Management and Conservation Article

Managing for Elevated Yield of Moose in Interior Alaska

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ABSTRACT Given recent actions to increase sustained yield of moose (*Alces alces*) in Alaska, USA, we examined factors affecting yield and moose demographics and discussed related management. Prior studies concluded that yield and density of moose remain low in much of Interior Alaska and Yukon, Canada, despite high moose reproductive rates, because of predation from lightly harvested grizzly (*Ursus arctos*) and black bear (*U. americanus*) and wolf (*Canis lupus*) populations. Our study area, Game Management Unit (GMU) 20A, was also in Interior Alaska, but we describe elevated yield and density of moose. Prior to our study, a wolf control program (1976–1982) helped reverse a decline in the moose population. Subsequent to 1975, moose numbers continued a 28-year, 7-fold increase through the initial 8 years of our study ($\lambda_{B1} =$ 1.05 during 1996–2004, peak density = 1,299 moose/1,000 km^2). During these initial 8 hunting seasons, reported harvest was composed primarily of males ($\bar{x} = 88\%$). Total harvest averaged 5% of the prehunt population and 57 moose/1,000 km^2, the highest sustained harvest-density recorded in Interior Alaska for similar-sized areas. In contrast, sustained total harvests of <10 moose/1,000 km^2 existed among low-density, predator-limited moose populations in Interior Alaska (≤417 moose/1,000 km^2). During the final 3 years of our study (2004–2006), moose numbers declined ($\lambda_{B2} = 0.96$) as intended using liberal harvests of female and male moose ($\bar{x} = 47\%$) that averaged 7% of the prehunt population and 97 moose/1,000 km^2. We intentionally reduced high densities in the central half of GMU 20A (up to 1,741 moose/1,000 km^2 in Nov) because moose were reproducing at the lowest rate measured among wild, noninsular North American populations. Calf survival was uniquely high in GMU 20A compared with 7 similar radiocollaring studies in Alaska and Yukon. Low predation was the proximate factor that allowed moose in GMU 20A to increase in density and sustain elevated yields. Bears killed only 9% of the modeled postcalving moose population annually in GMU 20A during 1996–2004, in contrast to 18–27% in 3 studies of low-density moose populations. Thus, outside GMU 20A, higher bear predation rates can create challenges for those desiring rapid increases in sustained yield of moose. Wolves killed 8–15% of the 4 postcalving moose populations annually (10% in GMU 20A), hunters killed 2–6%, and other factors killed 1–6%. Annually during the increase phase in GMU 20A, calf moose constituted 75% of the predator-killed moose and predators killed 4 times more moose than hunters killed. Wolf predation on calves remained largely additive at the high moose densities studied in GMU 20A. Sustainable harvest-densities of moose can be increased several-fold in most areas of Interior Alaska where moose density and moose:predator ratios are lower than in GMU 20A and nutritional status is higher. Steps include 1) reducing predation sufficient to allow the moose population to grow, and 2) initiating harvest of female moose to halt population growth and maximize harvest after density-dependent moose nutritional indices reach or approach the thresholds we previously published. (JOURNAL OF WILDLIFE MANAGEMENT 73(3):314–327; 2009)

Pursuant to 1994 legislation, the Alaska Board of Game selected areas for high or higher harvests of moose (*Alces alces*) and provided respective regulations (including predator control) to achieve and maintain elevated yield of moose. We define yield of moose as total estimated harvest among years. By 2006, state regulations specified that yield of moose was a priority use in 39% of the state (additional lands were specified but were excluded from this calculation because of status as federal parks, preserves, or refuges). During 2004–2006 the Alaska Board of Game passed implementation plans to reduce wolf (*Canis lupus*), grizzly (*Ursus arctos*), and black bear (*U. americanus*) predation in 9% of the state to increase sustained yield of moose.

One role of wildlife biologists in this regulatory process was to explain why sustainable yields differ among areas. Gasaway et al. (1992) reviewed yields and densities of moose in 31 moose populations in Alaska, USA, and Yukon, Canada. Gasaway et al. (1992) reported low sustainable yields of <10 moose/1,000 km^2 from low-density, predator-limited moose populations (≤417 moose/1,000 km^2) in Interior Alaska. In contrast, yields temporarily increased to >100 moose/1,000

km^2 in portions of South-central Alaska, for example, within and adjacent to settlements adjoining Alaska's largest population center, Anchorage, and on the Kenai Peninsula prior to and shortly after reestablishment of wolves. Gasaway et al. (1992) examined factors limiting moose at low densities and concluded that combined predation by bears and wolves kept moose densities and yields low where predators were lightly harvested. In cases where only wolves, or only bears, preyed on moose, moose reached high densities. Following multiyear experiments that substantially reduced predation, moose density increased (Gasaway et al. 1983, Larsen and Ward 1995, Boertje et al. 1996, Hayes et al. 2003, Keech 2005). Following 1-year experiments that substantially reduced predation, moose calf survival increased (Ballard and Miller 1990, Boertje et al. 1995).

Two case histories in our study area, Game Management Unit (GMU) 20A in central Interior Alaska, documented the prolonged increase in moose numbers from 183 to 1,020 moose/1,000 km^2 during early winter 1976–1994 and the role of 2 state wolf control programs (1976–1982 and 1993–1994; Gasaway et al. 1983, Boertje et al. 1996). The moose population in GMU 20A was uniquely poised to respond to wolf control in 1976, in part because of disproportionately low

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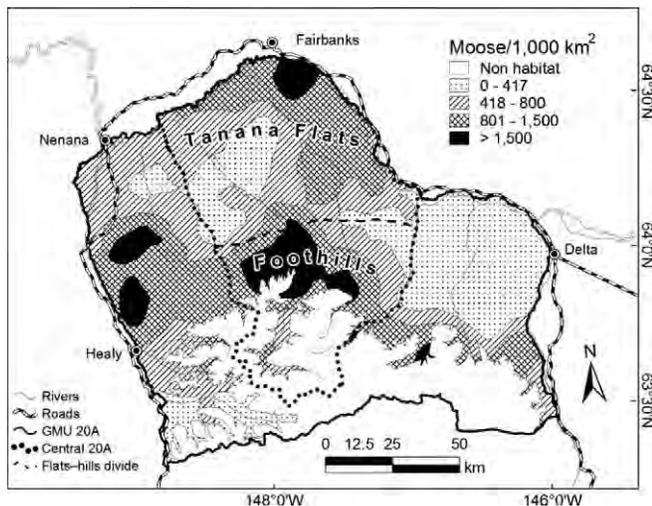
Figure 1. Distribution of moose densities in Game Management Unit (GMU) 20A and the central study area, Alaska, USA, November 1999–2003. We analyzed geospatial survey data using ordinary kriging, Geostatistical Analyst extension for ArcMap version 9.3.

moose densities and high wolf densities following the precipitous decline in moose numbers during 1965–1975 (Boertje and Stephenson 1992). The decline in moose densities was initiated by adverse weather during winters 1965–1967 and was sustained by predation, additional adverse weather (winters 1970–1971 and 1974–1975), and 3 years of ill-timed, excessive harvests of female moose (1972–1974; Gasaway et al. 1983). During the 1976–1982 wolf control program, moose calf, yearling, and adult survival increased simultaneously, which indicated wolf predation limited the moose population prior to wolf control (Gasaway et al. 1983).

After moose reached high densities, Boertje et al. (2007) ranked moose nutritional status in GMU 20A (1997–2005) as the lowest among 14 Alaska sites. Boertje et al. (2007) used these data to justify liberal harvests of female moose ($\geq 2.0\%$ of prehunt moose no.), which began in 2004 to slowly decrease the population and elevate yield. Young and Boertje (2004, 2008) and Young et al. (2006) discussed regulatory, social, and logistical challenges pertinent to increasing harvest of females and calves and maintaining male:female ratios in GMU 20A.

Our objectives were to 1) report and model empirical data on density and yield of moose, age-specific reproduction, and causes and rates of mortality in GMU 20A; 2) test whether wolf predation was similarly additive at the low and high moose densities studied; 3) contrast yield and demographic data from the high-density GMU 20A moose population with similar data from other moose–bear–wolf systems in Interior Alaska and Yukon; 4) discuss the pros and cons of managing for elevated yield; 5) describe how moose nutritional status and predation influenced management; and 6) identify the unique factors that contributed to high yields in GMU 20A.

STUDY AREA

Seasonal trails, waterways, and remote airstrips provided access to the 13,044 km^2 of moose habitat in GMU 20A in central Interior Alaska; <5% of the study area was accessible by road (Fig. 1). We defined moose habitat as all area, exclusive of large lakes, below the upper limits of vegetation used by moose. Human settlements were restricted to the perimeter of the area and totaled 86,200 people with 96% in the Fairbanks area (U.S. Census Bureau 2000). Gasaway et al. (1983) and Boertje et al. (1996) described the geography and vegetation of GMU 20A and the density and interaction of moose, caribou (*Rangifer tarandus*), and wolves during 1960–1994. During 1996–2007, we restricted radiocollaring of moose to the central half of GMU 20A (6,730 km^2 of moose habitat; Fig. 1). We subdivided this central area into the Alaska Range foothills and the Tanana Flats (Fig. 1).

METHODS

Estimating Moose Density and Composition of the Population

During early winter (late Oct–early Dec) 1996–1998, we used aerial surveys based on stratified random sampling techniques to estimate moose numbers and composition ratios in GMU 20A (Gasaway et al. 1983, 1986). We sampled from the entire 13,044 km^2 of moose habitat each year using 4 strata (high and low moose density in the foothills and flats). In 1996, we surveyed 102 of 402 sample units (about 32 km^2 each) at the standard search intensity of 1.5–2.3 minutes/km^2 and conducted 38 intensive searches (4.6–5.8 min/km^2) in portions of sample units to derive an observed sightability correction factor (SCF_o; Gasaway et al. 1986). We surveyed 27 units in 1997 and 40 units in 1998 at standard search intensity and applied the 1996 SCF_o and associated variance to estimate observable moose and 90% confidence intervals (Gasaway et al. 1986).

During early winter 1999–2001 and 2003–2006, we used a geospatial population estimation (GSPE) technique to estimate moose numbers and composition ratios in the 13,044 km^2 using 2 strata. We updated the stratification during 2003–2006 by using the prior years' survey data. The GSPE technique is a finite population version of block kriging. Ver Hoef (2008) provided the calculations used to derive an estimate and described the advantages compared with classical stratified random sampling. Calculating a GSPE population or composition ratio estimate involves measuring spatial correlation among samples, modeling that relationship as a function of distance, and using the model to predict population density or ratios and associated variances. Field methodology and descriptions of the spatial theory and data analysis are detailed in an operations manual (Kellie and DeLong 2006). A user's software manual provides steps for data entry, data management, and the planning of GSPE surveys (DeLong 2006).

We defined sample units (14 km^2) for GSPE surveys by 2 minutes of latitude and 5 minutes of longitude using a pilot-controlled global positioning device. In those units with 100% moose habitat, our search intensity averaged 3.0 minutes/km^2. Of 987 sample units, we surveyed 86 in 1999, 114 in 2000, 78 in 2001, 112 in 2003, 129 in 2004, 123 in

2005, and 115 in 2006 and applied a composite SCF of 1.21 (SE = 0.067) to estimate total moose numbers and 90% confidence intervals.

To estimate the composite SCF, we used data from 69 radiocollared moose in survey units during the 2003–2006 population surveys (Gasaway et al. 1986). While surveying, the pilot–observer teams did not know whether a radiocollared moose was in a survey unit, but the team radiotracked immediately after surveying a unit to estimate the SCF. We calculated the proportion of radiocollared moose observed during surveys ($\hat{p}_{\text{seen}}$) as the number of radiocollared moose seen in survey areas divided by the number of radiocollared moose in survey areas (n_{rc}). We estimated variance (V) of $\hat{p}_{\text{seen}}$ using Cochran (1977) as

$$\hat{V}(\hat{p}_{\text{seen}}) = \frac{\hat{p}_{\text{seen}}(1 - \hat{p}_{\text{seen}})}{n_{\text{rc}} - 1}$$

We calculated the SCF as

$$\text{SCF} = 1/\hat{p}_{\text{seen}}$$

We used the delta method (Seber 1982) to approximate $V(\text{SCF})$ as

$$\hat{V}(\text{SCF}) = \hat{V}(\hat{p}_{\text{seen}})/\hat{p}_{\text{seen}}^4$$

To estimate moose composition during the 1996–2006 population surveys, we circled each group of moose or single moose and classified moose as calves, yearling males, older males, and females. We calculated male:100 female ratios using moose older than calves. Calves had short faces and smaller body sizes. Yearling males had individual antler widths $\leq 1.3 \times$ the head width and antlers (spikes, 2- and 3-pointed poles, and paddles) had no brow palm development. We confirmed these criteria by observing known-age radiocollared 15-month-old males ($n = 51$) and 27-month-old males ($n = 31$) in GMU 20A in 2007 and 2008.

Moose Capture and Age Determination

Keech et al. (2000) described methods for capturing and monitoring newborn calves <6 days old. Boertje et al. (2007) described methods for capturing older moose. Capture-induced mortalities totaled 2 adult females, 8 newborns, and 10 9-month-old calves termed short-yearlings. We ultimately identified short-yearlings by the absence of adult incisors. We successfully radiocollared 83 newborns (1996–1997), 47 4-month-old calves (2006), 350 short-yearlings (1997–2007), 12 yearlings (1997–2006), and 277 older moose (1996–2007); 210 (76%) of the older moose were recaptures to replace aging radiocollars (Telonics, Mesa, AZ). Radiocollars had mortality switches that doubled the pulse rate to 114 beats/minute after being motionless for 1.5 hours (newborn collars) or 5.5 hours (remaining collars). We divided radiocollar samples equally between the Alaska Range foothills and Tanana Flats portions of the central study area. Males composed 40% of the sample of newborns, 49% of the 4-month-olds, 36% of the short-yearlings, 58% of the yearlings, and 8% of the older moose.

We knew adult ages on all but 67 females because we initially collared most 1- to 11-year-old moose as short-yearlings or yearlings. We based unknown ages on counts of cementum annuli (Gasaway et al. 1978) in canine teeth sent to Matson's Laboratory, Milltown, Montana, USA. We also collected canines from 25 known-age females (≤ 9 yr of age) that died from various causes. G. Matson examined these 25 canines to test accuracy of age estimation without prior knowledge of ages and with an assumed 1 June birth date. We conducted all aspects of research in accordance with acceptable methods for field studies adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998, Alaska Department of Fish and Game Protocol no. 04-003).

Estimating Annual Moose Reproduction, Survival, and Mortality

We estimated reproductive and mortality rates using radiocollared moose. Staff also flew transect-based, twinning surveys independent of radiocollared moose for 34 years during 1960–2007 in GMU 20A (Boertje et al. 2007). We radiotracked moose during March 1996–June 2007 at 24-hour (1996–1998) or 48-hour (1999–2007) intervals during the calving season, 2–4 times monthly until complete snow cover, and 1–2 times monthly during the period of snow cover.

Boertje et al. (2007) described methods for estimating moose reproductive rates from aerial surveys during 11 May through mid-June. Parturition rate (p) was the proportion of radiocollared females that gave birth, and twinning rate (t) was the proportion of producing females that gave birth to twins. Moose production rate (no. of calves born/F/yr) equaled $p \times (1 + t)$. To estimate production rates of females ≥ 36 months of age in GMU 20A, we weighted age-specific production rates as follows: 12.6% of the females in the precalving (10 May) population were 36 months old, 12.0% were 48 months old, and 75.4% were older females.

We derived composition of the precalving female population based on the average early winter composition from aerial population estimates (1996–2004), average age- and sex-specific survival rates, and a 50:50 sex ratio at 9–12 months of age. We determined the 50:50 sex ratio while darting short-yearlings ($n = 408$) in late winter 2000–2003 and 2007–2008. We distinguished female calves using the white vulval patch (Mitchell 1970) and lack of antler development. From a helicopter, we saw no diagnostic vulva patch or antler development on $\leq 5\%$ of calves; we darted these calves to fully evaluate the sex ratio. Survival rates differed among males and females after 12 months of age, so we calculated the number of yearling females in mid-November surveys based on differential survival and harvest rates of 12- to 18.5-month-old males and females. We calculated the number of 24-month-old females based on number of yearling females in November and the survival rate of radiocollared females 18.5–24 months of age. We then calculated the number of 36- and 48-month-old females based on the high annual survival rate of 24- to 48-month-old females.

Within each age-class of radiocollared females, we estimated production rate and 95% central credibility

Table 1. Moose population size and composition, total harvests, and harvest rates (%) in Game Management Unit 20A (13,044 km² of moose habitat), Alaska, USA, 1996–2006.

Sep–Dec	Nov population		% F ≥ 17 months of age	% M ≥ 17 months of age	% calves	% yearling M	No. M/100 F excluding calves	Total moose counted	Total no. M harvested[a]	Total no. F harvested[a]	Total prehunt harvest rate[b]
	Size	SE									
1996	11,532	885.4	55.5	21.5	23.0	6.8	39	3,343	736	73	6.5
1997	13,250	1,974.9	59.6	19.8	20.5	8.5	33	1,037	757	72	5.8
1998	11,414	1,343.9	61.6	19.1	19.3	5.7	31	1,268	740	84	6.7
1999	13,721	1,407.7	64.6	15.4	21.0	4.4	24	965	811	1	5.6
2000	13,565	1,902.8	64.8	14.4	21.2	3.4	22	1,377	652	84	5.1
2001	13,927	1,477.9	65.4	16.9	17.3	6.1	26	887	653	85	5.0
2002	No data	No data	No data	No data	No data	No data	No data	No data	437	138	3.5[c]
2003	17,768	1,702.0	62.3	19.9	17.1	7.1	32	1,483	416	191	3.3
2004	16,415	1,716.4	58.5	20.5	21.1	6.3	35	1,922	517	668	6.7
2005	16,151	1,704.5	59.6	22.5	18.1	5.5	38	1,684	596	761	7.7
2006	15,454	1,729.8	58.9	21.1	20.2	6.7	36	1,536	670	592[d]	7.5

[a] We estimated total harvest as reported harvest × 1.20 based on returns of radiocollars.

[b] We calculated prehunt harvest rate as [total harvest/(Nov population size + total kill by hunters)] × 100. We estimated total kill by hunters as reported harvest × 1.35 to account for unreported harvest and wounding loss, based on fate of radiocollared moose.

[c] We based prehunt total harvest rate during 2002 on average population size (15,848) during 2001 and 2003.

[d] A small proportion of harvest of F moose occurred during Jan–Feb of the following year.

intervals using Bayesian methods (Carlin and Louis 2000). We modeled observed production data (F with 0, 1, and 2 calves) as a multinomial distribution using WinBUGS software (Lunn et al. 2000), which implements Markov Chain Monte-Carlo techniques. We used a diffuse (non-informative) Dirichlet distribution as the prior for probability parameters of the multinomial distribution. We ran multiple chains (using a range of initial values) for 1 million iterations to simulate posterior distributions, eliminated the first 50,000 iterations for burn-in, and performed diagnostic tests to evaluate convergence. We verified convergence by examining run histories, autocorrelation functions for the simulated values, and the Gelman-Rubin convergence statistic, as modified by Brooks and Gelman (1998).

We estimated age- and sex-specific survival and mortality rates for moose using Kaplan–Meier staggered-entry design for telemetry studies (Pollock et al. 1989). We censored moose that died from human-related causes. We assigned causes of mortality to the respective mortality rates using proportions of radiocollared calves, yearlings, and adults that died during March 1996–April 2007.

We usually accessed mortality sites with a helicopter within 2–24 hours of locating a collar with a doubled pulse rate. To determine cause of death, we examined the site and any remains. Hemorrhaging associated with external puncture wounds, blood (noncoagulated) on collars or nearby snow or vegetation, or blood on remnants of hide served as evidence of a violent death. In these cases scats, tracks, hair, wounding patterns, other signs, and season of kill (bears hibernating in winter) served to identify the predator involved. Based on observations of bears and wolves killing collared moose, bears often scraped up portions of the tundra mat and buried the collar with pieces of bone and hide. In contrast, wolves often chewed the collar extensively and carried the bloody collar at least several meters from the kill site. During 2001–2007, K. Beckmen, Alaska Department of Fish and Game veterinarian,

necropsied 9 moose that died from causes unrelated to predation, harvest, or accidents.

Estimating Yield, Harvest Rates, and Total Kill by Hunters

Yield included total harvest (reported and estimated unreported) among years, but not wounding loss. Hunters reported harvest using mandatory harvest reports. Hunters received 1 or 2 reminder letters and usually telephone calls if we did not receive timely harvest reports. We estimated yield as 1.20 (55/46) times the reported harvest; 55 radiocollared moose were harvested but only 46 radiocollared moose were reported harvested ($n = 43$) or assumed to be reported ($n = 3$ unknown hunters). Evidence indicated that 9 radiocollared moose were shot illegally, so we presumed the hunters (unknown) did not report the harvest. Among 12 total radiocollared moose presumed shot by unknown hunters, we found 10 radiocollars discarded afield by hunters. We assumed 2 radiocollars ≤30 months old disappeared as a result of hunters because this disappearance was unprecedented and occurred during the hunting season.

We calculated harvest rates based on prehunt numbers as follows: (total harvest)/(Nov population size + total kill of moose by hunters). We estimated total kill by hunters (total harvest and wounding loss) to be 1.35 (62/46) times the reported harvest, based on 46 radiocollared moose reported harvested or assumed to be reported, 9 radiocollared moose harvested but likely unreported, and 7 radiocollared moose that died from gunshot wounds but were not harvested.

Modeling of Moose Population during Increase Phase, 1996–2004

To derive a conceptual, deterministic annual model of moose population dynamics in GMU 20A, we combined averages of annual estimates of population size, composition, and human-caused mortality from all of GMU 20A (Table 1) with telemetry-derived, age-specific reproductive and mortality rates from central GMU 20A. We assumed

birth and death rates and rates of growth were similar throughout GMU 20A during our study, because moose remained at proportionately high densities in central GMU 20A relative to the remainder of GMU 20A since studies began in the 1970s (Gasaway et al. 1983; Fig. 1). We used a Microsoft® Office Excel 2003® (Microsoft, Redmond, WA) spreadsheet to run the model. We used average aerial survey and harvest data from March 1996 to December 2004 but excluded the high harvest from 2004.

The 1-year model began with a precalving population derived from the average early winter population surveys minus overwinter mortality. We summed the precalving population and all calves born in the ensuing few weeks to calculate a postcalving population. Mortality on the postcalving population began after all calves were born. We calculated the ensuing 1-year mortality (no. dying and rates) based on this conceptual postcalving population, the peak in annual population size. We chose this modeling approach because several prior studies used a similar approach and we compare results among these studies (Larsen et al. 1989, Gasaway et al. 1992, Keech 2005).

Estimating Rate of Population Growth
We derived the annual finite rate of increase (λ) from the 1-year model as

$$\lambda = e^r$$

where

$r = (\ln P_2 - \ln P_1)$
P_1 = estimate of precalving population in year 1
P_2 = estimate of precalving population in year 2

To evaluate λ independent of our deterministic model, we estimated λ_{B1} and the associated 90% central credibility interval from 8 estimates of moose population size during the increase phase, 1996–2004. We also estimated λ_{B2} from 4 estimates of moose population size during the decline phase, 2003–2006. We used Bayesian methods and a 3-part hierarchical regression model following Ver Hoef (1996), except we performed a full Bayesian analysis using non-informative priors on all parameters. We also replaced the linear trend with a multiplicative trend incorporating the yearly change parameter λ. We used WinBUGS software to run the model. Run lengths, burn-in, and convergence diagnostics were the same as described for estimating moose production rates and associated credibility intervals.

Testing the Nature of Predation
To directly test whether wolf predation had a similar additive component at low and high moose density in GMU 20A, we analyzed early winter data from the 1970s (Gasaway et al. 1983) and 1990s (Boertje et al. 1996) wolf control experiments. We first analyzed data from each study independently using PROC GLM (Littell et al. 1991) in SAS® (SAS Institute, Cary, NC). Calves/100 females $\geq$29 months old was the response variable, and number of wolves was the explanatory variable. We then combined data from the 2 studies and performed an analysis of covariance (ANCOVA) using PROC GLM with study period (1970s

and 1990s) added as a second explanatory variable. This analysis required first testing for heterogeneity of slopes between study periods and then testing for differences in y-intercepts (Littell et al. 1991). We weighted linear models to account for unequal variances in the response variable; we based weights on numbers of females $\geq$29 months old observed in the respective surveys. To estimate number of females $\geq$29 months old, we subtracted the number of yearling males from the number of females $\geq$17 months old (Gasaway et al. 1983). We calculated exact 95% confidence intervals for calves/100 females $\geq$29 months old using the epitools package in R (R Foundation, Vienna, Austria).

To address normality and variance assumptions required for general linear models, we developed a Bayesian ANCOVA model to obtain posterior probability distributions for differences between the 1970s and 1990s slopes and y-intercepts. We modeled number of calves (successes) per number of females $\geq$29 months old (trials) as a binomial random variable following procedures previously described for Bayesian models, except we used 100,000 iterations with 10,000 for burn-in.

To test for differences in predation rates on calf moose by wolves, black bears, and grizzly bears for one sample of calves in GMU 20A, we followed Scott and Seber (1983). To test for differences in bear predation rates on calf moose between study areas, we used the chi-square test for independent samples (Cochran 1977).

RESULTS

Moose Population Rate of Growth and Density for GMU 20A, 1996–2006
From 8 early winter estimates of population size during 1996–2004 (Table 1), we estimated a multiplicative trend where λ_{B1} equaled 1.05 (90% central credibility interval = 1.029–1.072). Based on this trendline, density increased from 872 moose/1,000 km^2 (90% central credibility interval = 791–957) in 1996 to 1,299 moose/1,000 km^2 (90% central credibility interval = 1,155–1,436) in 2004. During 2003–2006, moose population estimates declined (λ_{B2} = 0.96; 90% central credibility interval = 0.883–1.029), as intended using liberal harvests of female moose (Table 1). Based on this trendline, moose density declined to 1,175 moose/1,000 km^2 (90% central credibility interval = 1,004–1,342) in 2006.

Moose were more concentrated in our central study area compared with the remainder of GMU 20A (Fig. 1). We estimated peak November density in the central study area as 1,741 moose/1,000 km^2 in 2004 (1,299 × 0.67 × 2), because 67% of the GMU 20A moose lived in the central 50% of GMU 20A during our most intensive survey in November 1996.

During spring and summer each year, we estimated moose concentrated in the Tanana Flats portion of the central study area (4,680 km^2) at 1.85 times the November density (Fig. 1). To estimate this concentrated density, we first estimated a spring migration rate from the foothills by plotting the distribution of birth sites of 104 moose

Table 2. Average precalving moose populations and numbers of moose produced and dying in a 1-year model we derived from average values, Game Management Unit 20A, Alaska, USA, March 1996–December 2004. When calculating average values, we excluded the high harvest from 2004.

Parameter	Moose age (months)			Totals
	≥24	12–24	0–12	
Precalving in yr 1	10,455	2,067	0	12,522
Calves produced	5,612	0	0	5,612
Killed by wolves	366	296	1,093	1,755
Killed by hunters[a]	650	164	20	834
Other human-caused mortality	105	30	35	170
Killed by grizzly bears	106	42	672	820
Killed by black bears	0	42	758	800
Died from poor nutrition, disease, drowning, thin ice, giving birth	224	42	253	519
Precalving in yr 2	9,005	1,450	2,782	13,237

[a] No. of moose killed by hunters included total estimated number harvested (741) and wounding loss (93), which totaled 1.35 × reported harvest, based on fate of radiocollared moose.

radiocollared in the central foothills; 337 (91%) of 371 of these birth sites were in the central Tanana Flats during 1996–2007. Combining this spring migration rate with the intensive survey in November 1996, we estimated 91% of 3,300 moose in the central foothills migrated to the central Tanana Flats in spring to join 4,400 resident moose. Moose north of GMU 20A also regularly migrated in spring to join resident moose on the Tanana Flats. We found 9% of 33 radiocollared newborn calves of unmarked females spent the spring and summer in the central Tanana Flats and wintered north of GMU 20A.

Yield of Moose, GMU 20A, 1996–2006

When the population was increasing (1996–2003), annual yield averaged 741 moose (SE = 35.4, n = 8 yr, 88% M), which constituted 5% of the average prehunt population (14,784 moose; Table 1) and 4% of the average postcalving population (18,134 moose; Table 2). When the population was decreasing (2004–2006), annual yield averaged 1,268 moose (SE = 49.7, n = 3 yr, 47% M), which constituted 7% of the average prehunt population (17,433 moose; Table 1).

Harvest-density averaged 57 moose/1,000 km^2 of moose habitat during the increase phase and 97 moose/1,000 km^2 during the decline. Calves constituted 1–2% of the reported harvest during 1996–2001 and increased to 6–7% during 2002–2006 after we encouraged harvest of calves.

Moose Reproduction, Central GMU 20A, 1996–2007

Reproductive rates varied with age (Fig. 2). Moose first produced newborns at 36 months of age, but at a low rate (30 calves/100 F, SE = 6.2, n = 5 yr, 121 F first collared as short-yearlings). Thus, most moose did not reproduce until 48 months of age. We observed no viable twins at 151 births sites of 36-month-old moose and 143 birth sites of 48-month-old moose. Age classes ≥48 months of age produced an average of 84 calves/100 females annually (SE = 0.032, n = 11 age-classes, 814 moose; Fig. 2).

During 1997–2007, females ≥36 months of age produced a weighted average of 75 calves/100 females annually based on age-specific production rates of radiocollared females (Fig. 2) and proportions of age classes in the population. Additionally, we observed 577 females ≥36 months of age
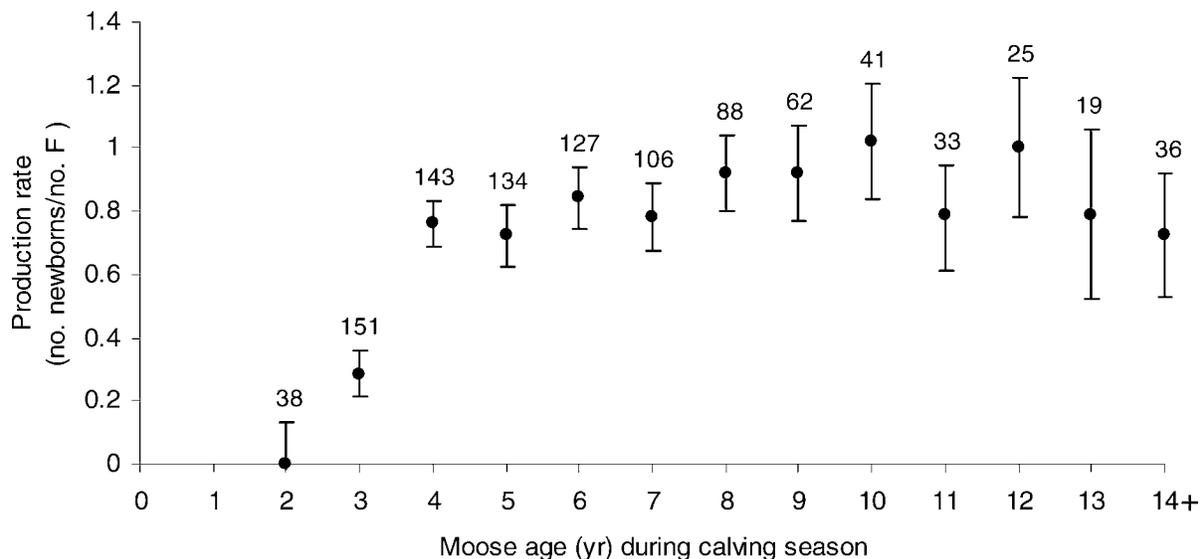
Figure 2. Age-specific production rates among moose (± 95% CI) in central Game Management Unit 20A, Alaska, USA, 11 May to mid-June 1996–2007. Data labels are numbers of female moose we aerially radiotracked for presence of newborns.
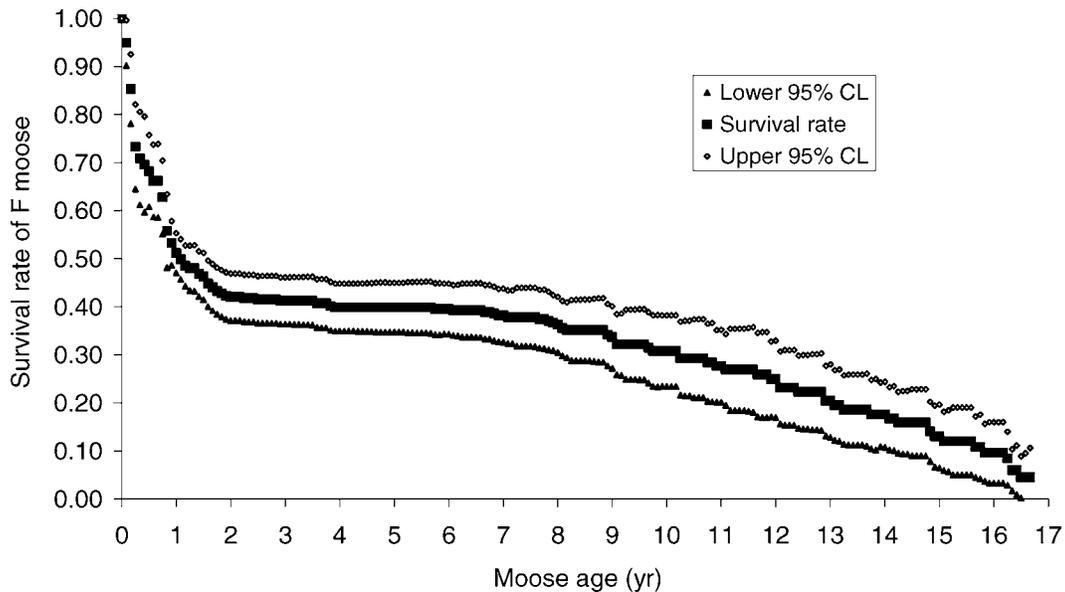
Figure 3. Cumulative survival rates (± 95% CI) to respective age classes for female moose, central Game Management Unit 20A, Alaska, USA, 1996–2007. Data are from 370 radiocollared female moose; we collared most (61%) at 9 months of age and replaced collars every 5 years. We censored human-caused mortality.

with calves on aerial transects (no telemetry) and calculated an average twinning rate of 7% (SE = 0.9%, n = 11 yr, range = 3–11%).

Moose Survival Rates Exclusive of Human-Caused Mortality, GMU 20A

Survival rates varied with age (Fig. 3). Annual survival rate was 51% among calves (95% CI = ±3.8%, n = 83–394 at risk depending on month) and 81% among yearlings (95% CI = ±4.6%, n = 227–337 at risk). Among females, annual survival rates peaked during the next 5 years of life ($\bar{x}$ = 98%, SE = 1.6%, n = 5 yr, 111–163 F at risk, range 96–100%). Also, among males, annual survival rate averaged 98% from 24 to 48 months of age (n = 27–66 at risk). Survival of older females slowly declined from 94% at 7 years of age (95% CI = 4.7%, n = 94–113 F at risk) to 85% at 12 years of age (95% CI = 13.8%, n = 22–27 F at risk).

The oldest radiocollared female moose was 17 years old and the oldest male was 8 years old. Males lived fewer years in part because hunters killed an average of 26% (SE = 0.9, n = 9 yr, range = 21–30%) of prehunt males ≥15 months old annually during 1993–2001. Our maximum age for males may have been biased low because our sample contained primarily 9-month-olds radiocollared during 2003–2007. We knew all male ages because we initially collared males as short-yearlings or yearlings. Likewise, we knew female ages, except in 67 cases where we estimated age based on counting annuli in canine teeth. Annuli counts were accurate in 20 (80%) of 25 cases where ages were known; 23 (92%) of 25 ages were accurate to ≤1 year of age.

Causes of Mortality Unrelated to Humans, Central GMU 20A, 1996–2007

Using data from 83 collared newborns that reunited with adults, predation was the proximate cause of death at 34 (92%) of 37 death sites. Wolves killed 13 collared calves,

black bears 9, and grizzly bears 8; differences were not significant ($p_{wolf} - p_{grizzly}$ = 0.17, 95% CI = −0.13 to 0.46, n = 30). In 4 cases, we could not determine the predator. We inferred that predators killed rather than scavenged calves, based on sign at kill sites and lack of scavenging for several days on 8 calves that died from capture-induced abandonment or trampling by maternal females. Drowning, malnutrition, and injuries inflicted from an adult male moose appeared to be the proximate causes of death at the remaining 3 death sites.

Wolf predation was the most important proximate cause of death among radiocollared moose ≥12 months of age. We examined remains of 50 radiocollared yearlings that died from causes unrelated to humans and determined that wolves killed 35 (70%), black bears 5 (10%), grizzly bears 5 (10%), and nonpredation accounted for 5 (10%) deaths. Likewise, we examined remains of 59 radiocollared moose ≥2 years of age and determined that wolves killed 31 (53%), grizzly bears 9 (15%), and nonpredation accounted for 19 (32%) deaths.

Of 24 moose ≥12 months of age that died from causes unrelated to predators, 17 died with signs of malnutrition (including ≥2 with pneumonia), 4 fell through the ice, 3 died giving birth, and 1 died from an internal rupture. Of 17 that died with signs of malnutrition, 11 died during March–May, 5 during November–February, and 1 in July. Deaths were distributed throughout the 12-year study. We failed to identify a consistent disease etiology despite necropsies of 9 moose ($\bar{x}$ age = 6.2 yr, SE = 1.31).

Modeled Moose Population During the Increase Phase, 1996–2004

We estimated the average postcalving population totaled 18,134 moose (5,612 newborn calves and 12,522 moose ≥1 year old, Table 2). We estimated 27% of the population
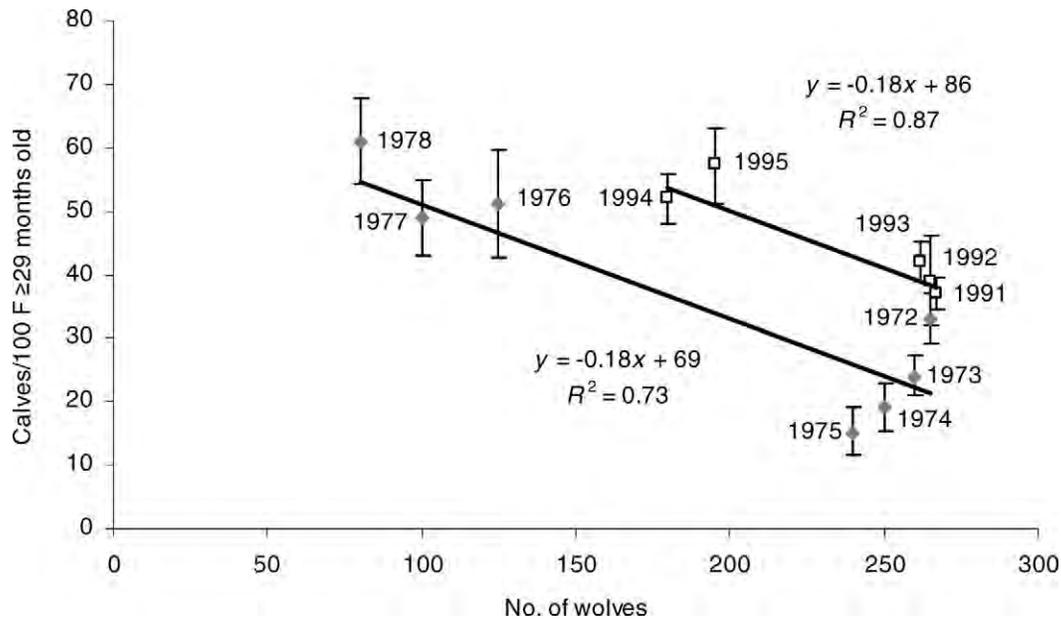
Figure 4. Increases in calves/100 females ≥29 months of age and respective 95% confidence intervals in early winter moose populations coincidental with 2 wolf control programs when moose were at low and high density, Game Management Unit 20A, Alaska, USA. Moose density varied from 250 moose/1,000 km^2 during the 1976–1978 wolf control program to 960 moose/1,000 km^2 during the 1994–1995 wolf control program. The 1994–1995 wolf control program was conducted to increase caribou numbers.

died annually; 19% from predation, 5% from hunters (4.1% harvest and 0.5% wounding loss), and 4% from other causes. Also, 4% (715 calves) were added to the subsequent year's population. Thus, the modeled population increased at a low rate ($\lambda = 1.06$), similar to the rate derived from the 1996–2004 population estimates ($\lambda_{B1} = 1.05$). The sum of 27% dying and 4% added to the subsequent year's population totaled 31%, which equaled calf production or potential recruitment in the postcalving population (5,612 calves born/18,134 = 0.31). Thus, the modeled postcalving population could have sustained a 31% loss and remained stable for 1 year.

We attributed 1,755 deaths to wolf predation during the year, compared with 820 to grizzly bears, 800 to black bears, and 834 to hunters (Table 2). Each predator killed mostly calves and 75% of the predator-killed moose were calves (Table 2). In contrast, 1–7% of hunter-killed moose were calves each year and hunters killed mostly males (88% in reported harvest, Table 1). Predators killed 852 moose older than calves, whereas hunters killed 814. We attributed 519 deaths to nonpredation causes unrelated to humans, and we attributed 175 (34%) of these 519 deaths to malnutrition. We attributed an additional 170 deaths to human causes unrelated to hunters; telemetry studies and independent reports indicated that moose died from snares, military exercises, and collisions with vehicles and trains.

Response of Moose to Wolf Control Experiments at Both Low and High Moose Density

Analyses indicated that removal of about 100 wolves resulted in about 18 more calves/100 females ≥29 months of age in early winter at both low (1970s, 250 moose/1,000 km^2) and high (1990s, 960 moose/1,000 km^2) moose density

in GMU 20A. Analyses also indicated a study period effect; 16 more calves/100 females ≥29 months of age existed prior to the 1990s wolf control experiment with 62 moose/wolf than prior to the 1970s experiment with 18 moose/wolf. Slopes of fitted lines were nearly equal (Fig. 4) and were different than zero (slope$_{1970s}$ = −0.18, SE = 0.048, P = 0.015; slope$_{1990s}$ = −0.18, SE = 0.039, P = 0.020). Based on the ANCOVA test for heterogeneity of slopes, slopes were not different ($F < 0.01$, df = 8, P = 0.990). The common slope was −0.18 (SE = 0.067, P = 0.030). The ANCOVA analysis demonstrated that the study period effect was significant (F = 20.93, df = 9, P = 0.001).

Estimates from the Bayesian ANCOVA models and general linear models were consistent. The 95% central credibility interval for the difference in slope coefficients was nearly centered on zero (−0.003, 0.002), indicating equal slopes. Using the common slope model, the 95% central credibility interval for the difference in intercept terms did not contain zero (−0.85, −0.62), indicating a study period effect.

DISCUSSION

Despite low reproductive rates (Tables 3–4; Boertje et al. 2007), moose attained high densities during our study largely because of low predation (Tables 3–5). Peak density of 1,299 moose/1,000 km^2 in 2004 was a 7-fold increase from the 1975 density in GMU 20A (183 moose/1,000 km^2; Boertje et al. 1996). Elevated moose densities in GMU 20A (1996–2007) exceeded by several-fold the densities reported by Gasaway et al. (1992) for Interior Alaska ($\bar{x}$ = 298 moose/1,000 km^2, SE = 62.5, n = 12 study populations, range = 88–751 moose/1,000 km^2).

High moose density in GMU 20A allowed for the highest recorded sustainable harvest-density in Interior Alaska for

Table 3. November moose densities, precalving numbers, reproductive rates, and numbers and percentages of moose produced and dying in 10,000 km^2 of habitat in Game Management Unit (GMU) 20E and GMU 20A, Alaska, USA, 1984–2004, and respective multipliers. Data from GMU 20E are from Gasaway et al. (1992).

Parameter	Low-density moose population in GMU 20E, 1984–1988, $\lambda = 1.04$	Multiplier	High-density moose population in GMU 20A, 1996–2004, $\lambda = 1.06$
Habitat	10,000 km^2	1.0	10,000 km^2
Average Nov moose density	130 moose/1,000 km^2	8.2	1,069 moose/1,000 km^2
No. moose next May prior to calving	1,167	8.2	9,600
Parturition rate for F $\geq$36 months of age	100%	0.75	75% during 1997–2007
Twinning rate for F $\geq$36 months of age	52%	0.13	7%
No. M:100 F excluding calves	44	0.68	30
No. calves produced	795	5.4	4,302
% calves in immediate postcalving population	41% of 1,962 moose	0.76	31% of 13,902 moose
No. moose killed by wolves	151	8.9	1,345
% of postcalving moose population killed by wolves	7.7%	1.3	9.7%
No. moose killed by grizzly bears	441	1.4	629
% of postcalving moose population killed by grizzly bears	22.5%	0.20	4.5%
No. moose killed by black bears	24	26	613
% of postcalving moose population killed by black bears	1.3%	3.4	4.4%
No. moose killed by nonpredation	108	3.7	398
% of postcalving moose population killed by nonpredation	5.5%	0.53	2.9%
No. of moose killed by hunters	30	21	639
% of postcalving population killed by hunters	1.5%	3.1	4.6%

similarly large areas, 57 moose/1,000 km^2 of moose habitat. The second highest total harvest-density during our study averaged 38 moose/1,000 km^2 of moose habitat, which occurred in and around Interior Alaska's largest settled area, the Fairbanks area (1996–2003, 12,600 km^2, central GMU 20B and Minto Flats). In contrast, total harvest-densities of <10 moose/1,000 km^2 existed in Interior Alaska systems with predator-limited, low-density moose (Gasaway et al. 1992).

In most of Interior Alaska, strong limiting effects of wolf and bear predation result in small sustainable yields (2–5% of prehunt populations) restricted primarily to male moose older than calves (Gasaway et al. 1992; Alaska Department of Fish and Game 2002, 2004, 2006). In these predation-limited systems, managers generally focus on maintaining male:female ratios of moose (excluding calves) above a minimum area-specific objective, which varied from 15 to 40 males/100 females depending on local hunter satisfaction (not a biological rationale).

In GMU 20A during 1996–2001, we used data on abundance of moose and high male:female ratios to gain approval for a total annual harvest rate of 5–7% of prehunt numbers (Table 1), an increase from previous harvest rates of 2–4% during 1987–1994 (Boertje et al. 1996). Public local advisory committees restricted these harvests to largely males (88% M, Table 1). As a result, male:female ratios declined below our objective of 30 males/100 females for moose older than calves (Table 1), yet the moose population continued to increase. Subsequently we gained approval to restrict harvest to a portion of adult males ($\geq$127 cm antler spreads) and yearling males (spike or fork antlers only) to protect males in the population (Young and Boertje 2008). As a result, average harvest rates declined to 3% of prehunt numbers during 2002 and 2003. The moose population continued to increase.

After gaining approval for liberal harvests of females to decrease the population during 2004–2006, total harvest rates reached 7–8% of the prehunt population (97 moose/1,000 km^2 of moose habitat). As a result, the population declined and male:female ratios increased to 35–38 males:100 females (Table 1). We conclude that the prehunt population and male:female ratio will likely stabilize if total harvest is 6% (60% M, 40% F) annually and underlying factors remain the same.

Pros and Cons of Managing Moose for High Density and Yield

Achieving high yield of moose fulfilled legal mandates, reduced demand for predator control, and should provide the impetus for protecting this system against uses incompatible with moose management. A disadvantage to managing for high yield of moose was the need for a more complex and expensive zonal management system (Young et al. 2006). In addition, we frequently need to defend harvests of female moose from public opposition, primarily because local hunters often oppose additional harvest that attracts additional nonlocal hunters (Young and Boertje 2004, Young et al. 2006).

A biological disadvantage to managing moose at reduced nutritional status is that the population may be more vulnerable to declines from severe weather. However, predicting effects and frequency of severe weather is problematic. Thirty-five years have passed since the last severe weather events precipitated noticeable declines in moose numbers in GMU 20A (Gasaway et al. 1983, Boertje et al. 1996).

Influence of Moose Nutritional Status on Management of Harvest and Habitat

Local public advisory committees vetoed liberal harvest of female moose until we documented density-dependent nutritional limitation. Moose reproductive rates declined noticeably during 1997–2007 compared with those during

Table 4. Moose calf mortality rates (%), moose production rates, moose calf:100 female ratios, and moose and predator densities among 8 radiotelemetry studies in Alaska, USA, and Yukon, Canada, 1977–2002.

| Study areas and sample sizes | Estimated % of collared calf moose killed | | | | | Calves produced/ 100 F ≥3 yr old | Early winter calves/ 100 F ≥17 months old[b] | Early winter moose and predator no./ 1,000 km² and references |
	Wolves	Grizzly bears	Black bears	Total annual predation[a]	Total annual mortality			
GMU 20A, Central AK; 83 calves, 2 cohorts; 1996–1997	18	11	13	45	47	75 during 1997–2007	35, 43	950 moose (this paper), 14–16 wolves (Boertje et al. 1996, Young 2000), 23 grizzly bears in the Alaska Range foothills (Reynolds 1997), uncommon black bears
GMU 13, South-central AK; 198 calves, 4 cohorts, 1977–1979, 1984	3	45	2	53	68	110	25, 24, 34, 34	710–844 moose (Ballard et al. 1991), 6–8 wolves, long-term public wolf control limited wolf no. periodically (Ballard et al. 1987), 24 grizzly bears but less in 1979 (Ballard and Miller 1990), 90 black bears (Miller et al. 1987)
GMU 15, Kenai Peninsula; 121 calves, 4 cohorts, 1977–1978, 1982–1983	3, May–Oct data only	4, May–Oct data only	35, May–Oct data only	No data	No data	>124[c]	27, 31, 40, 47	600–1,000 moose (Franzmann and Schwartz 1986), 11–20 wolves, wolves were extirpated during 1913–1960s and trappers limited no. through at least 1981 (Peterson et al. 1984), scarce grizzly bears (Bangs et al. 1989), 189–211 black bears (Schwartz and Franzmann 1991)
GMU 19D, West-central AK; 136 calves, 2 cohorts; 2001–2002	25	12	30	67	69	117	34	386 moose, 9 wolves, 97 black bears, 10 grizzly bears (Keech 2005; M. A. Keech, Alaska Department of Fish and Game, unpublished data)
GMUs 21B and 21D, West-central AK; 151 calves, 3 cohorts; 1988–1990	9	3	40	60	65	>130[c]	41, no data in 1989 or 1990	210–309 moose in 1988 and 1989 study sites and 512 moose in 1990 site, 7–11 wolves, common black bears, scarce grizzly bears (Osborne et al. 1991, Spindler 1992)
Southwest Yukon Territory; 96 calves, 2 cohorts; 1983, 1985	18	42	4	66	75	114	30	147 moose, 4–10 wolves with wolf control, 23 grizzly bears in moose habitat, 23 black bears (Larsen et al. 1989)
GMU 25D, Yukon Flats; 58 calves, 2 cohorts; 1998–1999	2	31	36	72	80	>145	35 in 1999	120–180 moose, 4 wolves, 10 grizzly bears, common black bears (Bertram and Vivion 2002)
GMU 20E, East-central AK; 33 calves, 1 cohort; 1984	13	52	3	68	80	152	22	105 moose, 5 wolves with wolf control (Gasaway et al. 1992), 10–12 grizzly bears (Boertje et al. 1987), scarce black bears

[a] Total annual predation rate includes all kills inferred to be from predators, including instances when we could not determine the species of predator.
[b] Ratios of calves:100 F ≥17 months old are from aerial population surveys in the respective study areas when radioed calf cohorts were 5 months of age.
[c] In GMUs 15 and 21, we calculated the production rate based on an average moose parturition rate of 85% (Schwartz 1998).

Table 5. Annual predation and mortality rates (%) measured among 4 postcalving moose populations during radiotelemetry studies in Alaska, USA, and Yukon, Canada, 1977–2004. The immediate postcalving population includes all adults and yearlings in mid-May plus all calves born in the ensuing few weeks.

Study area and moose population rate of increase (λ)	Estimated % mortality on total postcalving moose population during 1 yr							Reference
	Wolves	Grizzly bear	Black bear	Total predation	Other mortality not by humans	Total kill by hunters	Total mortality	
GMU 20A, 13,044 km², Central AK; 1996–2004; $\lambda = 1.06$	10	5	4	19	3	5	27	Table 2
GMU 19D, 1,347 km², West-central AK; 2001–2003; $\lambda = 1.01$	15	6	12	34	1	6	40	Keech 2005; M. A. Keech, Alaska Department of Fish and Game, unpublished data
Southwest Yukon Territory, 6,310 km²; 1983–1984; $\lambda = 0.91$	14	26	1	41	2	4	47	Larsen et al. 1989
GMU 20E, 9,700 km², East-central AK; 1984–1988; $\lambda = 1.04$	8	22	1	31	6	2	38	Gasaway et al. 1992

1960–1996 and rates reached the lowest levels recorded for wild, noninsular moose in North America (Boertje et al. 2007). Females ≥36 months of age produced an annual average of 7% twins and 75 calves/100 females during 1997–2007 in GMU 20A, in contrast to 28–64% twins and 114–152 calves/100 females in 5 studies of low-density moose (Table 4). Prior studies demonstrated the link between moose twinning rates and nutritional status using culling experiments with a fenced moose population (Blood 1974), fat depths of individual moose (Keech et al. 2000), and large-scale comparative population studies (Boertje et al. 2007).

In theory, liberal harvests of female moose could have begun in the early 1990s, rather than in 2004, to stabilize the population when moose were more productive (Boertje et al. 2007). In practice, it was more defensible to knowingly reduce the moose population with harvests of females after food stress became readily apparent, because local advisory committees required convincing data to approve harvests of females. Also, stabilizing a slowly growing moose population by harvesting females is problematic. Managers often require several years of survey data to determine trend in population size. Poorly timed and liberal harvests of female moose accelerated population declines in the early 1970s, and some hunters remained distrustful of agency recommendations for the harvest of female moose (Boertje et al. 2007).

We discourage managing for moose with greater density-dependent food stress than we observed in GMU 20A. Our rationale was that reduced reproduction was a major factor limiting yield when average twinning rates declined to 10%. Density-dependent mortality was a relatively minor factor limiting yield. We attributed only 3% of annual moose deaths solely to malnutrition during the period with 7% twinning (1997–2007). Also, with 11% twinning (SE = 5.0%, $n = 4$ yr, 1991, 1993–1995; Boertje et al. 2007) and elevated moose density (960 moose/1,000 km²), wolf predation was similarly additive compared with 21%

twinning (SE = 5.8%, $n = 4$ yr, 1975–1978) and low moose density (250 moose/1,000 km², Fig. 4).

Although density-dependent mortality was low, we used moose deaths attributed to malnutrition to help convince a skeptical public to initiate liberal harvests of female moose. These deaths accounted for only 1% of the postcalving population. However, malnutrition accounted for 16% ($n = 109$ mortalities not caused by humans) of deaths among yearling and adult moose and 24% ($n = 41$) of winter calf deaths. In contrast, Gasaway et al. (1992) detected no deaths from malnutrition among 46 mortalities of yearling and adult moose when moose were at low density.

To reduce food stress, we encouraged habitat manipulation. Periodic burning is useful to reverse succession and the effects of overbrowsing. For example, nonpreferred alders (*Alnus* spp.) were replacing preferred willows (*Salix* spp.) in the landscape at high moose densities (Butler and Kielland 2008), and fire would help reverse this trend. During all 12 years of our study, staff wrote prescribed fire plans and encouraged land managers to allow wildland fires in GMU 20A. Funding was available. Efforts to ignite prescribed fires failed because of unfavorable weather for burning, alternative objectives including protecting Fairbanks from smoke, and competition for qualified personnel and specialized equipment. However, land managers allowed 6 wildfires to burn sizeable areas ($\bar{x} = 352$ km², SE = 47.7) in eastern and western GMU 20A during our study.

Influence of Predation and Moose Reproduction on Management for Elevated Yields

Low predation rates in GMU 20A allowed moose to escape the low-density dynamic equilibrium, where lightly harvested bears and wolves maintain highly productive moose populations at low but fluctuating densities (≤417 moose/1,000 km² of moose habitat; Gasaway et al. 1992). Studies in Alaska and Yukon (Tables 3–5) clearly showed that predation was low in GMU 20A. Despite low annual calf mortality, early winter ratios of calves:100 females were not uniquely high in GMU 20A because of low reproduction

(Table 4). Predators killed 19% of the GMU 20A postcalving moose population annually in contrast to 31–41% in 3 studies of low-density moose where bear predation dominated (Table 5).

Predators impacted moose populations by selecting the most vulnerable cohorts at both low and high densities. Similar additive wolf predation on calves at low and high densities indicated calves were similarly vulnerable over a wide range of moose densities and moose:wolf ratios. Predators killed mostly calf moose; calves constituted 83–88% of the annual moose kills by wolves and bears in 3 study areas with low moose densities, compared with 75% in GMU 20A (Table 5). Predators rarely killed moose 2–6 years of age at low or high densities (Fig. 3; Gasaway et al. 1983, 1992).

Moose at high density were similarly affected by predation and reduced reproduction, in contrast to the dominating effects of bear and wolf predation on low-density moose (Gasaway et al. 1992). To quantify the effect of reduced reproduction, we substituted, in our conceptual model (Table 2), high moose productive rates from adjacent low-density moose in Denali National Park (125 calves/100 F $\geq$36 months of age and 35 calves/100 F 24 months of age, 1998–2002; Boertje et al. 2007). Results indicated an additional 3,614 calves would be born, similar to the annual number of moose deaths from predation (3,375; Table 2). Denali moose twinning rates ($\bar{x} = 44\%$) were the highest measured among long-term studies in Interior Alaska and were similar to rates measured in GMU 20A during 1977–1982 when moose density was low (Boertje et al. 2007).

Moose management in Sweden indicated sustained yields could be 6–8 times greater than in our study if predators were absent, moose reproduction was high, and habitat was improved. For example, in a small study area in Sweden (140 km^2) without predators and with high reproduction (117 calves/100 F $\geq$36 months of age), sustained yields were 650 moose/1,000 km^2 with calves constituting 48% of the harvest, prehunt densities were 1,950 moose/1,000 km^2, and prehunt sustainable harvest rates were 33% (Cederlund and Sand 1991). In contrast, in GMU 20A, with predation (Tables 3–5) and low reproduction (75 calves/100 F $\geq$36 months of age), sustained yields were 57–97 moose/1,000 km^2 with calves constituting 1–7% of the harvest, prehunt densities reached 1,741 moose/1,000 km^2 in central GMU 20A, and prehunt sustainable harvest rates averaged 5%.

Unique Factors Contributing to High Yields in GMU 20A

Replicating the elevated yields of GMU 20A elsewhere in remote Interior Alaska is problematic because GMU 20A had unique characteristics. Foremost, both bear species killed only 24% of radiocollared calves in GMU 20A compared with 39–67% in other areas ($\chi_1^2 \geq 4.85$, $P \leq 0.028$; Table 4). Also, both species of bears killed only 9% of the GMU 20A postcalving moose population annually compared with 18–27% in other study areas (Table 5). In contrast, wolves killed similar proportions of the postcalving populations (8–15%), hunters killed 2–6%, and other

factors killed 1–6%. Thus, 1 or 2 bear species strongly dominated moose population dynamics in other study areas relative to GMU 20A. Attempts to find practical methods, means, and incentives for the public to reduce bear predation in remote areas have failed to date (Boertje et al. 1995). As a result Interior Alaska has seldom managed for elevated yield of moose in large areas, except in and near settled areas, including agricultural areas.

Three mechanisms help explain why predation rates were low in GMU 20A (Table 4). First, grizzly and black bear densities were low in the poorly drained moose calving areas in GMU 20A. We observed no grizzly bears in the north-central Tanana Flats during our 12 years of surveys except in our final year. We observed an average of only 0.5 black bears/day during calving surveys (SE = 0.07, $n = 5$ yr). Hechtel (1991) concluded that black bear densities were naturally low, not harvest limited, in north-central GMU 20A. Second, the precalving movement of 91% of foothills females to the Tanana Flats for calving suggests an inherited trait with elevated survival compared with calving in the foothills. We hypothesize that spacing away from grizzly bear predation in the spring had important life-history consequences. Boertje et al. (1988) concluded that grizzly bear predation peaked during spring. Reynolds (1997, 1999) estimated grizzly density in the foothills was 10–17 bears $\geq$2 years of age/1,000 km^2 during 1981–2001. Grizzly bears have often been considered the most effective predator on moose calves (Boertje et al. 1988, Larsen et al. 1989, Ballard et al. 1991), and grizzly bear predation accounted for 26% of total predation on the postcalving moose population in GMU 20A (Table 5). Third, moose:wolf ratios were high in GMU 20A during our study ($\geq$54:1 in early winter and $\geq$100:1 in spring and summer with concentrated moose distribution in the central Tanana Flats). Gasaway et al. (1983) reported that wolf predation will not necessarily limit moose populations with >30 moose:wolf. The GMU 20A moose:wolf ratio was 13:1 in early winter 1975 (183 moose and 14.1 wolves/1,000 km^2) prior to Alaska Department of Fish and Game wolf control programs (1976–1982, 1993–1994; Boertje et al. 1996). After wolf control, the early winter wolf population was self-limited at $\leq$16.5 wolves/1,000 km^2, the highest density reported in Interior Alaska ($\leq$281 wolves in 17,000 km^2; Boertje et al. 1996; Young 2000; D. D. Young, Alaska Department of Fish and Game, unpublished data).

An additional factor allowing for an increasing moose population during 1976–2004 in GMU 20A included favorable weather. Snowfall was generally low during our study, 1996–2007 (National Weather Service 2007). Among radiocollared moose, we observed no multiple deaths from malnutrition that could be linked solely to severe weather. In contrast, in western Alaska where snow is typically deeper than in GMU 20A, snow depth >90 cm from mid-January to mid-April 2005 combined with unusual cold ($<-40°$ C for 14 days) coincided with 16 winterkills of calf moose (38% of 42 radiocollared calves that survived to winter; Keech 2005; M. A. Keech, Alaska Department of Fish and

Game, unpublished data). M. A. Keech reported no winterkills or predation among radiocollared yearling ($n = 25$) and adult moose ($n = 51$) during that exceptional winter and only 8 winterkills of calves in 5 additional winters of study (5% of 154 radiocollared calves that survived to winter). Gasaway et al. (1983) and Bishop and Rausch (1974) reported that adverse weather precipitated widespread declines of moose in GMU 20A and throughout Interior Alaska in the mid-1960s and early 1970s. Also, Boertje et al. (1996) implicated synergistic effects of adverse weather and predation in causing major declines of caribou in and near GMU 20A in the early 1990s.

Finally, factors affecting the GMU 20A moose population are changing. Substantial wildfires during 2001 and 2006 may result in increased moose reproductive rates, decreased mortality from malnutrition, and decreased predation (Boertje et al. 1995). Also, the recent decline in population size may result in improved moose reproduction, although an increase in twinning rates lagged well behind the 1960s decline in moose density in GMU 20A (Boertje et al. 2007). Data summarized here should enable moose managers to determine meaningful harvest and population objectives for any area in Interior Alaska given that basic, relative information is available on moose population nutritional status and composition, weather, and abundance of moose, wolves, and bears.

MANAGEMENT IMPLICATIONS

To attain similar elevated yields of moose in other areas of Interior Alaska with lower moose density, lower moose:predator ratios, low mortality from nonpredation, and higher moose nutritional status; we reaffirm that reductions in predation are necessary (Gasaway et al. 1992, Boertje et al. 1996). Where predation is sufficiently reduced to increase moose numbers, we expect eventual declines in density-dependent nutritional indices. When density-dependent nutritional indices reach or approach the thresholds we previously published, the harvest of female moose should be initiated or increased to halt population growth and maximize harvest (Boertje et al. 2007).

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