Alaska Department of Fish and Game
Division of Wildlife Conservation
July 2001

Population Dynamics of Moose and Predators in Game Management Unit 13

J. Ward Testa

Research Final Performance Report
1 July 1994–30 June 2000
Federal Aid in Wildlife Restoration
W-24-3 to W-27-3
Study 1.49

If using information from this report, please credit the author(s) and the Alaska Department of Fish and Game. The reference may include the following: Testa, J.W. 2001. Population dynamics of moose and predators in game management unit 13, 1 July 1994–30 June 2000. Alaska Department of Fish and Game. Federal aid in wildlife restoration research final performance report, grants W-24-3 through W-27-3, study 1.49. Juneau, Alaska. 43 pp.

RESEARCH FINAL REPORT

STATE: Alaska **STUDY** 1.49

GRANTS: W-24-3–W-24-5 and W-27-1–W-27-3

STUDY TITLE: Population dynamics of moose and predators in Game Management Unit 13

AUTHOR: J. Ward Testa

PERIOD: 1 July 1994–30 June 2000

SUMMARY

Historical trend data indicate the moose population in Game Management Unit 13 is at generally high density, but there is evidence for a decline in the population of adult female moose that is probably accelerating in recent years. The adult female segment of the moose population in Subunit 13A has declined ~25% in the past 4–5 years, primarily due to poor calf recruitment, with low-density areas apparently the most affected. In the northern part of the GMU (Subunits 13B and C), 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, but the adult female population has been stable since 1991. In eastern Subunit 13E large annual variability in counts of adult females mask potential trends, but calf:cow ratios declined 43% from the 1980s to the 1990s, and a decline in the adult population is probable. Subunit 15D, as indexed by a single count area, continues to display low moose density and recruitment without detectable trends.

In the intensive study site in western GMU 13A, the Nelchina Study Area (NSA), annual rates of parturition and twinning ranged between 0.63 and 0.90 and 9.1 and 24.4%, respectively. Twinning rates during 1994–1996 (9–15%) were among the lowest known for moose but have been increasing during the study (18–25% in 1997–2000). This may represent an improvement in productivity in response to recent mild winters or a density dependent response to lower density of moose. Browse utilization in winters 1996–1999 appeared to be moderate in comparison to other areas of Alaska. Survival of adult females was high (0.92) but declining. Calf survival was very low (0.20) and also declining. Yearling survival was 0.80. The severe winter of 1999–2000 probably affected other subunits of GMU 13 more than GMU 13A, but direct effects on survival and reproduction of radiocollared moose in the NSA (GMU 13A) were not detectable. Brown bears appear still to be the most important predator on moose calves, but the number of wolves in the NSA and throughout GMU 13 has increased substantially in the past few years. The moose:wolf ratio in the NSA is near the threshold at which Gasaway (1992) suggested that wolves can depress moose populations, even in the absence of bears.

There were both nutritionally driven and predator-driven life history tradeoffs in the moose studied here. Moose that successfully reared a calf to fall had lower parturition and twinning rates the following spring. These are considered to be bottom-up, or nutritionally driven life history tradeoffs because of clear links to body condition (Keech and others 2000; Testa and Adams 1998). Adult females with calves suffered greater losses to predation, and yearlings abandoned at the birth of their mothers' new calves had higher mortality than those remaining with their mother a second year. The interaction of these bottom-up and top-down life history tradeoffs appear to be mildly antiregulatory. That is, at the relative vulnerabilities estimated here, an increase in bottom-up costs to reproduction enhances survival of yearlings and adults enough to overcompensate for the loss of productivity of females that successfully reared a calf the previous year. The net difference in population growth rate (λ) caused by the interaction of fixed top-down costs to reproduction and bottom-up costs varying from 100 to 0% was 0.012. Relative to more direct ecological effects on population survival and reproductive parameters, the effect of such an interaction on λ may not be detectable. However, because of the antiregulatory nature of the change, subtle effects on the stability of predator-prey interactions cannot be excluded. Simulations that increased the effects of winter predation (more wolves) and decreased summer predation (fewer bears) reduced the interaction of the life history tradeoffs. Thus, it is possible that in addition to the predation load added to wolf-moose models by summer bear predation, life history interactions could contribute to the instability of a predator-prey equilibrium at high prey densities (Ballard and Van Ballenberghe 1997; Gasaway, Boertje, and others 1992; Messier 1994).

Key Words: *Alces alces*, brown bears, costs of reproduction, life history tradeoffs, moose, population dynamics, predation, reproduction, wolves.

CONTENTS

BACKGROUND

Ballard and others (1991) documented the recent management and ecological history of moose in Game Management Unit (GMU) 13 during 1952–1984. Indices to moose abundance indicated the population underwent a decline from 1963 to 1976 and 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 GMU 13. This report will summarize research results during 1994–2000.

STUDY AREA

I selected a study area of approximately 4200 km^2 of moose habitat near the townsite of Nelchina in GMU 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. Skoog described climate and vegetation in the region (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 precipitation from 22 to 42cm, mostly falling as 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 and others 1987) and 80–120 independent (noncub) 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

The main objectives of this 6-year research program were 1) to more accurately track the dynamics of the moose population in GMU 13, 2) determine which causal variables (e.g., weather, predation, habitat, hunting) are driving population changes as they occur, and 3) identify possible management strategies to anticipate or halt moose population declines and increase human harvests. Based on early results (Testa and Adams 1998) a further objective was added: to determine the possible consequences and importance of phenotypic life history tradeoffs to the population dynamics of moose. I hypothesized that measured phenotypic tradeoffs can contribute to the dynamics of the population, and subsequently focused on the interaction of top-down and bottom-up effects by modeling that part of a population trajectory when these effects were likely to change the most. That is, I modeled the population in the range when it approaches or retreats from K-carrying capacity (McCullough 1979) and when predator impact increases with the increasing ratio of predators to prey (Arditi and Ginzburg 1989; Gasaway 1992). These appear to be conditions in the study area.

METHODS

POPULATION-LEVEL ASSESSMENTS

COMPOSITION AND DENSITY OF MOOSE

Moose were surveyed from PA/18 aircraft in traditional count areas (CA's) of GMU 13 (Fig. 1) at an intensity of 0.6–1.1 min/km^2, roughly half the intensity used for density estimation (Gasaway and others 1986). Such surveys have been made for management purposes since 1955, but those prior to 1970 were excluded from analyses due to low and variable search effort. Those surveys after 1980 are considered the most consistent. Moose were identified as calves, adult females (older than calves), yearling males, and older males. Calves could be differentiated from adults based on their smaller size, distinctive light "saddle" around the shoulders, and short muzzle. Males were classified as yearlings or older based on size and conformation of antlers, admitting uncertainty to some of these classifications (Van Ballenberghe 1979). Yearling males have spike, forked, or slightly palmated antlers without brow tines. Pilots on these surveys each had many years of experience identifying moose to these categories. These data provided an index of moose densities for monitoring trends in abundance and estimates of composition.

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 and others 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 demographic trends and because cow moose are the most important segment to population growth, adult females (older than calves) are emphasized in these analyses. Also, I will present trend count data as moose or cows per km^2 for easier comparison to population estimates and appraisal of sighting probabilities. During 1994–1997 and 1999 the probability of sighting moose in count areas 13 and 14 was estimated from the proportion of radiocollared moose present that were seen during the survey. I determined the presence of radiocollared moose by radiotracking on the day of the survey.

Only Count Areas 3, 5, and 6, in the northern part of GMU 13, and count area 13 in the western part have been surveyed every fall from 1970 to 1999. Count Areas 10 and 16 were surveyed all years except 1989, and the data series for CA 15 excluded years 1970, 1974, 1992, and 1995. Count Area 14 was surveyed during 1970–76, 1978, 1980, 1984–88 and 1991–99. CA 7 was surveyed during 1970–86, 1990–92, and 1995–99. Other parts of GMU 13 have been surveyed for moose numbers and composition, but I included only those that have been surveyed at least 20 of the past 31 years. Count Areas in the NSA (CA's 13 and 14) composed 2000 km^2 of the 4200km^2 in the NSA.

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 during 1980–1998. These "deviations from the mean" will be graphically illustrated. To pool different CA's and report trends in entire subunits, I weighted the deviations from the mean by the size of each CA in the subunit. Because CA's 3 and 10 straddled subunit boundaries, I 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 CA's.

During 30 Oct–5 Nov, 1994, 2–5 Dec 1998 and 16–19 Nov 1999, estimates were made of the moose population in the western part of GMU 13A in areas under 1230 m in elevation. The area included all of the NSA, and a drainage of approximately 200 km^2 in the extreme NW of GMU 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 in 1994 was a modification of (Gasaway and others 1986) that employed a probability regression procedure (Sarndal and others 1992). This method relates the low-intensity "stratification" counts made by observers in a Cessna 185 on one day to intensive counts made by pilot/observer teams in PA/18 aircraft the following day. Rather than classifying these sample units into strata of different moose densities (Gasaway and others 1986), regression analysis was used to estimate the relationship between counts from the C-180 and more intensive counts from the PA/18 at approximately 1.5–2.3 min/km^2. This regression was then used to estimate the number of moose in sample units that were not surveyed by the PA/18 crews. Sightability correction factors (SCF's) were determined on the intensive sample units by resurveying a 2.6 km^2 subunit at 4–5 min/km^2 (Gasaway and others 1986). In 1998 standard stratification and estimation methods (Gasaway and others 1986) were used, including SCF's. In 1999 a modified Gasaway survey was done. Stratification of the area was accomplished subjectively by low-intensity surveys. Estimates were derived with the Geo-Statistical Population Estimator (GSPE) developed by J. Ver Hoef (ADF&G Fairbanks, personal communication). The principal statistical innovation of the GSPE is the incorporation of spatial autocorrelation in the estimates. Randomly selected units were flown at higher intensity (~2.5–4 min/km^2) than in a normal Gasaway survey, but sightability correction factors were not applied. Because this approached the intensity at which SCF plots were flown in the earlier surveys, I assumed bias in the 1999 method relative to earlier methods was small (<5%).

SNOW DEPTHS

Snow depths in GMU 13 were measured in cooperation with the Natural Resources Conservation Service (NRCS). Four new sites in the NSA were added in 1994, and a fifth was repaired after many years of disuse. These augmented 2 sites in moose habitat that have been monitored since 1968. Rick McClure (NRCS) compiled and distributed those results to users. Ballard and others (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). Based on Coady (1974), Ballard and others (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 7 sites in the NSA beginning in 1995. In order to compare winter snow conditions in the surrounding areas, mean snow depths were calculated from 2 to 3 representative sites in each of the other game management subunits.

BROWSING INTENSITY

The intensity of browsing in winter was determined in two important wintering areas, riparian habitats along Tyone Creek and Oshetna River where *Salix alexensis* is the principal forage species. Transects were selected in willow stands at systematic intervals along the stream in late winter (March) each year. At 5 m intervals along the transect, the nearest limb of *S. alexensis* was selected with the nearest twigs at 1 and 2 m above ground level; the terminal shoot was selected if it was ≤3m high. The diameter and length of current annual growth (DCAG & LCAG) were recorded for unbrowsed stems. Diameter at point of browse was recorded for browsed stems. Percent of stems browsed was calculated as an index of browsing pressure.

PREDATOR POPULATIONS

During 18 May–1 June 1998, a Capture-Mark-Resight (CMR) technique was applied to brown bears in a 2150 km^2 portion of GMU 13A, principally the northern half of the NSA, by Testa and others (2000*b*) following guidelines developed by Miller and others (1997). The study area for density estimation was chosen to represent habitats ranging from high mountain ridges in the Talkeetna Mountains to lower elevation (800 m) spruce bog in the Lake Louise Flats to the east. It was also chosen to encompass important concentrations of calving moose and caribou in the drainages of Tyone Creek and the Oshetna, Little Oshetna, and Black Rivers. CMR methods require that animals with radio collars be found within the study area boundary on the day (i) of each survey by an observer using a radio receiver and fixed-wing aircraft. These animals were considered “marks at risk,” M_i, and this number was determined each day of the survey by a pilot/observer team that was not involved in subsequent visual searching that day. The remaining pilots searched for all bears that they could find visually to determine whether the bears were collared with functioning radio collars (marked bears seen, or m_i) or “unmarked” (u_i). The key assumptions were that marked and unmarked bears each day were equally sightable, and this was partly assured by making the determination of M_i and m_i independent of one another.

Wolf density estimates were made in March 1995, February 1996, and March 1997 with the Sample Unit Probability Estimator (SUPE) (Becker and others 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 shapes 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. During 1998–2000 no formal estimates of wolf density were possible because snow conditions were inadequate for tracking. In those 3 winters, minimum estimates of wolf density were made by counting the number of packs present in the NSA, as determined by sightings of packs made in telemetry and composition survey flights during October–February. Only packs that could be excluded from possible double counting by color composition and numbers were included in these minimum estimates.

THE MARKED POPULATION

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 18 female moose 10–11 months old (short yearlings) were captured each April 1995–1997 and 1999, weighed from a portable tripod with a load cell dynamometer to the nearest kilogram and equipped with expandable radio collars. Except for 13 moose captured by helicopter net-gun on November 16–17, 1994, all captures were made by darting from a helicopter with a mixture of carfentanil-citrate and xylazine hydrochloride (Schmitt and Dalton 1987). Blood was collected for pregnancy determination by serum assay for pregnancy-specific protein B, PSPB (Rowell and others 1989; Stephenson and others 1995; Wood and others 1986), and assays were performed in R. G. Sasser's laboratory (University of Idaho, Moscow USA). I archived serum samples in the Fairbanks laboratory of Alaska Department of Fish and Game (R. Zarnke, personal communication).

ADULT SURVIVAL AND REPRODUCTION

Radiocollared moose were tracked by fixed-wing aircraft at least once each month during January–November, except from mid May to late June when they were tracked daily (weather permitting) and July when they were tracked 2–3 times per week. In May and June 1999 and 2000 we tracked each moose daily until parturition, then resumed a monthly tracking schedule thereafter. Adult survival was estimated by Kaplan–Meier procedure with staggered entry and censoring (Pollock and others 1989). A representative age structure was maintained by adding young animals that were tagged at 11 months of age to the adult population when they reached 2 years of age. 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 during normal search patterns 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 capture. 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 and others 1989). Tests related to predation were conducted by treating nonpredation deaths as censored data. Trend in the annual estimates was modeled with linear regression, weighting survival estimates by their SE^{-1}.

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 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 4 of each year. Sightings made within 1 km of those made previously that year were excluded from the sample. Parts of the NSA not usually traversed during telemetry flights were surveyed from helicopter for twinning rate information on 2 June 1995, 29 May 1996, 2–3 June 1997, 1–2 June 1998 and 31 May–1 June 1999 and 2000. Reproductive and twinning rates were modeled as response variables in logistic regression (Agresti 1990) with year, Winter Severity Index (WSI) in the two preceding winters, and previous reproductive success as covariates.

CALF SURVIVAL

Survival of calves was estimated by treating calves of radiocollared cows as if they were also radiocollared, applying Pollock's modified Kaplan–Meier estimator (Pollock and others 1989). During 1994–1997 calves were sighted daily until June 15, every 2–3 days in late June, and 3–5 days in July, weather permitting (Testa and others 2000*a*). 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. In 1999, calves were relocated at the end of each month, with a second flight at the end of June to confirm the absence of calves on the first flight. 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, although 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 was estimated monthly from birth to the end of June, then monthly until the end of April. At that point adults may force their calf to disperse, and their disappearance could not be presumed to indicate their death.

YEARLING SURVIVAL AND AGE OF PRIMIPARITY

Female calves of both collared and uncollared adults were captured and radiocollared in April 1995–1997 and 1999. They were weighed to the nearest kg by suspension under a tripod and load cell dynamometer. These calves were considered yearlings in May, and annual survival was calculated as for adults (Pollock and others 1989) by pooling all years 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 and others 1989) based on maternal company. 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. The effect of the yearling's mass on age of primiparity was tested with logistic regression of the observed reproduction of all moose at 3 years of age, the earliest age of primiparity.

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). The commonly measured parameters of survival, age of first reproduction, and adult fecundity are related to population growth rate (λ) by:

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

where

P0 = calf survival from birth to age 1
P1 = calf survival from age 1 to age 2
P = annual survival (excluding hunting mortality) thereafter
F = mean birth rate in female calves/adult female/year
a = age at first parturition

This assumes that, following 2 years of high juvenile mortality, adult mortality will be 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 ages present in the population, these assumptions are considered conservative. The model also assumes a stable age distribution. The possible violations of this assumption and their consequences will be discussed. 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 and reproductive estimates. An even sex ratio at birth was assumed.

LIFE HISTORY MODELS

My approach was to model the female component of the moose population in a stage-structured manner, extending the earlier approach of Testa (1998) for bottom-up costs and explicit changes to rates of calf survival. By considering the life history tradeoffs of individuals as having the same bottom-up or top-down ecological roots as populations, one can relate the familiar changes in population ecology (e.g., more predators, higher densities, less forage) to less familiar changes in individual risks and reproductive effort through time. Because the reduced reproductive output of adult moose following successful reproduction is well established in the NSA (Testa 1998; Testa and Adams 1998), I contrasted a baseline model that incorporates the reproductive tradeoffs measured in this study with one that incorporates both reproductive and survival costs to present reproduction. The term "costs" describes their effects on population growth as well as individual reproductive success: to reduce average reproduction or average survival and therefore reduce population growth rate. What is of interest is how the interaction of these two costs might affect the expected growth rate of moose populations. Both models employ costs as measured in this study, with adjustments meant to reflect plausible changes in nutritional and predator-driven constraints on the population. The scenarios to be explored will entail my changing the bottom-up and top-down costs simultaneously to identify how the interaction might alter the expected rate of population growth, remembering that each operating by itself would be negatively correlated with population growth.

The models were implemented in spreadsheet form with 4 age classes: yearlings, 2-year-olds, nulliparous 3-year-olds, and adults. Yearlings were classified as independent or accompanied by their mother. Adults were classified as having 0, 1 or 2 calves. Those having no calf were further divided into those that had born a lactation cost of reproduction (i.e., a calf surviving to the end of September or later) and those that had lost calves earlier or not given birth that year. Calves were tracked by reproductive status of the adults. Primiparous 3- and 4-year-old moose joined the adult classes as females with single calves in the same proportion as observed among radiocollared moose.

The models were iterated in 23 time steps beginning on May 25, the median birthdate. At the first step reproductive rates specific for each age/reproductive class were applied to moose that had survived the previous year. All primiparous females were assigned to the class of females with a single calf. The adult classes joined calving categories 0–2, depending on whether they had calves accompanying them the previous August. The two yearling classes were incremented by the number of surviving calves, depending on the parturition rates of females with calves. Abandoned yearlings became independent, but half of adult females that lost their new calves in the first 10 days after birth reacquired their yearling. Yearling classes were adjusted in the first 2 time steps to reflect this rate of re-adoption.

The next 13 steps simulated 5-day periods to the end of July. The remaining steps were monthly, except for December and January, which were pooled. At each step, every age/reproductive class was subjected to the mortality rate for that class. Where the interval being modeled was shorter than the period used in estimating survival, the appropriate root of the survival estimate was used in the model interval. Following mortality, classes with calves were adjusted to reflect the mortality of calves. Calf survival data during 1994–1997 (Testa and others 2000*a*) were used in the model because of the greater temporal resolution in those years. Half of twin calves that died in the first 15 days were assumed to die together up to that age, but independently thereafter (Testa and others 2000*a*). The models were iterated for 10 annual cycles based on experiments to determine that the stage-structure of simulations was stable by that point. The finite rate of population growth (λ) was determined from the growth in the final year, while calves/100 cows and spring reproductive parameters were monitored to assess realism of the models.

Two scenarios were simulated. The first was intended to simulate a population experiencing the average predation levels observed in this study while bottom-up costs of reproduction were varied. This might be viewed as a likely scenario where a moose population is increasing in spite of heavy predation on calves and moderate predation on adults, and the nutritional constraints on the population are growing. Rates of mortality were taken directly from those measured in the radiocollared population of moose. Predators would be an important factor in this scenario, but not acting in a manner that would regulate population growth (i.e., constant predation rate). Bottom-up constraints would be acting to regulate population growth, but in this model it can only act by increasing the cost of reproduction. That is, average reproduction was reduced by reducing rates of parturition by females that succeed in rearing a calf to the fall (100% to 0% of maximum rate), but maximum rates continued to apply to females that failed to rear a calf to fall. Reproductive rates were chosen that were close to those measured in the NSA and adjusted to produce a slow rate of growth when bottom-up costs of reproducing were zero (0). Twinning rate of adults was held constant.

In the second scenario I varied mortality rates along with costs of reproduction in order to maintain a population decline of 4% annually. Mortality was varied on all classes as a scalar multiplier to affect all classes without altering the inherent differences (e.g., those due to the top-down costs of reproduction) between classes. The intent was to maintain the observed differences in vulnerability between classes while increasing predation rates. This would be consistent with a predator-prey interaction controlled by predator encounter rate or ratio of predators/prey. This could be controlled separately in winter, when wolves were the only significant predator, and summer, when bears are likely to be the most significant agent of mortality (Ballard and others 1990; Ballard and others 1991; Testa and others 2000*a*). The baseline model without top-down life history tradeoffs in survival was used to simulate a population without the potential interaction of reproductive costs and survival costs to successful reproduction.

RESULTS

HISTORY AND ECOLOGICAL CONTEXT

POPULATION TRAJECTORY OF MOOSE IN GMU 13A

The number of adult female moose seen per km^2 during trend count surveys in GMU 13A is highly variable, but a downward trend beginning in the mid-1980s is indicated by the data in Figure 2. Calf:cow ratios in the 1990s were 20% lower than those in the 1980s, and the most recent 6 years include the 4 lowest recruitment records in the 30-year series. Estimates of the density of adult females in the NSA have declined 25% since 1994 (Table 1). That the change in density of moose in CA’s 13 and 14 is substantially less than that for the NSA in that period suggests that the decline is greatest in the eastern part of the NSA where moose densities are lowest.

The variability of counts from CA’s 13 and 14 remains an obstacle to recognizing real changes in population size in GMU 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. Changes in bull/cow ratios in GMU 13A have followed changes in hunting regulations, 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.

POPULATION TRENDS IN SURROUNDING SUBUNITS OF GMU 13

Moose density indices and geographic size differ substantially among CA's (Table 2). Game Management Subunits 13B and 13C (Figs. 3 and 4) 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 5–8 years of the series. With the exception of 1997, GMU 13B (Fig. 3) 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 for moose to the north (Alaska Range) and south (spruce bog) that limits migration. The 15% decline from the peak in cow moose observed in 1987 coincided with a decline in recruitment in GMU 13B, evidenced by the drop in the proportion of cows with calves after 1988 (29% to 20%, $P<0.01$). In GMU 13C, the CA's comprise a small proportion of the subunit (Fig. 1) where there is more annual variation in composition and in density index of moose than in GMU 13B. The pattern in cow moose abundance was similar to that in GMU 13B but with only a small drop in calf:cow ratios between the 1980s and 1990s.

Counts in GMU 13E (Fig. 5) in the northwestern part of the GMU are missing counts from its largest CA (7) in years when high densities of moose were reported in nearby areas of 13A and 13B. Because of the wide yearly variation in density of cow moose, there is little evidence for a trend in density in GMU 13E. However, calf:cow ratios have declined 43% in the 1990s from values of 24–35 calves:100 cows in the previous decade (Fig. 5). Such low recruitment, sustained for the past decade, indicates that a significant decline is occurring but is being masked by the wide annual variation in counts of adult cows. Bull to cow ratios have also declined to low levels (Fig. 5), apparently due to hunting pressure.

Subunit 13D in the southern part of the unit has the lowest density of moose (Table 2) and calf:cow ratios, but the highest bull:cow ratios (Fig. 6) 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. The traditional prevalence of bulls in the CA indicates that sexual segregation that occurs after the rut in moose (Miquelle and others 1992) affects this CA more than others.

SNOW DEPTHS

Winter snow depths in moose habitat in the NSA (Fig. 7) have generally been mild to moderate (Ballard and others 1991, Coady 1974). In the period of this study, only winter 2000 was severe in GMU 13A. In fact, since 1985 the values measured in GMU 13A are well below those for the remaining subunits of GMU 13 (Table 3), indicating that winter conditions are likely to be more important to moose in other subunits of the GMU.

BROWSE UTILIZATION

Browsing on the feltleaf willow (*S. alexensis*) was monitored along the Oshetna River and Tyone Creek, two important wintering areas for moose in the NSA. The winter utilization rate of terminal twigs of *S. alexensis* during 1995–2000 varied from 12 to 82% and was always substantially higher than that of lateral twigs (Table 4). The disparity among years indicates that winter range is probably not a limiting factor in most years in the NSA. The high rates of utilization in 1995 and 2000 correspond to the 2 winters of deepest snow (Fig. 7).

PREDATOR POPULATIONS

Although the late winter estimate of wolf density differed substantially in 1995–96 compared to surrounding years (Table 5), the annual harvest in that year was extremely light due to the unusually shallow, late snow. Effects of temporary wolf 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, 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 formal estimates of wolf density were made in 1998 through spring 2000 due to the absence of suitable snow conditions (Becker and others 1998). However, a total of 55 wolves in 9 packs were observed in the NSA from November 1998 to February 1999, a minimum density of 13.1 wolves/1000 km^2. In fall 1999 a minimum of 64 wolves were seen in 7 packs, a density of 14.5 wolves/1000 km^2. Both counts were considered conservative due to large tracts of the NSA that were not searched for wolves. The trend in harvest, especially in the last 2 years of study, also mirrored this upward trend in minimum numbers of wolves in fall (R.W. Tobey, Glennallen Area Biologist, personal communication).

The density of independent brown bears in a 2150 km^2 portion of the NSA in 1998 was 21.3/1000 km^2 (95% C.I. 18.4–25.9 (Testa and others 2000*b*). Although hunting of brown bears in the study area is significant, rates of harvest were near sustainable levels (Miller and others 1997) and therefore not likely to cause substantial changes in bear numbers in the short period of this study.

LIFE HISTORY ELEMENTS

REPRODUCTION

No moose gave birth before the age of 3 years in this study ($n = 31$), and only 13 of 22 (0.59) moose reaching 3 years of age gave birth. All 11 moose reaching 4 years of age were parous by that age. Mass at 11 months of age had no discernible effect on the number of 3-year-old moose that were primiparous ($t = 0.521$, $df = 18$, $P = 0.30$, 1-tailed).

Annual reproductive rates averaged 0.81 ($SE = 0.037$) among radiocollared females ≥4 years old from 1994 to 2000 (Table 6), but reproductive rates varied significantly among years ($G^2 = 10.1086$, $df = 1$, $P = 0.015$). The best fitting logistic regression model included the years 1994 and 2000, which were lower than average, as were the number of calves accompanying the female the previous fall (Table 7). Twinning rates of all moose seen with calves (Table 6) varied from 0.09 to 0.25 and were best modeled as an increasing trend in the 7 years studied ($G^2 = 4.029$, $df = 1$, $P = 0.045$), a period of declining population density. Winter Severity Index (WSI) in either of the preceding 2 winters did little to explain the variation in reproductive rate or twinning ($P > 0.75$). When only radiocollared females were analyzed, the annual trend toward increased twinning was undetectable with the smaller sample, but the number of calves accompanying a female in fall significantly reduced twinning rate among parturient females the next spring ($G^2 = 9.302$, $df = 1$, $P = 0.002$). When the analysis was limited to females that were parturient in successive years, the number of calves born the previous year was positively related, and the number of calves accompanying the female in fall was negatively related to rate of twinning in the second year (Table 8).

SURVIVAL

Adult females had an average annual survival of 0.92 (*SE* = 0.014) from 1994 to 2000 (Table 9). Both linear and quadratic terms entered the linear regression model of declining annual survival rates (Fig. 8). After the first 2 years of the study, annual adult survival was 0.90 (*SE* = 0.017).

Of 35 deaths occurring between March 1994 and July 2000, 21 were clearly attributable to predators (10 to wolves, 6 to brown bears, and 5 to unknown predators). In 3 other cases predation by wolves was probable, and predation by brown bear was possible in another. Four deaths were from unknown causes, but predation could not be excluded in 3 of those. Of 6 non-predation deaths, 1 adult died of distocia when giving birth to twin calves. Another apparently injured her hip on lake ice in January and starved to death 3 months later. Four other adults died in winter without evidence of predation, with 2 of these showing signs of starvation in late winter 2000. Predation was not excluded in two of the deaths from unknown causes. Adults with a calf showed a trend toward higher mortality than those without a calf (Table 10, $Z = 1.501$, $P = 0.133$). Mortality attributable to predation or suspected predation was significantly greater among females tending a calf (10% vs 4%, $Z = 2.058$, $P = 0.040$).

Annual survival of yearlings without considering maternal attendance (Table 11) was 0.79 (*SE* = 0.06). All 9 yearling deaths occurred from spring to midsummer (early May to early August). Three deaths were attributed to wolves and 2 to brown bears. Cause was uncertain in the other 4, but predation was considered the most probable cause because of the apparent good health of the moose when previously observed and the proximity of a predator to the fresh carcass. All of the wolf kills were in or next to small lakes, a common feature in 2 other cases in which cause of death was unknown.

Female yearlings abandoned by their mothers suffered higher mortality than yearlings that were able to maintain that association (0.35 versus 0.09, Table 12, $Z = 2.054$, $P = 0.040$). Neither survival nor abandonment of yearlings was related to yearling's body mass as a calf in April (Table 12). 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 within 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 that 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 13). Interannual variation in calf mortality to August was not significant during 1994–1998 (Testa and others

2000*a*). Sequential comparisons of each year's calf survival to the pooled survival of remaining years failed to identify any year as an outlier ($P = 0.067$). 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 (Testa and others 2000*a*). 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 number 13 in 1994. In one case a radiocollared wolverine was found feeding on the calf of a radiocollared moose the day after both moose were observed and apparently healthy. 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 (Table 13). In 4 cases calves disappeared and were presumed dead during winter after wolves had killed the mother. In another case wolves were observed eating the calf carcass, 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 6, 9, 11, and 13, was 0.989. This estimate was relatively insensitive to the variation seen in each of the population parameter estimates (Fig. 9) and indicates that for the period of study (1994–2000), the population of female moose represented by radiocollared animals in the NSA was slowly declining. The modeled population growth was most sensitive to adult, then calf survival in the range of the 95% confidence intervals for each parameter (Fig. 9). The model assumes a stable age structure and constant adult survival. Lower recruitment in later years would shift the age structure to older moose. This would buffer the model population from the depressive effects of low calf recruitment because of the assumption of constant adult survival. In reality, an adult moose population shifting to older age structure is likely to show increased mortality (Peterson 1977), as may be indicated by Figure 8. A trend to lower calf and adult survival suggests that the model might overestimate the early rate of decline and underestimate the current rate of decline. Also, there is a preponderance of radiocollared moose in high-density areas, while the survey results indicate that a greater population decline has occurred in areas of lower moose density. These factors indicate that the actual rate of decline in the NSA is higher than that modeled.

LIFE HISTORY MODELS

Baseline rates of survival of yearlings and adults in all categories were taken from the estimates given in Tables 9, 10, and 11. Calf survival rates were taken from Testa and others (2000*a*) and produced slightly higher annual survival than that given in Table 13. Sixty percent of females reaching 3 years of age were assumed primiparous. Maximum rate of adult parturition in scenario 1 was 0.95. Maximum twinning rate was set to 0.25. At 40% cost of reproduction, the modeled rates of parturition and fecundity were close to those observed. With these starting reproductive parameters, the rate of fecundity varied from 1.125 to 0.847 as the bottom-up cost of reproduction was increased from zero (0) to 100%. The contrast between the model excluding top-down tradeoffs in survival and one including those tradeoffs is shown in Figure 10. The null model illustrates that the loss of reproductive output imposed by the life history tradeoff in calving success is fairly small at these high rates of calf mortality and adult survival. The inclusion of top-down life history tradeoffs in a model of increasing bottom-up life tradeoffs causes the correlation between bottom-up reproductive costs and population growth rate to change sign. That is, the model predicts that the effect of the interaction between top-down and bottom-up life history tradeoffs is antiregulatory. The net difference in population growth rate (λ) caused by the interaction of fixed top-down costs to reproduction and bottom-up cost varying from 100 to zero (0)% was 0.012.

In the second scenario, the maximum reproductive rate was decreased to 0.84 and average predation was increased 30% so that 100% costs of reproduction (i.e., mandatory reproductive pause by females rearing a calf to fall) produced a 4% rate of population decline. As such a decline progressed, it is likely that reproductive tradeoffs would relax. As the reproductive tradeoffs were relaxed in these contrasting models, a 4% rate of decline in the null model was maintained by increasing the average rate of predation, and that increase was applied in both models. I explored the relative effects of bear and wolf predation by increasing mortality in summer (primarily bears) and, mostly, in winter (generally wolves). The effect on life history interactions of increasing the Nelchina pattern of annual mortality uniformly across the year was similar to that of scenario 1, a weakly antiregulatory compensation for increasing bottom-up reproductive costs (Fig. 11). Interestingly, the effect of altering the annual mortality patterns to increase the importance of wolf predation in winter removed much of the antiregulatory interaction in life history tradeoff (Fig. 11). This is probably due to the decoupling of calf mortality from the release from lactational costs when calf mortality is delayed to winter.

PREPARATION OF REPORTS AND PUBLICATIONS

The following technical papers were published or submitted for publication to professional journals during this project.

BERGER, J., J.W. TESTA, T. ROFFE, AND S.L.MONFORT. 1999. Conservation endocrinology: a non-invasive tool to understand relationships between carnivore colonization and ecological carrying capacity. Conservation Biology 13: 980–989.

HUNDERTMARK, K.J., M. MASTELLER, J.W. TESTA, R. TOBEY AND G. DEL FRATE. *In Press*. Selective harvest revisited: the effects of antler-based harvest strategies in three moose populations in Alaska. Alces 37: 000–000.

STEPHENSON, T.R., J.W. TESTA, G.P. ADAMS, R.G. SASSER, C.C. SCHWARTZ, AND K.J. HUNDERTMARK. 1996. Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. Alces 31: 167–172.

TESTA, J.W., E.F. BECKER AND G.R. LEE. 2000. Movements of female moose in relation to birth and death of calves. Alces 36: 155–162.

TESTA, J.W., E.F. BECKER AND G.R. LEE. 2000. Temporal patterns in survival of twin and single moose calves (*Alces alces*) in southcentral Alaska. Journal of Mammalogy 81: 162–168.

TESTA, J.W. AND G.P. ADAMS. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79: 1345–1354.

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

TESTA, J.W. 1996. Using annual approximations of birth rate in models for species with multiannual reproductive cycles. Marine Mammal Science 12: 428–433.

WHITE, K. S., J. BERGER and J. W. TESTA. *In Press*. Behavioral and ecological effects of differential predation pressure on solitary yearling moose in Alaska. Journal of Mammalogy.

DISCUSSION

Historical trend data indicate the moose population in GMU 13 is at a moderate density with changes in bull:cow ratios being driven by changes in harvest regime. Fall calf:cow ratios indicate heavy summer mortality, which has increased recently in most areas. Population growth appears dependent on those ratios exceeding ca. 24 calves/100 cows for a sustained period. The evidence for a population decline in the late 1980s is strongest in the northern part of the unit in Subunits 13B and 13C. Density of cow moose in these subunits is approximately 17% below historic highs during 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 the adult female segment of the population has changed little in the subunits since 1991. Trend counts in Subunit 13D are too variable to interpret trends with any confidence, but moose density and calf recruitment appear to be lower than elsewhere in GMU 13. The density of cow moose in Subunit 13E also has been too variable to detect a decline, but significantly reduced calf:cow ratios in the last decade, 57% of those in the 1980s, indicate that a decline in the adult population is probably ongoing.

Annual variation in the long-term record of indices to cow moose abundance in Subunit 13A was more than expected to result from natural dynamics of a closed population, particularly in the 1980s. There were no indications from composition that sharp annual changes in the cow moose index were preceded by appropriate changes in recruitment. During 1980–86, years in which CA 7 was surveyed north of 13A, the number of adult moose there showed a tendency to vary in an opposite direction to that seen in the adjacent CA 14 in GMU 13A, indicating temporary migration. There are no traditional CA’s in the portion of GMU 13D that borders the CA’s of GMU 13A so I have no way with present data to test the hypothesis that yearly variation in the counts in GMU 13A are caused from movements of moose across that boundary. However, radiotracking of moose captured in the southern and eastern parts of the NSA indicate that movements to GMU 13D and the unsurveyed portion of GMU 13A do occur. For these reasons, I believe that migration plays a significant 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 and others 1991) and in the western half of GMU 13A in 1987, 1994, 1998 and 1999. 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.

Near stability since 1994 was indicated by a model incorporating the population parameters estimated from radiocollared moose in the NSA ($\lambda = 0.99$). However, density estimates in the entire NSA in 1994, 1998 and 1999 showed a decline of over 25%. Most radiocollared moose contributing data to the model occupied areas of moderate to high density in CA 14 and the NE boundary of CA 13 (Fig. 1), areas showing only slight evidence for changing female density (Fig. 2). A model based on that sample may accurately represent what is occurring in those areas and not capture a declining trend in the southern and eastern part of the NSA. Alternatively, the estimated adult survival (0.92) is higher than that implied by age structure data in other studies of moose (e.g., Peterson 1977) and may be overestimated. A rate in the lower range of the estimated confidence interval would imply a 3–4% annual rate of decline (Fig. 9). Further, the fall calf:cow ratios in CA's 13 and 14 were 16% below the average of the previous 10 years, with the lowest values occurring most recently (Fig. 2). Calf survival at the low end of the confidence interval (Fig. 9) would contribute ca. 2% per year to the rate of population decline estimated from the model. The declining trends in annual adult survival (Fig. 8) and calf recruitment (Fig. 2) in the NSA also suggest that the decline in population density is accelerating.

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 before and year after the autumn 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 is an indicator of nutritional status of a moose population, and Gasaway and others (1992) compiled evidence that moose near a resource-dependent carrying capacity may have low twinning rates. Twinning rates in the NSA during 1994–96 (9–15%) were among the lowest recorded for moose throughout their range (Gasaway and others 1992), while twinning rates in the rest of the GMU were higher but not above the average 23–40% (R. Tobey, personal communication; 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 as density declined. Although low snowfall in most recent winters (Fig. 7) may have contributed to this improvement, overall density of moose has declined due to the heavy harvest of males from the population and the modest decline in adult females (Fig. 2), indicating that the increase in twinning may be density-dependent. The most recent rates of twinning in the NSA are nearer those of the remainder of GMU 13. In the NSA during 1995, browsing intensity also appeared to be high relative to 2 other drainages in Interior Alaska (Testa 1996), but recent browsing intensity in mild winters has been low. Two conclusions are relevant to moose in GMU 13. In the NSA, where moose densities were high, there was a moose-vegetation interaction that appears to have reduced moose productivity relative to that of moose in other parts of the GMU. The absence of better indicators of winter nutritional stress and the importance to ovulation rates of both body condition and forage quality in fall (Gunn and Doney 1975; Testa and Adams 1998) indicate that summer forage may constrain productivity of moose in the NSA more than winter forage.

Among radiocollared moose the phenotypic tradeoff between successful rearing of a calf to fall and subsequent calving and twinning (Tables 7 and 8) also indicates that nutritional constraints are operative in the NSA. In a large sample from Scandinavian populations of moose, negative effects of previous reproduction on pregnancy and ovulation rates were undetectable (Sæther and Haagenrud 1983; Sand 1998) presumably because the populations are kept well below K-carrying capacity by heavy hunting. Population density in red deer (*Cervus elaphus*) on Rhum was positively correlated with the nutritionally driven costs of reproduction (Clutton-Brock and others 1983).

The current rate of calf mortality in the NSA appears higher than that observed by Ballard and others (1991, 0.31 and 0.34 for male and female calves, respectively), although the timing of mortality (almost all in the first 60 days) has been similar (Testa and others 2000*a*). Sightings of brown bears on moose kills in spring are high; this supports the contention that brown bears remain the principal cause of calf mortality in the NSA and probably in the remainder of GMU 13 (Ballard and others 1991). Moose:wolf ratios in fall, calculated from Tables 1 and 5, have shifted substantially between 1994 (92 moose/wolf) and 1999 (<37 moose/wolf) and approached the threshold at which Gasaway and others (1983) suggested that wolves alone could limit moose populations. 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 must be considered an index, rather than an estimate for the entire NSA (Testa and others 2000*b*). Because I made the estimate during the calving season and in an area of high abundance of moose and caribou, the density of bears there may be higher than that in the entire NSA. Assuming little change in numbers of brown bears since 1994, the ratio of adult moose to bears probably is not lower than 25, having declined in the same proportion as the adult moose population (ca. 30%). The combined effects of wolves and bears remain a matter of speculation in an area where caribou also are abundant as alternative prey for part of the year (Gasaway and others 1992). Bears have historically had a greater effect on moose calf survival in GMU 13 than wolves (Ballard and others 1991), and one would expect effects of bears on moose population dynamics to be delayed through persistently poor recruitment more than directly through adult mortality in summer alone. Consequently, the expected trajectory of a moose population preyed upon most heavily by bears should follow a slow decline, rather than a rapid one. The chronically poor calf recruitment is now exacerbated by a recent increase in wolf numbers. The recent decline in calf survival is consistent with heightened summer predation on calves by wolves. The high wolf numbers, however, are expected to increase winter mortality of both young and adult moose and lead to an accelerating decline in moose numbers in the NSA.

Abandonment of the yearling by adult females in May and June lead to heavy yearling mortality due to predation by wolves and brown bears. The absence of even a weak correlation between yearling mass and subsequent mortality indicates that nutritional effects on vulnerability play little role in this phenotypic tradeoff between present and previous reproductive effort in the presence of effective predators. This appears to be an instance of a top-down effect on a life history tradeoff and represents more than a tripling in risk of summer mortality to yearlings when an adult attempts reproduction the following year. Given the high rate of calf mortality, it is likely that reproductive pauses were favored by selection under the conditions of this study (i.e., mild winters and moderate densities). Ballard and others (1991) found higher yearling mortality during winter than was evident in our study, some of it from starvation during a winter of deep snowfall. Nutritional constraints stemming from maternal investment in calf growth might play a larger role under those conditions, but I have no data to test for such a life history tradeoff in this population.

Facultative reduction of reproductive effort in the presence of high predation risk has been supported by models and experimental evidence as an effective strategy to maximize individual reproductive success (Dehn 1994; Oksanen and Lundberg 1995). The models explored here indicate that the reproductive strategies under bottom-up and top-down constraints on moose may interact in ways that can increase the instability of predator prey dynamics. A moose population able to increase under chronically high predation may reach a point at which nutritional constraints actually increase recruitment and survival of adults as a consequence of declining calf production. Similarly, a population being forced from a high population level by increased predation or hunting pressure might increase its calf production and accelerate the decline because of the increased vulnerability of independent yearlings and adult females. The apparent contradiction of the “optimum” evolutionary strategy and the population’s stability results from the fact that the “optimum” strategy under heavy calf predation does not change as nutritional constraints change. However, accurate cues to the degree of predation risk for calves or a physiological mechanism to override the nutritional influence on reproductive effort may be absent for moose.

There were both nutritionally driven and predator-driven life history tradeoffs in the moose studied in the NSA. The interaction of these bottom-up and top-down life history tradeoffs seems mildly antiregulatory. That is, at the relative vulnerabilities estimated here, an increase in bottom-up costs enhances survival of yearlings and adults enough to overcompensate for the loss of productivity due to the bottom-up costs. Relative to more direct ecological effects on population survival and reproductive parameters, the effect of such an interaction may not be detectable. However, because of the antiregulatory nature of the change, subtle effects on the stability of predator-prey interactions cannot be excluded. Moreover, the strength of this interaction may depend on the magnitude of predation-caused mortality and fecundity and on the magnitude of the top-down life history tradeoffs that were held constant in these models. The high rates of summer calf mortality in the study population leaves a small fraction of adult females available to change reproductive status for most of the year, so the increased risks of predation to females with calves have relatively small influence on adult mortality in the present situation. Simulations that increased the effects of winter predation (more wolves) and decreased summer predation (fewer bears) reduced the interaction of the life history tradeoffs. This is reasonable because winter predation occurs after the burden of lactation to individuals has been paid. The interaction is primarily the result of heavy spring mortality of calves, which has feedback effects through the energetic release from lactation burden for adult moose and possible re-adoption of surviving yearlings. Thus, it is possible that in addition to the predation load added to wolf-moose models by summer bear predation, life history interactions involving bear predation could contribute to the instability of a predator-prey equilibrium at high prey densities (Ballard and Van Ballenberghe 1997; Gasaway and others 1992; Messier 1994).

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 has modified harvest regulations in GMU 13 to increase the take of brown bears and wolves in order to increase moose calf survival. An increase in calf survival will be necessary to arrest the decline or increase moose numbers and to offset the increase in the mortality of aging adults. However, it is not clear the Board's actions on either predator species will be sufficient to obtain that increase in calf recruitment, particularly in the face of recent severe winters and high numbers of wolves.

ACKNOWLEDGMENTS

The following Alaska Department of Fish and Game staff participated in these studies and their efforts are greatly appreciated: Earl Becker, Suzan Bowen, Bill Collins, John Crouse, Craig Gardner, Howard Golden, Chris Hundertmark, Jackie Kephart, Enid Keyes, Kiana Koenen, Audrey Magoun, Brian Marston, Mark Masteller, Dennis McAllister, Mike McDonald, Boyd Porter, Jeff Sellinger, Tom Stephenson, Becky Strauch, Brad Scotton, Una Swain, Shelly Szepanski, Bill Taylor, Leigh Tutterow, David Vandenbosch, Kevin White, and Jim Woolington. Volunteers included DVM John Blake and DVM Kimberly Beckman (University of Alaska Fairbanks) and Layne Adams and Kurt Jenkins (National Biological Service). Earl Becker organized the first wolf survey and calculated density estimates. Jay Ver Hoef, Earl Becker, and Bill Taylor organized the moose population estimate in fall 1994. Collaborators Gregg Adams (University of Saskatchewan) and Knut Kielland (University of Alaska Fairbanks) were instrumental in the areas of ultrasonography and vegetation analysis, respectively. Bob Tobey and Brad Scotton generously shared management data and ideas from the GMU 13 area office. Pilots Harley McMahon, Chuck McMahon, Mike Meekin, Bill Wiederkehr, Rick Swisher, Al Lee, Paul Zaczkaoski and, especially, Jerry Lee were essential contributors to this research.

LITERATURE CITED

AGRESTI A. 1990. Categorical Data Analysis. New York: Wiley and Sons. 558pp.

ARDITI R, AND LR GINZBURG. 1989. Coupling in predator-prey dynamics: ratio-dependence. Journal of Theoretical Biology 139:311–326.

BALLARD WB, AND V VAN BALLENBERGHE. 1997. Predator/prey relationships. Pages 247–273 *in* Franzmann AW, Schwartz CC, editors. Ecology and Management of the North American Moose. Washington and London: Smithsonian Institution Press..

———, JS WHITMAN, AND CL GARDNER. 1987. Ecology of an exploited wolf population in southcentral Alaska. Wildlife Monographs 98:51.

———, SD MILLER, AND JS WHITMAN. 1990. Brown and black bear predation on moose in southcentral Alaska. Alces 26:1–8.

———, JS WHITMAN, AND DJ REED. 1991. Population dynamics of moose in southcentral Alaska. Wildlife Monographs 114:49.

BECKER EF, MA SPINDLER, AND TO OSBORNE. 1998. A population estimator based on network sampling of tracks in the snow. Journal of Wildlife Management 62(3).

CLUTTON-BROCK TH, FE GUINNESS, AND SD ALBON. 1983. The costs of reproduction to red deer hinds. Journal of Animal Ecology 52(2):367–383.

COADY JW. 1974. Influence of snow on behavior of moose. Le Naturaliste Canadien 101:417–436.

DEHN MM. 1994. Optimal reproduction under predation risk: consequences for life history and population dynamics in microtine rodents. PhD Thesis. Vancouver, British Columbia, Canada: Simon Fraser University. 90pp.

EBERHARDT LL. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

———, AND DB SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34(2):183–190.

FRANZMANN AW, AND CC SCHWARTZ. 1985. Moose twinning rates: a possible condition assessment. Journal of Wildlife Management 49:394–396.

GASAWAY WC, SD DUBOIS, DJ REED, AND SJ HARBO. 1986. Estimating moose population parameters from aerial surveys. Fairbanks: University of Alaska. Report nr 22. 108pp.

———, RO STEPHENSON, JL DAVIS, PEK SHEPHERD, AND OE BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl.Monogr. 84:50.

———, RD BOERTJE, DV GRANGAARD, DG KELLEYHOUSE, RO STEPHENSON, AND DG LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:59.

GUNN RG, AND JM DONEY. 1975. The interaction of nutrition and body condition at mating on ovulation rate and early embryo mortality in Scottish blackface ewes. Journal of Agricultural Science, Cambridge 85:465–470.

KEECH MA, RT BOWYER, JM VER HOEF, RD BOERTJE, BW DALE, AND TR STEPHENSON. 2000. Life history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64(2):450–462.

MCCULLOUGH DR. 1979. The George Reserve Deer Herd. Ann Arbor: The University of Michigan Press. 271pp.

MESSIER F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75(2):478–488.

MILLER SD. Detection of differences in brown bear density and population composition caused by hunting; 1990. 393–404.

———. 1997. Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Alaska Department of Fish and Game. Fed Aid Wildlife Res. W-24-4. 97pp. Juneau, Alaska USA.

MILLER SD, GC WHITE, RA SELLERS, HV REYNOLDS, JW SCHOEN, K TITUS, VG BARNES, RB SMITH, RR NELSON, WB BALLARD and others. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monographs 133:1–55.

OKSANEN L, AND P LUNDBERG. 1995. Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. Evolutionary Ecology 9:45–56.

PETERSON RO. 1977. Wolf Ecology and Prey Relationships on Isle Royale. Washington, D.C.: U. S. Government Printing Office. 210pp.

POLLOCK KH, SR WINTERSTEIN, CM BUNCK, AND PD CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53(1):7–15.

ROWELL JE, PF FLOOD, CA RUDER, AND RG SASSER. 1989. Pregnancy-specific protein in the plasma of captive muskoxen. Journal of Wildlife Management 53:899–901.

SÆTHER B-E, AND H HAAGENRUD. 1983. Life history of the moose (Alces alces): fecundity rates in relation to age and carcass weight. Journal of Mammalogy 64(2):226–232.

SAND H. 1998. Costs of reproduction in female moose (*Alces alces*) as measured by means of phenotypic correlations. Canadian Journal of Zoology 76(1):187–193.

SARNDAL C, B SWENNSON, AND J WRETMAN. 1992. Model Assisted Survey Sampling. New York: Springer-Verlag. 694pp.

SCHMITT SM, AND WJ DALTON. 1987. Immobilization of moose by carfentanil and xylazine and reversal with naltrexone, a long acting antagonist. Alces 23:195–219.

SKOOG RO. 1968. Ecology of caribou (*Rangifer tarandus granti*) in Alaska. PhD. University of California Berkeley. 699pp.

STEPHENSON TR, JW TESTA, GP ADAMS, RG SASSER, CC SCHWARTZ, AND KJ HUNDERTMARK. 1995. Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. Alces 31:167–172.

TESTA JW. 1996. Population Dynamics of Moose and Predators in Game Management Unit 13. Alaska Department of Fish and Game, Division of Wildlife Conservation. Fed Aid Wildlife Res. Grant W 24-4, Study 1.49. Juneau Alaska USA.

———. 1998. Compensatory response to changes in calf survivorship: management consequences of a reproductive cost in moose. Alces 34(1):107–115.

———, AND GP ADAMS. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammology. 79(4):1345–1354.

———, EF BECKER, AND GR LEE. 2000*a*. Temporal patterns in the survival of twin and single moose calves (*Alces alces*) in southcentral Alaska. Journal of Mammology. 81(1):162–168.

———, WP TAYLOR, AND SD MILLER. 2000*b*. Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Alaska: Alaska Department of Fish and Game. Fed Aid Wildlife Res. Grant W-24-5. Juneau Alaska USA.

VAN BALLENBERGHE V. 1979. Productivity estimates of moose populations: a review and re-evaluation. Proceedings of the North American Moose Conference and Workshop 15:1–18.

WOOD AK, RE SHORT, A-E DARLING, GL DUSEK, RG SASSER, AND CA RUDER. 1986. Serum assays for detecting pregnancy in mule and white-tailed deer. Journal of Wildlife Management 50:684–687.

PREPARED BY:

J. Ward Testa
Wildlife Biologist III

Donald Spalinger
Research Coordinator

APPROVED BY:

____
Wayne L. Regelin, Director
Division of Wildlife Conservation

Steven R. Peterson, Senior Staff Biologist
Division of Wildlife Conservation

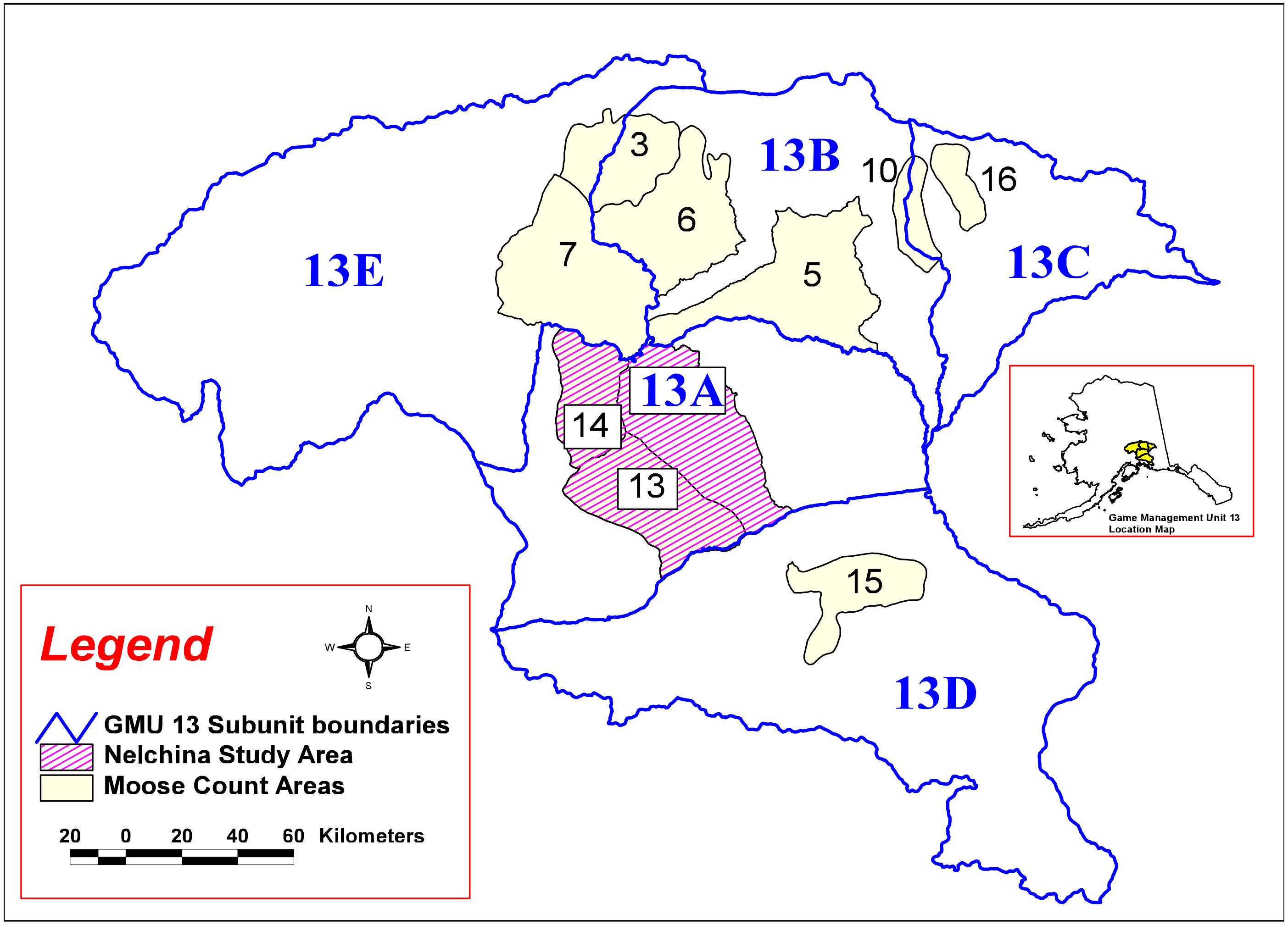
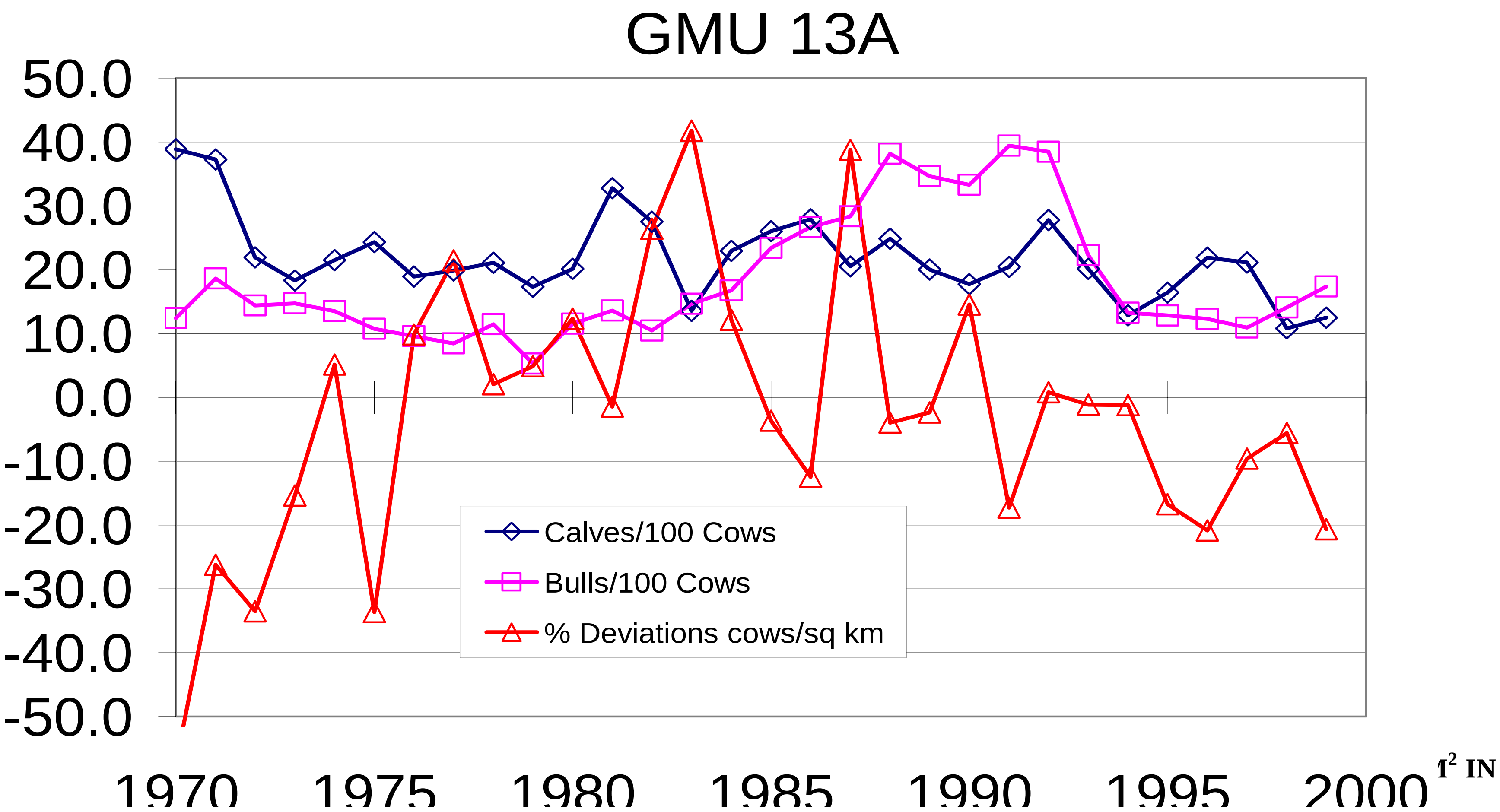


FIGURE 1. GAME MANAGEMENT UNIT 13 IN 5 SUBUNITS (A–E) IN SOUTHCENTRAL ALASKA, WITH TRADITIONALLY SURVEYED TREND COUNT AREAS AND BOUNDARY OF THE NELCHINA STUDY AREA (NSA) IN SUBUNIT 13A.


GMU 13A
50.0
40.0
30.0
20.0
10.0
0.0
-10.0
-20.0
-30.0
-40.0
-50.0
Calves/100 Cows
Bulls/100 Cows
% Deviations cows/sq km
1970
1975
1980
1985
1990
1995
2000
1² IN

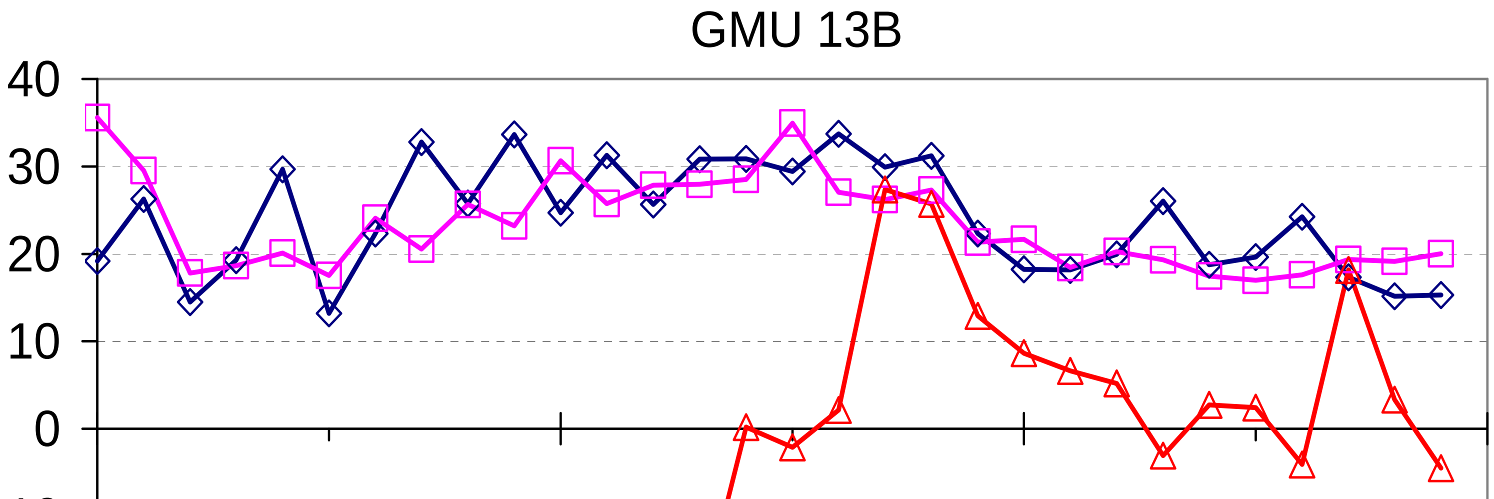

GMU 13B
40
30
20
10
0

Figure 3. Fall composition and annual deviations from the mean index of cow moose/km^2 in GMU 13B from 1970–1999.

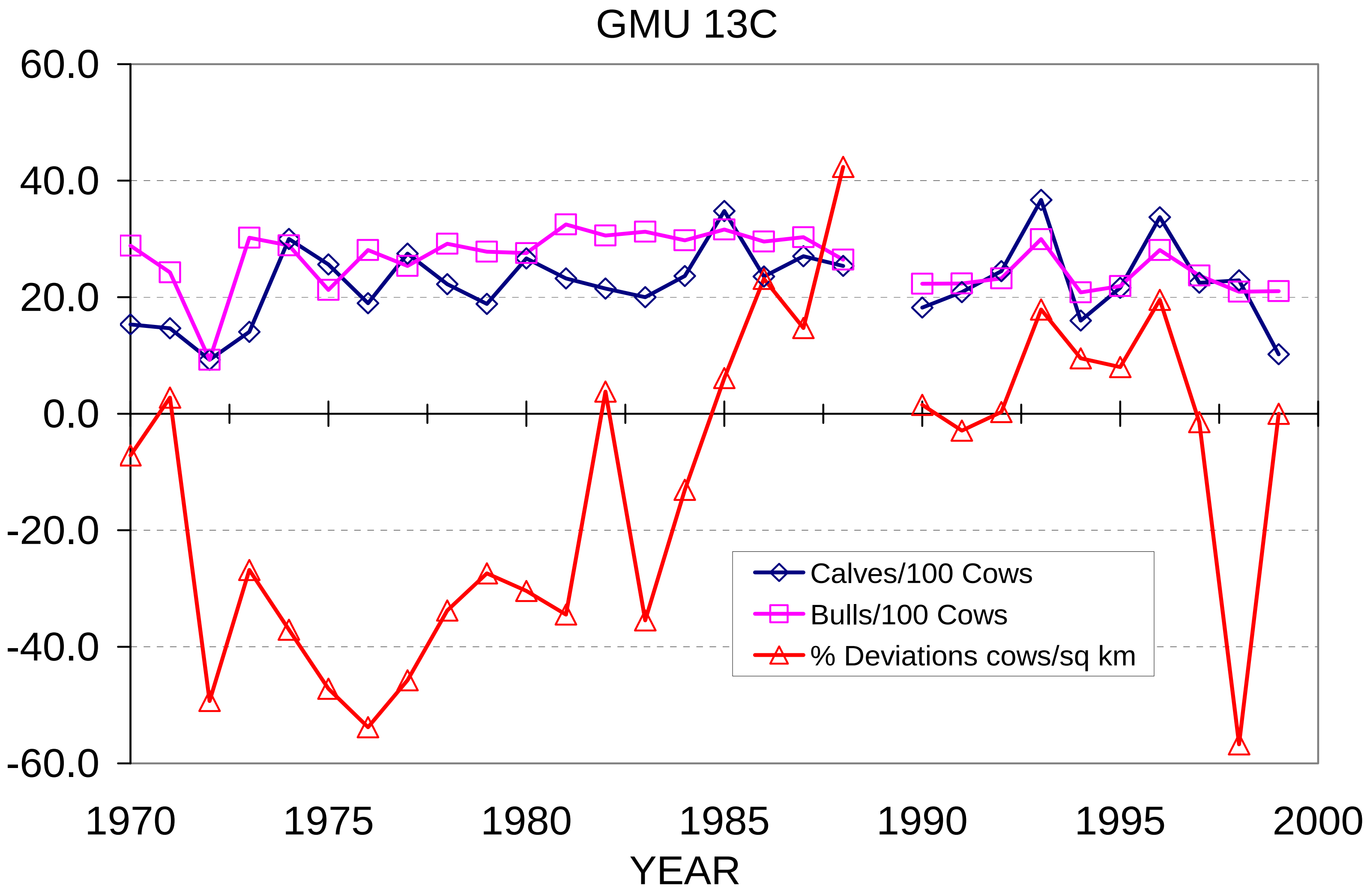


FIGURE 4. FALL COMPOSITION AND DEVIATIONS FROM THE MEAN INDEX VALUE OF COW MOOSE/KM^2 IN UNIT 13C FROM 1970–1999.

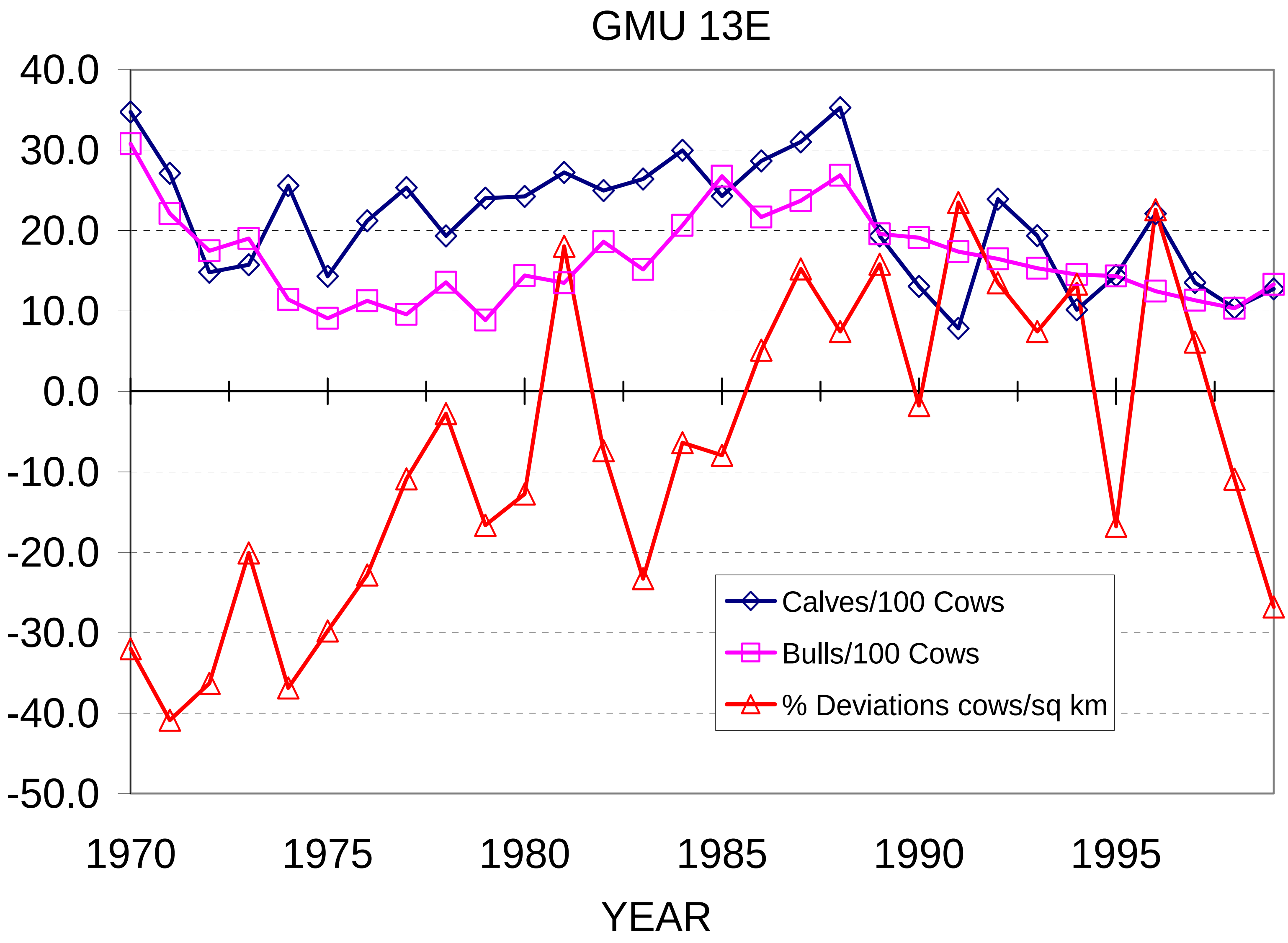


FIGURE 5. FALL COMPOSITION AND DEVIATIONS FROM THE MEAN INDEX VALUE OF COW MOOSE/KM^2 IN GMU 13E FROM 1970–1999. COUNT AREA 7 WAS NOT COUNTED IN 1987-1989 AND 1993–1995.

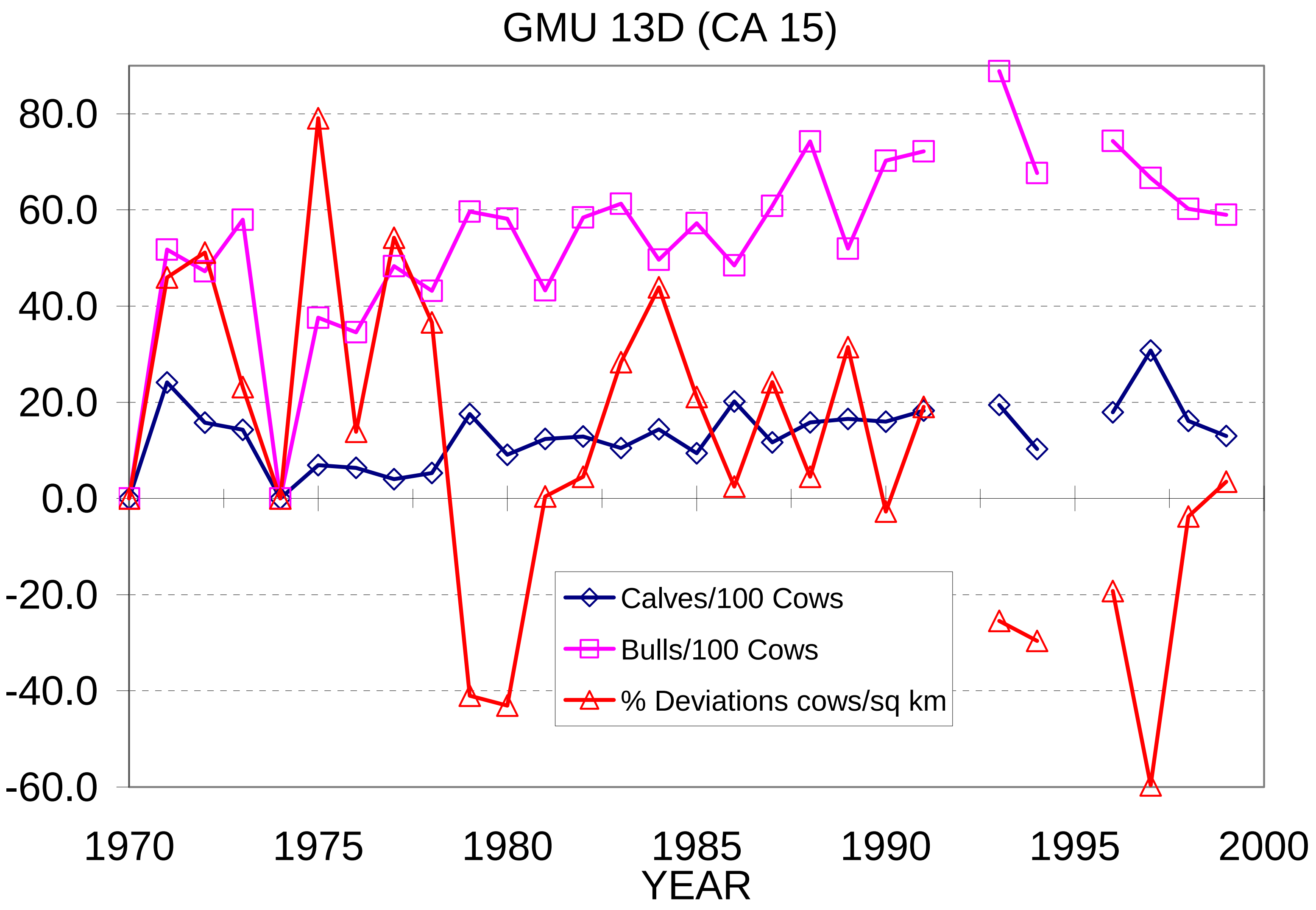


FIGURE 6. FALL COMPOSITION AND DEVIATIONS FROM THE MEAN INDEX VALUE OF COW MOOSE/KM^2 IN UNIT 13D FROM 1970–1999.

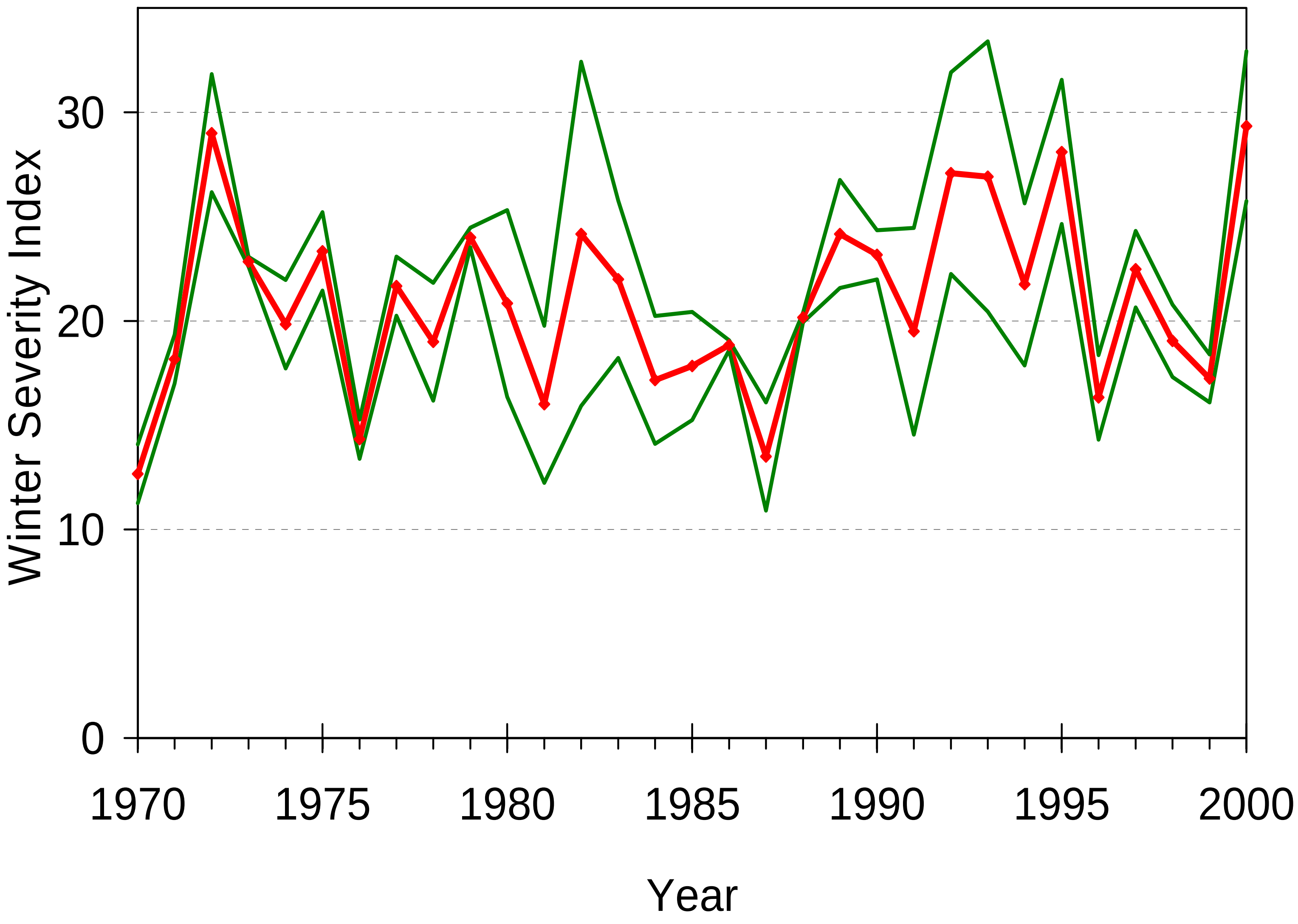


FIGURE 7. WINTER SEVERITY INDEX (± *SD* AMONG SITES) IN NELCHINA STUDY AREA FROM 1970–2000.

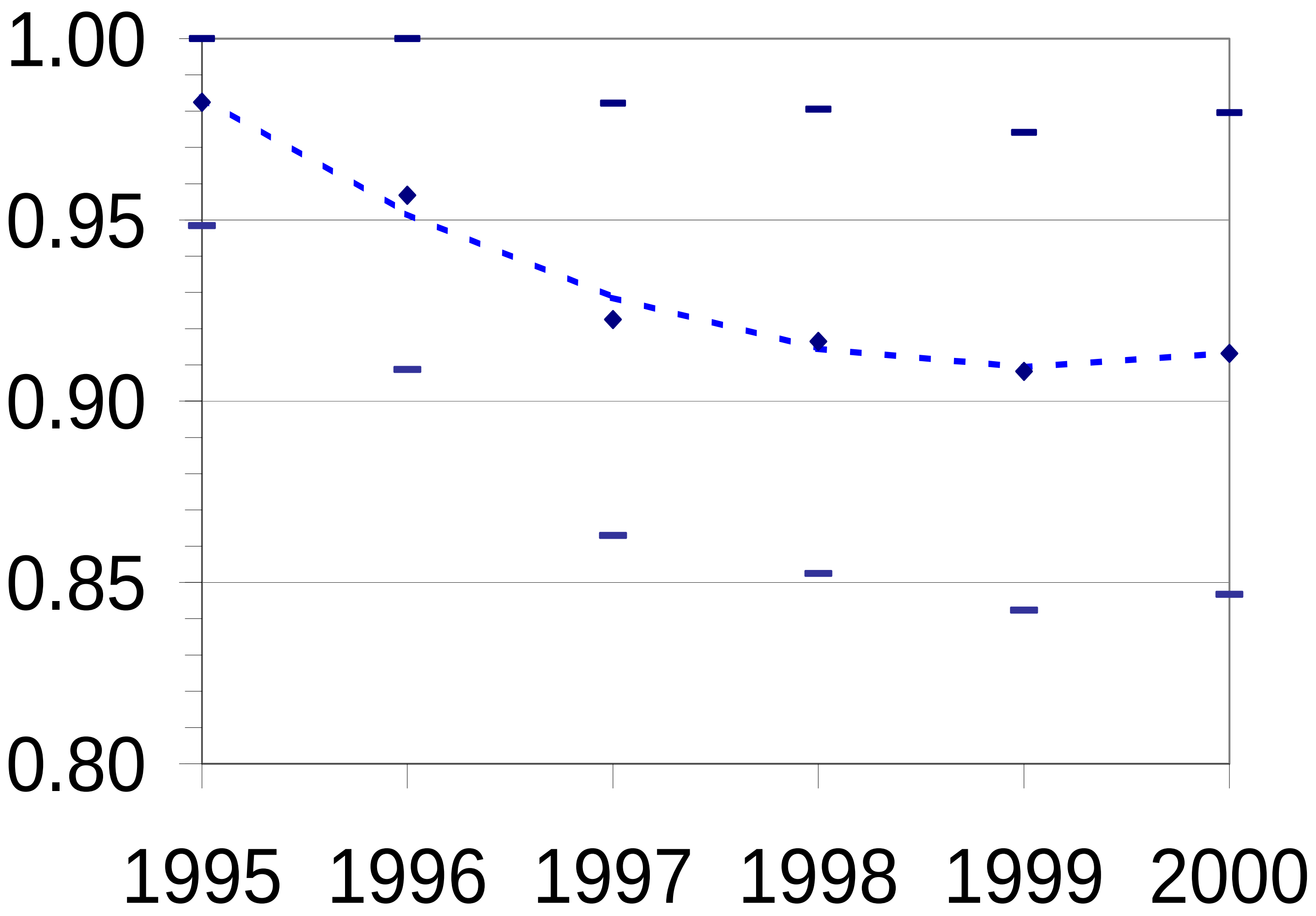
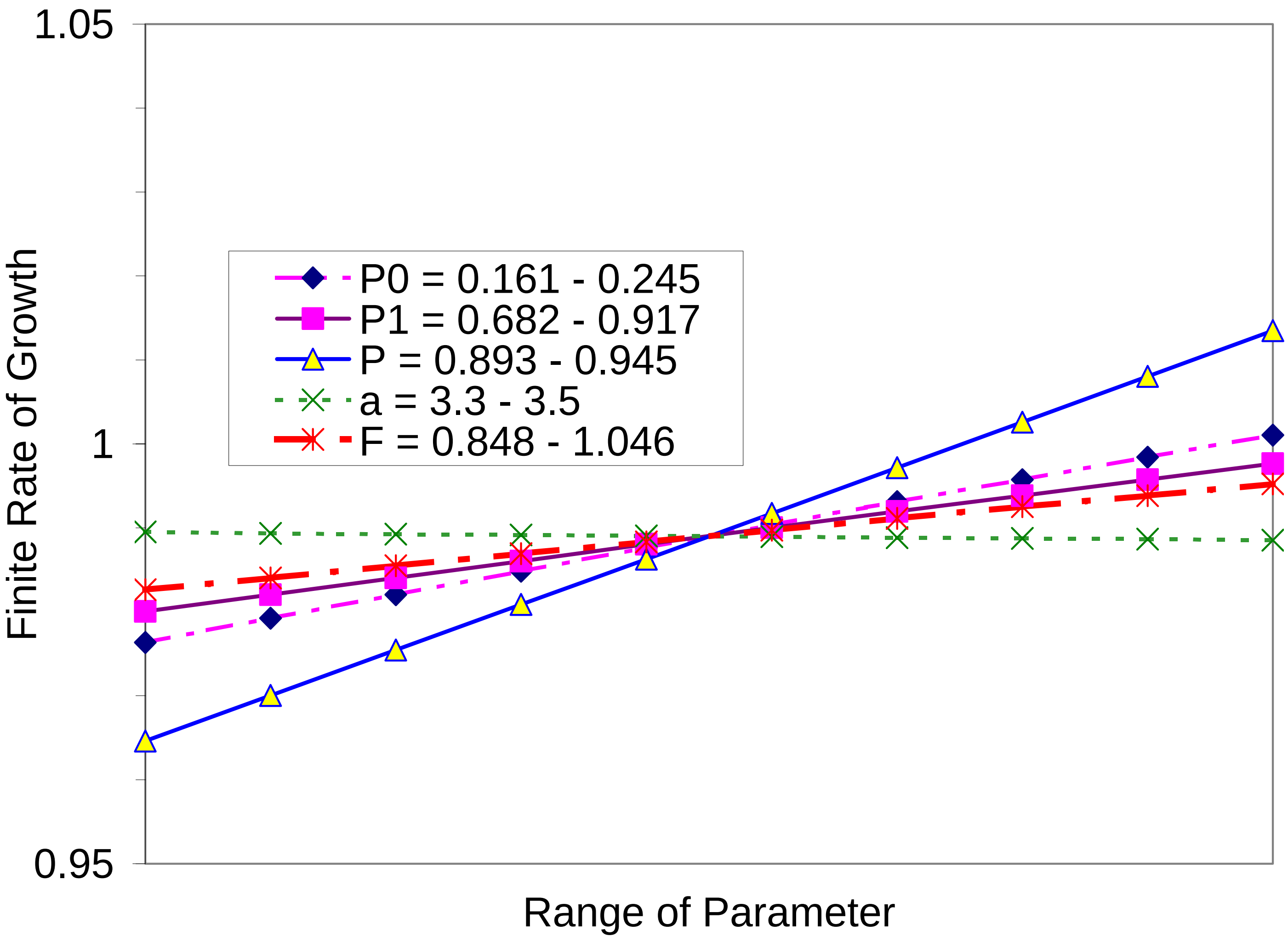
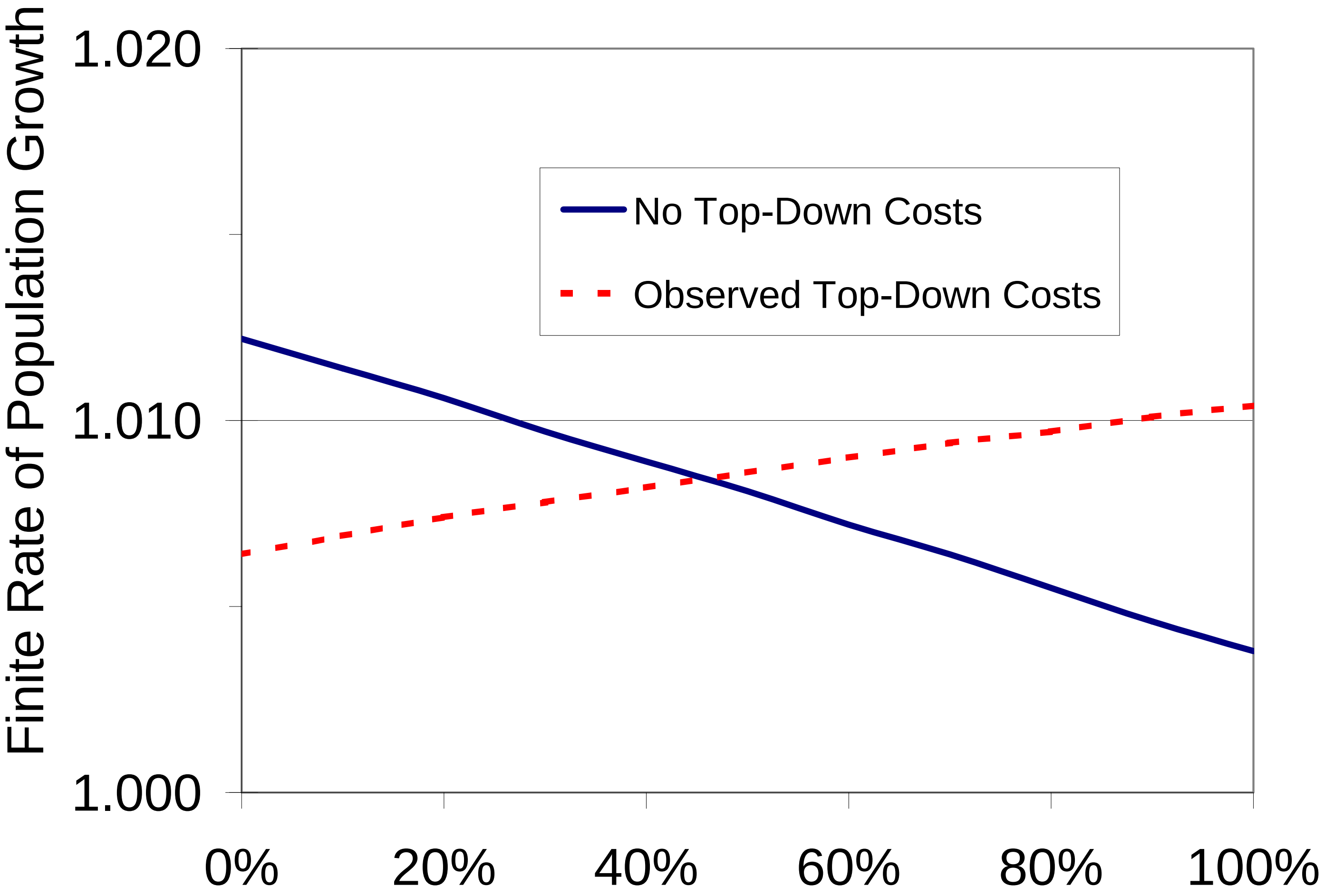


FIGURE 8. ANNUAL SURVIVAL (MAY-APRIL) OF ADULT FEMALE MOOSE IN THE NELCHINA STUDY AREA FROM 1994–2000 WITH FITTED POLYNOMIAL REGRESSION MODEL ($R^2 = 0.98$) AND 95% CONFIDENCE INTERVALS OF THE KAPLAN-MEIER ESTIMATES.



URE 9. SITIVITY OF MODELED POPULATION GROWTH RATE (λ = 0.99) 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).



FIGU
HIST
EXC
CON
RAD

UP LIFE
L THAT
ISKS IS
AMONG

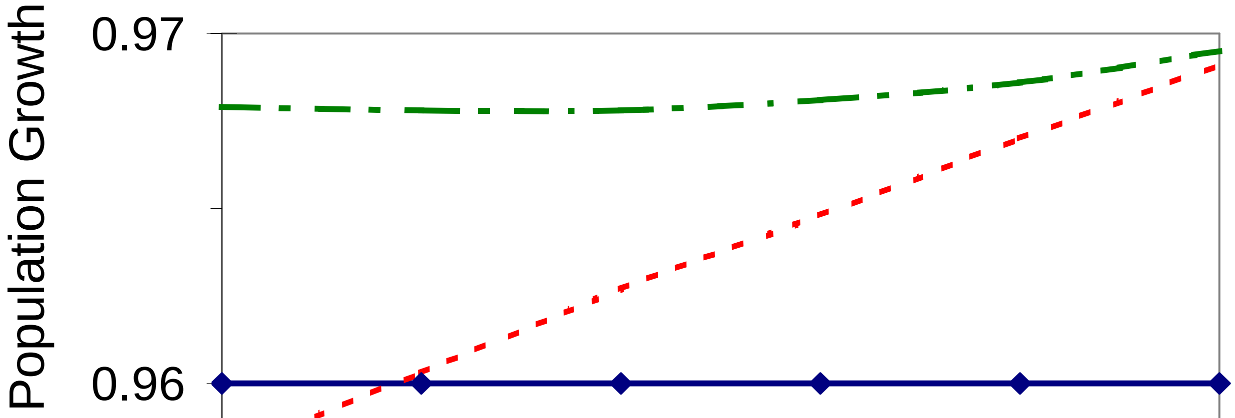


Figure 11. Finite rate of population growth (λ) modeled as a function of bottom-up life history tradeoffs between reproductive effort in successive years. The null model that excludes top-down tradeoffs between reproductive effort and predation risks is contrasted to one that includes the tradeoffs in mortality observed among radiocollared moose in the Nelchina Study Area, Southcentral Alaska, 1994–2000. The null model was modified by reducing the parturition rates and increasing predation mortality in summer and winter to produce a 4% rate of decline at all levels of bottom-up reproductive costs. The first contrasting model altered summer and winter predation rates equally while maintaining the relative vulnerabilities of moose in different reproductive classes. The second model reduced reduced summer (i.e., bear) predation by 40% and increased winter (wolf) predation.

TABLES

Table 1. Results of population estimates of the Nelchina Study Area and trend count surveys in Count Areas 13 and 14 within the Nelchina Study Area (fig. 1) from 1994–99. Standard errors of the population estimates are shown in parentheses. Apparent densities of the trend count surveys (rows 2–4) are minimum estimates, not corrected for moose sightability. Probabilities of sighting in count areas are shown for years in which the number of radiocollared moose seen and those present in the count area were determined (*SE* in parentheses).

	Population Estimates		Count Area Surveys		
Year	Moose/km^2	Cows/km^2	Moose/km^2	Cows/km^2	P(sighting)
1994	0.80 (0.066)	0.60 (0.054)	0.50	0.40	0.69 (0.090)
1995	-	-	0.43	0.32	0.71 (0.074)
1996	-	-	0.37	0.26	0.76 (0.066)
1997	-	-	0.48	0.36	0.83 (0.070)
1998	0.57 (0.042)	0.44 (0.034)	0.60	0.48	-
1999	0.53 (0.043)	0.43 (0.038)	0.64	0.44	0.72 (0.072)

Table 2. 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 1980–1999 (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

Table 3. Mean Winter Severity Indices (WSI) for the subunits of GMU 13 from 1985–2000.

GMS	Stations	WSI
13A	2	21.5
13B	3	27.7
13C	3	26.2
13D	2	26.5
13E	3	29.1

Table 4. Percentage of available twigs (lateral twigs at heights shown, and terminal twigs ≤3 m in height) of feltleaf willow (*Salix alexensis*) (with *SE*'s) that were browsed by moose in two important riparian wintering areas of the Nelchina Study Area, Southcentral Alaska.

Twig Height (m)	Oshetna River						Tyone Creek					
	1995	1996	1997	1998	1999	2000	1995	1996	1997	1998	1999	2000
0.5–1.5	-	9 (11)	10 (10)	13 (9)	-	-	-	4 (5)	5 (5)	7 (8)	-	-
1.5–2.5	-	11 (3)	11 (5)	12 (14)	-	-	-	5 (4)	7 (7)	9 (9)	-	-
Terminal	82 (22)	13 (12)	32 (12)	25 (10)	35 (13)	74 (31)	76 (16)	12 (13)	29 (10)	27 (10)	24 (14)	60 (30)

Table 5. Estimated density and harvest density of wolves (per 1000 km^2) in the Nelchina Study Area. In 1994/95 and 1996/97 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, and is therefore conservative. In 1998–99 and 1999-2000 a minimum density was estimated from packs identified in moose composition and telemetry flights from November-February, with total harvest/1000 km^2 shown.

Winter	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
1998/99			4.5	≥13.1
1999/2000			7.2	≥14.5

Table 6. Rates of parturition and twinning of adult moose (≥4 years) in the Nelchina Study Area, southcentral Alaska (sample sizes in parentheses), 1994–1998.

Year	Parturition Rate (n)	Twinning Rate (n)	Fecundity
1994	63% (40)	9.1% (77)	0.68
1995	86% (58)	12.6% (119)	0.97
1996	86% (68)	14.4% (139)	0.98
1997	87% (59)	21.2% (113)	1.06
1998	78% (52)	24.4% (82)	0.97
1999	90% (48)	18.0% (133)	1.07
2000	76% (54)	16.9% (130)	0.89
Total	82% (379)	16.6% (793)	0.97

Table 7. Logistic regression model predicting parturition rate among radiocollared moose in the Nelchina Study Area, southcentral Alaska, 1994-2000. G^2 and *P*-values are presented for sequential addition of listed variables (1 *df*) to the model.

Variable	Coefficient	SE	G^2	***P***
Intercept	2.879	0.289	-	-
Fall Calf	-1.660	0.296	30.890	0.000
Year 1994	-1.645	0.420	10.697	0.001
Year 2000	-1.292	0.411	9.212	0.002

Table 8. Logistic regression model predicting twinning rate among radiocollared moose in the Nelchina Study Area, southcentral Alaska, 1994-2000. G^2 and *P*-values are presented for sequential addition of listed variables (1 *df*) to the model. The analysis was limited to only those moose that were parturient in consecutive years.

Variable	Coefficient	*SE*	G^2	*P*
Intercept	-3.183	0.589	-	-
Fall Calf	-2.130	0.644	13.704	0.0002
Previous Twins	1.771	0.461	14.875	0.0001

Table 9. Average monthly survival of adult female moose from 1994–2000 in the Nelchina Study Area, Southcentral Alaska.

Month	At Risk	Died	Survival (SE)
5	469	1	1.00 (0.01)
6	452	8	0.98 (0.01)
7	430	5	0.97 (0.01)
8	376	1	0.97 (0.01)
9	384	1	0.96 (0.01)
10	367	2	0.96 (0.01)
11	365	3	0.95 (0.01)
1	411	3	0.94 (0.01)
2	407	1	0.94 (0.01)
3	405	5	0.93 (0.01)
4	428	5	0.92 (0.01)

Table 10. Comparison of survival rates of female moose in the Nelchina Study Area, Southcentral Alaska from 1994–2000, 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)	372	1	1.00 (0.00)	86	0	1.00 (0.00)
5 (12–21)	391	0	1.00 (0.00)	46	0	1.00 (0.00)
5 (22–31)	220	0	1.00 (0.00)	220	0	1.00 (0.00)
6 (1–10)	187	0	1.00 (0.00)	253	5	0.98 (0.01)
6 (11–20)	214	1	0.99 (0.01)	220	1	0.98 (0.01)
6 (21–30)	284	0	0.99 (0.01)	163	1	0.97 (0.01)
7	269	2	0.99 (0.01)	122	3	0.94 (0.02)
8	291	1	0.98 (0.01)	87	0	0.94 (0.02)
9	292	1	0.98 (0.01)	86	0	0.94 (0.02)
10	284	2	0.97 (0.01)	82	0	0.94 (0.02)
11	222	3	0.96 (0.01)	88	0	0.94 (0.02)
1	319	2	0.96 (0.01)	92	1	0.94 (0.02)
2	323	1	0.95 (0.01)	85	0	0.94 (0.02)
3	322	3	0.94 (0.01)	100	2	0.92 (0.02)
4	340	2	0.94 (0.01)	92	3	0.89 (0.03)

Table 11. Average annual survival rates of yearling female moose in the Nelchina Study Area, Southcentral Alaska, 1995–2000.

Month	At Risk	Died	Survival (SE)
All yearlings			
5	47	1	0.98 (0.02)
6	45	4	0.89 (0.05)
7	39	3	0.82 (0.06)
8	35	1	0.80 (0.06)
9–12	34-36	0	0.80 (0.06)
1–4	36-37	0	0.80 (0.06)
Yearlings with mother			
5	33	0	1.00 (0.00)
6	21	1	0.95 (0.05)
7	21	1	0.91 (0.06)
8	18	0	0.91 (0.06)
9–12	18	0	0.91 (0.06)
1–4	19-20	0	0.91 (0.06)
Independent yearlings			
5	13	1	0.92 (0.07)
6	22	3	0.80 (0.09)
7	18	2	0.71 (0.10)
8	17	1	0.67 (0.10)
9–12	15	0	0.67 (0.10)
1–4	15-16	0	0.67 (0.10)

Table 12. Comparisons of mass of female moose calves in April 1995–1999 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 13. 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	393	262	0.33	0.29	0.38
7	114	24	0.26	0.22	0.31
8	91	3	0.25	0.21	0.30
9	87	0	0.25	0.21	0.30
10	92	1	0.25	0.21	0.30
11	92	6	0.24	0.19	0.28
1	96	4	0.23	0.18	0.27
2	92	2	0.22	0.18	0.26
3	90	3	0.21	0.17	0.26
4	82	6	0.20	0.16	0.24