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Population Dynamics of Moose and Predators in Game Management Unit 13

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SUMMARY

An intensive study site in western Unit 13A, the Nelchina Study Area (NSA) was chosen for detailed study of moose population dynamics. Mortality of adult females there is low, while calf, and possibly yearling mortality, is high. The low survival of calves to adult age is probably not sustainable in the long term, given that the present adult age structure contains a high proportion of prime-age adults born before and during the peak of moose numbers around 1987. As these adults age, their susceptibility to mortality agents will probably increase (Peterson 1977) and increased calf recruitment will be necessary to offset increasing adult mortality. Studies in the NSA also have shown a relationship between the energy stores of adult female moose, as measured by rump fat thickness, and reproductive performance in both the year prior and year after the autumn of capture. This was especially apparent between pregnant and nonpregnant cows and was indicated by a trend toward fewer twins among cows with low rump fat measurements. Twinning rates in the NSA in 1994–1996 (9-15%) were among the lowest known for moose but have been increasing during the study (21–25% in 1997-1998). This may represent an improvement in productivity in response to recent mild winters and heavy harvest of male moose resulting in lower overall density of moose.

Historical trend data indicate the moose population in Unit 13 is at generally high density. The evidence for a population decline is strongest in the northern part of the unit, where cow moose density is approximately 17% below historic highs in 1986–87 and a decline of 30% has occurred in the calf/cow ratio in fall. The rate of decline was not as great as the rate of population increase in the 1970s and early 1980s. There is little evidence the adult female segment of the population has changed in the unit since 1991, with the possible exception of Unit 13D, which may be experiencing a decline in numbers. With respect to trend count indices to cow moose abundance, Unit 13A is the most variable subunit in Unit 13, making the detection of population trends there difficult. Because changes in the cow moose index were not accompanied by appropriate changes in calf:cow ratios, most of the historical variability in Unit 13A is probably related to temporary migrations.

Key Words: *Alces alces.*

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BACKGROUND

Ballard et al. (1991) documented the recent management and ecological history of moose in Game Management Unit (GMU) 13 from 1952–1984. Indices to moose abundance indicated the population underwent a decline from 1963–1976, then an increase through 1984. In recent years the population has stopped growing and has apparently declined since the late 1980s. This research program was undertaken in response to the perceived decline in moose numbers, and a management priority in the region of maximizing human harvest of moose and caribou in Unit 13. This annual report will summarize research results from 1994–1997 in addition to the current year.

I selected a study area of approximately 4200 km^2 of moose habitat near the townsite of Nelchina in Unit 13A (Fig. 1), primarily because of its proximity to air charter operators for logistical support, relatively high moose densities, and historical importance to consumptive users in

Southcentral Alaska. Climate and vegetation in the region were described by Skoog (1968). The Chugach and Talkeetna mountain ranges insulate the area from coastal influences on precipitation and temperatures. Annual temperatures range from -50 to 32C with 22–42cm of precipitation, mostly snow (Skoog 1968). The study area included subalpine heath and woody shrubs such as resin birch (*Betula glandulosa*), alder (*Alnus fruticosa*), and willow (primarily *Salix pulchra, S. alexensis, S. glauca*) in foothills of the Talkeetna Mountains in the west, progressing to a boreal forest of mixed birch (*Betula papyrifera*), aspen–poplar (*Populus tremuloides and P. balsamifera*), and spruce (*Picea glauca* and *P. mariana*) in hills and lowlands to roughly 800 m elevation. Bogs of sphagnum, sedges, and low shrubs, with scattered *P. mariana* were extensive in lower areas—predominantly the western portion of the study area from 800 to 620 m elevation. Previous studies indicated that an area this size should encompass 9–45 wolves in at least 3 packs (Ballard et al.1987) and 80–120 independent brown bears (Miller 1990). The Nelchina study area (NSA) also contained the principal calving area for the Nelchina caribou herd and its historic wintering range in the eastern part of the NSA.

OBJECTIVES

This 5-year research program will 1) more accurately track the dynamics of the moose population in Unit 13, 2) help us determine which causal variables (e.g., weather, predation, habitat, hunting) are driving population changes as they occur, and 3) help us identify possible management strategies to anticipate or halt moose population declines and increase human harvests.

METHODS

CAPTURE AND HANDLING

Adult female moose were captured and equipped with VHF radio collars in March, November, and December 1994, and November 1995 and 1997. Ten to 17 female moose 10–11 months old (short-yearlings) were captured each April 1995–1997, weighed from a portable tripod with a load cell dynamometer to the nearest kilogram and equipped with expandable radio collars. Except for 13 moose that were captured by helicopter net-gun on November 16–17, 1994, all captures were made by darting from a helicopter with a mixture of carfentinil-citrate and xylazine hydrochloride (Schmitt and Dalton 1987). Blood was collected for pregnancy determination by serum assay for pregnancy-specific protein B (PSPB) (Wood et al. 1986, Rowell et al. 1989, Stephenson et al. 1996), and assays were performed in G. Sasser's laboratory (University of Idaho, Moscow). We archived serum samples in the Fairbanks laboratory of Alaska Department of Fish and Game (R. Zarnke, pers. commun.).

In collaboration with Gregg P. Adams, theriogenologist from the University of Saskatchewan, I used ultrasonography to measure the maximum thickness of rump fat as an index to body condition in autumn of 1994 and 1995, and winter of 1996 (Stephenson et al. 1993). Transrectal ultrasonography was used in the field to diagnose pregnancy and incidence of twinning in utero in fall of 1994 and 1995 (Lenz et al. 1993, Stephenson et al. 1996, Testa and Adams In Press). Ultrasonagraphic assessments of pregnancy and rump fat thickness also were made in 1997 in collaboration with T. R. Stephenson, Moose Research Center, Soldotna.

ADULT SURVIVAL AND REPRODUCTION

Using fixed-wing aircraft, we tracked radiocollared moose at least once each month from January–November, except from mid May to late June when we tracked moose daily (weather permitting) and July when we tracked collared moose 2-3 times per week. Adult survival was estimated by Kaplan–Meier procedure with staggered entry and censoring (Pollock et al. 1989). Animals were counted as having been alive in a given month if they were tracked after the midpoint of that month and found alive. Only moose within radio range of the study area were included in survival analyses. Deaths were assigned to the month in which the moose was found dead, unless tracks in snow or other evidence indicated that death was before the beginning of that month. To avoid inclusion of capture-related mortality in the analysis, moose were excluded from survival analyses for 2 weeks after their captures. Cause of mortality was attributed to a predator if there was surface evidence of a chase or struggle, or if sightings were obtained daily and a predator was observed eating a moose that appeared healthy and active during the previous flight. Differences in annual survival rates between contrasting categories (e.g., females with calf versus those without) were tested by Z-test (Pollock, 1989).

We made daily radiotracking flights, including sightings of all radiocollared moose, from mid-May to mid-June to obtain parturition dates and reproductive rates. Parturition rates were calculated as the proportion of females that were sighted at least once with a calf in a given year out of those radiocollared females sighted on each occasion from 15 May to 30 June. Twinning rate was calculated as the proportion of adult females with calves that also had twins when first sighted with a calf. Twinning rate samples were augmented by observations of uncollared moose with calves during the telemetry flights before June 2 of each year. Sightings made within 1 km of those made previously were excluded from the sample. Parts of the NSA not usually overflown during telemetry flights were surveyed from helicopter for twinning rate information on 2 June 1995, 29 May 1996, and 2–3 June 1997. We compared data in each year with log-linear models (Agresti, 1990) for homogeneity before pooling. Differences between years were also tested with log-linear models (Agresti, 1990).

CALF SURVIVAL

Survival of calves was estimated by treating calves of radiocollared cows as if they were also radiocollared and applying Pollock's (1989) modified Kaplan–Meier estimator. In 1994-1997 calves were sighted daily until June 15, every 2–3 days in late June, and 3–5 days in July (weather permitting). In 1998 calves were sighted bimonthly after mid-June, with a follow-up flight the following day for any females whose calves were missing for the first time. Probability of sighting calves known to be alive was lowest in the first 2 months after birth, but still exceeded 96% per day. A calf was considered to have died when it was not observed with its mother on 4 consecutive flights. Date of death was then assigned to the first missing day or when 2–5 days separated the telemetry searches, assigned to the midpoint in the interval since its last sighting and first day missing. For even intervals, the midpoint was randomly selected from the 2 middle days. After July, calves were always sighted with the cows unless their disappearance was final and, again, death was assigned to the first month on which the calf was not sighted. Annual survival of calves was calculated from birth to May 1 of the following spring. Causes of calf mortality normally could not be determined, though in some cases a predator or freshly eaten calf carcass was found at the previous day's location of a missing calf, or dead calves were seen

alongside the collared adult and later recovered for necropsy. When adult females that were accompanied by a calf died, their calf was assumed to have died at the same time.

Mortality of calves in 1994–1997 was estimated daily, relative to both date and age until the end of July and 65 days of age, respectively. Survival estimates at these endpoints were equivalent due to low mortality after July and high birth synchrony. Thereafter, we calculated calf survival monthly until the end of April, when the animals were considered yearlings and their disappearance could relate to natural separation from the mother.

YEARLING SURVIVAL

Female calves of both collared and uncollared adults were captured in April, 1995–1997. They were weighed by suspension under a tripod and load cell dynamometer to the nearest kg. Radio collars were also attached. These calves were considered yearlings in May, and annual survival was calculated as for adults (Pollock 1989) by pooling all years from May–April.

A yearling female might remain with its mother for an entire year, be terminally separated at the birth of a new calf, or be temporarily abandoned until her mother's new calf died. Female yearling survival was calculated conditionally on whether the yearling was accompanied by its mother. During May and June, yearlings were considered independent if they were abandoned anytime during that month and remained independent through the end of the month. Staggered entry and exit was used to accommodate these contingencies in the Kaplan–Meier procedure and a Z-statistic used to test for difference (Pollock, 1989). Causes of yearling mortality were investigated as for adults. A rank-sum test with exact probability (Statistix) was calculated for yearlings permanently abandoned, or reacquired by parturient mothers, based on the age at which the new calf died.

MODELED POPULATION GROWTH

A model of the female segment of the moose population was programmed in spreadsheet software (Microsoft Excel) based on a formulation of the Euler–Lotka equation for marine mammals and bears (Eberhardt and Siniff, 1977; Eberhardt, 1985). This formulation relates the parameters measured via telemetry and surveys to population growth rate. This assumes that, following a fairly short period of high juvenile mortality, adult mortality will be low and relatively constant across age classes. Similarly, once maturity is reached, age-specific variation in fecundity will be small and relatively unimportant. Because these parameters have been estimated from a sample representing a cross section of the ages present in this population, these assumptions are considered conservative. The commonly measured parameters of survival, age of first reproduction, and adult fecundity are related to population growth rate, λ, and are incorporated into spreadsheet models by the following formula:

$$1 = \lambda^{-a} * P0 * P1 * P^{a-2} * F * (1-P/\lambda)^{-1}$$

where

P0 = cub survival from birth to age 1
P1 = cub survival from age 1 to age 2
P = annual survival (excluding hunting mortality) thereafter

F = mean birth rate in female cubs/adult female/year
a = age at first parturition

Sensitivity curves for each parameter were generated by holding the other variables constant at their best estimate as each parameter was varied across the 95% confidence intervals of survival estimates and the range of observed reproductive estimates.

SNOW COURSE MEASUREMENTS

We continued to measure snow depths in Unit 13 in cooperation with the Natural Resources Conservation Service (NRCS). Five new sites in the NSA were added in 1994, and a sixth was repaired after many years of disuse. These augmented 2 sites in moose habitat have been monitored since 1968. Rick McClure (NRCS) compiled and distributed those results to users. Ballard et al. (1991) used the mean snow depth (in inches) measured monthly from late January to late March in the Susitna River Study Area, north and west of the NSA, as a “Winter Severity Index” (WSI). Ballard et al. (1991) considered a WSI >29 as indicative of a "severe" winter that could reduce moose survival. WSI was calculated from 2 snow course sites (Square Lake and Lake Louise) that were considered within moose habitat (elevations <1230 m) in the NSA for 1970-1994, and from all 8 sites in the NSA beginning in 1995.

WOLF DENSITY ESTIMATES

Wolf density estimates were made in March 1995, February 1996, and March 1997 with the Sample Unit Probability Estimator (SUPE) described by Becker et al. (1998). The NSA was divided into a grid of 101 square sample units of 42 km^2 and classified into strata of low, medium, and high probability of finding wolves or wolf tracks. Border units of uneven shape were combined to keep the area of each to approximately 42 km^2. Area pilots and Alaska Department of Fish and Game biologists familiar with wolf abundance in the area assigned sample units to strata based on habitat quality and tracks seen in previous flights in the area. Surveys were flown in randomly selected quadrats within a few days of fresh snowfall, and tracks were followed to determine the number of quadrats containing tracks, and the numbers of wolves associated with the tracks. Wolves harvested before the surveys, as determined from mandatory reporting forms submitted by trappers and hunters, were added to the survey results to estimate fall density of wolves in the NSA. In 1998 we made no formal estimate of wolf density because of the absence of suitable snow conditions.

POPULATION ESTIMATES, TREND COUNTS, AND COMPOSITION SURVEYS

On 30 Oct–5 Nov 1994, a moose population estimate was conducted on the western part of Unit 13A in areas under 1230 m in elevation. The area included all of the NSA, plus an area of approximately 200 km^2 in the extreme NW of Unit 13A that lies just outside the NSA. The total area was approximately 4400 km^2. Sample units of approximately 40km^2 were drawn on a map of the area, choosing boundaries that could be easily identified from the air. The method used was a modification of Gasaway et al. (1986) that employed a probability regression procedure (J. Ver Hoef and E. Becker, in prep.). This was used to relate low-intensity “stratification” counts made by observers in a Cessna 185 (C–185) on one day to intensive counts made by pilot/observer teams in PA–18 aircraft the following day. Regression analysis was used to

estimate the relationship between partial counts from the C–185 and more intensive complete counts from the PA–18. The regression relationship was then used to estimate the number of moose in sample units that were not surveyed by the PA–18 crews. Sightability correction factors were determined on the intensive sample units by resurveying a 2.6km^2 subunit at higher intensity (Gasaway et al.1986).

Trend count surveys to index moose abundance and determine herd composition are routinely made for management purposes in traditional Count Areas (CA's) around Unit 13, and 2 of these occur in the NSA (Fig. 1). As part of this study, surveys from PA–18 aircraft were made in CA's 13 and 14 in late October 1994, and mid-November 1995–1997. The search procedure entailed a systematic search by a pilot and observer at 50–150 m height above ground level in a pattern chosen by the pilot for safety and efficient search coverage. When a moose or group of moose was spotted, the pilot would circle the group to identify sex and age composition. Calves, cows, yearling bulls (identified by antler size), and adult bulls were identified and counted in each group. Management reports from the area commonly standardize these counts by reporting moose per unit of time searched (moose/hour), or per unit of area searched, which can be used as an index of moose abundance.

ANALYSES OF TREND COUNT DATA

The task of exploratory data analyses and modeling is ongoing. At this time, only a preliminary summary of moose population trends in Unit 13 will be presented. The most continuous record of moose abundance in Unit 13 is the series of counts in autumn of traditional count areas. The boundaries for these units are shown in Fig. 1, but early surveyors (prior to 1980) often shifted boundaries in an effort to get larger counts and, therefore, better composition information. For this reason, we considered only counts from 1980 onward. The trend count database for Unit 13 is current, but analyses are preliminary. Traditional analyses of these data have focused on moose per hour of counting as an indicator of moose population size in the game management unit (Ballard et al. 1991). Moose counted per unit area show very similar trends, but slightly higher year to year variability. Bull/cow ratios and calf/cow ratios vary substantially from year to year, due to harvest of bulls and annual changes in calf recruitment. Because these may obscure trends in the demography and because cow moose are the most important segment to population growth, my approach is to emphasize the adult females in population analyses. Also, I will present trend count data as moose or cows per km^2 for easier comparison to population estimates and appraisal for sighting probabilities.

Only Count Areas 3, 5, and 6, in the northern part of Unit 13, and count area 13 in the western part have been surveyed each fall from 1980 to 1995. Count Areas 10 and 16 were surveyed all years except 1989, and the data series for CA 15 excluded years 1992 and 1995. Count Area 14 was surveyed in 1980, 1984–88 and 1991–95. CA 7 was surveyed in 1980–86, 1990–92, and 1995–97. Other parts of Unit 13 have been surveyed for moose numbers and composition, but I included only those that have been surveyed at least 12 of the past 18 years.

Summaries presented in this report were based on cow moose per km^2. Because moose density, habitat quality, and size of each CA vary and population trends are of the most interest, the data from each CA were standardized by subtracting the mean value for that CA from 1980–1997.

These “deviations from the mean” will be graphically illustrated. To pool different CA’s and report subunitwide trends, we weighted the deviations from the mean by the size of each CA in the subunit. Because CA’s 3 and 10 straddled subunit boundaries, we weighted deviations by half the area of those CA's and included them in both subunit calculations. Composition in the subunits was based on all moose seen in the respective CA’s, except for CA 3 and CA 10 where totals were divided evenly between subunits sharing those CAs.

RESULTS

REPRODUCTION

No moose gave birth before the age of 3 years in this study (n = 15), and only 7 of 12 moose reaching 3 years of age gave birth. All 7 moose reaching 4 years of age were parous by that age. Mass as yearlings had no discernible effect on primiparity among 3-year-olds (t = 0.839, df = 9, P = 0.423). Annual reproductive rates averaged 0.82 among females >2 years old from 1994-1998 (Table 1), but reproductive rates varied significantly among years (P = 0.019); 1994 was 25% below the average from 1995-1998 (0.843, SE = 0.023). No differences were detected among the years 1995-1998 (P = 0.448). Twinning rates (Table 1) varied from 9.1-25.3%, and increased every year of the study (P = 0.022).

SURVIVAL

Adult females had an average annual survival of 0.94 (SE = 0.015) from 1994-1998 (Table 2). Of 16 deaths, 10 were clearly attributable to predators (4 to wolves, 5 to brown bears, and 1 to an unknown predator). In 3 other cases predation was probable. Only 3 deaths were clearly not related to predation. Adults with a calf showed a trend toward higher mortality than those without a calf (Table 3, Z = 1.60, P = 0.09), and deaths attributable to predation (Z = 2.75, P = 0.01) or suspected predation (Z = 2.14, P = 0.03) were significantly greater among females tending a calf.

Annual survival of yearlings without considering maternal attendance (Table 4) was 0.75 (SE = 0.07). All 8 yearling deaths occurred in spring to midsummer (early May to early August). Three were attributed to wolves and 2 to brown bears. Cause was uncertain in the other 3, but predation was considered the most probable cause because of the apparent health of the moose when previously observed and proximity of a predator to the freshly dead carcass. All of the wolf kills were found in or next to small lakes, a feature also observed in 2 cases where cause of death was unknown.

Female yearlings abandoned by their mothers suffered higher mortality (0.49) than yearlings that were able to maintain that association (0.49 versus 0.07, Table 4, Z = 2.87, P = 0.002). Neither survival nor abandonment of yearlings was related to yearling’s body mass as a calf in April (Table 5). Nine of 12 (75%) nonparturient females with yearlings of either sex kept that yearling to at least August, but no male yearlings of 3 that remained with their mother in June were seen with their mother past August. Hunting season opened on August 20, and yearlings with spike or fork antlers were legal game.

Age of the new calf at death might influence rate of reassociation between yearlings and mothers (P = 0.058). All reassociations took place when calves died in less than 10 days (2, 7, and 10 days), while 2 opportunities for reassociation were missed in that period (8 and 10 days) and no reassociations occurred when calves died after 10 days of age (n = 5). In the 3 cases where yearlings rejoined their mother, reassociation took place within 1–3 days of the calf's death. One female yearling was attended closely by her mother for the entire year, despite the birth and survival of her mother's new calf.

Most calf mortality occurred between parturition and the end of July (Table 6). Interannual variation in calf mortality to August was not significant (Testa, Becker and Lee In Review). Age-specific mortality was essentially a linear, declining function of calf's age from a rate of 4%/day at birth to nearly 0 at 64 days (Fig. 2). Because calves were not radiocollared, cause of death usually was unknown. However, occasionally the dead calf was observed, or the fate of the mother led to presumptive causation. Three single calves and 2 pairs of twins were either observed or presumed dead when their mothers were killed by brown bears in June. A brown bear was observed killing the calf of moose #13 in 1994. In one case a radiocollared wolverine was found feeding on the calf of a radiocollared moose. Also, one calf carcass was observed near its radiocollared mother and was fed upon only by eagles; it was splayed forward on its sternum and opened from the back, suggestive of having been killed by an eagle.

Mortality of calves for the remainder of the year was low, with a small surge in April. In 3 cases calves disappeared and were presumed dead during winter when the mother was killed by wolves. In another case the calf carcass was observed being eaten by wolves, and the radiocollared mother was resting, wounded, nearby. She died the following day, presumably from her wounds.

MODELED POPULATION GROWTH

Population growth (λ) in the NSA, as modeled from the population parameters in Tables 1, 2, and 6, was 1.01. This estimate was relatively insensitive to the variation seen in each of the population parameter estimates (Fig. 3), and indicates that for the period of study (1994–1998), the population of female moose in the NSA has been stable.

SNOW COURSE MEASUREMENTS

Winter snow depths in moose habitat in the NSA (Fig. 4) have been mild to moderate (Ballard et al. 1991, Coady 1974). In fact, since 1970 the values measured in Unit 13A (Fig. 4) are well below those reported by Ballard et al. (1991) for Unit 13, indicating that subunit 13A tends to have less accumulated snow than the rest of the unit. Without severe winters, we had no opportunity to observe their effects on moose demography.

WOLF DENSITY ESTIMATES

Although late winter estimates of wolf density differed substantially in 1995–96 compared to surrounding years (Table 7), the annual harvest in that year was extremely light due to the unusually shallow, late snow pack. Effects of temporary emigration (2 packs) were felt by local pilots to be greater in 1995 than in 1996, though this probably involved only 2–3 wolves/1000

km^2. Fall densities apparently differed little between years, but due to the low, late harvest in the 1995–96 winter, the effects of wolves should have been greater in that winter, and possibly the winter of 1996–97 than in the winter of 1994–95. Several wolf-killed or injured moose calves were seen near wolves during the wolf estimation flights of 1995–96. No estimate of wolf density was made in 1998 due to the absence of suitable snow conditions (Becker et al. 1998).

MOOSE POPULATION ESTIMATE AND RECENT TREND COUNTS

Nelchina Study Area–Unit 13A

The number of moose seen per flight hour and per km^2 during trend count surveys declined from 1994 to 1995 and remained low until 1997 (Table 8). However, the observed difference may not represent changes in population density because survey conditions were poor in 1995 and 1996. With only slightly better conditions in 1997 the counts increased. There were no changes in mortality or recruitment estimates obtained from radiocollared moose ($\lambda = 1.01$) or in herd composition (Table 7) that would explain such wide variation in population density. The variability of counts from CA's 13 and 14 remain an obstacle to recognizing real changes in population size in Unit 13A, although composition of the counts appears to be a valid indicator of production and effects of hunting on the male segment of the population. The November 1994 moose population estimate yielded an assessment of 0.81 moose/km^2 and 0.60 cows/km^2 in the NSA (Table 8).

Changes in bull/cow ratios in Unit 13A have followed harvest regime changes, which have favored bulls and involved a hiatus on adult bull harvest from the late 1980s to 1992. There was limited protection for 2–3-year-old bulls via selective antler restrictions when the season reopened in 1993, but harvest rates were high and the bull/cow ratio declined sharply. Surveys reveal almost no bulls in the most accessible parts of the CA's in spite of antler restrictions, indicating that illegal harvest is a problem. Calf recruitment in recent years was 15% below the long-term average. This is in accord with the high calf mortality seen in calves of radiocollared cow moose in the NSA, and may warn of pending changes in the adult age structure and moose abundance if recruitment does not improve.

Remainder of Unit 13

Moose density indices and geographic size differ substantially among CA’s (Table 9). Differences from the mean density of cow moose for each of the subunits of Unit 13 for which we have consistent CA data are shown graphically in Fig. 6. Subunits 13A and 13D are the most variable in Unit 13, making interpretation of short-term changes in moose density in these subunits more difficult.

Units 13B and 13C (Figs. 7, 8) show the clearest trends in cow moose abundance: a period of strong growth until the late 1980s, followed by a small decline and relative stability for the last 5–6 years of the series. With the exception of the most recent count, Unit 13B (Fig. 7) has the most stable series of cow density indices, possibly due to the large proportion of the subunit that lies within CA's and relatively poor habitat to the north and south that limits migration. The 15% decline from the peak in cow moose observed in 1987 coincided with a decline in recruitment in Unit 13B, evidenced by the drop in the proportion of cows with calves after 1988 (29% to 20%,

P<0.01). In subunit 13C, the CA's comprise a small proportion of the subunit (Fig. 1), where there is more annual variation in composition and density index of moose than in Unit 13B. The pattern in cow moose abundance was similar to that in Unit 13B, but with only a small drop in calf:cow ratios between the 1980s and 1990s.

Data from Unit 13E (Fig. 9) in the northwestern part of the unit (Fig. 1) are missing counts from its largest CA in years when high densities of moose were reported in nearby areas of Units 13A and 13B. While there is little evidence for a trend in cow moose density amid the yearly fluctuations in Unit 13E, calf:cow ratios have declined 43% in the 1990s from values of 24-35 calves:100 cows in the 1980s. Bull to cow ratios also have declined to low levels (Fig. 9).

Subunit 13D in the southern part of the unit has the lowest density of moose (Table 9) and calf:cow ratios, but the highest bull:cow ratios (Fig. 10) in the unit. The small size of the subunit's only CA and low density of moose probably exacerbate fluctuations in the survey counts and ratios because of the potential for migration across CA boundaries.

PREPARATION OF REPORTS AND PUBLICATIONS

The following technical papers were published or submitted for publication to professional journals in the past year.

TESTA, J.W., E.F. BECKER AND G.R. LEE. (In Review). Temporal patterns in survival of twin and single moose calves (*Alces alces*) in southcentral Alaska. Canadian Journal of Zoology.

———, AND G.P. ADAMS. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79 (4): 000-000.

———. 1998. Compensatory response to changes in calf survivorship: management consequences of a reproductive cost in moose. Alces 34: 107-116.

DISCUSSION

The status of moose in Unit 13 is of great interest to public user groups and resource managers in the state. Historical trend data indicate the population is at generally high density. The evidence for a population decline is strongest in the northern part of the unit, Subunits 13B and 13C, where cow moose density is approximately 17% below historic highs in 1986–87 and the fall calf/cow ratio since 1988 is 30% less than that observed before 1988. The rate of decline was not as great as the rate of population increase in the 1970s and early 1980s, and we have little evidence the adult female segment of the population has changed in the unit since 1991. With respect to trend count indices to cow moose abundance, Unit 13A is the most variable subunit in Unit 13. Because changes in the cow moose index were not accompanied by appropriate changes in calf:cow ratios, this variability must be related to temporary (interannual) migrations of moose in Unit 13A. Although composition data from that area appear fairly stable and consistent with studies of calf mortality and changes in hunter harvest, they are probably representative of an area larger than that defined by the boundaries of the NSA and subunit.

Annual variation in the long-term record of indices to cow moose abundance in Unit 13A was more than expected to result from natural dynamics of a closed population. From 1980–86, years in which CA 7 was surveyed, the number of adult moose there showed a tendency to vary in an opposite direction to that seen in the adjacent CA 14 in Unit 13A. There are no traditional CA's in the portion of Unit 13D that borders the CA's of Unit 13A, so we have no way, with present data, to test the hypothesis that year to year variation in the counts in Unit 13A are caused from movements of moose across that boundary. Radiotracking of moose captured in the southern part of the NSA do indicate that some movements to Unit 13D and the eastern, unsurveyed portion of Unit 13A occur. There were no indications from fall composition surveys that sharp changes in the cow moose index were preceded by appropriate changes in recruitment. For these reasons, I believe that migration plays a substantial role in the sudden changes of moose abundance observed in CA's 13 and 14 from year to year and that short-term changes in moose counts from CA's 13 and 14 must be interpreted cautiously.

Direct estimates of moose abundance were made in CA 14 in 1983 (Ballard et al. 1991) and in the western half of Unit 13A in 1987 and 1994. The estimated density of moose in 1983 in CA 14 was nearly identical with that for the NSA in 1994, but the estimate in 1987 was 55% higher than either value. While this might be considered evidence for a peak in 1987 that was substantially above population levels now, the trend count data (Fig. 5) indicate the elevated density estimate in 1987 was the result of an influx of moose that was reversed the following year. It should not be considered a legitimate baseline on which to manage the population. Due at least in part to the variability in CA data from the subunit, I see no compelling evidence in these data for a trend in numbers of adult cow moose in Unit 13A in the last 2 decades. Stability since 1994 is also indicated by the population parameters estimated from radiocollared moose in the NSA ($\lambda = 1.01$). A new density estimate in the NSA is planned in fall 1998.

Studies in the NSA have shown a relationship between the energy stores of adult female moose, as measured by rump fat thickness, and reproductive performance in both the year prior and year after the autumn in which they were measured (Testa and Adams 1998). This was especially apparent in the proportion of cows with calves and was suggested by a trend toward fewer twins among cows with low rump fat measurements the previous fall. Franzmann and Schwartz (1985) suggested that spring twinning rate indicates nutritional status of a moose population, and Gasaway et al. (1992) compiled evidence that moose near a resource-dependent carrying capacity may have low twinning rates. Twinning rates in the NSA in 1994–96 (9–15%) were among the lowest recorded for moose (Gasaway et al. 1992), while twinning rates in the rest of the unit in recent years were higher, but not above average (23–40%: R. Tobey, pers.commun. and J.W. Testa unpublished).

As indexed by twinning rate, productivity of the female segment of the population of moose in the NSA has improved in the last 5 years. Although low snowfall in recent winters (Fig. 4) has probably contributed to this improvement, overall density of moose has declined due to the heavy harvest of males from the population (Fig. 5), indicating a density-dependent increase in twinning. The most recent rates of twinning in the NSA are nearer those of the remainder of Unit 13. In the NSA in 1995, browsing intensity appeared also to be high relative to 2 other drainages in Interior Alaska (Testa 1996), but recent browsing intensity in mild winters has been low (W. Collins, pers. commun.). Two conclusions are relevant to moose in Unit 13. In the NSA, where

moose densities are high, there is a moose-vegetation interaction that appears to have reduced moose productivity relative to that of moose in other parts of the unit. Recent improvements in twinning rates in the NSA may be density dependent, stemming from high harvest of males and resulting lowered density of adult moose. Indications of moose nutritional status elsewhere in the unit are no better than average.

Mortality of adult females in the NSA is low, while calf and possibly yearling mortality is high. The low survival of calves to adult age is probably not sustainable in the long term because the present adult age structure contains a high proportion of prime-age adults born before and during the peak of moose numbers prior to 1988. As these adults age, their susceptibility to mortality agents will probably increase (Peterson 1977), and increased calf recruitment will be necessary to offset increasing adult mortality.

The current rate of calf mortality in the NSA has been somewhat higher that that observed by Ballard et al. (1991), though the timing of mortality (almost all in the first 60 days) has been similar (Testa et al., in review). Sightings of brown bears, often on moose kills in the spring, is high and supports the contention that brown bears remain the principal cause of calf mortality in the NSA and probably in the remainder of Unit 13 (Ballard et al. 1991). Brown bears also killed more adults than any other causative agent observed so far, although total number of adults dying was low. Assuming that changes in moose numbers were related solely to changing composition relative to adult females, and using the average overwinter wolf densities, moose/wolf ratios in the NSA ranged between 80 and 115 from 1994–95 to 1996–97. These are above the densities at which Gasaway et al. (1983) suggested that wolves could limit moose populations, but probably within the range at which wolves plus bears limit the moose population (Gasaway et al. 1992). The density of brown bears older than 2 years in a 2400 km^2 section of the NSA was estimated at 21 per 1000 km^2 (95% CI = 18–26) in spring 1998, but this estimate was considered an index, rather than an estimate for the entire NSA (Testa et al. 1998). Because we made the estimate during the calving season and in an area of high abundance of moose and caribou, the density of bears may be higher than that in the NSA. This would indicate that the ratio of adult moose to bears probably is not lower than 38. However, the combined effects of wolves and bears remain a matter of speculation in an area where caribou also are abundant as alternative prey (Gasaway et al. 1992). Bears appear to have a greater effect on moose calf survival in the NSA and Unit 13 than do wolves, and we would expect effects of bears on moose population dynamics to be delayed through persistently poor recruitment, rather than direct through adult mortality. Consequently, the expected trajectory of a moose population preyed upon most heavily by bears may follow a slow decline, rather than a rapid one.

The management of predator numbers for the purpose of increasing human harvest of moose and caribou in Alaska is a matter of heated debate. The Board of Game modified harvest regulations in Unit 13 to increase the take of brown bears in order to increase moose calf survival. An increase in calf survival will be necessary to increase moose in areas where that is the objective and to offset an expected increase in the mortality of aging adults, although that increase has yet to be seen. Because of the feedback loop between calving success and energy stores of adult female moose, increases in calf survival to autumn that may follow reductions in predator populations could compensate decreases in calving and twinning rates. Given the high densities and low productivity of moose in some parts of Unit 13 (notably 13A and 13E), and rather

average productivity in areas where moose have declined, care must also be taken that moose densities are not allowed to increase beyond what the range will support. Predator impact is distributed fairly evenly over the moose population. If management actions successfully reduce predation pressure on moose, human harvest of moose "released" from predation pressure should mimic normal predator impact as much as possible to avoid local irruption or overharvest of the moose population.

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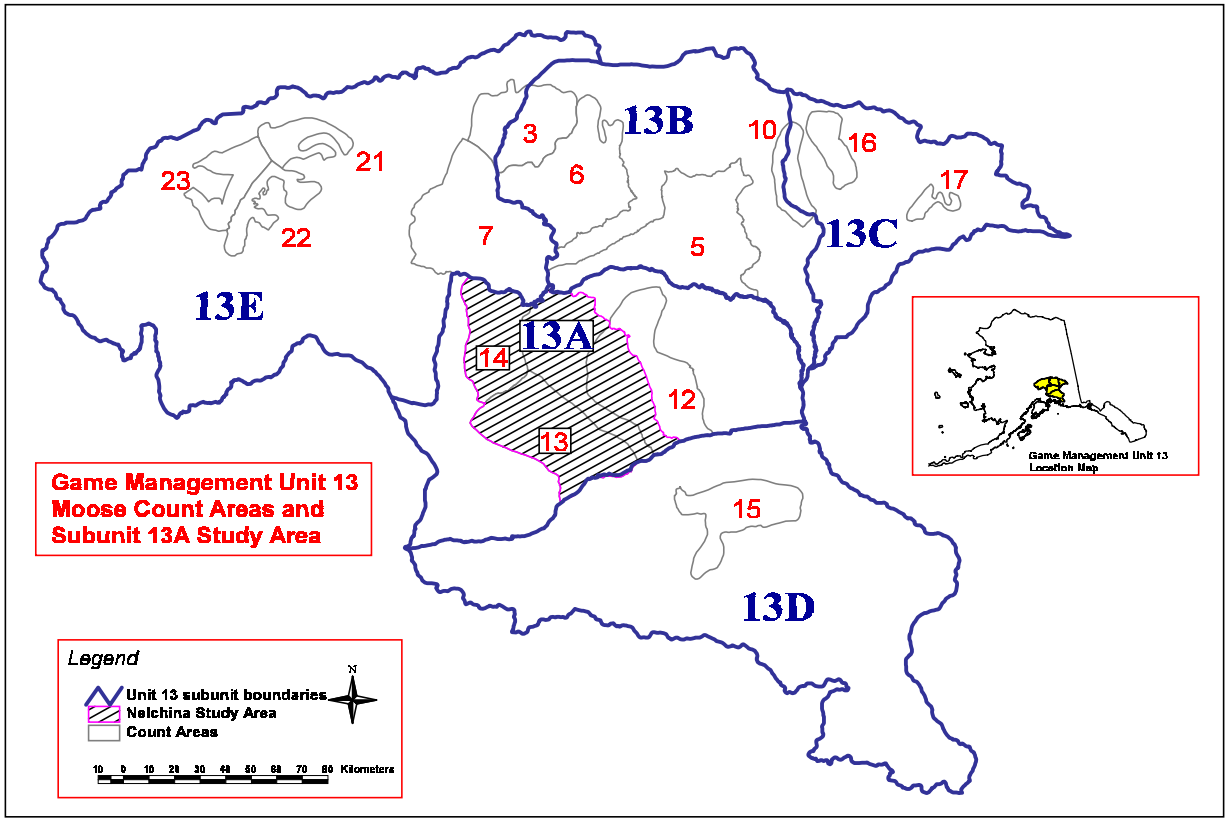

Figure 1. Game Management Unit 13 in 5 subdivisions (A–E) in Southcentral Alaska, with traditionally surveyed trend count areas and boundary for Nelchina Study Area (NSA).

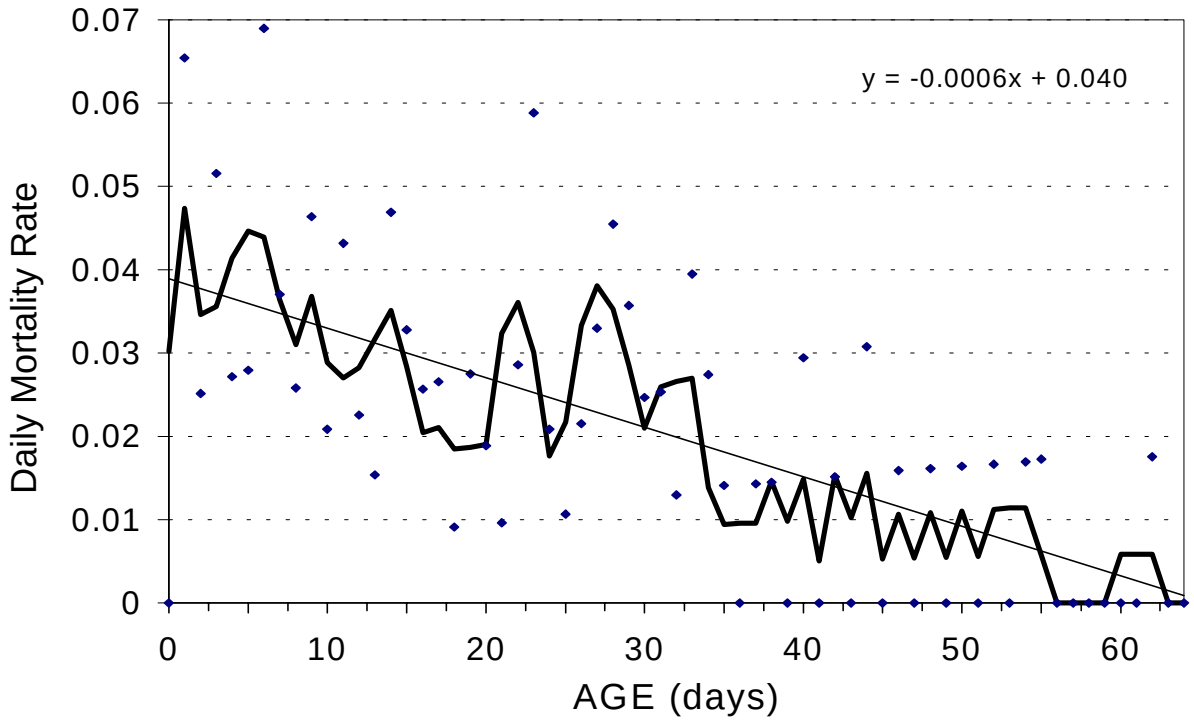

Figure 2. Age-specific daily mortality rate of moose calves in the Nelchina Study Area in spring 1994–1997, with 7-day running average (bold) and least squares regression lines superimposed.

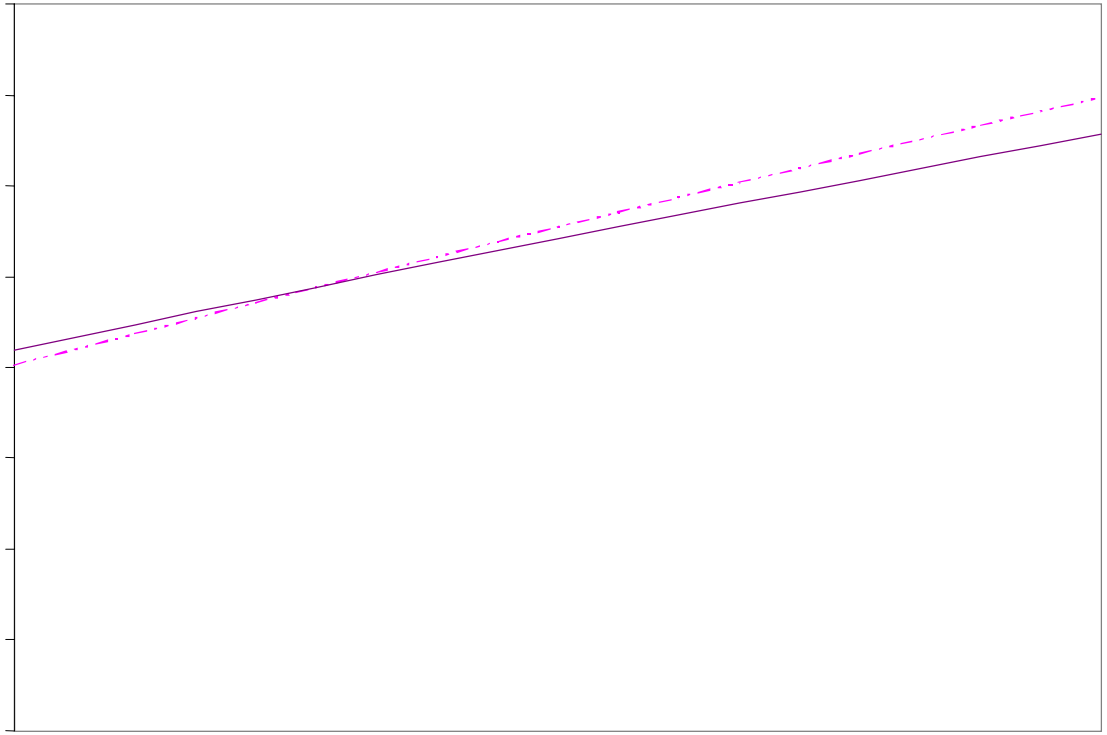

Figure 3. Sensitivity of modeled population growth rate (λ = 0.01) to uncertainty in population parameters estimated from telemetry and survey data from moose in the Nelchina Study Area, Southcentral Alaska. Parameters are annual rates of survival of calf (P0), yearling (P1) and adult moose (P), age of primiparity (a), and adult fecundity (F).

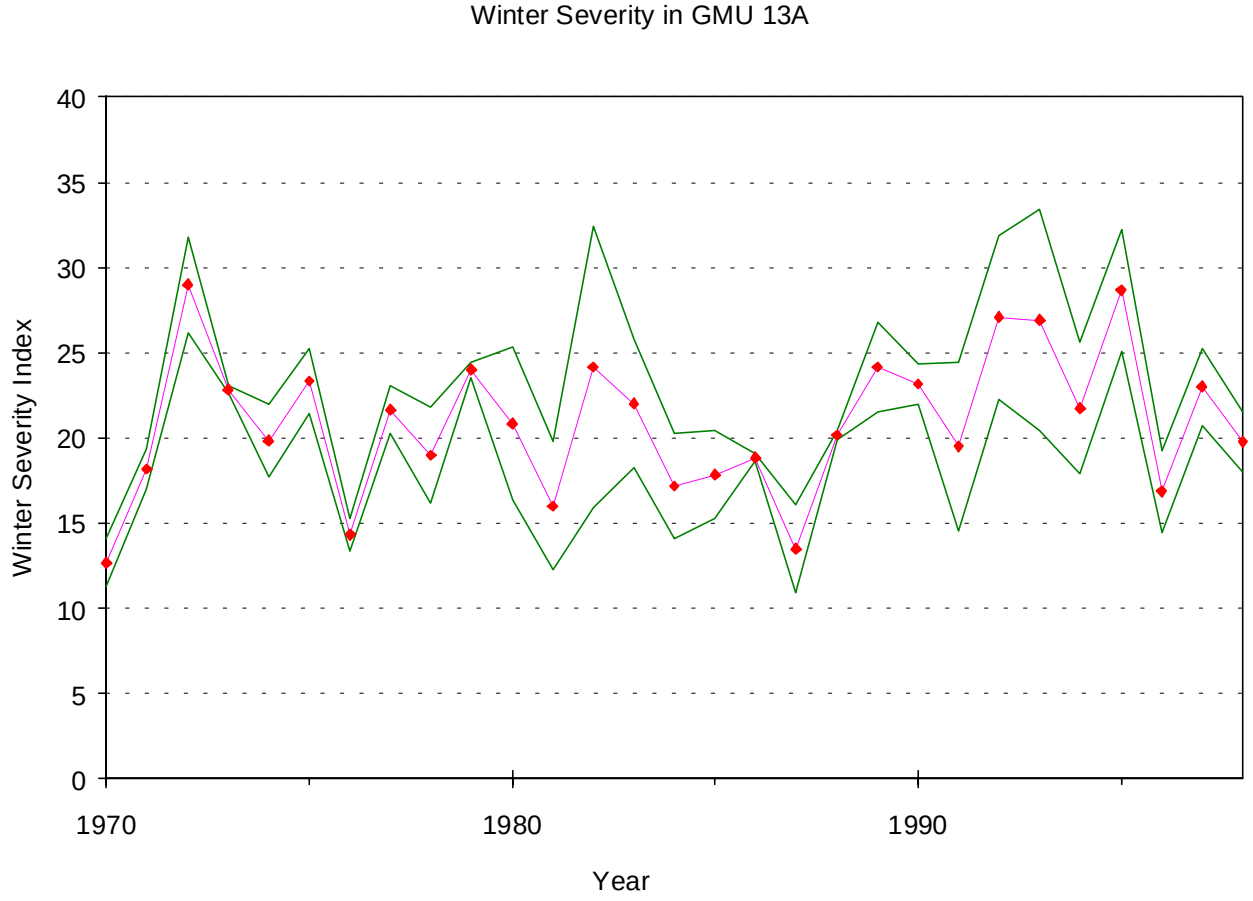

Figure 4. Winter severity index (± *SD* among sites) in Nelchina Study Area from 1970–1996.

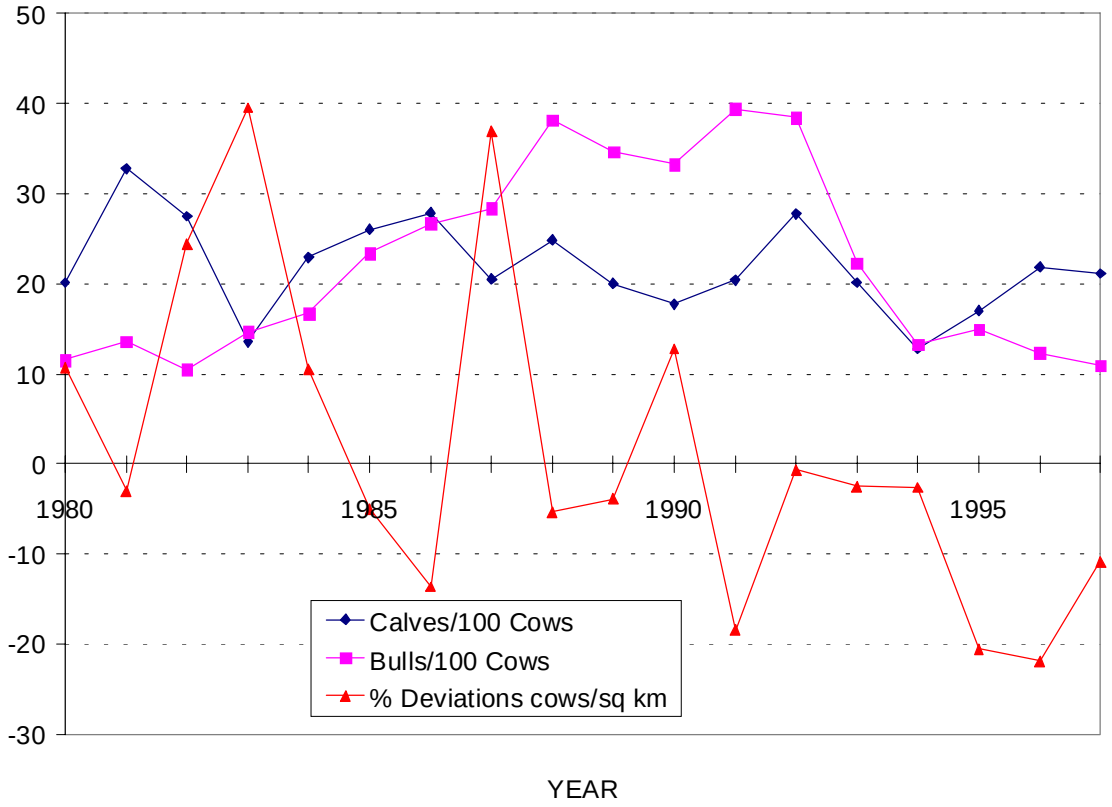

Figure 5. Fall composition and annual deviations from the mean index of cow moose/km^2 in the Nelchina Study Area (Count Areas 13 and 14) from 1980-1997.

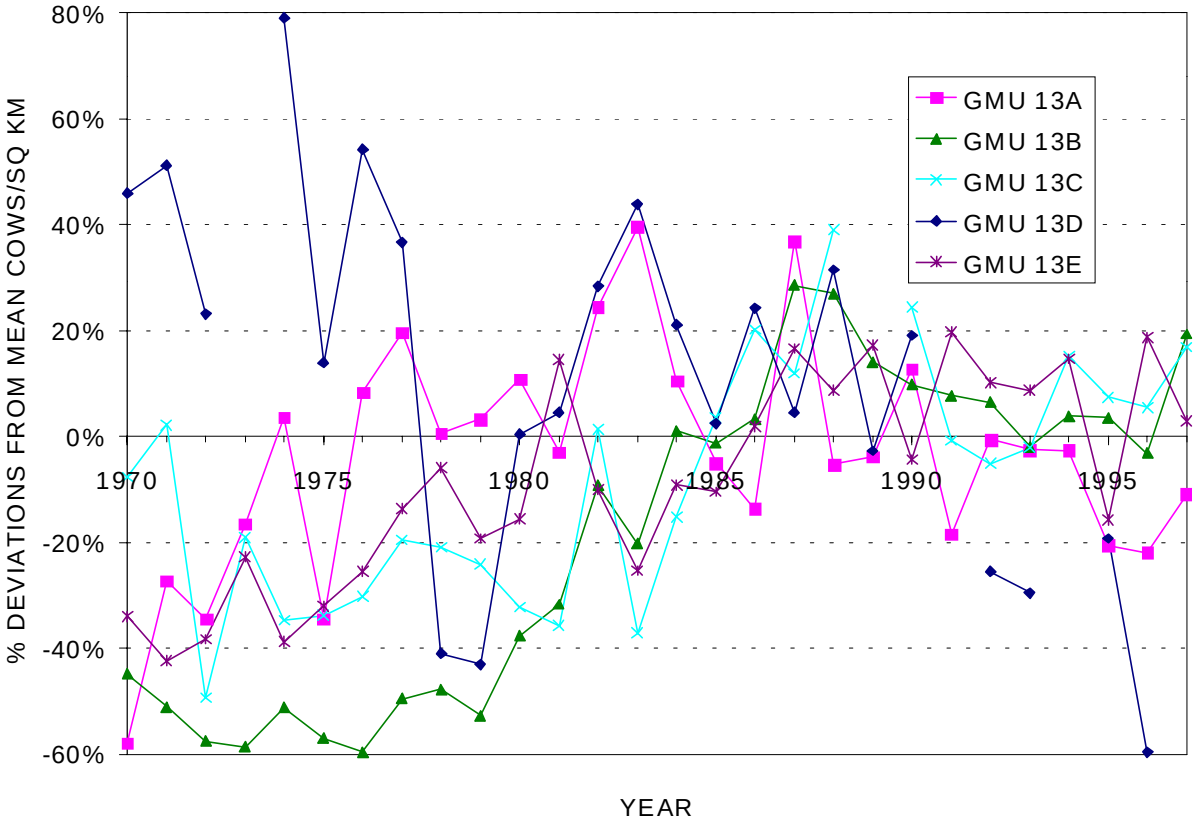

Figure 6. Annual deviations from the mean index (1970–1997) of cows/km^2 in the major subunits of Unit 13.

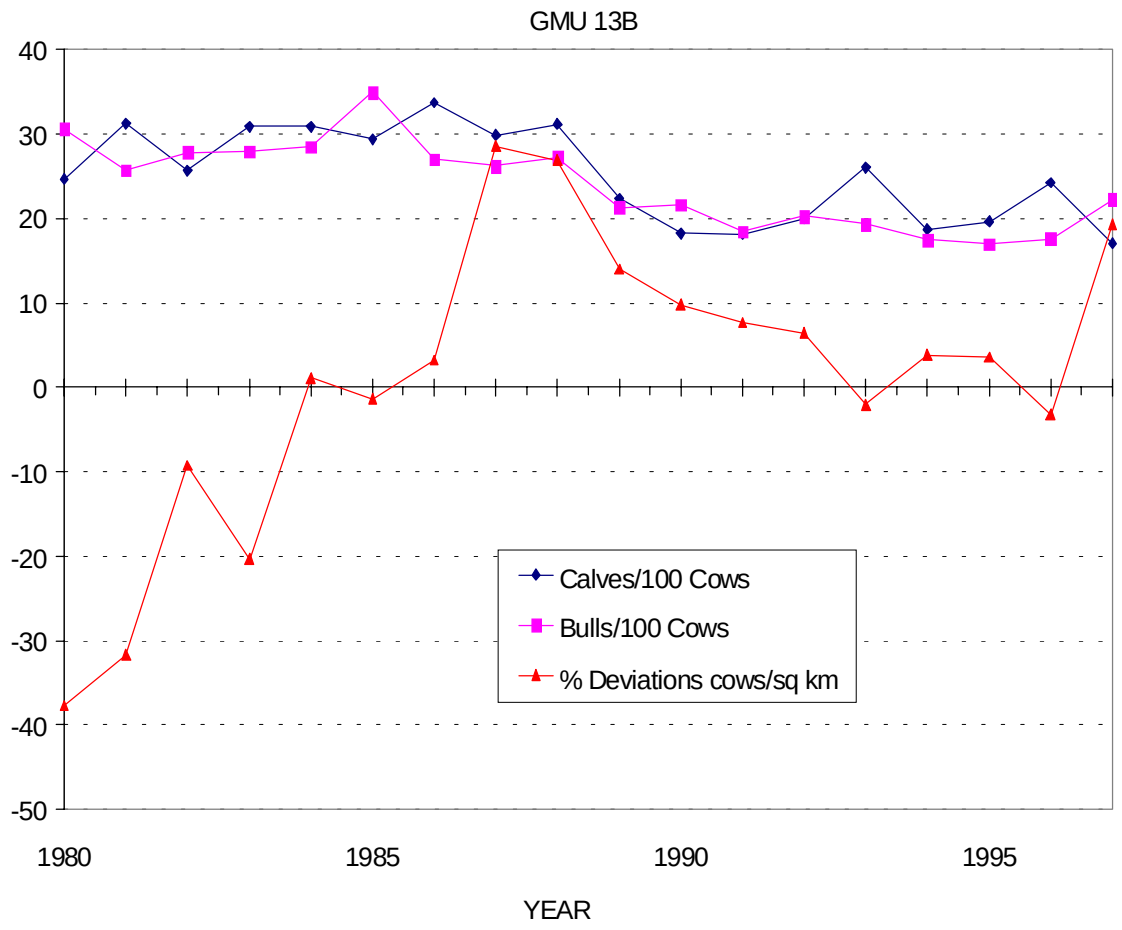

Figure 7. Fall composition and annual deviations from the mean index of cow moose/km^2 in Unit 13B from 1980–1997.

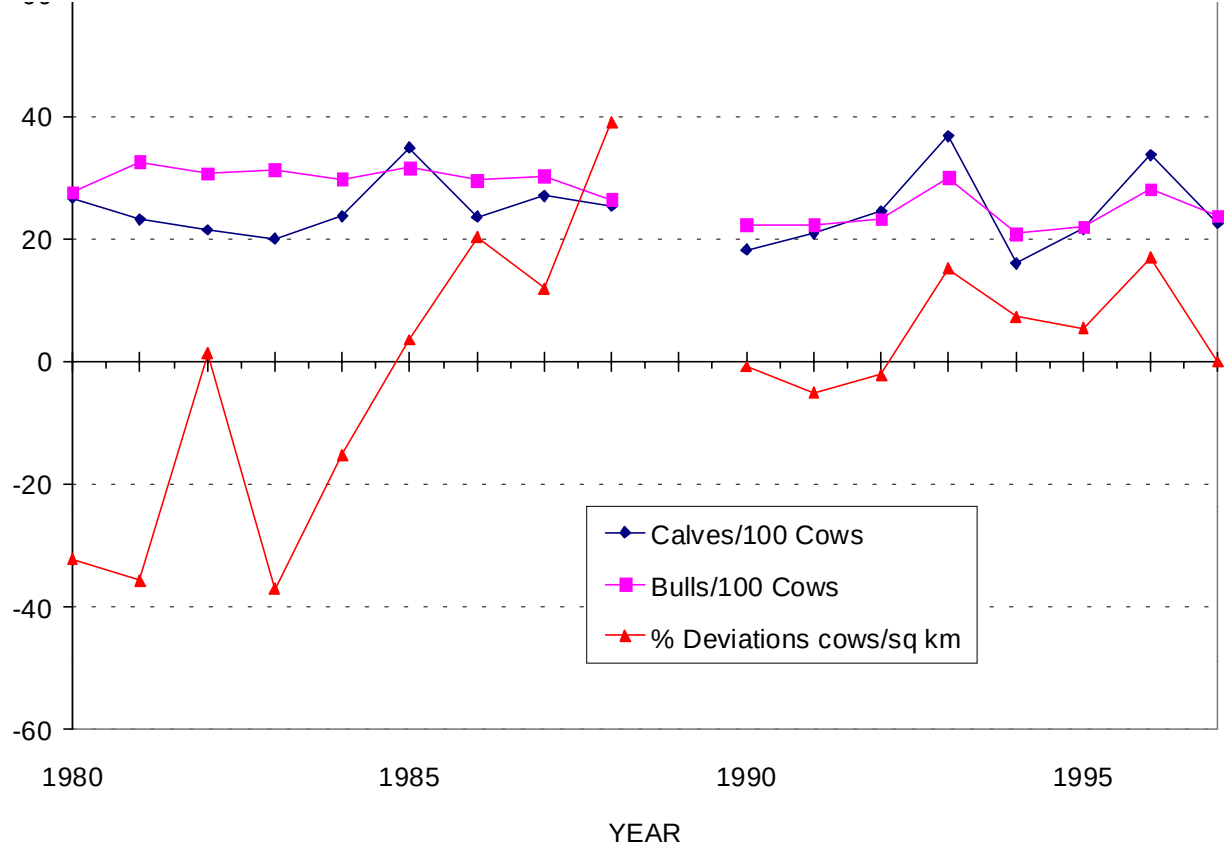

Figure 8. Fall composition and deviations from the mean index value of cow moose/km^2 in Unit 13C from 1980–1997.

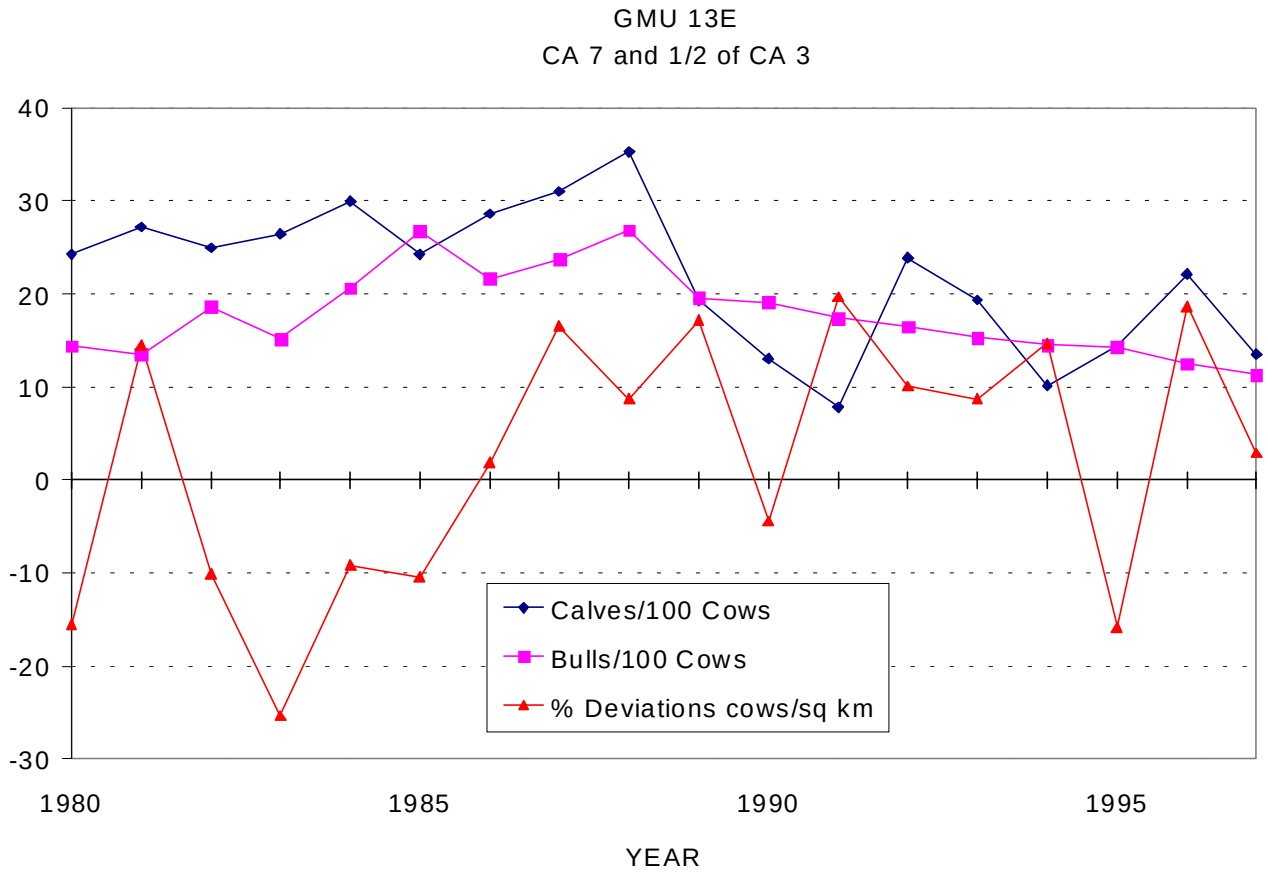

Figure 9. Fall composition and deviations from the mean index value of cow moose/km^2 in Unit 13E from 1980–1997. Count Area 7 was not counted in 1987–1989 and 1993–1995.

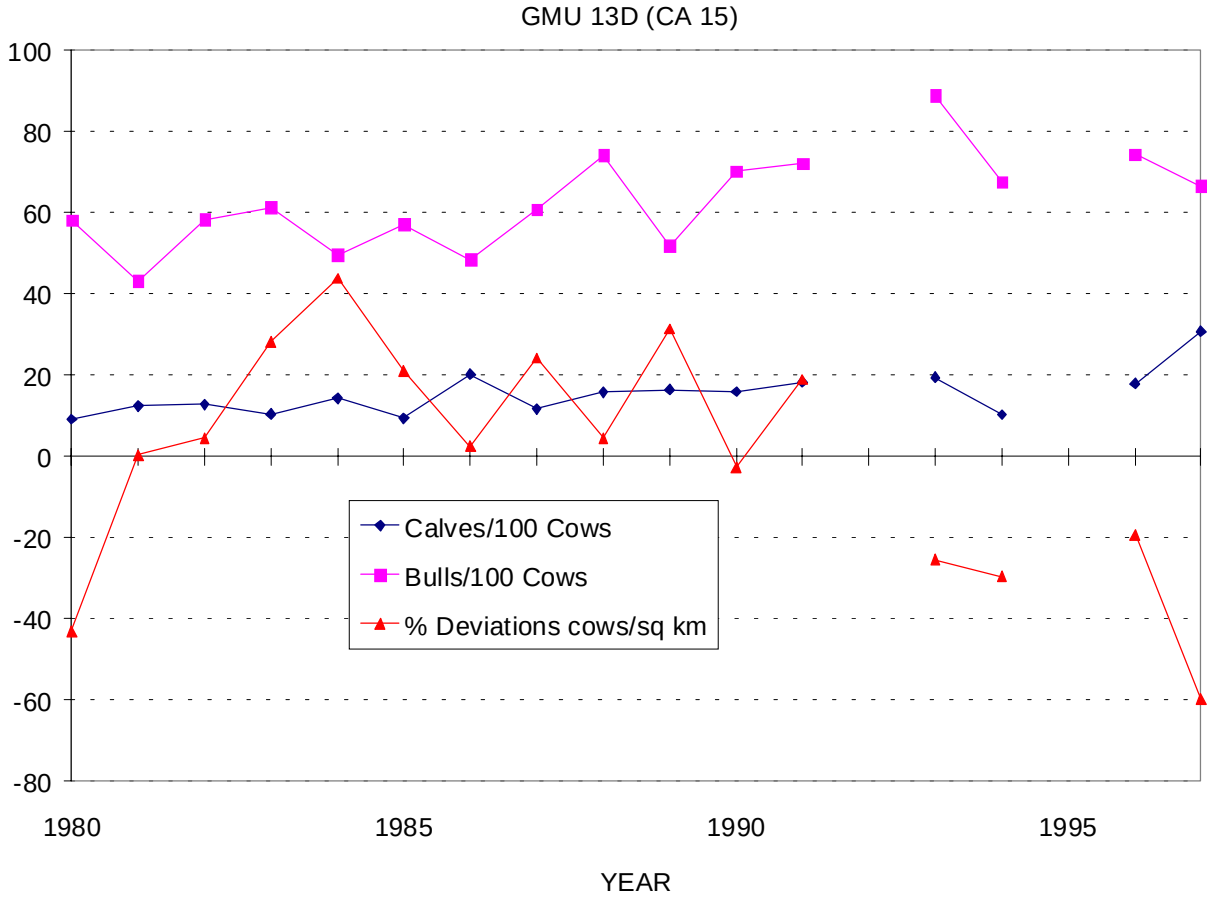

Figure 10. Fall composition and deviations from the mean index value of cow moose/km^2 in Unit 13D from 1980–1997.

Table 1. Rates of parturition and twinning of adult moose in the Nelchina Study Area, Southcentral Alaska (sample size in parentheses), 1994–1998.

Year	Parturition Rate (n)	Twinning Rate (n)	Fecundity
1994	63% (40)	9.1% (77)	0.69
1995	86% (58)	12.1% (116)	0.96
1996	88% (68)	15.0% (140)	1.01
1997	84% (50)	21.0% (113)	1.02
1998	78% (59)	25.3% (83)	0.98
Total	81% (275)	16.4% (529)	0.94

Table 2. Average monthly survival of adult female moose from 1994–1998 in the Nelchina Study Area, Southcentral Alaska.

Month	At Risk	Died	Survival (*SE*)
5	331	0	1.00 (0.00)
6	328	5	0.99 (0.01)
7	310	1	0.98 (0.01)
8	245	0	0.98 (0.01)
9	245	0	0.98 (0.01)
10	243	2	0.97 (0.01)
11	226	0	0.97 (0.01)
12	268	0	0.97 (0.01)
1	276	1	0.97 (0.01)
2	273	1	0.97 (0.01)
3	274	1	0.96 (0.01)
4	305	5	0.95 (0.01)

Table 3. Comparison of survival rates of female moose in the Nelchina Study Area, Southcentral Alaska from 1994–1998, conditioned on the presence of a calf.

	Females alone			Females with calf		
Month (days)	At risk	Died	Survival (*SE*)	At risk	Died	Survival (*SE*)
5 (1–11)	196	0	1.00 (0.00)	58	0	1.00 (0.00)
5 (12–21)	205	0	1.00 (0.00)	34	0	1.00 (0.00)
5 (22–31)	90	0	1.00 (0.00)	147	0	1.00 (0.00)
6 (1–10)	91	0	1.00 (0.00)	146	4	0.97 (0.01)
6 (11–20)	114	0	1.00 (0.00)	118	1	0.96 (0.02)
6 (21–30)	153	0	1.00 (0.00)	91	0	0.96 (0.02)
7	171	1	0.99 (0.01)	72	0	0.96 (0.02)
8	188	0	0.99 (0.01)	55	0	0.96 (0.02)
9	188	0	0.99 (0.01)	54	0	0.96 (0.02)
10	187	2	0.98 (0.01)	55	0	0.96 (0.02)
11	168	0	0.98 (0.01)	55	0	0.96 (0.02)
12	207	0	0.98 (0.01)	60	0	0.96 (0.02)
1	212	1	0.98 (0.01)	62	0	0.96 (0.02)
2	211	1	0.97 (0.01)	60	0	0.96 (0.02)
3	211	0	0.97 (0.01)	74	1	0.95 (0.02)
4	235	2	0.97 (0.01)	71	3	0.91 (0.03)

Table 4. Average annual survival rates of yearling female moose in the Nelchina Study Area, Southcentral Alaska, 1995–1998.

Month	At Risk	Died	Survival (*SE*)
All yearlings			
5	33	1	0.97 (0.03)
6	31	4	0.84 (0.06)
7	27	2	0.78 (0.07)
8	25	1	0.75 (0.07)
9–12	22-24	0	0.75 (0.07
1–4	24-25	0	0.75 (0.07)
Yearlings with mother			
5	20	0	1.00 (0.00)
6	15	1	0.93 (0.06)
7	16	0	0.93 (0.06)
8	14	0	0.93 (0.06)
9–12	13-15	0	0.93 (0.06)
1–4	13-16	0	0.93 (0.06)
Independent yearlings			
5	11	1	0.91 (0.09)
6	14	3	0.71 (0.12)
7	10	2	0.57 (0.13)
8	10	1	0.51 (0.13)
9–12	7-10	0	0.51 (0.13)
1–4	8-10	0	0.51 (0.13)

Table 5. Comparisons of mass of female moose calves in April 1995–1997 in the Nelchina Study Area, Southcentral Alaska in relation to alternative categories of maternal attendance and mortality the following summer.

Yearling Category	Mean mass (kg)	Sample size	*SE*	*t*-statistic	*P*
Abandoned	157.5	16	4.17		
Not abandoned	155.42	12	4.73	0.33	0.49
Killed	153.75	8	4.56		
Survived	158.31	26	3.14	0.73	0.47

Table 6. Average monthly survivorship of calves of radiocollared moose in the Nelchina Study Area, Southcentral Alaska, 1994–1998. Survival in months 5–6 is an estimate from parturition to the end of June.

Month	At Risk	Deaths	Survival	Lower 95%	Upper 95%
5-6	214	139	0.35	0.29	0.41
7	75	17	0.27	0.21	0.33
8	58	2	0.26	0.20	0.32
9	55	0	0.26	0.20	0.32
10	56	1	0.26	0.20	0.32
11	56	2	0.25	0.19	0.31
12	63	0	0.25	0.19	0.31
1	65	0	0.25	0.19	0.31
2	65	2	0.24	0.18	0.30
3	76	1	0.24	0.18	0.29
4	72	4	0.22	0.17	0.28

Table 7. Estimated density and harvest density of wolves (per 1,000 km^2) in the Nelchina Study Area. In 1994–95 essentially all harvest took place before the population estimate in March. In 1995–96, due to unusually late snowfall, a harvest of 1.22 wolves/1,000km^2 took place after the population estimate in February. Fall density of wolves was calculated as the sum of the spring estimate and pre-survey harvest.

Year	Estimate	90% CI	Pre-Survey Harvest	Fall Density
1994/95	4.5	(3.2–6.9)	4.2	8.7
1995/96	9.9	(9.7–11.3)	0.0	9.9
1996/97	5.9	(5.2–8.9)	6.4	12.3

Table 8. Results of surveys during a 1994 population estimate of the Nelchina Study Area (top row) and during trend count surveys in Count Areas 13 and 14 within the Nelchina Study Area (fig. 1) from 1994–97. Apparent densities of the trend count surveys (rows 2–4) are minimum estimates, not corrected for moose sightability.

Year	Moose/hr	Cows/hr	Moose/km^2	Cows/km^2	Calves/100 cows	Bulls/100 cows
1994 NSA Estimate	-	-	0.81	0.60	17.1	16.8
1994	60.5	48.0	0.50	0.40	12.8	13.2
1995	35.0	26.5	0.43	0.32	17.0	14.9
1996	33.1	23.3	0.37	0.26	26.9	15.1
1997	55.7	44.2	0.48	0.36	21.1	10.9

Table 9. Area and average count indices of moose observed in aerial surveys of traditional Count Areas (CA's). Indices of moose abundance are mean values obtained in survey flights for the period 1980–1997 (see methods). Survey flights were not intended to estimate actual densities, so values obtained each year were minimum moose densities.

CA	Area(km^2)	Moose/km^2	Cows/km^2	Moose/hr	Cows/hr
3	1103	0.424	0.293	65.83	45.32
5	2130	0.560	0.358	54.43	34.84
6	1677	0.252	0.174	50.36	34.76
7	2215	0.427	0.305	51.41	36.74
10	423	0.472	0.305	57.14	36.86
13	1594	0.679	0.513	61.89	46.74
14	968	0.462	0.355	51.38	39.54
15	924	0.100	0.059	23.00	13.75
16	341	0.381	0.249	43.33	28.33

APPENDIX: ABSTRACTS TO PAPERS SUBMITTED OR IN PRESS.

Testa, J.W. 1998. Compensatory response to changes in calf survivorship: management consequences of a reproductive cost in moose. Alces 34: 107-116.

Life history tradeoffs are a well-documented feature in many large mammal species but the management consequences of such tradeoffs usually are not explored. A cost to present reproduction, in terms of future reproductive success, for female moose was implied in recent work by Testa and Adams (*in press*). In that paper, rump fat thickness differed in moose with and without a calf at heel in autumn, and was correlated in logistic regression models to subsequent calving. This suggests an energetic link that results in lower reproductive success for female moose in years after successfully rearing a calf to autumn. In the present paper, a model of their results linking present and future calving success through rump fat changes was favorably compared to a second sample of female moose for which reproductive histories in successive years was known. This individual cost of reproduction in moose may play a role in populations having high and variable rates of additive perinatal mortality due to predation. The cost for individual moose of having and rearing a calf to autumn was estimated, and incorporated into a population model in which perinatal mortality was manipulated to simulate managed reduction of predation rates on neonates. The expectation was that the tradeoff between current and future reproductive success in individuals could reduce the harvest benefits expected from reducing calf mortality. The estimated cost of successfully rearing a calf to the fall in this study was a 44% reduction in fecundity, which led to modeled reductions of 10-13% in the gains expected from better calf survival. This effect could be greater in years of unusually low reproduction, or after an increase in population density.

Testa, J.W. and G.P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79: 000-000.

We studied condition and reproduction of moose (*Alces alces*) in southcentral Alaska using ultrasonography to determine rump-fat thickness and numbers of corpora lutea and embryos in early gestation, and intensive radio-tracking of the same animals in spring to measure rates of calving and neonatal survival. Rump-fat thickness, pregnancy rate, and embryo size were less among female moose accompanied by a calf in autumn. Fifteen percent of ovulations failed to result in a detectable embryo, and additional reproductive losses occurred between early gestation and birth. Body condition in the autumn was correlated positively with pregnancy and calving rates and negatively with reproductive losses in both early and late gestation and neonatal mortality. Our study documents the extent to which body condition and prior reproductive success affect adjustments to reproductive effort made by female moose within a single reproductive cycle.

Testa, J.W., E.F. Becker and G.R. Lee. (In Review). Temporal patterns in survival of twin and single moose calves (*Alces alces*) in Southcentral Alaska. Journal of Mammalogy.

We studied survival of 220 calves of radiocollared moose from birth to the end of July in Southcentral Alaska from 1994-1997. Prior studies have established that predation by brown bears (*Ursus arctos*) is the primary cause of mortality on moose calves in the region. Survival of moose calves to the end of July was 0.27 (SE = 0.03) and their age-specific rate of mortality showed a linear decline in that period. Mean annual survival was 0.22 (SE = 0.03). Previous winter's snow depths and survival of the previous year's calf had no detectable effects on neonatal survival. The hazard of death increased by 6.6% with each daily increase in parturition date. While there was no significant difference in survival of twin and single moose calves, most twins (83%) disappeared in pairs up to 15 days of age, suggesting that predators kill both when encountered up to that age.