Research Article

Ranking Alaska Moose Nutrition: Signals to Begin Liberal Antlerless Harvests

RODNEY D. BOERTJE,[1] *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1599, USA*

KALIN A. KELLIE, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1599, USA*

C. TOM SEATON, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1599, USA*

MARK A. KEECH, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1599, USA*

DONALD D. YOUNG, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1599, USA*

BRUCE W. DALE,[2] *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1599, USA*

LAYNE G. ADAMS, *United States Geological Survey – Alaska Science Center, 1011 E. Tudor Road, Anchorage, AK 99503, USA*

ANDREW R. ADERMAN, *United States Fish and Wildlife Service, Togiak National Wildlife Refuge, P.O. Box 270, Dillingham, AK 99576, USA*

ABSTRACT We focused on describing low nutritional status in an increasing moose (*Alces alces gigas*) population with reduced predation in Game Management Unit (GMU) 20A near Fairbanks, Alaska, USA. A skeptical public disallowed liberal antlerless harvests of this moose population until we provided convincing data on low nutritional status. We ranked nutritional status in 15 Alaska moose populations (in boreal forests and coastal tundra) based on multiyear twinning rates. Data on age-of-first-reproduction and parturition rates provided a ranking consistent with twinning rates in the 6 areas where comparative data were available. Also, short-yearling mass provided a ranking consistent with twinning rates in 5 of the 6 areas where data were available. Data from 5 areas implied an inverse relationship between twinning rate and browse removal rate. Only in GMU 20A did nutritional indices reach low levels where justification for halting population growth was apparent, which supports prior findings that nutrition is a minor factor limiting most Alaska moose populations compared to predation. With predator reductions, the GMU 20A moose population increased from 1976 until liberal antlerless harvests in 2004. During 1997–2005, GMU 20A moose exhibited the lowest nutritional status reported to date for wild, noninsular, North American populations, including 1) delayed reproduction until moose reached 36 months of age and the lowest parturition rate among 36-month-old moose (29%, $n = 147$); 2) the lowest average multiyear twinning rates from late-May aerial surveys ($\bar{x} = 7\%$, SE = 0.9%, $n = 9$ yr, range = 3–10%) and delayed twinning until moose reached 60 months of age; 3) the lowest average mass of female short-yearlings in Alaska ($\bar{x} = 155 \pm 1.6$ [SE] kg in the Tanana Flats subpopulation, up to 58 kg below average masses found elsewhere); and 4) high removal (42%) of current annual browse biomass compared to 9–26% elsewhere in boreal forests. When average multiyear twinning rates in GMU 20A (sampled during 1960–2005) declined to <10% in the mid- to late 1990s, we began encouraging liberal antlerless harvests, but only conservative annual harvests of 61–76 antlerless moose were achieved during 1996–2001. Using data in the context of our broader ranking system, we convinced skeptical citizen advisory committees to allow liberal antlerless harvests of 600–690 moose in 2004 and 2005, with the objective of halting population growth of the 16,000–17,000 moose; total harvests were 7–8% of total prehunt numbers. The resulting liberal antlerless harvests served to protect the moose population's health and habitat and to fulfill a mandate for elevated yield. Liberal antlerless harvests appear justified to halt population growth when multiyear twinning rates average ≤10% and ≥1 of the following signals substantiate low nutritional status: <50% of 36-month-old moose are parturient, average multiyear short-yearling mass is <175 kg, or >35% of annual browse biomass is removed by moose. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):1494–1506; 2007)

In 1960, the first moose (*Alces alces gigas*) managers in the new state of Alaska, USA, acquired several high-density moose populations from federal managers. These high moose densities resulted in part from previous widespread federal predator control, favorable winters, favorable habitat, and the lack of antlerless harvests (Bishop and Rausch 1974, Rausch et al. 1974). The new state managers immediately initiated conservative antlerless harvests. These harvests evolved into liberal antlerless harvests by the early 1970s, although moose densities had already substantially declined from adverse winters and increasing predator numbers during 1965–1971 (Gasaway et al. 1983). We categorize an antlerless harvest as liberal when the number of antlerless moose harvested is ≥2.0% of the total prehunt population

and the general intent is to stabilize or decrease the moose population.

The rationale for liberal antlerless harvests during 1971–1974 was to reduce suspected low nutritional status. However, moderate, not low, nutritional status was apparent during 1971–1974 in Game Management Unit (GMU) 20A based on browse surveys and twinning rates, and densities of moose were low (Gasaway et al. 1983). Unfortunately, these liberal antlerless harvests clearly contributed to further declines in moose numbers (Rausch et al. 1974, Gasaway et al. 1983). Consequently, the state legislature transferred the authority to implement antlerless harvests to the local citizen advisory committees. Thirty years later, these committees still have annual veto power affecting antlerless moose harvests and are skeptical of the need for antlerless harvests, despite a 1994 mandate to manage for elevated yields. Young et al. (2006) discussed the

[1] E-mail: rod_boertje@fishgame.state.ak.us
[2] *Present address: Alaska Department of Fish and Game, 1800 Glenn Highway, Suite 4, Palmer, AK 99645-6736, USA*
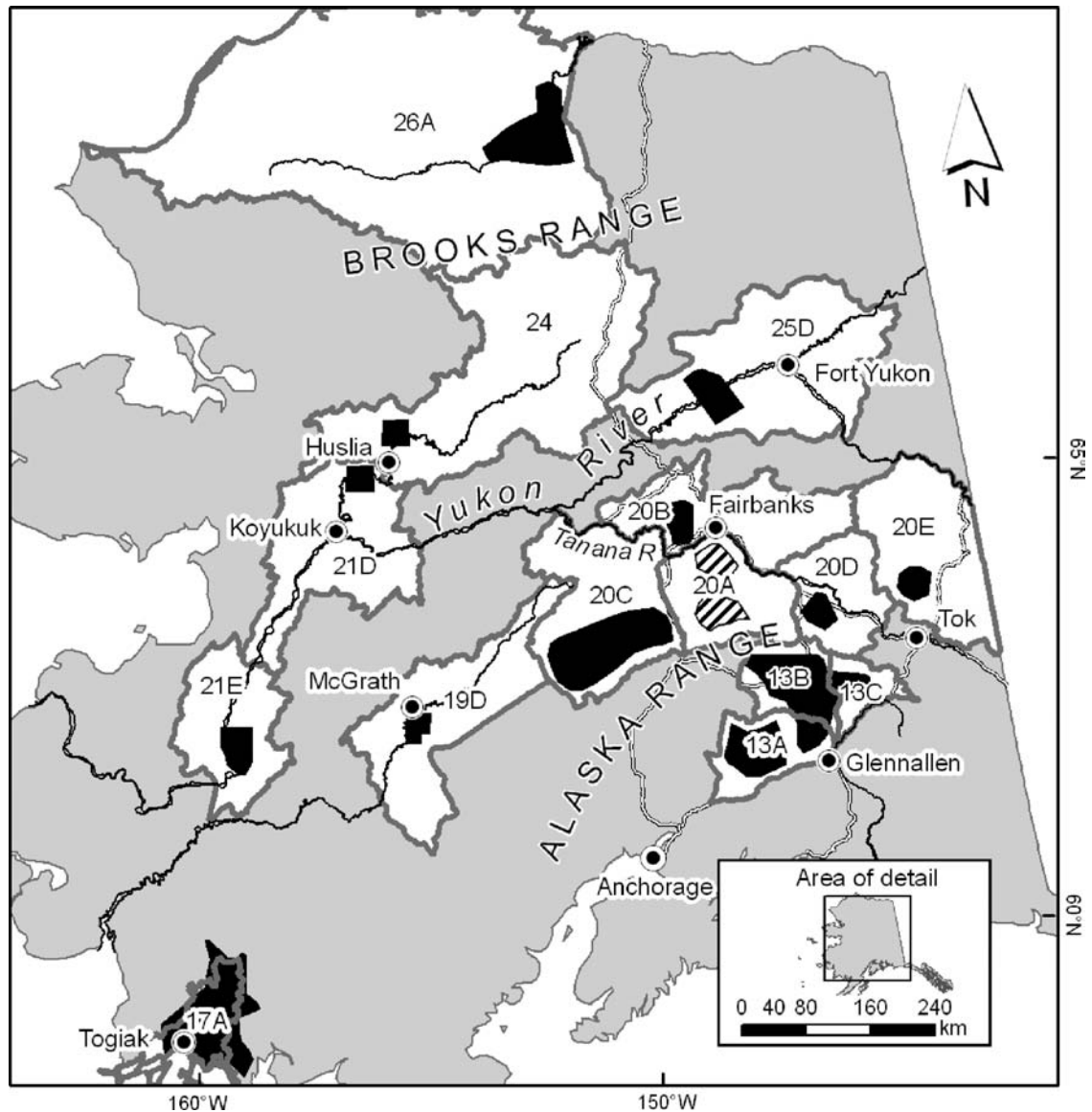
Figure 1. We focused on 2 subpopulations (hatched) of moose in the Tanana Flats and adjacent Alaska Range foothills of central Game Management Unit 20A, immediately south of Fairbanks, Alaska, USA, 1996–2005. In addition, we compared data from 13 other moose populations (black) throughout much of Alaska, 1994–2005.

1994 mandate and legal, social, and logistical challenges pertinent to elevating yield of moose in GMU 20A.

Our primary objectives are to describe the lowest nutritional status found to date among wild, non-insular, North American moose populations and to provide signals of low or declining nutritional status that can be used in combination with information on population trend to initiate liberal antlerless harvests. To provide a broad contrast, we ranked nutritional status in 15 Alaska moose populations based on a continuum of multiyear twinning rates. Prior literature substantiated the relationship between moose twinning rate and nutritional status (Blood 1974, Boer 1992, Gasaway et al. 1992, Keech et al. 2000). We further substantiate this twinning-based ranking and the low nutritional status in GMU 20A, using age-specific reproductive data and short-yearling masses from 6 of the 15 populations. Several prior authors suggested using repro-

ductive data (e.g., Franzmann 1977, Franzmann and Schwartz 1985) and short-yearling mass (Sæther et al. 1996) to rank moose nutritional status. We present browse removal rates in 5 of the areas as implied indices to range use and nutritional status, not as supporting evidence for the twinning-based ranking. We discuss the relative value of the nutritional indices and use of these data in management scenarios.

STUDY AREA

We compared data from 15 distinct moose populations or subpopulations: 13 in boreal forest communities (lowland and upland habitats) and 2 in coastal tundra communities (Fig. 1; Table 1). We focused primarily on 2 subpopulations within GMU 20A (13,044 km^2 of moose habitat) and present data from 13 other areas for contrast. The subpopulation in the central Tanana Flats of GMU 20A

Table 1. Ranked moose populations[a] and respective nutritional indices, May 1994–June 2005, Alaska, USA.

Moose population or subpopulation	Yr of study	Population trend, relative moose density[b], and reference	Parturition rates of radiocollared F Age first parturient
1: Game Management Unit (GMU) 20A north-central, central Tanana Flats	1997–2005	Increasing; high density; this paper	36 months; 27% of 70
2: GMU 20A south-central, central Alaska Range foothills	1997–2005	Increasing; high density; this paper	36 months; 30% of 77
3: GMU 13A west, foothills	1994–2003	Declining; moderate density; Testa 2004	36 months; 59% of 22
4: GMU 20B west, Minto Flats	1998–2005	Increasing; high density; D. D. Young, Alaska Department of Fish and Game (ADFG) files	
5: GMU 20D southwest; hills, lowlands, and agricultural fields	2000–2005	Increasing; high density; S. DuBois, ADFG files	
6: GMU 21D north-central, Koyukuk River	1994–2005	Declining; high riparian density; G. Stout, ADFG files	
7: GMU 13A east, 13B, and 13C; foothills and flats	1999, 2001, 2002, 2004	Stable, low and moderate densities; R. Tobey, ADFG files	
8: GMU 20E south-central, hills and flats, Fortymile	2004–2005	Stable; low density; J. Gross, ADFG files	
9: GMU 21E central, lower Innoko River	2000–2004	Stable; moderate riparian density; E. Lenart, ADFG files	
10: GMU 24 west, Huslia area	2003–2005	Stable; high riparian density; G. Stout, ADFG files	
11: GMU 26A east-central, Colville River	1996–2003	Increasing; low riparian density; G. Carroll, ADFG files	
12: GMU 19D local McGrath area, Kuskokwim River	2001–2005	Increasing; moderate riparian density; M. Keech, ADFG files	36 months; 76% of 34
13: GMU 20C south, foothills and flats, Denali National Park	1998–2002	Stable; low density; L. Adams, United States Geological Survey files, Anchorage, AK	24 months; 35% of 40
14: GMU 25D west, Yukon Flats	1998–1999	Stable; low density; Bertram and Vivion 2002; C. T. Seaton, ADFG files	
15: GMU 17A, Togiak area	1998–2005	Rapidly increasing; low riparian density on previously unused range; A. Aderman, United States Fish and Wildlife Service files, Dillingham, AK	24 months; 74% of 19

[a] The ranking (1–15) begins with the lowest nutritional status and is based on twinning rates. Age-specific reproductive indices and short-yearling masses provide supportive evidence for the twinning-based ranking in most cases. Browse removal rates are an implied index to nutritional status.

[b] Low moose density was <400 moose/1,000 km² over large areas (>2,000 km² of moose habitat; Gasaway et al. 1992). Moderate density was 400–800 moose/1,000 km², and high density was >800 moose/1,000 km². Some densities were from only riparian portions of the annual range as detailed above; densities outside riparian corridors were much lower.

was nonmigratory. The subpopulation in the central Alaska Range foothills migrated to the Tanana Flats during late March and April for calving in May and early June and returned to the foothills during late June through September.

Gasaway et al. (1983), Boertje et al. (1996), and Keech et al. (2000) described the GMU 20A study area and factors limiting moose density during 1960–1997. The moose population increased during 1976–2003, partly from wolf (*Canis lupus*) reductions during 1976–1982 and 1993–1994, and low black bear (*Ursus americanus*) and grizzly bear (*U. arctos*) predation relative to other moose mortality studies in Alaska (Boertje et al. 2000). Relatively high moose survival allowed moose numbers to reach 16,000–17,000 during

early winter 2003–2005, well above the population objective of 10,000–12,000 (Young et al. 2006).

METHODS

Ranking Nutritional Status and Comparing Nutritional Indices for the 15 Populations

To rank moose nutritional status among the 15 areas, we used summary statistics on multiyear twinning rates. To allow further comparisons of nutritional status in several of these areas, we provided summary statistics and sampling periods for age-specific reproductive indices, short-yearling masses, and browse removal rates (Table 1). Short-yearlings ranged from 9 months to 10 months of age in these studies.

Table 1. Extended.

Parturition rates of radiocollared F — Mature parturition rate	Twinning rates of parturient F in late May–early Jun	F short-yearling mass	Browse biomass removal rate
$\bar{x} = 0.70$, SE = 0.043, n = 9 yr, 297 F ≥48 months	$\bar{x} = 0.07$, SE = 0.009, n = 9 yr, 462 uncollared F; $\bar{x} = 0.07$, SE = 0.023, n = 9 yr, 169 radiocollared F ≥60 months of age; First twins at 60 months of age, 3% of 36	$\bar{x} = 155$ kg, SE = 1.6, n = 5 yr, 95 F in Mar	0.41, SE = 0.012, winter 1999–2000, 48 sites, 325 plants
$\bar{x} = 0.80$, SE = 0.037, n = 9 yr, 285 F ≥48 months	$\bar{x} = 0.12$, SE = 0.021, n = 9 yr, 167 radiocollared F ≥60 months of age; First twins at 60 months of age, 14% of 35	$\bar{x} = 172$ kg, SE = 2.4, n = 5 yr, 96 F in Mar	0.43, SE = 0.013, winter 1999–2000, 49 sites, 233 plants
$\bar{x} = 0.82$, SE = 0.037, n = 7 yr, 379 F ≥48 months	$\bar{x} = 0.17$, SE = 0.020, n = 7 yr, 793 uncollared F	$\bar{x} = 159$ kg, SE = 2.9, n = 7 yr, 74 F in Apr	
	$\bar{x} = 0.18$, SE = 0.025, n = 8 yr, 467 uncollared F		
	$\bar{x} = 0.21$, SE = 0.021, n = 5 yr, 273 uncollared F		0.26, SE = 0.011, winters 1999–2001, 15 sites, 113 plants
	$\bar{x} = 0.23$, SE = 0.031, n = 12 yr, 544 uncollared F		
	$\bar{x} = 0.24$, SE = 0.046, n = 4 yr, 338 uncollared F		
	$\bar{x} = 0.27$, SE = 0.027, n = 2 yr, 70 uncollared F		
	$\bar{x} = 0.30$, SE = 0.039, n = 4 yr, 155 uncollared F		
	$\bar{x} = 0.32$, SE = 0.023, n = 3 yr, 186 uncollared F		
	$\bar{x} = 0.32$, SE = 0.056, n = 8 yr, 149 uncollared F		
$\bar{x} = 0.86$, SE = 0.048, n = 5 yr, 135 F ≥48 months	$\bar{x} = 0.41$, SE = 0.031, n = 4 yr, 156 uncollared F; $\bar{x} = 0.37$, SE = 0.066, n = 5 yr, 139 radiocollared F ≥36 months of age; First twins at 36 months of age, 8% of 26	$\bar{x} = 182$ kg, SE = 2.9, n = 5 yr, 75 F in Mar	0.20, SE = 0.008, winter 2002–2003, 39 sites, 235 plants
$\bar{x} = 0.87$, SE = 0.030, n = 5 yr, 219 F ≥36 months	$\bar{x} = 0.44$, SE = 0.054, n = 5 yr, 190 radiocollared F ≥36 months of age; First twins at 36 months of age, 22% of 32	$\bar{x} = 204$ kg, SE = 4.4, n = 19 F in Mar	
$\bar{x} = 0.90$, SE = 0.103, n = 2 yr, 55 F of all ages	$\bar{x} = 0.64$, SE = 0.030, n = 2 yr, 60 radiocollared F of all ages		0.09, SE = 0.005, winter 1999–2000, 40 sites, 234 plants
	$\bar{x} = 0.67$, SE = 0.079, n = 8 yr, 161 radiocollared F ≥36 months of age; First twins at 24 months of age, 29% of 14	$\bar{x} = 213$ kg, SE = 4.3, n = 25 F in Apr	

Moose Capture, Measurement, and Telemetry in GMU 20A, 1996–2006

Each year, we radiocollared moose in equal numbers across both subpopulations. During a 2-day to 5-day period in March (range = 3–18 Mar), we immobilized and weighed 224 female short-yearlings (34–42 in 1997–2001, 20 in 2002, and 10 in 2003) and 82 male short-yearlings (1–3 in 1998–2001, 10 in 2003, and 21–23 in 2004–2006). Capture-related mortalities totaled 10 of 324 (3%) short-yearlings. We immobilized short-yearlings with 1.2 mg (0.4 cc) carfentanil citrate (Wildnil®; Wildlife Pharmaceuticals, Fort Collins, CO) and 60 mg (0.6 cc) xylazine hydrochloride (Anased®; Lloyd Laboratories, Shenandoah, IA) delivered via a 1-cc projectile syringe (1.9-cm needle) fired from a short-range Palmer Cap-Chur™ (Douglasville, GA) pistol or rifle while in slow flight in an R-22 Robinson (one passenger) or R-44 Robinson (3 passenger) helicopter. We

reversed the tranquilization with 125 mg (2.5 cc) naltrexone hydrochloride (Trexonil®; Wildlife Pharmaceuticals) and 200 mg (2.0 cc) tolazaline hydrochloride (Tolazine®; Lloyd Laboratories) using 2 or 3 intramuscular injections. We conducted all aspects of this 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 04-003 for GMU 20A).

We weighed short-yearlings with a dynamometer (227 kg; Dillon, Fairmont, MN) or electronic, calibrated strain gauge (450 kg; Cardinal Scale Manufacturing Co., Webb City, MO) hung from a helicopter or tripod and hoist. We deployed expandable radiocollars on short-yearlings. We used Telonics (Mesa, AZ) model 605-NH transmitters on CB-8 collars. We helped design extra overlapping collar belting and attachment of a bungee to accommodate

growth. We experimented with recapturing these moose at 21 months and 33 months of age and found no problems with the collar design. We usually replaced expandable collars with non-expandable collars when moose reached 69 months of age.

We recaptured known-age adult moose during most years ($n = 175$ total, 1996–2006) and radiocollared unknown-age adults in 1996 ($n = 44$) and 2000 ($n = 16$). Keech et al. (2000) described capture methods during 1996 and 1997; methods were similar thereafter. Stephenson et al. (1998) described ultrasonic measurements of rump fat. We initially radiocollared most of the 2-year-old through 9-year-old moose as short-yearlings; as a result, we knew most of the moose ages. We based all other ages on counts of cementum annuli in canine teeth (Matson's Laboratory, Milltown, MT). We analyzed blood sera for pregnancy-specific protein B (PSPB; Bio Tracking, Moscow, ID; Sasser et al. 1986). We reevaluated the 1997 samples using PSPB analyses in 2002. T. Stephenson (AK Department of Fish and Game) diagnosed pregnancy status using ultrasonography to view cotyledons in 1996 (Stephenson et al. 1995). We categorized pregnancies that did not result in observed live births as unsuccessful.

To monitor reproductive success with telemetry, we observed radiocollared adults ≥36 months of age every 24 hours (1996–1998) or 48 hours (1999–2005) from 11 May through mid-June. We used surveys of newborn calves to monitor reproductive success because predation on spring and summer calves is a dominant, largely additive factor limiting many Alaskan moose populations (Ballard and Miller 1990, Gasaway et al. 1992, Boertje et al. 1995, Testa 2004, Keech 2005). In study areas with improved nutritional status, we observed radiocollared moose ≥24 months of age every 24 hours or 48 hours (weekly in GMU 17A) during the respective calving periods. Deriving parturition rates of radiocollared mature adults required excluding data from the youngest producing cohort in the respective study areas.

Estimating Moose Twinning Rates without Telemetry
We calculated twinning rate as the number of adult females observed with ≥2 newborns divided by the number of adult females observed with ≥1 newborn (Boer 1992, Gasaway et al. 1992). Staff flew late-May or early June transect surveys in the central Tanana Flats during 32 years from 1960 to 2005 to estimate moose twinning rates without telemetry. Staff flew transect surveys during 1-day to 4-day periods in Bellanca Scout or Piper PA-18 aircraft with both an observer and pilot searching for newborns; staff circled to determine if twins were present. In 1989, we followed the Bellanca Scout with a Bell 206 helicopter (3 observers and pilot) to determine if we could detect more twins using a helicopter.

During most springs, we made preliminary flights to detect the first day during which we could observe large numbers of newborns. Using radiocollared moose from 1996 to 2005, we deemed twinning surveys most appropriate beginning about 25–28 May in the Tanana Flats, a few days after the median calving date. During earlier flights, we often observed insufficient numbers of females with newborns. Our objective was to observe ≥50 females with newborns, although this was impractical in study areas with low moose density.

Estimating Browse Removal Rates
We estimated browse removal rate in 5 study areas as sum biomass removed by moose on sampled plants divided by sum biomass of current annual growth on sampled plants. We used diameter of twigs at the base of current annual growth to predict browse production, and diameter of twigs at point of browsing to predict removal (Oldemeyer 1982). We measured diameter of twigs from late March to early May (Seaton 2002). We clipped unbrowsed twigs throughout the winter to estimate regression coefficients relating twig diameter to dry mass (Telfer 1969, Seaton 2002). We derived unique regression coefficients for each browse species and study area, and selected browse plots based on systematic sampling (C. T. Seaton, Alaska Department of Fish and Game, unpublished data). We estimated browse removal only on paper birch (*Betula papyrifera*), quaking aspen and balsam poplar (*Populus* spp.), and willow (*Salix* spp.) that exhibited current annual growth between 0.5 m and 3.0 m above the ground. We derived browse removal estimates using one winter of data in each study area, except in GMU 20D (2 winters). We based standard errors for percent removal per plant on the binomial distribution (Cochran 1977).

Estimating Moose Density
Moose density estimates in GMU 20A during 1960–1994 are from Gasaway et al. (1983) and Boertje et al. (1996). During 1978–1998, we used stratified–random methodology and sightability correction factors derived from intensive searches (Gasaway et al. 1986). During 1999–2005, we used geospatial survey methodology (DeLong 2006, Kellie and DeLong 2006) and a composite sightability correction factor (Gasaway et al. 1986) of 1.21 derived from proportions of radiocollared moose observed during 2003–2006 surveys. Alaska Department of Fish and Game (2002, 2004, 2006) moose management reports describe specific methodology for estimating moose numbers in the respective GMUs.

Statistics
We tested for subpopulation differences in GMU 20A. We used a paired 2-tailed t-test to test for subpopulation differences in parturition rates, and a 2-sample t-test with equal variances to test for subpopulation differences in the mean mass of female short-yearlings (Zar 1999). We used a z-test to test for differences in twinning rates before and after the median calving date (Remington and Schork 1970). We calculated 95% confidence intervals for age-specific parturition and twinning rates using binomial confidence intervals (Cochran 1977). We did not test for differences among other moose population statistics because of differences in years sampled and sample sizes.
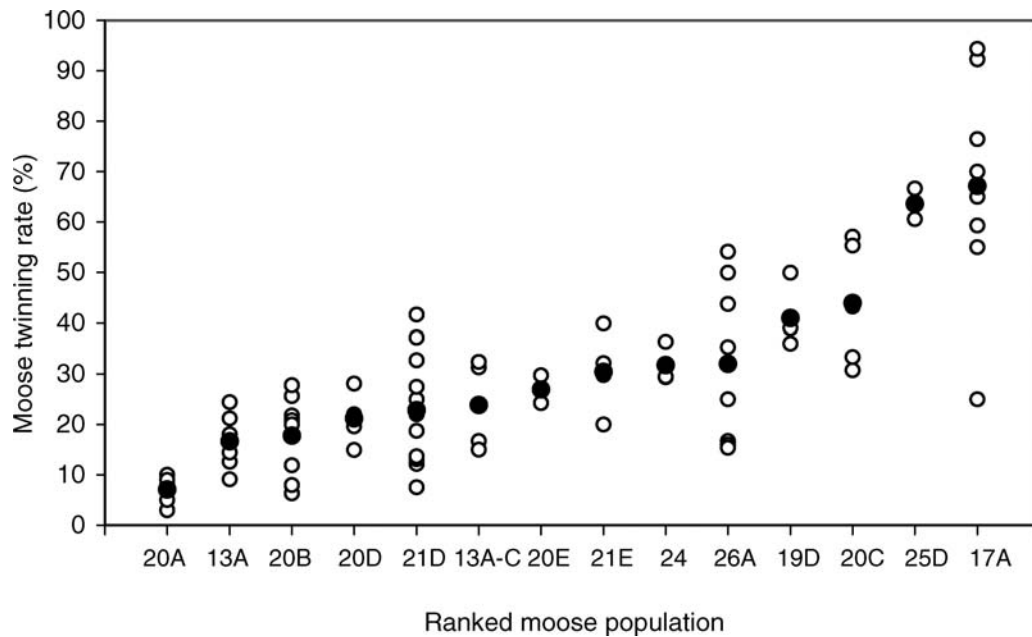
Figure 2. Annual (white) and mean (black) twinning rates from Game Management Unit (GMU) 20A and 13 other moose populations, Alaska, USA, 1994–2005. We ranked the 14 moose populations using respective mean twinning rates to illustrate relative nutritional status from the lowest nutrition (GMU 20A) to the highest (GMU 17A).

RESULTS

Comparative Data from 15 Study Areas in Alaska, 1994–2005

We summarized multiyear twinning data from 15 moose populations or subpopulations in Alaska to rank the respective populations' apparent nutritional status (Table 1; Fig. 2). Using additional data on reproduction and short-yearling mass in 6 of these 15 areas, we highlighted consistencies and inconsistencies in the twinning-based ranking (Table 2). Results largely supported the twinning-based nutritional ranking and an inverse relationship between twinning rates and browse removal rates (Table 2). We ranked each population using ≥2 years of twinning data to reduce the effects of a year of unusual weather; we found no evidence that a multiyear ranking resulted largely from unusual weather.

Unsuccessful Pregnancies or Births, Central GMU 20A, 1996–2005

Based on observations at 24-hour intervals, we failed to observe births among 15% of 41 pregnant females in 1996 and 13% of 23 pregnant females in 1997. Based on observations at 48-hour intervals, we failed to observe births among 10% of 79 pregnant females during 1999–2005. We verified these 143 pregnancies using PSPB analyses from March blood samples. Incorrect diagnosis of pregnancy (false positives) was unlikely because we confirmed the presence of cotyledons with ultrasound in 1996. It is unlikely that we missed many successful births during our flights at 24-hour or 48-hour intervals, because no calf mortality occurred in the first 48 hours after we collared 83 newborns in the Tanana Flats in 1996 and 1997 (Keech et al. 2000). We observed 4 stillbirths and 1 nonviable twin

dwarf among 575 calves born to radiocollared females in GMU 20A.

Relationship between Moose Age and Natality, Central GMU 20A, 1996–2005

Based on observations of live births of radiocollared moose in central GMU 20A, 36-month-old moose gave birth at a low rate (29%, $n = 150$), whereas mature age classes regularly gave birth with age-specific rates ranging from 64% to 85% (Fig. 3). Annual 36-month-old parturition rates ranged from 12% (3/26) to 48% (10/21) during 1999–2004 ($n = 17$–27). We detected no pregnancies among 38 22-month-old moose using PSPB analyses from blood sera. We confirmed the validity of PSPB analyses in March 1996, when transrectal ultrasonography provided consistent results with PSPB analyses ($n = 44$ adult moose).

We observed no viable twins among 43 births of 36-month-old moose and 102 births of 48-month-old moose. Older age classes twinned at rates of 8% to 18% when sample sizes were ≥34, and twinning rates appeared to peak when moose reached 10 years of age (Fig. 4). We consider the twinning data for moose ≥10 years old as preliminary until known-age cohorts reach these ages, particularly because the sample of 11-year-old moose has yet to produce twins.

Parturition Rates, Central GMU 20A, 1997–2005

Annual observed parturition rates among radiocollared moose ≥48 months old averaged 75% (SE = 3.2%, $n = 9$ yr, 602 moose) and ranged from 63% ($n = 93$ moose) to 89% ($n = 102$ moose) during 1997–2005, when twinning rates were ≤10% (Fig. 5). Parturition rates were lower for moose that remained in the Tanana Flats ($\bar{x} = 70\%$, SE = 4.3%, annual range = 55–85%) compared to those that

Table 2. Relationships between twinning rates and other indices of nutritional status in 8 Alaska, USA, moose populations ranked from low to high nutritional status,[a] May 1994–June 2005.

Moose population or subpopulation	Twinning rate (%)	Age when first twinning (months)	Age of first cohort to produce (months)	Parturition rate of first cohort to produce (%)	Parturition rate of mature F (%)	Mar–Apr F short-yearling mass (kg)	Browse biomass removed (%)
GMU 20A, Tanana Flats	7[b,c] 7[d]	60	36	27	70	155	41
GMU 20A, Alaska Range foothills	7[b,c] 12[d]	60	36	30	80	172	43
GMU 13A West	17[c]		36	59	82	159	
GMU 20D Southwest	21[c]						26
GMU 19D, McGrath area	41[c]	36	36	76	86	182	20
GMU 20C South	44[d]	36	24	35	87	204	
GMU 25D West	64[d]				90		9
GMU 17A	67[d]	24	24	74		213	

[a] Data are simplified from Table 1 to highlight consistencies and inconsistencies in the ranking by twinning rate. Sources of data and variability of estimates are in Table 1 for the respective game management units (GMU).

[b] The 7% twinning rates are from central GMU 20A moose when the 2 subpopulations (Tanana Flats and Alaska Range foothills) are mixed on the Tanana Flats.

[c] Data are from aerial surveys without telemetry.

[d] Data are from radiocollared moose and usually from specific age classes of moose.

consistently migrated to the adjacent foothills ($\bar{x} = 80\%$, SE = 3.7%, annual range = 66–95%), and differences were significant ($t = 2.439$, df = 8, $P = 0.041$).

Twinning Rates, Central GMU 20A, 1960–2005

A primary indicator of recent low nutritional status in GMU 20A was the consistent pattern of twinning rates of ≤10% during 9 consecutive years (1997–2005), after many years of moderate and high moose densities (Fig. 5). Historically, twinning rates were highest ($\bar{x} = 37\%$, SE = 2.9%, range = 30–47%, 1977–1982) when moose density was increasing from low levels ($\lambda = 1.15$; Boertje et al. 1996), as expected if

twinning rates increase with an improvement in density-dependent nutrition. In contrast, twinning rates varied from 0% to 22% ($\bar{x} = 12\%$, SE = 1.0%, $n = 33$ yr) when moose density was moderate to high, declining from highs, or first reaching low levels.

Paired airplane and helicopter surveys in 1989 indicated no significant sightability handicap while using an airplane to conduct transect surveys in the Tanana Flats. We observed a twinning rate of 15% from the airplane ($n = 41$ F with newborns) and 16% from the helicopter ($n = 45$).
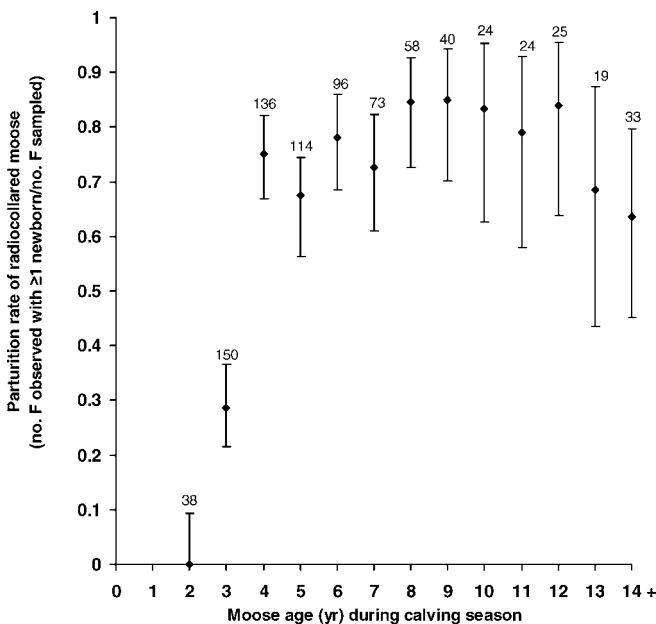

Figure 3. Age-specific observed parturition rates (± 95% CI) of moose in central Game Management Unit 20A, Alaska, USA, from mid-May to mid-June, 1996–2005. Data labels are numbers of radiocollared females sampled for the presence of newborns.
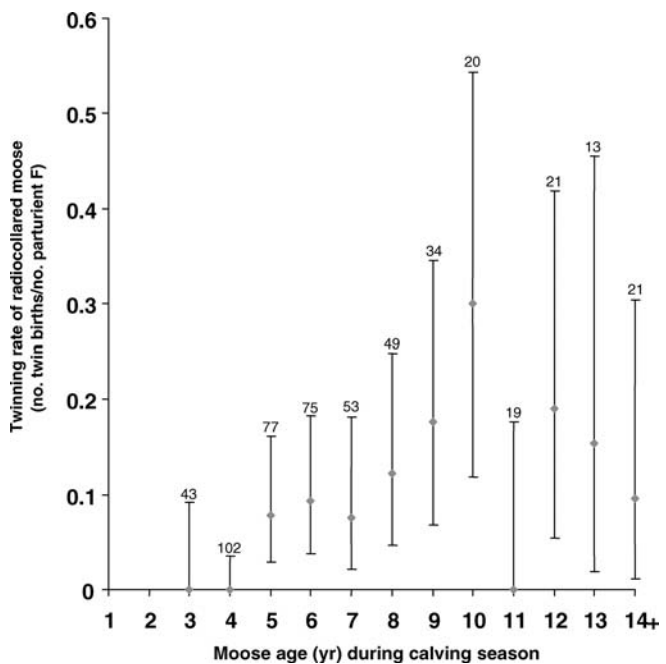

Figure 4. Age-specific observed twinning rates (± 95% CI) of moose in central Game Management Unit 20A, Alaska, USA, from mid-May to mid-June, 1996–2005. Data labels are numbers of radiocollared females observed with ≥1 newborn.
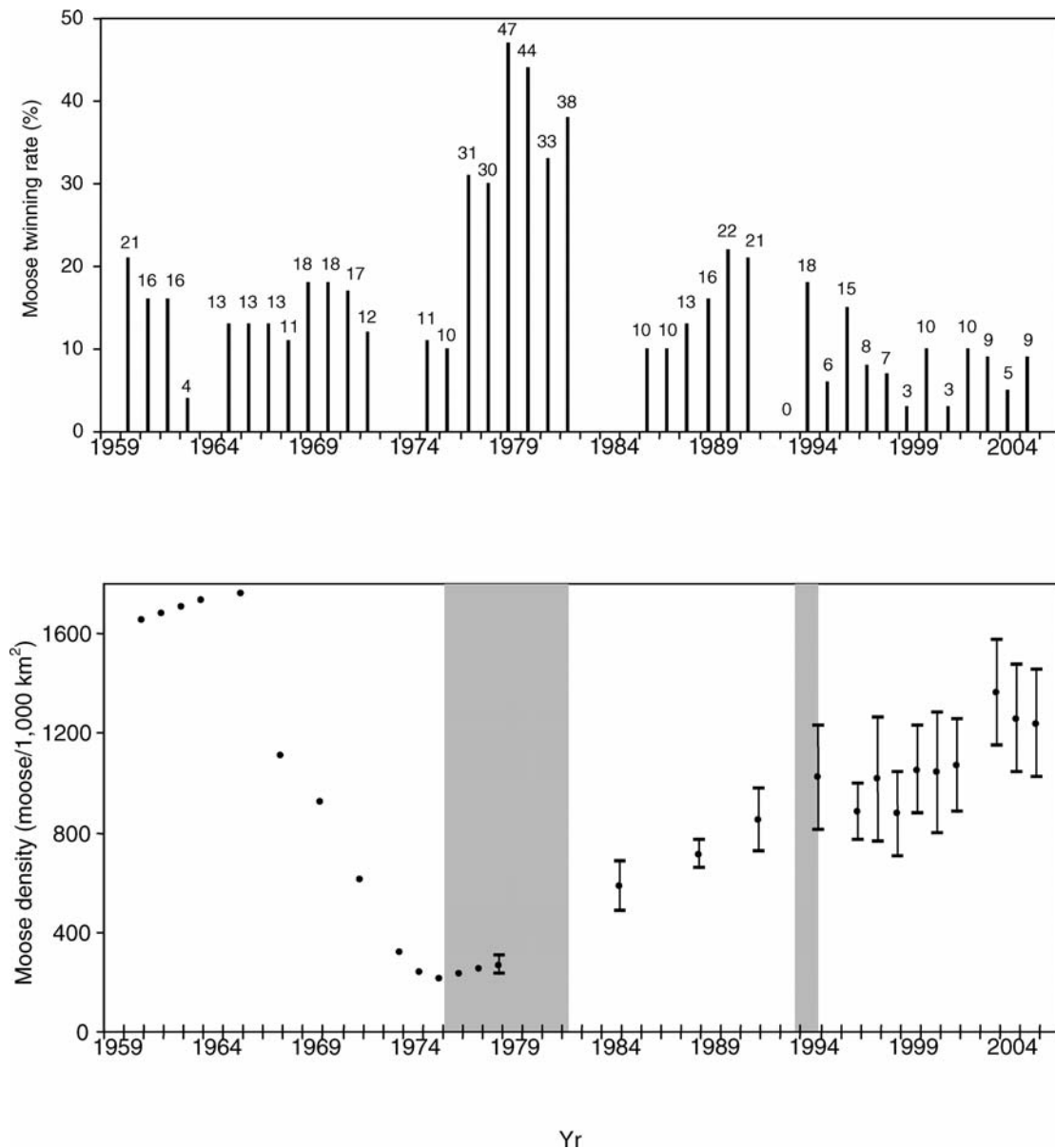
Figure 5. Annual moose twinning rates and corresponding moose densities, Game Management Unit 20A, Alaska, USA, 1960–2005. Twinning rates are from aerial surveys flown in late May or early June in the central Tanana Flats. Exceptions occurred during 1978–1982 and 2000–2001 when twinning rates were from radiocollared moose. Shaded areas correspond to periods of agency wolf control (Boertje et al. 1996).

Twinning was distributed throughout the calving periods, so no bias existed by surveying a few days after the median calving date. No significant differences ($z = 1.21$, $P = 0.226$) existed in the percentage of twins observed before versus after the respective years' median calving dates. Of the 43 twin births documented during this 10-year study, 24 (56%) occurred prior to the respective years' median calving dates and 15 (35%) occurred after the median calving dates.

Mass of Short-Yearlings in the Tanana Flats and Adjacent Foothills Subpopulations

Average mass of short-yearlings was lower in the Tanana Flats compared to that in the foothills during each of the 10 years, 1997–2006. Also, average mass of female short-yearlings was significantly different between the 2 sub-populations during each of the 4 years when sample sizes were ≥37 ($t = 2.55$–3.16, df = 35–40, $P = 0.003$–0.015). Combining females and males, the 10-year average mass was 157 kg (SE $= 1.8$, $n = 153$) for the Tanana Flats and 170 kg (SE $= 1.7$, $n = 153$) for the foothills subpopulations. Overall, average annual masses of short-yearlings varied between 147 kg (SE $= 4.0$, $n = 23$) in 2005 and 180 kg (SE $= 6.2$, $n = 20$) in 2002 compared with a 10-year average mass of 164 kg (SE $= 1.3$, $n = 306$). Although we did not capture large numbers of both males and females during any March to test for possible gender differences, gender differences were small (5 kg) compared to habitat-based subpopulation differences (14 kg). The average mass of males was 160 kg (SE $= 2.3$, $n = 82$), and the average mass of females was 165 kg (SE $= 1.6$, $n = 224$).

Browse Removal Rate in the Tanana Flats and Adjacent Foothills, GMU 20A

During winter 1999–2000, moose removed 41% of the current annual browse biomass sampled in the central Tanana Flats and 43% in the adjacent foothills (Table 1; Seaton 2002). Moose removed a slightly higher rate (46%) of quaking aspen and balsam poplar in the Tanana Flats and willow in the foothills, but a majority of the biomass was not removed for several reasons. Moose apparently did not consider all current annual biomass as preferred food; for example, moose removed an average of only 61% of the current annual biomass on browsed twigs. Also, moose browsed only 32% of the twigs we measured. Moose presumably did not encounter all measured twigs and considered some twigs as unpalatable or too costly to browse, for example, too small or too large in diameter, too low or too high, or shielded by snow or plant architecture (Seaton 2002).

Rump-Fat Depths, Central GMU 20A, March 1996–2000

Maximum rump-fat depths of adult female moose averaged 1.6 cm in 1996 ($n = 43$, SE $= 0.16$), 1.0 cm in 1997 ($n = 30$, SE $= 0.16$), and 0.4 cm in 2000 ($n = 16$, SE $= 0.11$). Overall, maximum rump-fat depths averaged 1.2 cm ($n = 89$, SE $= 0.11$). Short-yearlings ($n = 21$ in 1997) and 21-month-old moose ($n = 20$ in 1998) had no detectable rump fat.

DISCUSSION

Moose nutritional status in GMU 20A ranked as the lowest studied to date in Alaska, based on the indices presented (Table 1; Fig. 2). Also, using historical and current data on twinning rates within GMU 20A (1960–2005; Fig. 5), we inferred that moose nutrition during this study (1996–2005) was lower than during any similar period since 1960, presumably because of the cumulative effects of moose foraging on this habitat. These data were successfully used to implement liberal antlerless harvests in 2004 ($n = 600$) and 2005 ($n = 690$), in contrast to the conservative antlerless harvests of 61–76 moose during each of 5 prior years (1996–1998 and 2000–2001). We deemed the 2004 and 2005 antlerless harvests prudent both to benefit moose hunters and to benefit the short-term and long-term health of this increasing moose population. Total harvests were 7–8% of total prehunt numbers during each of these 2 years, including 388–434 antlered moose and estimates of unreported moose harvest. Prior annual harvests and harvest rates were lower since reporting began in 1960, except during 1972–1974 when excessive harvest rates (10–19%) caused population declines (Gasaway et al. 1983, Boertje et al. 1996, Young et al. 2006).

Only in GMU 20A did nutritional indices reach low levels where justification for halting population growth was apparent, which supports prior findings that nutrition is a minor factor limiting most Alaska moose populations compared to predation (Gasaway et al. 1992; Boertje et al. 1996, 2000; Keech et al. 2000). Although low nutritional status was the primary justification for implementing liberal antlerless harvests in GMU 20A, we also justified these harvests based on an increasing population trend that had resulted in 4,000–5,000 more moose than prescribed in the population objective (Young et al. 2006). However, population objectives were subject to change and therefore had less influence on our decision. We observed stable or declining population trends in most of the other 13 study areas (Table 1), and population objectives were to increase moose numbers except in GMUs 20B and 20D (Alaska Department of Fish and Game 2002, 2004, 2006).

We discuss several indices to nutritional status below and the utility of these data to encourage prudent integration of nutritional indices into management programs, particularly in areas with reduced predation. Currently, the regulatory boards often base population objectives on historically high population levels or demands for harvest often without a perspective on relative nutritional status. To be most useful, we believe an index to nutritional status should 1) generally agree with the multiyear twinning-based ranking, 2) have a wide-ranging scale across the extremes of nutritional status, 3) be cost-effective, and 4) exhibit low annual variability during a few consecutive years within a study area, unless unusual weather occurs (Albright and Keith 1987, Ballard et al. 1996, Boertje et al. 1996).

Age-of-First-Reproduction and Parturition Rates of Young Cohorts

The percentages of 24-month-old and 36-month-old moose observed with calves in May provided a ranking consistent with twinning rate and exhibited a wide-ranging and stepwise scale across the extremes of nutritional status (Table 2). These 24-month-old and 36-month-old moose were known-age moose collared as short-yearlings. Annual values in GMU 20A did not overlap totals from other areas. Apparently, the low mass of short-yearlings in GMU 20A delayed the age-of-first-reproduction, consistent with findings elsewhere (Blood 1974; Sæther and Haagenrud 1983, 1985; Ferguson et al. 2000). As age-of-first-reproduction and age-of-first-twinning decreased, parturition rates increased (Table 2) presumably because of improved nutrition (Franzmann 1977, Mautz 1978).

Boer (1992) reviewed indicators of reproductive performance in moose populations across North America and reported that both yearling pregnancy rates and adult twinning rates changed at approximately the same rate in moose populations at different levels of nutritional status. Thus, both rates appeared to be influenced by the same factors. We provide data showing that, in areas where 24-month-old moose fail to give birth, the percentage of 36-month-old moose giving birth is an additional index to relative nutritional status that apparently can allow differentiation among areas of moderate and low nutritional status (Table 2).

Parturition Rates of Mature Adults

Multiyear average parturition rates for females ≥36 months or ≥48 months old provided a ranking consistent with the ranking of twinning rates in the 6 areas from which similar

data were gathered (Table 2). We recommend caution when using average adult parturition rates to rank nutritional status because these rates had a narrow-ranging scale (70–90%) across the extremes of nutritional status. Also, given the high annual variation in these parturition rates (e.g., 55–85% in the Tanana Flats subpopulation), a single year of adult parturition rates can be an insensitive index to nutritional status (Schwartz 1998). Averaging values among several years increased the value of this index (Table 2), but the capture and observation of adequate samples of adult moose for multiple years is a slow and costly approach to ranking nutritional status. The Tanana Flats subpopulation exhibited the lowest average observed parturition rate reported to date among wild moose populations in North America (Table 2; Schwartz 1998).

Twinning Rates

Moose twinning rates were the most widely available index to nutritional status in Alaska (Fig. 2). Biologists favor twinning rate as an index to nutritional status because twinning rates are the easiest and often the least costly index to obtain and because several studies of penned and wild moose recognized that twinning rates varied with nutritional status (Blood 1974, Franzmann and Schwartz 1985, Boer 1992, Gasaway et al. 1992, Keech et al. 2000). We used only multiyear twinning rates to rank nutritional status (Table 1; Fig. 2) because of the variability that can exist between consecutive years (Fig. 5).

The 39 years of twinning rates and moose density in GMU 20A (Fig. 5) lends support to the use of multiyear twinning rates to rank nutritional status. The highest twinning rates occurred during a period of low and increasing moose numbers, when density-dependent factors would have had the least influence on limiting fecundity. Also, the decade of lowest twinning rates occurred during this study, presumably due to the cumulative effect of having moderate to high moose densities for most years since 1960 and the lack of widespread habitat rejuvenation. The only important burn benefiting moose in GMU 20A from 1958 through 2000 was a 500-km^2 burn in 1980 (Gasaway et al. 1989).

Twinning rates did not recover in 1975 and 1976 when moose density first reached its lowest level. We inferred that a few years of browse recovery might be required before twinning rates would increase (cf. Blood 1974). Based on weather data from the mid-1970s in Fairbanks, we discounted that short summers caused the low 1975 and 1976 twinning rates (as observed in 1993; Boertje et al. 1996, National Weather Service 1960–2005).

The scale of twinning rates reported here ranged from 0% in 1993 in GMU 20A (Fig. 5), following an extremely short summer (Boertje et al. 1996), to an 8-year average of 67% (SE = 7.9%) in GMU 17A, where moose recently colonized unbrowsed ranges (Table 1). Average multiyear twinning rates of 7% (SE = 0.9%) from transect surveys in central GMU 20A (1997–2005; Fig. 5) indicated low nutritional status relative to other recent and past multiyear Alaska studies of wild moose (17–71% twinning; Table 2; Gasaway

et al. 1992). However, multiyear twinning rates among wild Alaska populations can decline further than the 7% observed to date based on multiyear penned moose studies (0% twinning; Schwartz 1998) and studies on the island of Newfoundland, Canada (1–3%; Albright and Keith 1987). Thus, we found no empirical evidence that the increasing GMU 20A moose population was going to enter a rapid decline because of failed reproduction or nutritional feedback.

We achieved relatively large, inexpensive, and unbiased samples of twinning rate with transect surveys ($\bar{x}$ = 72 moose, SE = 10.5, n = 32 yr of data) compared with following radiocollared moose, which often have a biased age structure. For example, the absence of young radio-collared cohorts can bias twinning rates high where nutrition is lowest (Fig. 4). Historically, staff surveyed twinning rates from 20 May to 28 May, even after adverse winters in GMU 20A, although calving occurs later in other areas of the state (Ballard et al. 1991). Surveying soon after the median calving date helps maximize sample size while minimizing the underestimating bias that can exist when, in particular, black bears kill one calf of a set of young twins (Osborne et al. 1991). Where moose density is very low and or cover is dense, measuring twinning rates may require radiocollaring females in winter and several subsequent May and June flights to document calving success.

Mass of Short-Yearlings

Mass of short-yearlings was particularly useful in differentiating between the 2 subpopulations of moose in GMU 20A (Table 1). These subpopulations overlapped in ranges during most of April, May, and June, yet masses of female short-yearlings were significantly different between the 2 subpopulations during each of the 4 years when sample sizes totaled $\geq$37. We found no other index that provided this level of differentiation between the 2 subpopulations (Table 2). Also, the wide-ranging scale across current extremes of nutritional status ($\bar{x}$ = 155–213 kg; Table 2) increases the value of this index. Sæther and Haagenrud (1985), Sæther and Heim (1993), and Sæther et al. (1996) discuss the relationship between yearling mass and age of first reproduction.

We noted 4 drawbacks to relying on short-yearling mass to rank nutritional status. First, an inconsistency occurred in GMU 13A where average April female short-yearling mass (159 kg; SE = 2.9, n = 74) was similar to the average March female short-yearling mass in GMU 20A (165 kg; SE = 1.6, n = 224), yet reproductive success was less in GMU 20A (Table 2). Differences in the mass required to reach puberty may help explain why the GMU 13A moose population reproduces at a higher rate than in GMU 20A (cf. Sæther et al. 1996). We rejected the hypothesis that moose may grow faster from short-yearling age to reproductive age in GMU 13A than in GMU 20A because data indicate moose do not compensate for low calf body mass later in life (Keech et al. 1999, Hjeljord et al. 2000).

A second drawback to relying on short-yearling mass to rank nutritional status was the logistical problem of locating

adequate numbers of female short-yearlings in areas with low moose density, low calf survival, or both. We recommend measuring mass of males and females in these areas because gender differences were small compared to subpopulation differences in GMU 20A. A third drawback is that annual variation in short-yearling mass can be fairly great with small sample sizes. For example, the annual average ranged from 147 kg (SE = 4.0, $n = 23$) to 180 kg (SE = 6.2, $n = 20$) in GMU 20A in recent years. As a result, we recommend >1 year of data to rank nutritional status, except where average weights are $\geq$190 kg. A final drawback is that no fecundity data are gathered, and measuring fecundity is a more accepted approach to ranking nutritional status. However, weighing short-yearlings appears to be an adequate baseline step to ranking nutritional status, particularly if average weights are high ($\geq$190 kg).

Browse Biomass Surveys
Browse biomass removal rates of >35% appear to indicate low moose nutritional status (Table 2). Currently this implied index fills the need for an affordable vegetative index that appears useful for ranking nutritional status. We recognize that this index may be useful only where winter moose rely largely on measurable browse species. We did not measure incidental browsing on alder (*Alnus* spp.), shrub birch (*Betula glanduolsa*), or dwarf birch (*B. nana*) which are among the most abundant but least preferred shrubs in Alaska (Bryant and Kuropat 1980, Seaton 2002).

A relatively high proportion of preferred willow in the diet of foothills moose (Seaton 2002) may have been a factor causing significantly greater parturition rates and short-yearling masses in the foothills moose compared to the flats moose (Table 1). For example, 95% of the browse biomass removed in the foothills was preferred willow compared to 9% in the flats, and the average mass of current annual growth of willow twigs in the foothills was 2.4 times greater than in the flats (Seaton 2002). Regardless of these apparent differences in diet quality, the nutritional status of both subpopulations ranked as low, presumably because moose were consuming a high proportion of the available palatable food relative to other areas in Alaska (Table 2; Fig. 2); that is, moose were having difficulty finding adequate food.

Rump-Fat Depths
Originally, we measured rump-fat depths to evaluate whether young cohorts had sufficient rump fat to help distinguish favorable versus unfavorable weather patterns. However, we found no rump fat on March calves and yearlings in the GMU 20A study area.

The fattest winter adult females are more likely to be pregnant and not tending a calf (Testa and Adams 1998, Keech et al. 2000). However, moose can apparently utilize most rump fat by March in areas with high and low nutritional status. For example, Bertram and Vivion (2002) reported median March rump-fat depths of 1.0 cm (SE = 0.19, range 0–1.8 cm, $n = 13$) in adult female moose in GMU 25D, where moose fecundity was high (Table 1; Fig. 2). These rump-fat depths were similar to median March rump-fat depths in GMU 20A (0.8 cm; SE = 0.11, range 0–3.8 cm, $n = 89$). Therefore, March rump fat can be an insensitive index to a population's reproductive success.

Using Signals to Begin Antlerless Harvests
We recommend that an increasing population trend be well documented before initiating successive annual liberal antlerless harvests because of the risk of accelerating declines and alienating users (Gasaway et al. 1983). We specifically recommend against initiating liberal antlerless harvests based solely on average twinning rates of 10–30% (Fig. 2). We caution that twinning rates of 12–18% (Fig. 5) were inappropriate signals to begin liberal antlerless harvests in the early 1970s in GMU 20A because the population was declining. In 2006, we successfully implemented conservative antlerless harvests in and near settled portions of GMUs 20B and 20D (Fig. 1; Table 1), where moose densities were high and increasing, and predation was reduced. Associated twinning rates of 18% and 21%, alone, did not signal that liberal antlerless harvests were prudent. Instead, we based these harvests and the potential for liberal harvests on increasing population trend, increased human–moose conflicts, and demand for additional yield.

We recommend at least one of the following signals to substantiate low twinning-based nutritional status: <50% of 36-month-old moose are parturient, average multiyear short-yearling mass is <175 kg, or >35% of annual browse biomass is removed by moose. The choice among these 3 indices will ultimately depend on the personnel involved and the logistical and economic trade-offs unique to a study area. For example, surveying reproductive rates and weighing calves may be more economical than browse surveys in remote areas accessed by helicopter, particularly considering the additional personnel and time required to analyze browse data. We currently recommend the documentation of $\geq$2 indices to nutritional status, in part because of the daunting task of convincing a skeptical public to allow a liberal antlerless harvest. Many people remain opposed to the liberal antlerless harvests in GMU 20A (Young and Boertje 2004, Young et al. 2006), in part because they prefer to see the maximum number of moose on the landscape and remember that antlerless harvests contributed to population declines in these predator-dominated systems in the 1970s.

To the public, the most persuasive, data-driven argument favoring liberal antlerless harvests in GMU 20A in 2004 was that further stockpiling of moose was clearly detrimental to the moose population's health and habitat (Table 2; Figs. 2, 5). A secondary argument was that a precipitous population decline might be imminent and therefore liberal antlerless harvests should begin before the moose die (Fig. 5). This argument was less convincing for 2 reasons. First, a weather-induced decline may not be imminent; for example, weather-induced declines of moose have not been documented in most of Interior Alaska during the last 35 years, despite record-level deep snow in the early 1990s (Boertje et al. 1996). Second, we found no evidence that density-dependent feedback would soon cause a precipitous decline in this growing population (Fig. 5; cf. Albright and Keith

1987, Sæther et al. 1996), despite obvious density-dependent factors (Table 2; Fig. 2).

MANAGEMENT IMPLICATIONS

A system is now available for ranking the nutritional status of a moose population within a continuum of values and between the extremes likely to be found in Interior Alaska. When moose nutritional status declines to values similar to that in GMU 20A, our recommended thresholds to low nutritional status should be sufficient to convince the public to allow liberal antlerless harvests to halt moose population growth. When a moose population initially declines from liberal antlerless harvests, there may be little or no immediate increase in nutritional status, so we recommend caution to prevent an accelerated decline to low densities (cf. Gasaway et al. 1983). Where moose nutritional ranking is higher than in GMU 20A and a moose population is stable or declining, non-nutritional factors are apparently the major factors limiting population growth (cf. Gasaway et al. 1992).

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