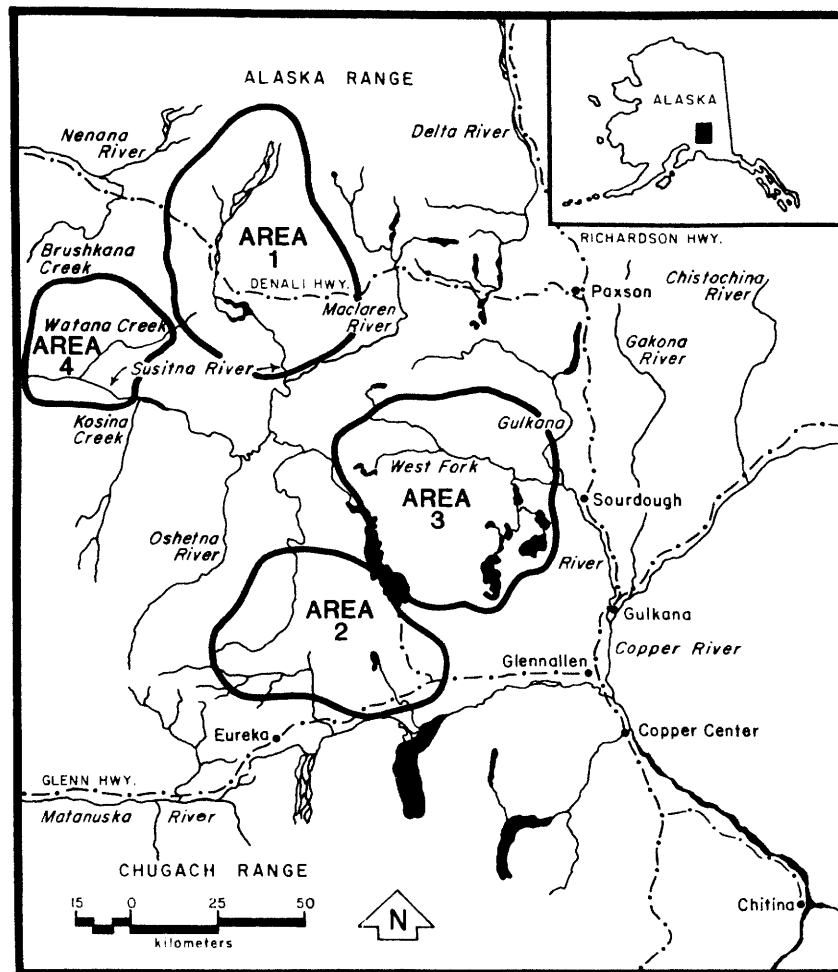


Fig. 7. Location of 4 study areas within GMU 13 where moose calf sex ratios, twinning rates, and causes of mortality were determined, 1977–79, 1980, and 1984.

within this sample. Pimlott (1959) reported that moose twinning rates ranged from 5 to 28% in North America, and Markgren (1982) reported they ranged from 17 to 65% in Sweden. Franzmann and Schwartz

(1985) suggested that twinning rates reported in the literature had been collected by several different methods over several months and were not comparable. For example, Pimlott's (1959) rates were ob-

Table 3. Twinning rates of adult cow moose by area as determined during calf mortality studies and frequent monitoring of radio-collared cows during 1977–84 in south-central Alaska.

Year	Area 1		Area 2		Area 3		Area 4		Subtotal		Uncollared calves ^a		Pooled	
	% twins	No. of cows	% twins	No. of cows	% twins	No. of cows	% twins	No. of cows	% twins	No. of cows	% twins	No. of cows	% twins	No. of cows
1977	17	23	20	25					19	48	30	23	23	71
1978	35	23	20	20	38	16			31	59	32	28	31	87
1979	52	23							52	23			52	23
1980											58	19	58	19
1984							63	38	63	38			63	38
\bar{x} or total	35	69	20	45	38	16	63	38	38	168	39	70	38	238

^a Radio-collared cows (calves uncollared) ranged into and beyond areas 1 and 3 in 1977 and 1978, whereas in 1980 the cow sample ranged over area 4 and beyond.

tained in autumn, after most neonate mortality had occurred (Franzmann et al. 1980; Ballard et al. 1981a,b).

Markgren (1982) attributed differences in twinning rates in Sweden to climate and nutrition. Franzmann and Schwartz (1985) also attributed differences in twinning rates on the Kenai Peninsula, Alaska, to differences in quality and quantity of browse in burned and unburned areas. There were no apparent changes in habitat quality within GMU 13 during our study that would account for the 3-fold differences in twinning rates among years. Also, if winter severity prior to parturition had strongly diminished annual twinning rates, the 1979 twinning rate (following the severe winter of 1978–79) should have been the lowest, and the 1977, 1978, and 1984 rates (following mild winters) should have been highest. Only 1 year fit the expected pattern; consequently, the observed annual variations in observed twinning rates could not be explained based on current literature and may have been related to sampling variation or other factors.

Edwards and Ritcey (1958) reported that migratory cows had higher twinning rates and, therefore, were more productive than resident cows at Wells Gray Park, British Columbia. However, we found that of the intensively monitored radio-collared cows in 1977, 1978, and 1980, residents produced proportionately more twins than migratory cows ($\chi^2 = 5.5$, 1 df, $P < 0.05$). When all years were pooled, the same was true ($\chi^2 = 7.6$, $P < 0.05$) contrary to the findings of Edwards and Ritcey (1958). Although number of twins produced was greater for residents than migrating cows, the numbers of calves surviving the first year of life were not different ($\chi^2 = 0.7$, $P > 0.05$).

Sex ratios among neonates were not significantly different from 50:50 each year (103.9 males:100 females, $n = 155$, $\chi^2 = 0.8$, $P = 0.85$) except in 1977 when males predominated (233 males:100 females, $\chi^2 = 8.0$, $P < 0.005$). A higher proportion of single calves than of twin calves was males in Area 2 during 1977 ($\chi^2 = 6.5$, $P < 0.05$), but not in other years ($P > 0.05$). Verme

and Ozoga (1981) reported a relationship between the interval following onset of estrus and subsequent insemination and the sex ratio of fawns produced in white-tailed deer (*Odocoileus virginianus*); females bred late in estrus produced higher proportions of male fawns. They implied that in heavily hunted populations where male densities were greatly reduced, does may have mated later due to scarcity of males, resulting in higher male sex ratios at birth. Although speculative, there may have been a relationship between adult sex ratios and neonate sex ratios during the present study. The lowest adult bulls:100 cows ratio in the calf mortality study areas occurred in 1977 (11 males:100 females). Thereafter, bull:cow ratios increased from 17:100 in 1978 to 24:100 in 1984.

Several investigators have expressed concern that low bull:cow ratios could influence conception rates and neonate sex ratios in ungulates (Bishop and Rausch 1974; McIlroy 1974; Bailey et al. 1978; Crete et al. 1981; Verme and Ozoga 1981; A. W. Franzmann, Alaska Dep. Fish and Game, pers. commun.). Smaller fetus sizes (indicating late mating) have been noted in several Alaskan moose populations where bull:cow ratios have been relatively low (Rausch 1967b; J. C. Didrickson, Alaska Dep. Fish and Game, pers. commun.; V. Van Ballenberghe, U.S. For. Serv., pers. commun.). Whether observations of small fetuses and skewed neonate sex ratios during some years were the result of relatively low bull:cow ratios has not been determined and further investigation appears warranted.

Survival and Natural Mortality

Calves <6 Months of Age.—Causes of moose neonate mortality were studied within 4 areas of GMU 13 during 1977–79 and 1984 (Fig. 7). Areas 1, 2, 3, and 4 were studied during 1977–79, 1977–78, 1978, and 1984, respectively. A total of 218 moose calves was captured and radio collared (Table 4). Twenty calves (9%) died as a result of being abandoned or trampled by their cows during capture activities.

Table 4. Numbers of moose calves collared and subsequent causes of mortality in GMU 13 of south-central Alaska during 1977–79 and 1984, May through October.

Calves	Area 1				Area 2			Area 3	Area 4	All areas		Grand total	
	1977	1978	1979	Total	1977	1978	Total	1978	1984	1977	1978	n	%
Radio-collared	25	31	29	85	31	26	57	24	52	56	81	218	
Abandoned	2	4	1	7	4	2	6	1	6	6	7	20	
Remaining	23	27	28	78	27	24	51	23	46	50	74	198	100.0
Death from													
Brown bear predation	8	11	12	31	16	10	26	7	24	24	28	88	44.4
Wolf predation	0	0	0	0	1	0	1	1	3	1	1	5	2.5
Unknown predation	0	0	0	0	1	1	2	1	0	1	2	3	1.5
Miscellaneous	1	1	4	6	2	1	3	1	5	3	3	15	7.6
Unknown cause	0	1	0	1	2	0	2	1	1	2	2	5	2.5
Black bear predation	0	0	0	0	0	0	0	0	4	0	0	4	2.0
Coyote predation	0	0	0	0	0	0	0	0	1	0	0	1	0.5
All causes	9	13	16	38	22	12	34	11	38	31	36	121	61.0

These calves were excluded from survival and mortality calculations.

Sixty-one percent of the calves died during the first 5 months of life. Ninety-six percent of early natural mortality occurred before 9 July of each year. Predation by brown bears was the largest cause of calf moose mortality (Table 4), accounting for 73% of total mortality. The second largest cause of mortality was attributed to miscellaneous factors (12%) such as accidental injury inflicted by the cow, drownings, and pneumonia. Wolf predation and unknown causes each accounted for 4%. Predation from all causes accounted for 83% of total mortality during the first 5 months of life.

Survival rates (Table 5) for collared and uncollared moose calves from June through October were compared to determine if collaring predisposed the calves to death. There were no significant differences in rates of calf moose survival in 1977 ($t = 1.4$, 68 df, $P = 0.20-0.10$), 1978 ($t = 0.3$, 74 df, $P > 0.50$), or pooled for all years ($t = 1.0$, 204 df, $P > 0.50$).

Timings of mortality between radio-collared calves in 1977–79 and 1984 and of calves of radio-collared cows in 1977, 1978, and 1980 were not significantly different (Kolmogorov-Smirnov test, $P > 0.05$) (Sokal and Rohlf 1969:440) (Fig. 8), except between collared calves in 1984 and uncollared ones in 1978 (Kolmogorov-Smirnov test, $D = 159$, $P < 0.05$). Overall, the

timing of mortalities suggests that the causes of mortality between the 2 groups were similar. Ninety-four percent of natural mortality for both groups occurred before 19 July each year. After that date, nearly all calves survived to at least 1 November each year; thereafter, survival was dependent on winter severity and predation. We conclude that neither the collars nor the capture process predisposed calves to death.

Recently, Ozoga and Clute (1988) compared mortality rates between marked and unmarked white-tailed deer fawns and concluded that marked fawns suffered less mortality. This was because healthy fawns survive longer, whereas those dying of inadequate nutrition die immediately postpartum and are not available for capture. While searching for newborn moose calves, we found only 3 of 221 calves had been stillborn or died immediately postpartum. Therefore, because we found no differences in survival rates between collared and uncollared calves and there was an apparent low rate of stillbirths, we conclude that this source of bias was minimal in this study.

There were differences in calf survival rates among study areas and years ($P < 0.05$) (Table 5). The lowest survival rate occurred within the SRSA (Area 4) during 1984. Area 4 was selected for study because of its dense populations of black bears (Miller 1984) that could have been an im-

Table 5. Survivorship of radio-collared and uncollared moose calves in GMU 13 of south-central Alaska from May through October 1977-80 and 1984.*

Area and year	Jun		Jul		Aug		Sep		Oct	
	Rate	SE	Rate	SE	Rate	SE	Rate	SE	Rate	SE
Radio-collared calves										
Area 1										
1977	0.739	0.079	0.609	0.092	0.609	0.102	0.609	0.102	0.609	0.102
1978	0.519	0.069	0.519	0.096	0.519	0.096	0.519	0.096	0.519	0.096
1979	0.607	0.072	0.429	0.079	0.429	0.098	0.429	0.098	0.429	0.108
Total	0.615	0.043	0.513	0.052	0.513	0.057	0.513	0.057	0.513	0.059
Area 2										
1977	0.259	0.043	0.259	0.084	0.185	0.063	0.185	0.075	0.185	0.075
1978	0.708	0.078	0.542	0.089	0.500	0.098	0.500	0.107	0.500	0.107
Total	0.471	0.048	0.392	0.062	0.333	0.061	0.333	0.068	0.333	0.068
Area 3										
1977	0.565	0.078	0.565	0.103	0.522	0.100	0.522	0.109	0.522	0.109
Area 4										
1984	0.217	0.028	0.174	0.050	0.174	0.056	0.174	0.056	0.174	0.056
All areas										
1977	0.480	0.049	0.420	0.065	0.380	0.065	0.380	0.069	0.380	0.069
1978	0.595	0.044	0.541	0.055	0.514	0.057	0.514	0.060	0.514	0.060
1977-84	0.480	0.025	0.409	0.032	0.389	0.034	0.389	0.035	0.389	0.036
Uncollared calves										
1977	0.400	0.057	0.233	0.059	0.233	0.077	0.233	0.077	0.233	0.077
1978	0.595	0.062	0.541	0.078	0.514	0.080	0.487	0.080	0.487	0.082
1980	0.467	0.062	0.233	0.055	0.233	0.077	0.233	0.077	0.233	0.077
Total	0.495	0.036	0.351	0.041	0.340	0.047	0.330	0.047	0.330	0.047

* Calculated using methods described by Pollock et al. (1989a).

portant source of calf mortality (Franzmann et al. 1980) not previously documented in GMU 13. Because black bears would likely be drastically reduced as a result of hydroelectric development (Miller 1984), it was conceivable that a reduction in the black bear population could be beneficial to the moose population. Black bears were responsible for 11% of the total calf mortality in 1984 (Table 4). Similar to previous years, predation by brown bears was the largest source of calf mortality (62%).

Pooled survival rates for twin (0.373) and single (0.439) calves were not different ($P > 0.05$). Sex was not a significant factor in explaining variations among mortality rates ($\chi^2 = 17.4$, 1 df, $P > 0.20$) from June through October. Survival rates during the first 5 months of life varied from 17% in Area 4 in 1984 to 61% in Area 1 in 1977 (Table 5). Differences in survival rates

among areas and years may have been related to differences in densities of predator species, although most observed differences could not be explained. For example, in 1977, wolf densities were greatly reduced in Area 1 but not in Area 2, and calf survival that year was greater in Area 1 than in Area 2. The same trend was not evident in 1978, but wolf populations in Area 2 had been greatly reduced (Ballard et al. 1981a). In 1979, predation by brown bears was expected to have been greatly reduced in Area 1 because brown bear populations were reduced by about 60% (Miller and Ballard 1982a,b). Although moose sex-age composition and census data suggested that reductions in bear density greatly increased calf survival (Ballard and Miller 1990), radio-collared calf survival data suggested no improvement. This discrepancy occurred largely because the small sample of radio-collared calves was

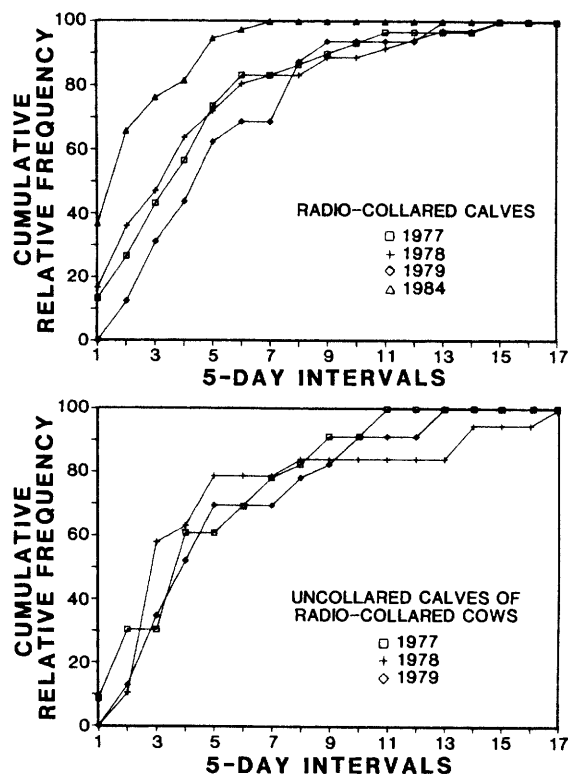


Fig. 8. Dates of mortalities of radio-collared and uncollared moose calves within GMU 13 of south-central Alaska, 1977–84. First 5-day interval begins on 26 May and the last 5-day interval ends on 3 August (Interval No. 14). Intervals 15–17 correspond to August through September.

killed (67% of mortalities) by only 2 bears that had not been removed. From 1977 through 1984, overall calf survival during the first 5 months of life averaged 39% (61% mortality).

Calves 6–12 Months of Age.—During this study, 14 mortalities of radio-collared calves occurred between 1 November and 31 May. Of the 14 deaths, starvation (or winterkill) was the largest source ($n = 11$, 79%) of calf mortality, whereas 2 were caused by brown bear predation and 1 by an unknown predator. Nine of 11 starvation deaths occurred during the severe winter of 1978–79.

Annually there were no differences ($P > 0.05$) in calf survival rates between sexes from 1 November to 31 May of each year except during the winter of 1978–79 ($t = 2.7$, 43 df, $P < 0.01$) (Tables 6, 7). During that relatively severe winter, male calf survival was 55%, whereas female calf survival was 88%. During severe winters, male calves suffered higher ($P < 0.01$) rates of mortality than female calves.

Annual Calf Survival Rates.—Average annual calf survival rates for female and male calves were 34 and 31%, respectively (Table 8); these rates were determined by multiplying the rate from Table 5 times the rates from either Table 6 or 7. Although male calf survival rates were lower than female rates from 1 November to 31 May during severe winters, overall annual survival rates were not different ($P > 0.05$).

Ranges of annual calf moose survival rates that have occurred or potentially could occur under differing predator densities and winter severities in GMU 13 were

Table 6. Annual survival rates of radio-collared cow moose in GMU 13 of south-central Alaska during 1976–86.^a

Year	Adults			Yearlings			Calves ^b		
	n	Rate	SE	n	Rate	SE	n	Rate	SE
1976–77	38	1.000	0.000	2	1.000	0.000			
1977–78	44	0.977	0.023				1	1.000	0.000
1978–79	46	0.922	0.050				37	0.881	0.065
1979–80	53	0.907	0.040	22	1.000	0.000	16	0.938	0.061
1980–81	75	0.968	0.021	16	1.000	0.000	9	1.000	0.000
1981–82	80	0.921	0.030	8	0.750	0.153			
1982–83	70	0.970	0.023						
1983–84	52	0.961	0.030						
1984–85	41	0.951	0.041						
1985–86	25	0.914	0.155						
\bar{x}	52	0.949	0.041	12	0.938	0.038	16	0.955	0.032
Pooled	524	0.948	0.011	48	0.951	0.033	63	0.880	0.045

^a Survival rates calculated using methods described by Pollock et al. (1989a).

^b Seven-month rate from 1 Nov through May.

Table 7. Annual survival rates of radio-collared bull moose in GMU 13 of south-central Alaska during 1978–86.^a

Year	Adults			Yearlings			Calves ^b		
	n	Rate	SE	n	Rate	SE	n	Rate	SE
1978–79							26	0.550	0.107
1979–80	3	1.000	0.000	14	0.727	0.120	18	0.941	0.057
1980–81	10	0.875	0.117	17	1.000	0.000	7	1.000	0.000
1981–82	16	0.750	0.108	6	1.000	0.000			
1982–83	13	0.833	0.108						
1983–84	9	0.778	0.139						
1984–85	7	0.714	0.171						
1985–86	5	0.400	0.204						
\bar{x}	9	0.764	0.121	12	0.909	0.040	17	0.830	0.055
Pooled	63	0.754	0.055	37	0.909	0.048	51	0.806	0.055

^a Survival rates calculated using methods described by Pollock et al. (1989a).

^b Seven-month rate from 1 Nov through May.

estimated from combinations of summer and winter calf survival rates (Table 8). These rates are presented to provide managers with some indication of the potential survival rates possible under the conditions we measured. Rate no. 4 represents the lowest annual survival rate possible from available data (i.e., 15 and 10% annual survival for females and males, respectively). The summer rate was obtained from an area with relatively high densities of brown bears (28/1,000 km²—Miller et al. 1987), black bears (90/1,000 km²—Miller et al. 1987), and wolves (3/1,000 km²—W. B. Ballard, unpubl. data) and can be considered representative of an area where predation was severe. The winter rate was obtained during the severe winter of 1978–79 when starvation mortality was greatest. At the other extreme, the highest potential annual calf survival rate was represented by rate no. 5. The summer rate was representative of an area with low wolf densities following intensive predator control (2 wolves/1,000 km²—Ballard et al. 1987) whereas the winter rate occurred during mild weather conditions. Both summer and winter data were collected consecutively during 1978 and 1979. The estimated survival rates for those years fell within the range of extreme values.

Yearling and Adult Females.—Annual survival rates for yearling and adult radio-collared cow moose were based on 43 and 532 moose years, respectively. Overall, yearling and adult female annual survival

rates each averaged 95% (Table 6) and were not significantly different ($t = 0.02$, $P < 0.01$). Lowest adult survival occurred in 1985–86, but because that rate was only through January 1986, it was not representative of the entire year. Adult female survival rates also were relatively low in 1978–79 (i.e., a relatively severe winter), 1979–80, and 1981–82, averaging about 92%. Lowest yearling survival (75%) occurred in 1981–82.

In general, radio-collared yearlings and adults were not monitored frequently enough to accurately determine causes of mortality. However, there were periods when monitoring intensity was sufficient to allow causes of mortality to be determined—during parturition in 1977 and 1978 when cows were monitored 3–5 times/week, and during late winter in 1978–79 when cows and 9–10-month-old calves were monitored once per week. From October 1976 through January 1986, 21 adult radio-collared females died. Of that total, 10 died from unknown causes. Predation accounted for 8 of 11 mortalities where cause of death was determined: brown bears killed 5, wolves killed 2, and unknown predators killed 1. Three adults starved. Causes of death for 2 yearlings were starvation and wolf predation. Contact with 37 adult radio-collared females was lost; therefore, their fates were unknown. Dates of lost radio contact were equally divided between snow-free (May–Oct) and snow-cover periods.

Table 8. Hypothetical and actual annual survival rates of radio-collared calf moose in GMU 13 of south-central Alaska, 1977–84 (from Tables 5, 6, and 7).^a

Sex and rate nos.	Survival rates ^b		
	Jun through Oct	Nov through May	Annual ^c
Females			
1.	Pooled (1977–84) 0.389	Pooled (1976–86) 0.880	0.342
2.	Pooled (1978–79) 0.514	Pooled (1978–79) 0.452	0.232
3.	Pooled (1979–80) 0.429	Pooled (1979–80) 0.938	0.402
4.	Lowest (area 4—1984) 0.174	Lowest (1978–79) 0.881	0.153
5.	Highest (area 1—1977) 0.609	Highest (1980–81) 1.000	0.609
6.	Pooled (1977–84) 0.389	Lowest (1978–79) 0.881	0.342
7.	Lowest (area 4—1984) 0.174	Pooled (1976–86) 0.880	0.153
Males			
1.	Pooled (1977–84) 0.389	Pooled (1978–81) 0.806	0.313
2.	Pooled (1978–79) 0.514	Pooled (1978–79) 0.550	0.282
3.	Pooled (1979–80) 0.429	Pooled (1979–80) 0.941	0.403
4.	Lowest (area 4—1984) 0.174	Lowest (1978–79) 0.550	0.096
5.	Highest (area 1—1977) 0.609	Highest (1980–81) 1.000	0.609
6.	Pooled (1977–84) 0.389	Lowest (1978–79) 0.550	0.214
7.	Lowest (area 4—1984) 0.174	Pooled (1978–81) 0.806	0.140

^a Survival rates calculated using methods described by Pollock *et al.* (1989a).

^b Of 7 calculated rates for each sex, rate nos. 1–3 were actual rates based on pooled data or data from individual years. Rate nos. 4–7 are hypothetical estimates based on combinations derived from areas having different predator densities and/or different winter severities.

^c Annual rates estimated by multiplying Jun–Oct rate times Nov–May rate.

Yearling and Adult Males.—Survival rates for yearling and adult radio-collared bull moose were based on 34 and 72 moose years, respectively (Table 7). Overall, adult bulls had significantly lower ($t = 2.1$, $P < 0.05$) survival rates (75%) than yearling bulls (91%). Prior to 1980, any bull was legal for human harvest. Following that date, only bulls with 3 brow tines on at least 1 antler or antler spreads ≥ 91 cm were legal. Also, in 1984 only spiked or forked antlered males were legal in the SRSA, whereas after that year the regulation applied only to subunit GMU 13A. Yearling bulls had their lowest survival in 1979–80 when they were legally harvested (2 of 3 mortalities). Thereafter, yearling

bull survival was relatively high, ranging from 86 to 100%.

According to annual survival rates and aerial sex–age composition data, adult bull survival declined as the study progressed (Table 7; $r_s = -0.87$, $P < 0.01$), suggesting increased vulnerability with age when bulls with antler spreads ≥ 91 cm were legally available for hunting. Lowest adult bull survival rate occurred in 1985–86 (Table 7). However, that rate applied only through January 1986 and may have been biased. Radio-collared bulls had relatively low rates of natural mortality after they attained 2 years of age. Of 13 adult bull mortalities, 12 were due to human harvest and 1 to unknown causes.

Hunting Mortality

While the GMU 13 moose population was declining (i.e., 1963–71), moose hunting seasons and bag limits were relatively liberal (Appendix A). Annual reported harvests during that period averaged 1,524 (SD = 189) (Table 9). Hunting of cow moose was open to all hunters with relatively short seasons (2–7 days) during all but 1 year when it was closed. In 1970–71 and 1971–72, cow moose hunting was regulated by permits. During the 7 years that cow moose hunting was allowed, cows composed 21.2% of the total harvest. Following the severe winter of 1971–72, legal harvests of cow moose were eliminated.

Only bull moose were legally harvested from 1972 through 1985 (Appendix A), and an average of 751 moose (SD = 104, >98% bulls) were killed annually. The result of elimination of cow moose seasons and the shortening of the bull season after 1971 was a 49% reduction in the average annual reported harvest (Table 9). Bull moose hunting seasons became progressively more conservative. By 1980–81, after it became clear that harvests of bull moose were skewing bull:cow ratios (Figs. 4, 5; Table 9) to low levels in some areas (e.g., 5.3 bulls:100 cows), bull moose hunting was further restricted; legal bulls were restricted to those with antler spreads ≥ 91 cm or ≥ 3 brow tines on at least 1 antler (Appendix A). The logic behind the regulation was to provide full protection to the yearling age class, which was disproportionately vulnerable to hunting mortality. Although largely successful, this strategy placed disproportionate pressure on large-antlered bulls. The age structure among remaining bulls became skewed to yearling and 2-year-old classes, causing concern that most breeding was being conducted by these younger age classes (W. B. Ballard, unpubl. data). By 1982–84, over half of bulls counted from fixed-wing aircraft during autumn sex-age composition surveys within the 15 count areas (Fig. 3) were yearlings with antler spreads of ≤ 76 cm; within 4 of the count areas, yearlings composed $\geq 75\%$ of total bulls counted.

Biologists have debated for many years the potential impacts of skewed sex ratios on ungulate populations. Identified potential impacts often have involved the following: (1) concern over significant numbers of females not being bred because of low bull densities (Peterson 1955); (2) parturition occurring over a wide range of dates leading to late, less viable calves (K. N. Child, B.C. Minist. of Environ., pers. commun.); (3) conception occurring over 2–3 estrus cycles, resulting in calves of various sizes (Bishop and Rausch 1974; K. N. Child, B.C. Minist. of Environ., pers. commun.); (4) sociological implications (Bubenik 1972); and (5) potential physical deterioration caused by continual breeding by young, smaller-bodied, genetically inferior bulls (Harmel 1982). Although direct evidence of problems created by heavily skewed sex ratios in moose are difficult to detect, some observations are available. In the Matanuska Valley, Alaska, bull:cow ratios were reduced to low levels (4–9 bulls:100 cows), but these low ratios did not adversely affect pregnancy rates, which were about 90% (Rausch 1967*b*). However, there were indications that conception dates were variable. Considerable size differences occurred both in unborn fetuses (Lent 1974) and in calves present in autumn (J. C. Didrickson, Alaska Dep. Fish and Game, pers. commun.). Smaller calves presumably died at higher rates during winter.

As a result of the above concerns, an alternative harvest strategy was initiated in 1983 (Appendix A). Within portions of GMU 13, only bulls with a spike or forked antler on at least 1 side were legal. Preliminary results suggest that bull:cow ratios improved and recruitment of older bulls into the moose population increased over areas where harvest seasons were not modified (R. W. Tobey, Alaska Dep. Fish and Game, unpubl. data).

Numbers of moose harvested within the SRSA prior to 1975 were not determined. As in the remainder of GMU 13, only bull moose were harvested during this study. Numbers of bulls harvested in the SRSA were not correlated ($P > 0.05$) with num-

Table 9. Summary of reported moose harvests and hunter success in GMU 13 and SRSA in south-central Alaska from 1963 to 1985.

Year	Number killed			GMU 13 total	SRSA ^a total	No. hunters	% success
	Bulls	Cows	Unknown sex				
1963	1,385	343	7	1,735			
1964	1,213	394		1,607			
1965	1,318	3	10	1,331			
1966	1,336	181	36	1,553		4,163	37
1967	1,217	319	16	1,552		4,027	39
1968	1,240	243	29	1,512		4,476	34
1969	1,204	7	8	1,219		2,553	48
1970	1,141	220	30	1,391		3,535	39
1971	1,126	670	18	1,814		4,881	37
1972	689	7	16	712		3,199	22
1973	604	4	10	618		2,513	25
1974	768	3	23	794		2,770	29
1975	690	2	23	715	119	2,978	24
1976	708	1	23	732	96	3,122	23
1977	684	1	13	698	120	2,299	30 ^b
1978	846	1	16	863	170	3,034	28
1979	845	0	3	848	189	2,377	36 ^b
1980	525	1	31	557	107	2,859	20
1981	793	0	1	794	176	3,105	26
1982	620	0	3	623	144	2,919	21
1983	885	4	15	904	153	3,243	28
1984	830	3	6	839	71	3,426	25
1985	812	4	7	823	196	3,576	23
1986	1,023						

^a Only bulls were legally harvested.

^b Absence of reminder letters in 1977 and 1979 may have resulted in inflated percent success relative to previous years because those that responded without reminder letters probably had higher success rates.

bers harvested elsewhere in GMU 13. The percentage of the unit harvest that reportedly was taken from the SRSA increased during the study concurrent with reduced predator populations and mild winters; percent of harvest attributed to SRSA within GMU 13 increased progressively from 13.1% in 1976 to 23.1% in 1982 (1975–83, $r = 0.55$, $P = 0.13$, 1984 excluded because of different harvest regulations; see Appendix A). Increases in calf survivorship resulting from reductions in wolf and bear numbers, and mild winters (Ballard et al. 1987, 1990) also were reflected by increases in harvests of bull moose in subsequent years.

MOVEMENTS, DISTRIBUTION, AND HABITAT USE

Group Size

Differences in observed mean group sizes per month were determined for radio-

collared adult cows from 1977 to 1985. There were no differences among years; therefore, all years were pooled. During January through August, 30% of all observations of instrumented moose were of single animals. In September that proportion began declining, and by October only 19%

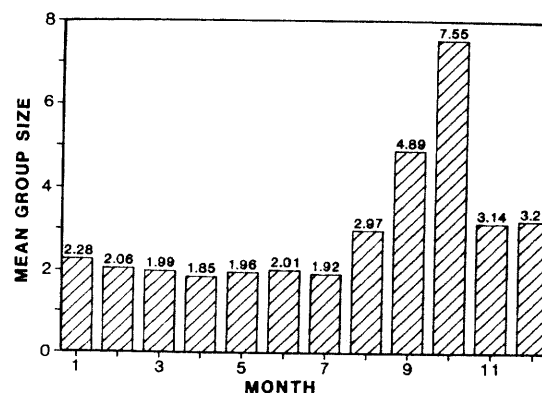


Fig. 9. Average group size containing 1 or more radio-collared moose by month of observation in GMU 13 of south-central Alaska, 1976–85.

of the observations were of lone individuals, reflecting rutting concentrations. Proportions of lone moose again increased in November and December. Average group size exhibited similar trends. Average group size was about 2 moose from January through July (Fig. 9). Average group size increased to 3.0 in August, 4.9 in September, and 7.6 in October. After October, group size decreased to 3.2.

Our results were similar to other studies, indicating that moose aggregations (excluding cows with calves) were highest in late autumn and early winter (LeResche 1974, Peek et al. 1976). Largest group sizes occur during the rut and immediately following the rut. Generally, cows with calves do not associate with the large rutting groups.

Movement Patterns

Moose exhibited all of the movement patterns described by LeResche (1974) as well as many undescribed variations. Moose were classified into 2 basic categories, based on overlapping or nonoverlapping of winter and summer home ranges: residents—individuals with movements confined to relatively small areas and with portions of their winter and summer home ranges overlapping; migratory—individuals that moved over relatively large areas and whose winter and summer home ranges did not develop. Three periods of movement were identified: movements to rutting areas, autumn migration, and spring migration.

Movements During Rut.—Movements during rut were most pronounced for resident moose. During late September and October, several moose made distinct movements to upland areas not used during other seasons. These areas appeared to have greater numbers of large-antlered bulls than other areas, and, consequently, bull density and behavior may have been an attraction. Major identified rutting areas within the project area had poor human access, and fewer bulls were killed there than in other areas. For example in CA 7 (Fig. 3), an area with relatively poor

human access, 22% of the bulls counted in autumn 1984 had antler spreads ≥ 102 cm. In contrast, only 4% of the counted bulls had antler spreads ≥ 102 cm in adjacent areas with relatively easy human access (CA's 13 and 14). Migratory moose also may have moved to specific rutting areas, but these were not easily identifiable because of the large areas occupied.

Autumn Migration.—Dates of initiation of autumn migration were variable, ranging from 17 August to as late as 11 February (Table 10). Both LeResche (1974) and Van Ballenberghe (1978) reported that weather, particularly snowfall, was a contributing factor in moose migrations. Although we did not directly measure snow depths on the ground, heavy snow accumulations (>0.3 m) appeared to stimulate autumn migration if it had not already been initiated. Response to lesser-intensity storms or accumulations was not predictable. During years of low snowfall, migratory and resident moose did not move to lower elevation areas until early winter (Jan–Feb) (*see* Elevation Use Versus Winter Severity). Rapid movements to winter range coincided with heavy initial snowfall, whereas slower movements occurred when there was a gradual accumulation of snow.

LeResche (1974) and Pierce and Peek (1984) suggested that winter snow depths, forage availability and quality, habitat suitability, and their various combinations determined whether particular winter habitats were used. In years of moderate snowfall, forage and habitat were probably more available at upland sites than during severe winters because snow depths were relatively shallow. During these types of winters, moose did not arrive on winter range until late winter, if at all, and then they may have remained on winter range for only 2–4 weeks. During the relatively severe winter of 1978–79, several moose used winter areas they had not used during previous mild winters. For example, from 1976 through 1978, 1 individual moose maintained a summer range near Maclaran River and a winter range along the Susitna River. From 21 December 1978 to

Table 10. Ranges of dates of migration for migratory moose in GMU 13 of south-central Alaska, 1976–83.

Year	No. moose	Initiation of autumn migration		Arrival on winter range		No. moose	Initiation of spring migration		Arrival on summer range	
		Earliest	Latest	Earliest	Latest		Earliest	Latest	Earliest	Latest
1976–77	8	2 Nov	16 Dec	22 Nov	19 Jan					
1977–78	5	30 Sep	5 Oct	5 Oct	22 Nov	7	30 Mar	30 Aug	22 Apr	5 Oct
1978–79	3	17 Aug	21 Dec	22 Sep	21 Dec	6	31 Mar	18 Sep	26 Apr	14 Oct
1981–82	3	1 Oct	1 Oct	17 Nov	5 Jan	4	5 Mar	8 Jun	15 Apr	9 Jul
1982–83	3	30 Oct	11 Feb	15 Nov	2 Mar	4	13 Apr	19 Jul	5 May	11 Aug

14 April 1979, she was relocated 82 km to the south below the Glenn Highway. In subsequent years (1980–84), she used her traditional winter and summer ranges and did not return to the 1979 winter location. Moose may only use certain habitats or areas during relatively severe winters.

Spring Migration.—Dates of spring migration were as variable as those observed during autumn movements, ranging from March through mid-July (Table 10). LeResche (1974) suggested that spring movements were in response to disappearance of snow and/or plant development. Rate of movement to summer range also was variable. Van Ballenberghe (1978) reported that moose departure to summer range occurred from mid-April through mid-June in the eastern portion of GMU 13. Most moose were on summer range by late April or early May where they calved. During some years, moose remained on winter range for calving, with migration to summer range not occurring until mid-summer; these latter movements appeared to be in relation to plant development.

Seasonal and Total Home Range Sizes

All moose exhibited seasonal movements within their total home ranges. Distances between winter and summer ranges of migratory moose averaged 48 km and ranged from 16 to 93 km. The longer distances were associated with moose that summered in distant upland areas and wintered in riparian habitats along major river systems.

Use of seasonal home ranges by adult moose was traditional, although at least 1

adult permanently changed its home range. LeResche (1974) suggested that traditional use of home ranges persisted over several generations, but whether these conditions persist during severe winters is not known. Also, because more yearling bulls than yearling females disperse (*see* Dispersal and Home Range Formation), traditional use of parental home ranges (LeResche 1974) is probably much lower for male than female moose.

Seasonal and total home range sizes of resident and migratory adult cow moose increased ($P < 0.05$) with numbers of relocations. This analysis suggested that, although we had not completely defined home range size using Mohr's (1947) method, home range sizes appeared to begin leveling off when numbers of relocations ranged between 60 and 90/moose. We estimated that about 75% or more of total home range size was defined when numbers of relocations were ≥ 40 . For this discussion, we considered seasonal and total home range sizes for resident moose to be adequately defined when numbers of relocations exceeded 13 and 39, respectively (Appendix C and Fig. 10). Using these criteria, winter, summer, autumn, and total home ranges for resident moose averaged 113, 103, 157, and 290 km², respectively. Resident winter home ranges were not different in size ($P = 0.60$) from summer ranges, but autumn home ranges were larger than winter ($P = 0.12$) and summer ($P = 0.02$) home ranges (Mann-Whitney *U* test).

Winter, summer, autumn, and total home range sizes of migratory adult cow moose averaged 151, 263, 322, and 505 km², respectively (Appendix C). There

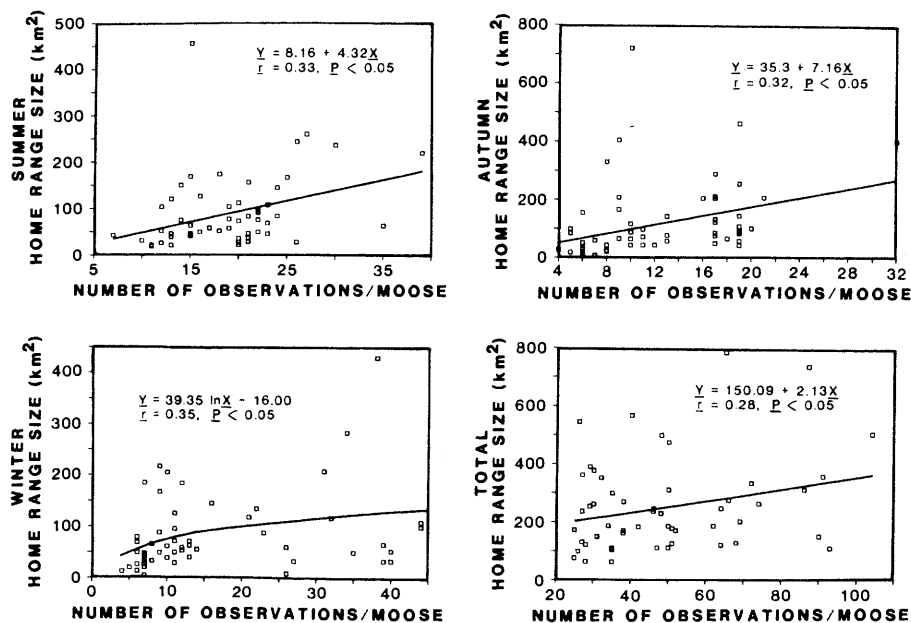


Fig. 10. Relationship between total numbers of relocations for each resident moose and sizes of seasonal and total home range sizes in GMU 13 of south-central Alaska, 1976–85. Each data set refers to a tracking period for each moose of 1–9 years.

were no differences ($P = 0.31$) between winter and summer ranges of migratory moose, but autumn ranges were larger than both winter ($P = 0.11$) and summer ($P = 0.11$) ranges (Appendix C).

Migratory moose had larger ($P < 0.001$) total home range sizes than resident moose (Appendix C). They also had larger autumn ($P < 0.10$) and summer ($P < 0.01$) home ranges, but there was no difference ($P = 0.82$) between sizes of winter ranges. The larger autumn home ranges of both groups reflected increased movements of moose during the rut (Houston 1968, Phillips et al. 1973, LeResche 1974, Hauge and Keith 1981). LeResche (1974) reported that seasonal home ranges of moose in North America seldom exceeded 5–10 km², regardless of how far a moose moved between seasons. Cederlund and Okarma (1988) reported that summer home ranges of Swedish moose were twice as large as those in winter. Home ranges in this study followed that trend but the differences were not significant ($P > 0.05$). Home ranges for resident and migratory moose in this study were 10–20 times larger than those reported in the literature, even though they were minimum areas and not fully defined.

LeResche (1974) indicated that cows with calves had smaller home ranges than other moose. Ballard et al. (1980a) reported that home ranges of cow-calf pairs in late spring and early summer averaged 25 km². This average was larger than reported previously in the literature but smaller than those of other sex-age classes in this study, providing additional evidence that this group uses smaller areas.

Adjusted Home Range Sizes.—Large areas of null habitats (i.e., unused areas) were included in seasonal and total home range calculations using Mohr's (1947) method. To provide a better estimate of actual home range size, Mohr's method was modified by basing calculations on actual habitat use (see Methods). Many of the studies reported by LeResche (1974) concerning home range sizes occurred in areas where elevation relief was usually less than that found in GMU 13. However, even in those areas, unused habitats were included in home range calculations. Less than 1% of 4,700 relocations of radio-collared adults in GMU 13 occurred at elevations $> 1,220$ m, and only 3% occurred at elevations $> 1,097$ m. Thirty-one percent (18,800 km²) of GMU 13 (61,600 km²) is composed of unusable habitat for moose

Table 11. Comparison of mean seasonal and total home range sizes (km²) by method of calculation for radio-collared resident and migratory adult cow moose studied in GMU 13 of south-central Alaska during 1978–84.

Season	Residents (n = 9)				Migratory (n = 4)			
	Mohr's ^a method		Adjusted ^b method		Mohr's ^a method		Adjusted ^b method	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Winter	58.0	9.9	36.5	5.4	134.9	72.4	52.6	32.5
Summer	55.9	10.9	21.0	5.1	152.6	39.9	43.8	3.9
Total	258.0	68.2	81.8	11.2	507.9	84.2	173.5	29.8

^a Described by Mohr (1947).

^b Unused areas (lakes, glaciers, elevations >1,220 m) not included; see Methods.

(i.e., lakes, glaciers, or areas >1,220 m elevation).

Ideally home range sizes excluding null habitats would have been calculated for all adult moose and the resulting estimates compared with the traditional unadjusted method. However, because the adjusted method was labor intensive and could not be computerized, a representative sample had to be selected. Thirteen cows (9 residents and 4 migrants) that also were used for dispersal analyses and home range formation analyses were selected for paired comparisons. These cows had from 35 to 89 relocations each ($\bar{x} = 60$, SE = 9) gathered over a 3–5-year period. Adjusted estimates of seasonal and total home range sizes (Table 11) were still larger than those reported in the literature. However, they probably still represent minimum areas because of the relatively low numbers of relocations and methods of calculation. Winter and summer home ranges calculated by each method were not significantly different ($P > 0.05$), but total home range sizes were different ($P < 0.05$). Winter home range sizes were not different from summer ranges ($P > 0.05$) for resident and migratory moose using Mohr's method, but, with the modified method, winter home ranges were larger ($P = 0.08$) than summer home ranges for resident moose. Also, there was no difference ($P = 0.60$) between winter ranges of migratory versus resident moose. Restriction of movements because of winter snow depths may have affected both categories of moose equally. Both methods indicated that summer and total home ranges of migratory

moose were larger ($P = 0.03$) than those of resident moose.

Dispersal and Home Range Formation

During March 1981, 16 calves (8 males and 8 females) and 1 female yearling associated with radio-collared cows were captured and radio collared in an attempt to investigate timing of parent–offspring separation, rates of dispersal, and home range formation of subadults. Immediately following capture, radio contact with 2 calves was lost due to unknown causes.

Timing of Separation.—Average age of separation from parents was 14 months (SE = 1.0). Gasaway et al. (1985) reported that only 2 of 20 yearlings remained with their cows after 1 year of age in interior Alaska. In this study, 13 of 16 yearlings remained with their cows >1 year (Fig. 11). Five of the separations occurred during late June and July, and 8 occurred during September and October. Separations at that time appeared induced by aggressive behavior of either cows or bulls during the rut.

Gasaway et al. (1985) reported that once initial separation of parent and offspring occurred in interior Alaska, it was permanent. In this study, 5 of 15 yearlings and the 2-year-old were observed in 1–6 ($\bar{x} = 2$, SE = 0.9) temporary reassociations with their cows. During parturition, adult cows that were still in association with the calf of the previous year exhibited varying degrees of aggressive behavior toward the yearling. If the new calf survived, separation between cow and yearling usually

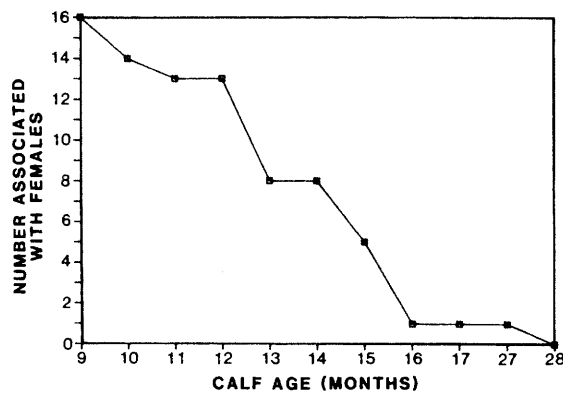


Fig. 11. Ages that moose offspring separated from adults in GMU 13 of south-central Alaska, 1981–84.

was permanent. However, if the new calf died, there was a tendency (5 of 8) for the yearling to remain with the cow at least through summer months. Therefore, magnitude and timing of early neonatal mortality (monthly predation) may influence the timing of parent–offspring separation.

Types and Rates of Dispersal.—Gasaway et al. (1985) reported that offspring selected home ranges that partially overlapped those of their parent; offspring's home range in interior Alaska overlapped at least half of parental home range. The maximum distance that offspring were observed from parental home ranges was 10 km (Gasaway et al. 1985). In the present study, yearlings and 2-year-olds exhibited a different pattern. Dispersal was classified into 3 categories based on subsequent movements and home ranges of offspring in relation to those of the parent:

1. No dispersal—offspring shared both summer and winter home range of mother. Exploratory movements outside of traditional home ranges sometimes occurred during autumn of first and second years following separation.
2. Partial dispersal—offspring shared either winter or summer range of mother, but at least 1 of seasonal ranges was separate and distinct from the parent. Offspring may ultimately share home range of mother but only after extensive movements outside of historical parental home range for at least 1 year.
3. Full dispersal—offspring established

separate winter and summer home ranges that were not shared or, if shared, separated temporally from that of the mother. Development of new home ranges may occur over several seasons.

Nine of 15 offspring partially ($n = 4$) or fully ($n = 5$) dispersed from the parental home range. More male than female ($P < 0.05$) offspring dispersed. No male offspring remained fully within the home range of its mother. Six of 8 females occupied the home ranges of their dams. Dispersal rates were comparable to those reported by Houston (1968) in Wyoming but higher than those reported for interior Alaska (Gasaway et al. 1985) and portions of Sweden (Cederlund et al. 1987).

Several factors influence dispersal in moose populations (Houston 1968, Gasaway et al. 1985, Cederlund et al. 1987), but density and social stress may be particularly important. In interior Alaska where full dispersal rates were low, moose densities ranged from 200 moose/1,000 km² in 1975 to 300–600 moose/1,000 km² in 1978 and 1984, respectively (Gasaway et al. 1985). Moose densities during the present study ranged from 600 to 800 moose/1,000 km² and were increasing. Moose densities that were 3–4 times greater than those in interior Alaska may partially account for the higher dispersal rates.

Dispersers appeared to move to areas of lower moose density. The receiving areas had greater hunting pressure and lower bull densities than areas from which dispersal occurred. Most dispersers were bulls that moved to either the Denali Highway area or Lake Louise flats.

Home Range Formation and Size.—Average adjusted home range (excluding null habitats) sizes of cows and those of their offspring were positively correlated ($P < 0.05$) (Fig. 12). Adjusted home range sizes for offspring were computed for a total 2–3-year period following separation, whereas for mothers all relocations before and after separation were used. Offspring of cows with relatively large home ranges also had large home ranges. Male offspring had larger seasonal and total adjusted home

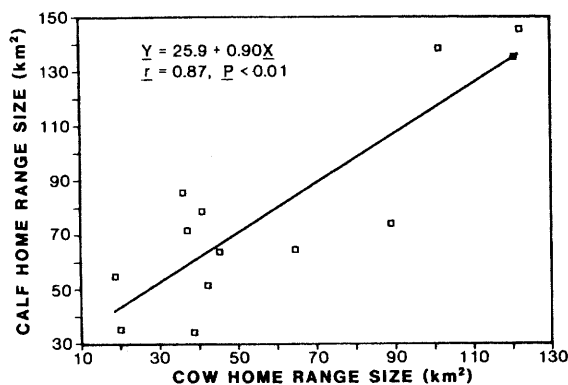


Fig. 12. Relationship between parent and offspring total home range sizes following separation of offspring from adult moose in GMU 13 of south-central Alaska, 1977–85.

ranges ($P < 0.05$) than female offspring. Winter, summer, and total adjusted home ranges for male offspring averaged 34, 28, and 88 km², respectively, whereas those for female offspring averaged 19, 16, and 76 km², respectively. Changes in location and size of offspring's seasonal adjusted home ranges were variable, and some changes did not occur until about 2.5 years following separation from the cow (Table 12).

Moose use of seasonal home ranges is traditional (Goddard 1970, Van Ballenberghe and Peek 1971, Berg and Phillips 1974, LeResche 1974, Cederlund and Okarma 1988). During this study, only 1 of 101 (1%) radio-collared adult females dispersed from their traditional home

range. This moose occupied a relatively small home range in the vicinity of the Susitna River from March 1977 through mid-August 1978. By 26 October 1978, she was relocated 177 km from her previous location at the Dadina River. She maintained a resident home range in the Dadina area at least through 1981, when last relocated. Prior to this documented movement, the longest reported moose movement was 170 km in the Northwest Territories (Barry 1961).

Vegetation Use

Preliminary analyses based on overstory vegetation indicated that spruce and willow vegetation types were preferred habitats within the moose study area, and tundra habitats were avoided (Ballard et al. 1985). These analyses did not indicate why a particular type was selected. We reasoned that if moose select habitats based primarily on the quantity of food, such analyses based upon overstory vegetation could provide misleading conclusions. Consequently, we were interested in comparing production, use, and availability of browse species with actual moose usage.

Becker and Steigers (1987) measured browse distribution, production, and use in relation to the proposed Susitna Hydroelectric Project along the middle Susitna River basin. Because of differing ($P < 0.05$)

Table 12. Comparison^a of individual moose offspring seasonal home range use to that of their mothers in GMU 13 of south-central Alaska from 1981 to 1984.

Season	Dispersal status ^b							
	Partial				Full			
	Male No. 690	Female No. 693	Male No. 696	Male No. 672	Male No. 675	Male No. 676	Male No. 677	Female No. 685
Summer 81	0	0	—	0	0	X	0	0
Winter 82	0	0	—	X	—	X	—	X
Summer 82	0	X	—	—	X	X	—	—
Winter 83	0	X	—	—	X	X	X	X
Summer 83	X	0	—	—	X	X	X	—
Winter 84	0	X	X	—	X	X	—	—
Summer 84	X	0	—	—	—	X	—	—

^a 0 = same home range as mother; X = different home range from mother; — = home range partially overlaps with mother.

^b Partial dispersal—offspring shared either winter or summer range of mother, but at least 1 of seasonal ranges was separate and distinct from the parent. Offspring may ultimately share home range of mother but only after extensive movements outside of historical parental home range for at least 1 year. Full dispersal—offspring established separate winter and summer home ranges that were not shared or, if shared, were separated temporarily from that of the mother.

Table 13. Comparison of browse quantity with usage by radio-collared moose along the middle Susitna River Basin of south-central Alaska, 1976-85.

Browse class ^a	Range of \bar{x} (g/m ²) ^b	Hectares available	Winter			Summer			Autumn			Total		
			Observed no. relocations	Expected no. relocations	χ^2	Observed no. relocations	Expected no. relocations	χ^2	Observed no. relocations	Expected no. relocations	χ^2	Observed no. relocations	Expected no. relocations	χ^2
High	1.0-2.2	15,710	59	54.8	0.3	63	48.4	4.4*	59	31.8	23.3*	181	132.9	1.4*
Medium	0.5-1.7	25,327	69	88.3	4.2*	60	77.9	4.1*	61	51.3	1.8*	190	213.5	2.6
Low	0.6-0.7	84,923	347	296.3	8.7*	252	261.2	0.3	221	171.9	14.0*	820	717.3	14.7*
Very low	0.5-0.6	123,442	449	430.5	0.8	452	379.9	13.7*	229	249.7	1.7	1,067	1,041.5	0.6
Scarce	0.3-0.7	162,544	530	566.7	2.4	438	498.4	7.3*	256	328.8	16.1*	1,224	1,369.9	15.5*
Zero	0.1	15,048	35	52.4	5.8*	47	463.0	0.01	38	30.5		120	126.9	0.4

* $P < 0.05$.^a From Becker and Steigers (1987) for willow (*Salix* spp.) biomass.^b Modified from Becker and Steigers (1987).

quantities of browse within and surrounding the proposed impoundment areas, Becker and Steigers (1987) stratified vegetation into 3 subpopulations. Because 1 of these subpopulations was judged to be low quality moose habitat with few moose, we used 2 of their vegetation subpopulations to compare with actual moose usage.

Comparison of radio-collared adult moose relocations with browse quantity suggested that although browse quantity was possibly an important factor, other factors also were important in determining habitat use (Table 13). During winter, moose avoided ($P < 0.05$) medium and zero browse quantity categories but selected the low quantity category. High, very-low, and scarce types were used in proportion to their availability. During summer, high and very-low categories were selected ($P < 0.05$), whereas medium and scarce types were avoided. We attribute these differences between summer and winter to elevation, snow depths, and ultimately food availability. A high proportion of the high and medium browse categories were found in higher upland sites, which were not frequented by moose during winter (*see* next section). Although higher elevations typically had higher browse production (Becker and Steigers 1987), they also generally had deeper snow in winter (W. D. Steigers, Jr., W. B. Ballard, and E. F. Becker; March 1985 snow depth survey in the middle Susitna River Basin, Alaska; LGL Alaska Res. Assoc., Inc., Anchorage; Unpubl. rep., 33pp., 1985). Even though lower elevation sites had lower browse production, browse was more available to moose due to shallow snow depths. During summer, moose were widely distributed over GMU 13. In autumn, food availability apparently did not affect moose distribution; therefore, areas apparently were used on the basis of factors other than food.

Other factors such as thermal and escape cover, traditional use, snow depths, elevation, slope, and aspect influenced where moose were located. Based on over-story vegetation, spruce cover types were important habitats for wintering moose in

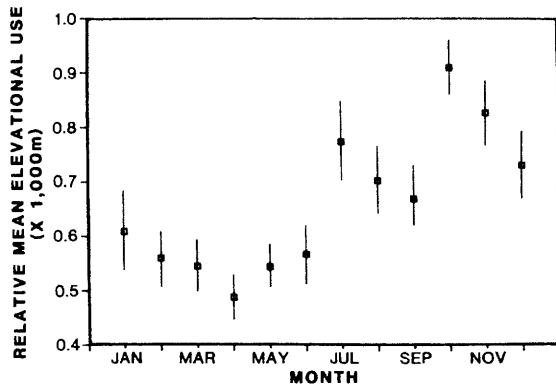


Fig. 13. Average monthly relative elevation use by radio-collared moose in GMU 13 of south-central Alaska, 1976–84. Standard deviation of average values denoted by solid lines. Original data were composed of individual mean values for each moose per month.

south-central Alaska (Ballard et al. 1985). Nineteen percent of the study area was composed of spruce stands, and 35% of total observations of radio-collared moose during 1976–81 were in spruce overstory habitats.

Elevation Use

Different elevations were used both seasonally and annually by moose. Use of low-est elevation strata occurred in April. Moose moved to higher elevations in May and June as snow melted (Fig. 13). In July after calving, moose moved to even higher elevations. Downward movements occurred during August and September. During the rut (Oct), high elevations were again selected. In November, moose began movements toward lower elevations, continuing this descent into March and April. The latter movements were apparently in response to deepening snows and lower browse availability at higher elevations.

Shifts in elevation use also were evident among seasons when percent frequencies of occurrence of relocations were compared among elevations. Peak elevation use during winter occurred near 792 m elevation, whereas the peak ranged from 853 m to 914 m elevation in summer and autumn, respectively.

Elevation and vegetation use by Susitna moose in winter depended to a large extent on the severity of individual winters. As

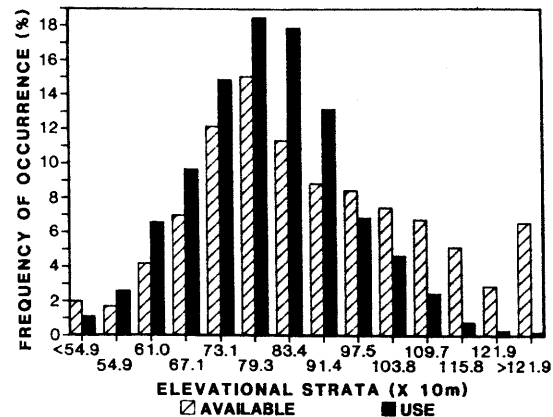


Fig. 14. Comparison of year-round use of various elevations by radio-collared moose in relation to availability of elevations within the moose study area along the Susitna River of south-central Alaska, 1976–84.

winter severity increased, the percent of moose using lower elevations increased (*see* Effects of Snow on Moose Distribution). Elevations from 549 to 914 m were used disproportionately greater ($P < 0.05$) than their occurrence (Fig. 14). Elevations over 914 m were used less than their occurrence ($P < 0.05$), indicating an avoidance of the higher elevations where food and cover were less abundant. Only 16 of 2,984 observations (0.5%) from 1981 to 1984 were at elevations $>1,158$ m.

Slope and Aspect Use

During winter, slopes were used by moose in proportion to their occurrence ($\chi^2 = 0.01-0.1, P > 0.05$) (Fig. 15). During

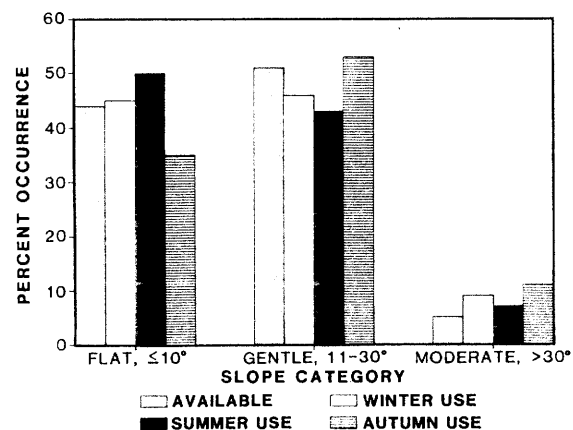


Fig. 15. Use of slopes by radio-collared moose in comparison to slope availability along the Susitna River of south-central Alaska, 1976–84.

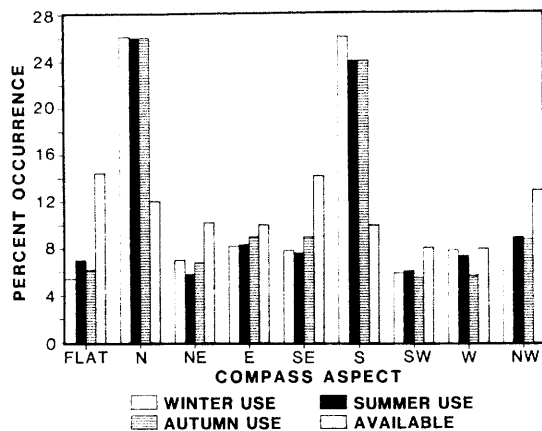


Fig. 16. Annual use of terrain compass aspects by radio-collared moose in relation to aspect availability along the Susitna River in GMU 13, 1976-84.

summer, flat ($\chi^2 = 11.7$, $P = 0.005$) and moderate ($\chi^2 = 6.2$, $P = 0.04$) slopes were preferred, and gentle ($\chi^2 = 5.2$, $P = 0.07$) slopes were avoided. During autumn, gentle ($\chi^2 = 10.4$, $P = 0.01$) and moderate ($\chi^2 = 9.0$, $P = 0.02$) slopes were preferred, and flat areas were avoided ($\chi^2 = 21.4$, $P = 0.005$). During autumn, moose used higher elevations where terrain was more varied. During winter, snows apparently forced moose to use lower elevations and whatever slopes were available.

No significant differences ($P > 0.05$) in aspect use occurred among seasons. Annually, moose preferred north- and south-facing slopes ($P < 0.05$), whereas east ($P = 0.13$) and west ($P = 0.44$) aspects were neither avoided nor preferred (Fig. 16). Other aspects (flat, northeast, southeast, southwest, and northwest) were avoided ($P < 0.05$).

Effects of Snow on Moose Distribution

Assessment of winter severity is critical to understanding movements, habitat use, and population dynamics of moose. Winter 1972-73 caused substantial moose mortality in the GMU 13 moose population, especially in calf and yearling cohorts. From 1977 to 1985, elevation use by moose was correlated ($r = -0.74$, $P < 0.05$) with winter severity; during deep-snow years,

moose used lower elevations. To assess impacts of severe winters on moose population dynamics, it is important that managers be alerted early in the year when a severe winter is in progress. Consequently, we developed a method to predict winter severity early in the year (based on total snow depths) and to quantitatively assess the severity in relation to previous winters.

Winter Severity Index.—The winter severity index (WSI) was based on U.S. Soil Conservation Service (SCS) snow-survey data collected from the winters of 1963-64 to 1985-86. Four SCS snow sites in and near the SRSA were used to develop the index (Ballard and Whitman 1988). Three snow-depth readings (1 each during late Jan-Mar) from each of 4 snow courses (i.e., Fog Lakes, Lake Louise, Monahan Flats, and Square Lake) were summed and divided by the number of courses that were measured during that period. The WSI was composed of the average 3-month cumulative snow depths. The index was based on the following assumptions:

1. Amount of snow cover during mid to late winter (Jan-Apr) was more important in terms of moose mortality than early winter snow depths.
2. Snow depth was the most important factor causing malnourishment in moose because as depths increased, browse became less available. To use browse covered by snow, moose must crater, which requires additional energy expenditure per unit of food. Movements eventually become restricted and moose starve, or, as in this study, they move to habitats of lower browse production where forage is more available due to shallow snow depths.

Based on inspection and interpretation of moose mortality data, 3 general categories of winter were identifiable using the WSI: severe winters when $WSI \geq 28.0$, moderate winters when WSI ranged 18.1-27.9, and mild winters when $WSI \leq 18.0$ (Fig. 17). The winters of 1971-72 ($WSI = 31.8$) and 1978-79 ($WSI = 28.3$) were considered severe, resulting in substantial moose mortality (Stephenson and Johnson

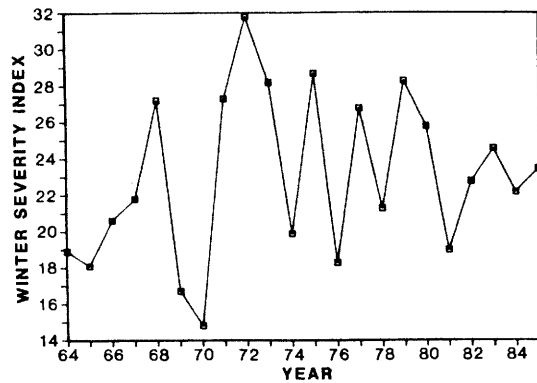


Fig. 17. Comparison of annual winter severity indices (based on snow depth during Jan, Feb, Mar) in the middle Susitna River Basin of south-central Alaska, 1964–85.

1973, Ballard and Gardner 1980, Eide and Ballard 1982). The winter of 1974–75 (WSI = 28.7) also was considered relatively severe based on autumn moose calf survival (W. B. Ballard, unpubl. data).

Prediction of winter severity by early February was obtained by the following method: January snow depths from the 4 SCS snow surveys were averaged for each of 22 years and used as the January WSI. Annual WSI's were then plotted against January snow depths for the same 22 years. Regression analysis was used to predict final winter severity (Fig. 18). Revised winter severity predictions also could have been made following February snow course readings using the same procedures.

Elevation Use Versus Winter Severity.—Monitoring intensity of radio-collared adult moose was increased during the winters of 1981–84 to determine winter use of areas along the Susitna River. There appeared to be a relationship between elevation use by moose and winter severity. The proportion of radio-collared moose at elevations ≤ 671 m increased ($P < 0.05$) with the WSI. Sixteen percent of radio-collared moose relocations were at elevations ≤ 671 m during May through December. These moose probably represented year-round residents along lower elevations of the middle Susitna River Basin. As snow accumulated, moose present at higher elevations moved downward, and the proportion of the moose population using lower elevations increased.

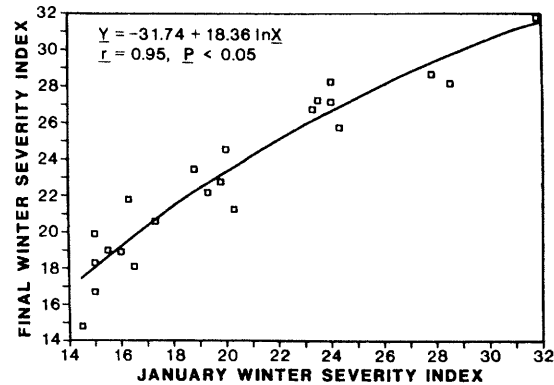


Fig. 18. Relationship between annual and January winter severity indices each year within the middle Susitna River Basin of south-central Alaska, 1974–85. January winter severity index equals average of Soil Conservation Service snow depth readings during January in 4 areas.

MANAGEMENT CONSIDERATIONS

This study was initiated to determine causes of the moose population decline in GMU 13 that occurred in the 1960's and early 1970's. It was initiated 1 year after the moose population had reached record low levels in 1975. Consequently, many of our findings occurred after the decline had been reversed. Because we had no accurate population or mortality estimates during the decline, actual causes can only be inferred.

Severe winters appeared to be 1 of the key factors causing the moose population decline (Bishop and Rausch 1974). Bishop and Rausch (1974) also suggested that deteriorating range conditions contributed to the decline; however, the importance of that factor remains unclear. Because no moose population estimates were available, it was impossible to assess mortality rates from human harvest, but Bishop and Rausch (1974) did not believe harvests were a significant cause of mortality. Ironically, harvests of cow moose were initiated in 1963 after the population had peaked and was in the process of declining. The reported annual harvests of females (181–670) during 1963–71 were probably not the largest cause of mortality, but this factor also contributed to the population decline.

Bishop and Rausch (1974) suspected that wolf predation was a relatively large con-

tributing factor to the decline but, more importantly, that it prevented population recovery during intervening years of mild winters. Comparison of recently completed wolf predation studies in relation to historical wolf population trends (Ballard et al. 1987, Bergerud and Ballard 1988) suggests that wolf predation was probably not the largest source of mortality when the moose population declined but that it contributed to the decline once in progress.

Prior to this study, brown bears were not considered significant predators of moose in North America (Ballard and Larsen 1987), and they were not mentioned as an important cause of mortality by Bishop and Rausch (1974). Results from this and other recently completed studies (Ballard et al. 1979, 1981a, 1990; Ballard and Larsen 1987; Boertje et al. 1987, 1988; Larsen et al. 1988; Ballard and Miller 1990) suggest that brown bears can be a significant cause of moose mortality. Ballard and Larsen (1987) suggested that bears have always been a significant predator of moose and other ungulates and that this "recent discovery" was due to advances in radio-telemetry rather than recently learned behavior. If correct, predation by brown bears probably could be added to the list of factors that contributed to a moose population decline in GMU 13. Similar to wolves, bear numbers were thought to have been reduced by poisoning in the late 1940's and early 1950's. Consequently, reduced bear populations in the 1950's may have contributed to a moose population increase, whereas in the 1960's the increasing bear population may have contributed to the moose population decline. However, like wolf predation, bear predation alone was not solely or primarily responsible for the decline; rather, it was a contributing factor and may have been the largest cause of mortality.

When this study was initiated, wolves were relatively abundant and wolf predation may have been of sufficient importance to have reduced calf survival to low levels (Ballard et al. 1987:41). Therefore, a combination of apparent high levels of wolf and bear predation could have been

great enough to suppress recruitment and prevent the moose population from increasing, if predator densities had not been reduced. A model of the GMU 13 and SRSA moose population was used to test and partially verify this hypothesis (Ballard et al. 1986; W. B. Ballard, unpubl. data).

During this study, predation by brown bears was the largest cause of radio-collared calf mortality followed by starvation and miscellaneous factors. Bear predation was the largest cause of adult female mortality, followed by starvation and wolf predation. Human harvest, however, was the largest source of adult bull mortality. Wolf populations were greatly reduced both in the SRSA and GMU 13 (Ballard et al. 1987). There were significant negative correlations in spring wolf densities and subsequent autumn moose calf survival, suggesting that wolf predation constituted a measurable source of mortality. As the study progressed, bear densities also were reduced in GMU 13 because of liberalized hunting seasons and resulting increased bear harvests. The reductions in bear density were disproportionately greater within a 1,300-km² portion of the SRSA than the remainder of the unit because of a temporary 60% reduction in bear numbers as a result of a transplant program in 1979 (Miller and Ballard 1982a,b; Ballard and Miller 1990). Because about 40% of the translocated adult bears did not return to the area, the beneficial impact on moose calf survival may have been longer than expected. Other than the severe winter of 1978-79, which appeared to affect only calves, winters were relatively mild from 1976 through 1986; moreover, moose hunting seasons and bag limits were relatively conservative (i.e., bulls only). Lower predator densities, mild winters, and conservative harvest strategies resulted in an increase in the moose population, which was still increasing when this study was terminated (Figs. 4, 5) (Ballard et al. 1986, 1987, 1990; Ballard and Miller 1990).

This study was conducted to seek practical solutions to an immediate management problem (i.e., a declining moose pop-

ulation) and to provide insight for dealing with similar problems in the future. Our findings illustrate the difficulties that managers must consider in selecting appropriate actions that involve complex species interactions. Even decisions to "let nature take its course" have consequences, and a sound understanding of them is necessary for enlightened management. When a singular, obvious factor such as wolf predation is limiting a prey population (Bergerud et al. 1983, Gasaway et al. 1983, Messier and Crete 1985, Bergerud and Snider 1988), it may be possible to select management actions on the basis of existing or easily obtainable information. However, as in the case of GMU 13 moose, when several factors that may be independent of each other are limiting the population, the risk of management error greatly increases.

Rarely will agencies be able to conduct in-depth, long-term studies such as presented here to answer single, localized management problems. Yet, even here, a number of questions remain, restricting our ability to predict the consequences of allowing densities of 1 or more of the key species to move above or below the observed ranges. Therefore, for the foreseeable future, managers will have to continue making decisions with a less-than-optimum understanding of the consequences of those decisions and accept some risk of error. A re-examination of the moose situation in GMU 13, in light of recent findings in North America (Gasaway et al. 1983; Keith 1983; Messier and Crete 1984, 1985; Peterson et al. 1984; Ballard et al. 1987; Ballard and Larsen 1987; Crete 1987; Van Ballenberghe 1987; Bergerud and Snider 1988; Gasaway 1988; Messier 1989) with the benefit of hindsight, may illustrate some ways of minimizing the seriousness of such errors.

Faced with a continued decline in the moose population in GMU 13, managers attempted to identify the most probable cause by simplifying the problem through a series of questions that could be answered sequentially, starting with the most basic. From the available information, it was concluded that (1) the food supply was

adequate (Ballard and Taylor 1980) to allow an increase in the number of moose during a series of moderate winters, (2) adequate numbers of moose were being born, (3) total mortality was severe, and (4) mortality during the first 6 months of life constituted a major portion of that mortality. In 1975, wolves and humans were initially suspected as the 2 major causes of mortality. Harvest by humans was no longer considered a limiting factor because only bull moose were being taken at the time and their remaining numbers were adequate for breeding purposes, even though sex ratios were becoming heavily skewed in favor of females. Wolves were the likely causal factors because of their suspected density and because of the sex and age composition of moose being killed.

This study was initiated, in part, as an experiment to test the hypothesis that wolves were the primary cause of moose calf mortality. Reductions in wolf numbers failed to greatly improve calf survival quickly and, thus, other mortality factors became suspect (Ballard et al. 1987). Calf mortality studies were initiated, and we now know that either brown bear, black bear (Franzmann et al. 1980), or wolf (Gasaway et al. 1983) predation can produce the pattern of calf mortality observed in GMU 13.

Moose managers in the future will have to determine which of the 3 predator species are the primary cause of calf mortality. It might be possible to exclude 1 or more of them, based on available data (e.g., black bears are scarce in many portions of GMU 13 where calf mortality is high), but the possibility of other unidentified causes remains. The manager can select the most likely key factor and manipulate it. However, if his choice is wrong (e.g., as in GMU 13) and other major factors are involved, the results may be confusing. Calf mortality studies of the type used in GMU 13 have provided a fast and reliable approach for determining causes of mortality as long as the rate of mortality is high enough to be detected with moderate sample sizes.

If 2 or more major mortality factors act in combination, the next step may be dif-

difficult because further observations may not allow reliable predictions of what could occur or what has actually occurred. At that point, manipulation of 1 or more of the principal predator species may be necessary to begin understanding the key relationships. However, even this approach may have pitfalls. In this study, a concentrated 60% reduction in brown bear densities (by removal plus transplanting to other areas) demonstrated that bear predation was additive to other mortality factors and that a reduction in adult bears would allow a moose population to increase (Ballard and Miller 1990). However, the effect of a more moderate reduction on bear, wolf, and moose populations remains unknown. A well-documented, costly, experimental-management regime ultimately becomes necessary if predator and moose populations are to be managed.

The choice of which component of the ecosystem to manipulate can be difficult. A manager must consider practicality and conflicting management goals. Any management action should preferably satisfy 2 important criteria: (1) a high likelihood of attaining the immediate objective (e.g., allowing the moose population to increase), and (2) side effects that are predictable, easily measurable, moderate in magnitude, of short duration, and easily reversible. The 4 basic courses of action available to managers in GMU 13 appear to be as follows:

1. No action—This course would have violated both of the above criteria. The moose population may have continued to decline; perhaps, it would not have recovered for decades (Gasaway et al. 1983, Ballard and Larsen 1987). Wolf populations ultimately also would have declined because of the decline of their major prey. Management goals for both species would have been compromised, and the situation would have been difficult to reverse.
2. Reduce harvest by humans—This course would not violate management
3. Reduce brown bear densities—This course clearly has the highest probability of satisfying the first criterion; however, a permanent 60% reduction in bear numbers could cause long-term consequences for the bear population. Whether a lesser reduction in bear numbers would have a desirable effect on the moose population cannot be determined without further experimentation. Recent comparison of rates of bear predation on calf moose in areas having different moose densities and similar bear densities suggests that bear predation may not be dependent on densities of moose calves (Boertje et al. 1988, Ballard et al. 1990) and that causes of moose calf mortality were not proportional to relative densities of predator species (Ballard et al. 1990). Also, there were no significant differences ($P > 0.05$) in rates of predation on calf moose by sex, age, or family class of bear in GMU 13 (Ballard et al. 1990). However, Boertje et al. (1988) detected greater predation rates for large single bears in east-central Alaska. Because bears are not obligate carnivores, the feedback between bear and ungulate populations could be loose and insensitive (Ballard et al. 1987). Also, effects of reductions on the bear population are uncertain. Brown bear management objectives could be compromised, and

criteria, but, at the time when cow harvests were terminated, biologists suspected that total natural mortality exceeded recruitment. After 1971, human harvest was limited to bull-only hunting to ensure increased productivity (i.e., reducing percent of bulls and increasing numbers of calves per adults in the population). A further restriction on bull harvest would have allowed males to increase in the short term, but the regulation may have had little effect on the recovery of the moose population because female mortality was a key concern. The halt of cow moose hunting after 1971 probably contributed to the moose population recovery after 1975.

the low reproductive rates of bears and lack of practical techniques for estimating numbers could retard attempts to reverse a detrimental action. This option would have to be applied as a carefully monitored management experiment to minimize the degree to which the second criterion was compromised.

4. Reduce wolf densities—The efficacy of this action and the previous depends on how close the moose population is to carrying capacity. If they are close to carrying capacity of the habitat, there could be little to gain from such actions, but, if they are below carrying capacity and if wolf predation is a significant mortality factor, a significant increase in moose density may be achieved (Gasaway et al. 1983, Messier and Crete 1985). This course of action would compromise wolf management objectives for a shorter period than number 1. Wolf population levels are relatively easily monitored, and reductions or even localized extirpations are quickly reversible.

A combination of the second, third, and fourth courses of action was chosen. Moose hunting seasons were reduced to bulls-only seasons, hunting season lengths were shortened, and beginning in 1980 only certain age classes of bulls were legal. Concurrently, liberal hunting and trapping seasons allowed the public to reduce wolf densities to low levels (3 wolves/1,000 km²). During 1979, brown bears were experimentally translocated from a small study area, and, beginning in 1980, bear harvests were increased through liberalization of hunting seasons and bag limits (Miller and Ballard 1982*a,b*; Miller 1985; Ballard et al. 1987). Lower predator densities and reduced human harvests along with mild winter conditions appear to have been sufficient to allow a slow increase in the moose population. However, had the moose population been lower, these actions might not have been sufficient. At some point, even the elimination of wolves would have been insufficient to allow a moose population to

increase. Even now, some event, such as a severe winter, could alter the predator-prey ratio so that predation could limit the population.

Although moose populations increased during our study, particularly following the reduction in bear density (Ballard and Miller 1990), the number of moose that can be supported indefinitely by existing habitat is unknown. Certainly the moose population cannot increase indefinitely without causing range deterioration and a probable moose die-off. Because of fire suppression policies by land management agencies during the last 35 years, spruce forests are advancing toward climax, providing presumably less than optimum moose habitat. Establishment and implementation of a sound fire management plan for GMU 13 could markedly increase forage quantity and quality as well as the potential for GMU 13 to support greater numbers of moose and predators.

Probably the most serious threat to the future of ungulate, wolf, and bear populations in GMU 13 is loss of habitat through increased human settlement and development (e.g., construction of a hydroelectric development project along the Susitna River). As a result of the Alaska Native Claims Settlement Act and governmental land management policies, large areas of undeveloped land are or have been in the process of being transferred to private ownership or developed for mineral extraction or grazing. This could have major effects on the distribution and abundance of ungulates and predators, and on the potential for managing populations and habitat. This development, occurring simultaneously with increased demands for human harvests of ungulates, will greatly intensify the need for a better understanding of predator-prey relationships.

The role of predation in regulating moose populations in North America has been intensively studied here and elsewhere during the past decade. Many of these studies were recently reviewed by Ballard and Larsen (1987) and Van Balenbergh (1987). Nearly all, if not all, of

the studies have suggested that predation can and often does regulate moose population growth at levels below food carrying capacity. What is not clear, however, are the conditions under which regulation occurs and duration of regulation. Areas where moose are subjected to predation from multiple, naturally-regulated predator species will in the long term have fewer moose available for human harvest than those subjected to no predation or those where predator species are managed.

Although this study provided some valuable insight into predator-prey relationships and the dynamics of moose populations, a number of interesting and perplexing questions remain:

1. What, if anything, could moose managers have done differently to have prevented a population decline?
2. When, if ever, should managers halt the current growth of the moose population?
3. How should the harvest be managed at various moose densities?
4. Will bear and wolf predation rates change with increasing moose densities?
5. Is permanent predator control required to indefinitely maintain high moose densities or to satisfy increasing human demands?

These and many other perplexing questions will merit further investigation before managers can accurately and efficiently manipulate the predator-prey system to achieve reasonable sustained human use.

CONCLUSIONS

1. Moose populations in GMU 13 and the SRSA increased in the 1940's and 1950's. According to the numbers of moose observed per hour of survey, the population peaked about 1963. Sex and age composition and recruitment indices were exhibiting declines earlier. The moose population declined through the 1960's and into the 1970's reaching a record low in 1975. From

1975 through 1986, moose populations increased. More calves were produced and survived from 1976 to 1984 than from 1963 to 1975. Increases were attributed to mild winters, reduced predation from bears and wolves, and reduced human harvest. In recent years, moose densities within GMU 13 were relatively high (603-741 moose/1,000 km²) in comparison to those elsewhere in Alaska. On winter range, moose densities ranged from 154 to 1,930 moose/1,000 km². Moose typically used lower elevations during winter than summer. Observability of moose from fixed-wing aircraft in spruce-forest habitats during winter was low.

2. Average age of captured cow moose was 7.7 years. Observed pregnancy rates for our sample averaged 81%, but the average for the population was probably higher. Parturition occurred between 25 May and 10 June. Twinning rates averaged 38%. Calf sex ratios did not differ from 1:1. Rates of mortality during the first 5 months of life were not different between males and females.
3. During the first 5 months of life, calf moose survival averaged 39%. Predation by brown bears was the largest cause of neonate calf mortality accounting for 73% of total mortality. Wolf predation and unknown causes each accounted for 4% of the mortality. Black bears accounted for 11% of the mortality in 1984 in an area where black bears were twice as dense as brown bears. Mortality rates for twin calves were similar to those for single calves.
4. Starvation was the largest cause of calf mortality from November through May; however, 9 of 11 starvation mortalities occurred during the severe winter of 1978-79. Female calves had higher ($P < 0.05$) rates of survival than males during severe winters but not during winters of moderate severity. Annual calf survival rates from 1976 to 1986 averaged 34% for females and 31% for males.

5. Annual survival rates of yearling and adult cow moose averaged 95%. During the severe winter of 1978–79, annual adult cow survival was 92%. Predation accounted for 8 of 11 mortalities where cause of death was determined.
6. Annual survival rates for radio-collared adult bulls averaged 75%. Adult bull survival rates declined as the study progressed because of increased hunting pressure on them (i.e., only bulls with antler spreads ≥ 91 cm or 3 brow tines on at least 1 antler were legal). Radio-collared bulls had low rates of natural mortality after 2 years of age. Yearling radio-collared bull survival averaged 91% annually. Hunting was the largest cause of adult bull mortality.
7. Moose hunting seasons and bag limits were relatively liberal from 1963 to 1971. Following the severe winter of 1971–72, hunting seasons became more conservative; harvests were reduced to an average of 51% of the 1963 to 1971 levels. Beginning in 1980, only bulls with antler spreads ≥ 91 cm or 3 brow tines on 1 antler were legal. Beginning in 1983 in portions of GMU 13, only bulls with a spike or forked antler on 1 side were legal. The net result of these regulations was to improve bull:cow ratios and recruitment of older bulls into moose populations.
8. Excluding cow-calf pairs, moose were not highly gregarious during much of the year. Largest group sizes occurred during the rut and during post-rut aggregations. Three periods of movements were identified: autumn, spring, and rut. Dates of autumn and spring migration were variable. Autumn migration occurred from October through January. Moose did not always move to winter range. During years of moderate snowfall, moose arrived on winter range by February or March. During severe winters, some moose used wintering areas not used during years of moderate severity. Dates of spring migration ranged from March through mid-July. Most moose were on summer range by late April or early May where they calved.
9. All moose exhibited seasonal movements within their annual home range. Moose were classified as migratory or sedentary depending on whether their winter and summer home ranges overlapped. Distances between winter and summer ranges of migratory moose ranged from 16 to 93 km. Seasonal and total home range sizes were positively correlated with number of relocations for both resident and migratory moose. Use of seasonal home ranges was traditional. Total home ranges for resident and migratory moose averaged 290 and 505 km², respectively. Autumn home ranges were larger than other seasonal ranges. An alternate method of computing home ranges was described that eliminated large areas of null (unused) habitats from calculations.
10. Average age of offspring separation from the cow was 14 months. Dispersal was classified into 3 categories: no dispersal, partial, and full. More male than female offspring dispersed from the maternal cow's home range. Nine of 15 offspring partially or fully dispersed. No male offspring remained fully within the home range of their mother. Moose density may be an important factor in determining rate of dispersal. Dispersers appeared to move from areas of high moose density to areas of low moose density. Home range sizes of cows and their dispersed offspring were positively correlated. Males had larger home ranges than females.
11. Spruce forest and willow vegetation types were selected out of proportion to their availability. Moose did not select habitat types based solely on browse biomass. Use of lowest elevations occurred during April, whereas the highest elevations were used in July. Winter elevation and vegetation use appears to depend on severity of individual winters. High elevation use was negatively correlated with snow

depths. Elevations from 549 to 914 m were used in higher proportion than their availability. Elevations above 1,158 m were rarely used. Flat and moderate slopes were preferred by moose during summer, whereas no preference was detectable during winter. Annually, north- and south-facing slopes were preferred.

12. A winter severity index based on snow depths during January through March was developed for SRSA. Use of the index allows managers to predict whether or not a severe winter will occur as early as January. The winter severity index was related to moose mortality.
13. Management of predators and large ungulates such as moose is controversial and complex. Management actions should minimally satisfy 2 criteria: (1) a high likelihood of attaining the immediate objective (e.g., allowing the moose population to increase) and (2) side effects that are predictable, easily measurable, of moderate magnitude, of short duration, and easily reversible. Four courses of action are typically available to a moose manager facing population declines similar to those we observed in GMU 13: no action, reduce harvest by humans, reduce brown bear densities, or reduce wolf densities. All 4 options have biological and sociological consequences that may dictate the preferred action (Ballard and Larsen 1987).

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APPENDIXES

Appendix A. Summary of moose hunting seasons and bag limits in GMU 13 of south-central Alaska from 1960 through 1986.

Harvest year	Area(s)	Dates	Bag limits
1960-64	13	20 Aug-30 Sep 1 Nov-30 Nov	1 moose—antlerless moose may be taken only from 24 Sep to 30 Sep.
1965	13	20 Aug-30 Sep 1 Nov-30 Nov	1 bull.
1966	13	20 Aug-30 Sep 1 Nov-30 Nov	1 moose—antlerless moose may be taken only from 29 Sep to 30 Sep.
1967-68	13	20 Aug-30 Sep 1 Nov-20 Nov	1 moose—antlerless moose may be taken only from 29 Sep to 30 Sep except 13A East was closed to antlerless harvests.
1969	13	20 Aug-30 Sep 1 Nov-20 Nov	1 bull.
1970-71	13A, D	20 Aug-20 Sep 1 Nov-20 Nov	1 bull.
	13B, C	20 Aug-20 Sep 1 Nov-20 Nov	1 moose—400 antlerless permits for 13B; 300 antlerless permits for 13C.
1972	13A	20 Aug-20 Sep	1 bull.
	13B, C, D, E	20 Aug-20 Sep 1 Nov-20 Nov	1 bull.
1973	13A, B, D, E	20 Aug-30 Sep	1 bull.
	13C	No open season	
1974	13	20 Aug-20 Sep	1 bull.
1975-79	13	1 Sep-20 Sep	1 bull.
1980-82	13	1 Sep-20 Sep	1 bull having antler spread of at least 91 cm or 3 brow tines on at least 1 side.
1983	13	1 Sep-20 Sep	Sport hunting—1 bull having antler spread of at least 91 cm or 3 brow tines on at least 1 side. Subsistence* hunters—1 bull by drawing permit only; 100 permits issued.
1984	13 except portions of 13B & E	1 Sep-20 Sep	Sport hunting—1 bull having antler spread of at least 91 cm or 3 brow tines on at least 1 side. Subsistence* hunting—1 bull by drawing permit only; 100 permits issued.
	13 B & E Maclaren River to Nenana River	1 Sep-20 Sep	Sport hunting—1 bull having a spike or forked antler on at least 1 side.
1985	13 except 13A West	1 Sep-20 Sep	Sport hunting—1 bull having antler spread of at least 91 cm or 3 brow tines on at least 1 side. Subsistence* hunting—1 bull by drawing permit only; 200 permits issued.
	13A West	1 Sep-20 Sep	Sport hunting—1 bull having a spike or forked antler on at least 1 side.
1986	13 except 13A West	1 Sep-20 Sep	Sport hunting—1 bull having antler spread of at least 91 cm or 3 brow tines on at least 1 side. Subsistence* hunting—1 bull by registration permit only; unlimited number of permits issued.
	13A West	1 Sep-20 Sep	Sport hunting—1 bull having a spike or forked antler on at least 1 side.

* Priority harvests to satisfy need of local rural residents.

Appendix B. Summary of reported moose densities in Alaska from 1980 through 1987 attained from aerial surveys using quadrat sampling methods identical or similar to those described by Gasaway et al. (1986). Densities listed from lowest to highest.

Location of census	Year	Moose density (no./1,000 km ²)	Size of study area (km ²)	Source
Western Yukon Flats GMU 25D West	1983	50 ^a	16,107	R. A. Nowlin, Alaska Dep. Fish and Game, unpubl. data
Taylor Highway GMU 20E	1981	86 ^b	7,500	Boertje et al. 1987
Western Yukon Flats GMU 25D West	1986	93 ^a	16,107	R. A. Nowlin, unpubl. data
Yukon River corridor GMU's 20E, 25B & C	1987	120 ^b	9,210	R. A. Nowlin, unpubl. data
Squirrel River GMU 23	1985	148 ^b	4,101	D. N. Larsen et al., Alaska Dep. Fish and Game, unpubl. data
Selawik Natl. Wildl. Refuge GMU 23	1985	168 ^b	11,162	D. N. Larsen et al., unpubl. data
Lower Nowitna and Yukon rivers GMU 21B	1986	194 ^a	4,026	Haggstrom and Osborne 1981a
Upper Nowitna and Innoko rivers GMU 21A	1980	201 ^a	9,832	Haggstrom and Osborne 1981b
Eastern Yukon Flats GMU 25D East	1984	234 ^a	13,888	R. A. Nowlin, unpubl. data
Bristol Bay GMU 17	1982	255 ^b	4,750	Taylor 1984
Beaver Creek GMU 25	1985	270 ^b	1,849	Nowlin 1987
Tanana Flats and surrounding area GMU 20	1978	277 ^b	12,650	Gasaway et al. 1983
Mulchatna River GMU 17B	1987	286 ^a	4,183	K. P. Taylor, Alaska Dep. Fish and Game, unpubl. data
Central Alaska Peninsula GMU 9E	1987	340 ^b	3,380	Sellers and McNay 1984
Lower Nowitna and Yukon rivers GMU 21B	1980	345 ^a	4,026	T. O. Osborne, Alaska Dep. Fish and Game, unpubl. data
Seward Peninsula GMU 22B	1987	348 ^a	5,451	R. R. Nelson, Alaska Dep. Fish and Game, unpubl. data
Kaiyuk Flats GMU 21D	1987	417 ^a	4,076	T. O. Osborne, unpubl. data
Middle Noatak River GMU 23	1985	312–508 ^a	5,414	D. D. James and K. Cannon, Alaska Dep. Fish and Game, unpubl. data 1985
Beluga-Drift River GMU 16B	1985	453 ^a	3,685	J. B. Faro and W. P. Taylor, Alaska Dep. Fish and Game, unpubl. data
Koyukuk River GMU 21D	1987	530 ^a	8,556	T. O. Osborne, unpubl. data
Tanana Flats and surrounding area GMU 20	1984	643 ^b	12,650	Jennings 1986
Tok River GMU 12	1980	734 ^a	1,166	Kellyhouse 1981
Upper and middle Susitna River GMU 13	1980–83	741–603 ^b	3,156–7,588	This study
Kenai Natl. Wildl. Refuge GMU 15A & B	1976–81	800 ^a	4,973	Bailey 1978
Kenai Peninsula GMU 15A	1987	816 ^a	3,317	T. H. Spraker and W. P. Taylor, Alaska Dep. Fish and Game, unpubl. data
Lower Susitna River GMU 16A	1984	832 ^a	2,556	J. B. Faro and W. P. Taylor, un- publ. data

Appendix B. Continued.

Location of census	Year	Moose density (no./1,000 km ²)	Size of study area (km ²)	Source
Matansuka Valley GMU 14B	1987	1,015 ^b	2,777	W. P. Taylor, unpubl. data
Nelchina River GMU 13A West	1987	1,217 ^b	4,861	W. P. Taylor, unpubl. data
Lower Yentna and Kahiltna rivers GMU 16B	1984	1,236 ^a	2,602	J. B. Faro and W. P. Taylor, unpubl. data

^a Winter density.^b Autumn density.

Appendix C. Mean seasonal and total home range sizes for adult resident and migratory cow moose studied during 1976–84 in GMU 13 of south-central Alaska. Home range sizes of individual moose were computed for multiyear periods.

Type of home range	Winter home range (km ²)					Summer home range (km ²)					Autumn home range (km ²)					Total home range (km ²)				
	No. locations	No. moose	\bar{x}	SE	Range	No. moose	\bar{x}	SE	Range	No. moose	\bar{x}	SE	Range	No. locations	No. moose	\bar{x}	SE	Range		
Resident	4-13	35	61	8.5	4-202	11	46	10.5	19-121	33	105	24.6	6-720	25-39	25	209	24.6	63-545		
	14-23	5	110	16.7	55-146	34	87	13.3	23-456	20	144	23.0	43-462	40-54	14	261	39.8	113-568		
	24-33	5	87	35.6	10-209	7	168	33.3	29-262	1	404			55-69	7	280	87.2	123-787		
	34-43	7	137	59.1	35-430	2	144	78.6	65-222					70-84	2	301	35.4	266-337		
	44-53	2	106	4.6	101-111									85-104	6	366	95.6	111-739		
\bar{x}	14-53	19	113	23.3	10-430	43	103	12.8	23-456	21	157	25.1	43-462	40-104	29	290	33.9	111-787		
Migratory	4-13	8	173	50.8	15-375	2	389	233.2	155-622	12	333	64.5	89-955	25-39	5	1,061	228.0	454-1,703		
	14-23	3	193	89.4	38-347	4	234	105.2	60-519	3	280	74.1	133-371	40-54	3	603	98.8	411-740		
	24-33	4	75	12.0	48-106									55-69	4	497	84.8	263-667		
	34-43	4	75	12.0	48-106									70-84	1	398	153.1	274-580		
\bar{x}	4-43	15	15	32.8	15-375	15	263	55.0	60-622	15	322	53.0	89-955	40-104	10	505	52.1	263-740		