Research Article

Effects of Predator Treatments, Individual Traits, and Environment on Moose Survival in Alaska

MARK A. KEECH,[1] *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*

MARK S. LINDBERG, *Department of Biology and Wildlife, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-7000, USA*

RODNEY D. BOERTJE, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*

PATRICK VALKENBURG,[2] *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*

BRIAN D. TARAS, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*

TOBY A. BOUDREAU,[3] *Alaska Department of Fish and Game, P.O. Box 230, McGrath, AK 99627-0230, USA*

KIMBERLEE B. BECKMEN, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*

ABSTRACT We studied moose (*Alces alces*) survival, physical condition, and abundance in a 3-predator system in western Interior Alaska, USA, during 2001–2007. Our objective was to quantify the effects of predator treatments on moose population dynamics by investigating changes in survival while evaluating the contribution of potentially confounding covariates. In May 2003 and 2004, we reduced black bear (*Ursus americanus*) and brown bear (*U. arctos*) numbers by translocating bears ≥240 km from the study area. Aircraft-assisted take reduced wolf (*Canis lupus*) numbers markedly in the study area during 2004–2007. We estimated black bears were reduced by approximately 96% by June 2004 and recovered to within 27% of untreated numbers by May 2007. Brown bears were reduced approximately 50% by June 2004. Late-winter wolf numbers were reduced by 75% by 2005 and likely remained at these levels through 2007. In addition to predator treatments, moose hunting closures during 2004–2007 reduced harvests of male moose by 60% in the study area. Predator treatments resulted in increased calf survival rates during summer (primarily from reduced black bear predation) and autumn (primarily from reduced wolf predation). Predator treatments had little influence on survival of moose calves during winter; instead, calf survival was influenced by snow depth and possibly temperature. Increased survival of moose calves during summer and autumn combined with relatively constant winter survival in most years led to a corresponding increase in annual survival of calves following predator treatments. Nonpredation mortalities of calves increased following predator treatments; however, this increase provided little compensation to the decrease in predation mortalities resulting from treatments. Thus, predator-induced calf mortality was primarily additive. Summer survival of moose calves was positively related to calf mass ($\beta > 0.07$, SE = 0.073) during treated years and lower ($\beta = -0.82$, SE = 0.247) for twins than singletons during all years. Following predator treatments, survival of yearling moose increased 8.7% for females and 21.4% for males during summer and 2.2% for females and 15.6% for males during autumn. Annual survival of adult (≥2 yr old) female moose also increased in treated years and was negatively ($\beta = -0.21$, SE = 0.078) related to age. Moose density increased 45%, from 0.38 moose/km² in 2001 to 0.55 moose/km² in 2007, which resulted from annual increases in overall survival of moose, not increases in reproductive rates. Indices of nutritional status remained constant throughout our study despite increased moose density. This information can be used by wildlife managers and policymakers to better understand the outcomes of predator treatments in Alaska and similar environments. © 2011 The Wildlife Society.

KEY WORDS additive, *Alces alces*, *Canis lupus*, condition, indices, limitation, predation, survival, *Ursus americanus*, *Ursus arctos*.

Effective management of moose (*Alces alces*) populations in many northern systems requires that managers understand the effects of predation by wolves (*Canis lupus*), brown bears (*Ursus arctos*), and black bears (*U. americanus*). These 3 predators have been important sources of mortality for moose at both low (Boertje et al. 1988, Larsen et al. 1989, Bowyer

et al. 1998, Bertram and Vivion 2002*a*) and high moose densities (Franzmann and Schwartz 1980, Ballard et al. 1981, Gasaway et al. 1983). Moose survival and density have been increased by reductions in predator numbers (Gasaway et al. 1983, Stewart et al. 1985, Ballard and Miller 1990, Boertje et al. 1996, Hayes et al. 2003). However, relevant detailed individual and environmental covariate data have been lacking in manipulative moose predation studies to date.

Identifying the effects of predator treatments requires evaluating the contribution of variables other than predator treatments that can influence survival (White et al. 2010). Condition of individual moose affects their susceptibility to predation (Testa and Adams 1998, Keech et al. 2000, Swenson et al. 2007) and density, age, and weather can influence moose survival independent of predator treatments (Van Ballenberghe and Ballard 1997; Boertje et al. 2007, 2009). By assessing survival in this broader ecological context, we could potentially increase our understanding of additive versus compensatory mortality and proximate versus ultimate factors affecting predator-ungulate dynamics (Linnell et al. 1995, Ballard and Van Ballenberghe 1998, Zager and Beecham 2006).

We had a unique opportunity to investigate the effects of predation, individual traits, and environmental covariates on survival of moose following predator treatments. Our principle objective was to examine the relationship between moose survival and predator treatments. Our study included 2 untreated years (2001 and 2002) and 5 treated years (2003–

2007), allowing us to compare survival before and following predator treatment. Treatments consisted of 2 yr of bear translocations (2003 and 2004) and 4 complete years (2004–2007) of aircraft-assisted take of wolves. In addition, we investigated the effects of individual moose characteristics, moose density, and environmental conditions on moose survival to gain better insights on the potential effects of predator treatments. We also estimated and compared cause-specific rates of moose mortality during untreated and treated years, analyzed moose population trends, and quantified the effect of harvest on the moose population.

STUDY AREA

We studied moose in a 1,368-km^2 area (62°58′N, 155°35′W) on the upper Kuskokwim River, near McGrath in western Interior Alaska, USA. The area was comprised primarily of the broad floodplains of the Kuskokwim and Takotna rivers and adjacent rolling hills. Elevations varied between 102–566 m, and moose used all available habitats (Fig. 1).

Two large rivers played a major role in the creation of shallow oxbow lakes and mixed-age successional plant communities. In these areas, early successional willow (*Salix* sp.) and alder (*Alnus* sp.) graded into stands of mature cottonwood (*Populus balsamifera*), white spruce (*Picea glauca*), and paper birch (*Betula papyrifera*) ultimately replaced by climax bogs and older forests of black spruce (*Picea mariana*) and tamarack (*Larix laricina*). In the hills, lower elevations were characterized by stands of white and black spruce, paper birch, and quaking aspen (*Populus tremuloides*), whereas
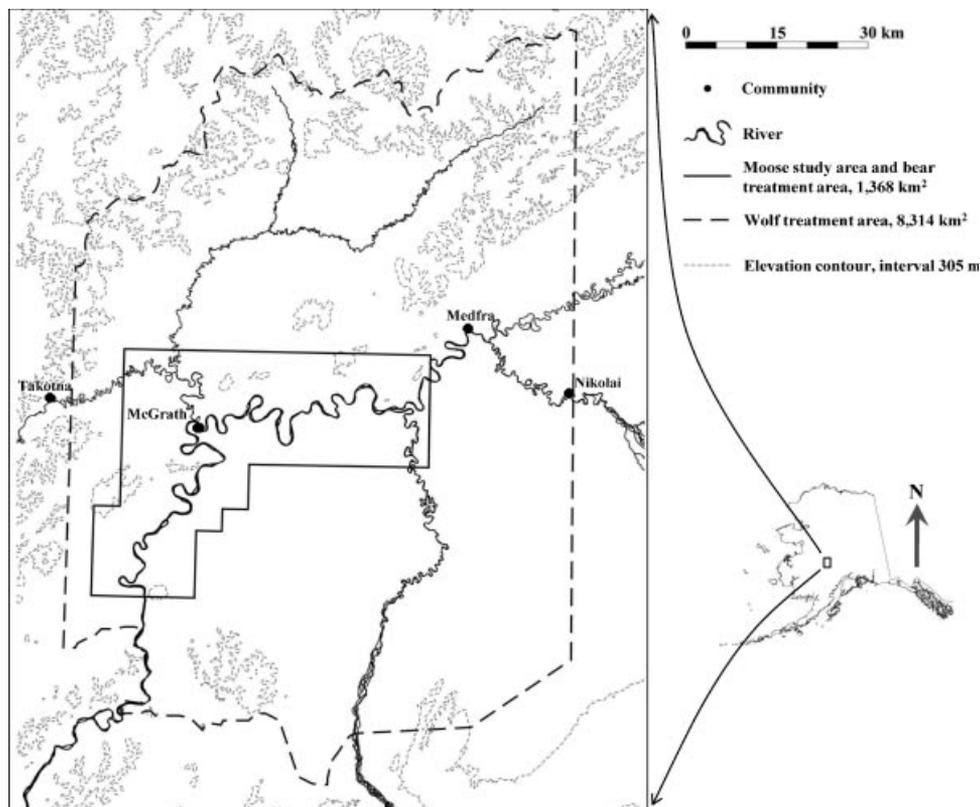

Figure 1. Locations of the 1,368-km^2 moose study area and bear treatment area, and the 8,314-km^2 wolf treatment area, western Interior Alaska, USA, 2001–2007.

shrub communities of willow, dwarf birch (*B. glandulosa* and *B. nana*), and alder predominated at higher elevations. A natural fire regime, including a fire that burned 16.5% of the study area during summer 2002, contributed to a mosaic of shrub, young spruce forest, and older mixed taiga. The 2002 burn occurred in upland spruce forest and radiocollared moose movements were not influenced during our study. Substantial regrowth did not occur until 3–4 yr post-burn.

Temperatures ranged 31° C in summer to −47° C in winter, and early March snow depth ranged 41–104 cm ($\bar{x} = 61$ cm, SE = 7.7). In general, this region experienced more frequent snowfall and snow accumulation than elsewhere in Interior Alaska. During 2000–2007 average late-winter snow depth (Ballard et al. 1991) was 65 cm (2000), 51 cm (2001), 25 cm (2002), 49 cm (2003), 98 cm (2004), 47 cm (2005), 47 cm (2006), and 65 cm (2007). The period of snow cover usually extended from late October to the beginning of May.

Large predators of moose included wolves, black bears, and brown bears. Caribou (*Rangifer tarandus*) were the only alternate large prey and occurred sporadically in low numbers at the northern edge of the study area.

METHODS

Black and Brown Bear Treatments and Capture

During 2003 and 2004 translocation efforts, we employed 3 methods for catching black and brown bears: 1) aerial search and darting ($n = 94$ black bears and 5 brown bears) in the entire study area; 2) baited cubbies with Aldrich spring-activated foot snares (Beecham and Rohlman 1994) set along major waterways ($n = 15$ black bears and 2 brown bears); and 3) breakaway radio-snares (Boertje et al. 1987) set at moose carcasses to enable later aerial darting ($n = 2$ brown bears). We moved 75 black bears (including 8 dependent young) and 8 brown bears (including 2 dependent young) from within and immediately outside (<3.5 km) the study area during 11–31 May 2003. We moved 34 black bears (including 8 dependent young) and 1 independent brown bear from the study area during 12–22 May 2004. We attempted to minimize study-induced abandonment of young by avoiding capture of female black bears with cubs of the year and some females with yearling cubs; we purposely did not capture 16 adult female black bears associated with 33 dependent cubs in the study area in 2003. In May 2004, we observed no cubs of the year and removed all observed bears.

We immobilized bears using 4.4–8.8 mg/kg Telazol® (Fort Dodge Laboratories, Inc., Fort Dodge, IA), administered intramuscularly via 3–8 cubic centimeter (cc) darts. We marked all bears with an upper lip tattoo and ear tags. With the exception of 14 bears taken to the University of Alaska Fairbanks, we translocated bears by aircraft to sites ≥240 km from our study area. We assumed 240 km would be an adequate distance to minimize return to the study area based on home range movements of Interior Alaska black bears (Bertram and Vivion 2002b). We confirmed this assumption based on the relatively few recaptures in years that followed

(2 of 37 captures during 2006 and 2007). We kept bears sedated during transport (2–6 hr) with supplemental doses of Telazol, ketamine hydrochloride, and diazepam hydrochloride.

Estimating Black and Brown Bear Abundance

To estimate untreated abundance of black bears and the proportion of bears removed, we used removal estimators (Gould and Pollock 1997) while accounting for female bears with dependent cubs intentionally left in the study area. We estimated the abundance of independent black bears because cubs were unlikely to kill moose calves. To estimate females with dependents remaining in the study area after 2003 treatments, we used the known number of bears remaining, an estimate of family size, and an inflation factor to account for unobserved family groups. We estimated the inflation factor using an average probability of encounter from the removal analysis. Because we could not quantify the uncertainty in this inflation factor, the standard error for the untreated black bear abundance is approximate. We based our estimate of black bear numbers in 2004 solely upon the removal estimator because we removed all bears encountered during 2004.

To determine removal estimates, we ran the closed capture models in Program MARK (version 5.1, updated 15 Nov 2008; White and Burnham 1999) constraining recapture probabilities to zero. The global model (M_{tbh}) accommodated temporal and behavior effects as well as individual heterogeneity (Otis et al. 1978, White et al. 1982, Norris and Pollock 1996, Pledger 2000). We considered models with bears grouped by sex and models with relative effort as a temporal covariate. For 2003 we developed a relative-effort metric based on a qualitative weighting of the 2 capture methods (foot snares and aerial darting) used for black bears. We did not use daily effort as a covariate in 2004 as it was nearly constant. For the removal models as well as the mark–resight and survival analyses that follow, we developed a set of candidate models, selected models using Akaike's Information Criterion for small sample sizes (AIC_c; Sugiura 1978, Hurvich and Tsai 1989) and Akaike weights (Burnham and Anderson 2002), and, where applicable, assessed model fit using the variance inflation factor ($\hat{c}$).

Although treatments were not specifically designed to determine bear abundance we considered our estimates of the proportion of black bears removed reliable. Daily coverage of the study area was sufficient to approximate a similar capture probability for all bears, and although we did not assess closure during the treatments, telemetry data from the mark–resight survey described below support an assumption of limited movement during this time period. Additionally, we determined that uncertainty in the relative-effort covariate values and our estimate of females remaining after the 2003 treatments had little effect on our estimate of initial population size.

During May 2007, we used mark–resight techniques to estimate abundance of independent black bears using the study area (Miller et al. 1987, 1997). We captured and radiocollared (model 500; Telonics, Inc., Mesa, AZ,

modified to drop-off as described by Hellgren et al. 1988) bears in 2006 and 2007 (20 bears during 12–15 May 2006 and 17 bears during 2–4 May 2007) to minimize the potential for marking bias based on reproductive status. We used aerial search and darting with drug doses described in the previous section for all captures. For the survey, we partitioned the study area into 5 sections, each approximately 275 km^2, and searched all sections daily 1–8 May, totaling 8 sampling occasions. We searched areas using small aircraft (Piper PA-18, Piper Aircraft Corporation, Lock Haven, PA, or Bellanca 8GCBC, American Champion Aircraft Corporation, Rochester, WI) at approximately 1.2 min/km^2. Additionally, we located all radiocollared bears on each sampling occasion to identify marked bears present within the study area. For all bears located during the survey we recorded the location, the general habitat type, and the number of dependent young present.

We determined the 2007 black bear abundance using an extension of the nonlinear logit-normal mixed effects estimator (LNE; McClintock et al. 2009). This approach modified the LNE to account for immigration and emigration (IELNE) by adding a binomial term to the likelihood, modeling the probability that an animal was in the search area (McClintock and White 2011). The IELNE allowed for the introduction of marks between sampling occasions, produced estimates of the number of animals using the study area during the survey (i.e., the super population) and an average of the number of animals in the study area on each occasion, and enabled us to assess whether density within the study area was constant throughout the survey. The IELNE did not require all animals to have the same sighting probability within occasions, and variability in resighting probabilities was accounted for by including a random effect for individual heterogeneity and temporal and individual covariates.

We did not directly estimate brown bear abundance in our study area. We assumed that the untreated (2003) brown bear density was similar to other areas of Interior Alaska with comparable habitat (i.e., continental climate, forested, and limited salmon [*Oncorhynchus* spp.] resources). Miller et al. (1997) reported brown bear densities of 6.4–11.4 bears ≥2 yr old/1,000 km^2 based on mark–resight techniques for similar Interior Alaska study areas. We used the midpoint of this range (9 bears/1,000 km^2) to approximate untreated abundance of brown bears in our study area. We calculated abundance following treatment by subtracting the number of bears removed from the untreated approximation.

Wolf Treatment

To reduce wolf predation on moose during February 2004–April 2008 the Alaska Board of Game established an 8,314-km^2 wolf treatment area (Fig. 1), which encompassed our study area. Private citizens familiar with aircraft-assisted take of wolves received special permits to shoot wolves in winter within the wolf treatment area with no limit. Aircraft-assisted take involved pilots or pilot–passenger teams using aircraft to locate and shoot wolves directly from the air or immediately after landing near wolves.

In addition, liberal conventional hunting and trapping seasons for wolves occurred within the wolf treatment area during the entire study. Hunting season was 10 August–30 April during 2001–2003 and 1 August–31 May during 2004–2007, with a daily limit of 10 wolves during all years. Trapping season was 1 October–30 April with no limit. Any individual who possessed a valid harvest license could hunt and trap wolves.

Estimating Wolf Density

We conducted wolf surveys (Stephenson 1978, Gasaway et al. 1983, Hayes and Harestad 2000) during 21–24 February 2001, 17–19 March 2005, and 14–17 March 2006 to estimate wolf density. Wolves have large territories (500–2,500 km^2; Mech et al. 1998) in Interior Alaska, and our study area was comparatively small (1,368 km^2) and contained only portions of pack territories. Therefore, we used estimates of wolf density for the 8,314–km^2 wolf treatment area (Fig. 1).

We conducted surveys several days following a fresh snowfall (<8 days). We used 3–4 small aircraft flown by pilots experienced at snow-tracking wolves. We searched the entire area, generally using parallel transects, with increased effort along likely wolf travel routes, following tracks until we sighted the wolves or until the tracks were lost. If we did not observe wolves or if they were obscured by cover, we estimated wolf numbers from tracks where individuals traveled separate paths. Survey teams met daily to summarize observations and to resolve potential discrepancies. To estimate population size, we totaled the number of wolves believed to occupy territories primarily within the survey area plus 50% of wolves believed to occupy territories substantially overlapping survey area boundaries.

Capture and Monitoring of Adult and Short-Yearling Moose

We captured 25 adult female moose (>33 months old) during 24–28 March 2001 and 15 during 26–27 March 2002. We also captured 15 short-yearling (10-month-old) female moose annually during late March or early April 2001–2007. We identified short-yearling moose prior to capture by behavior, pelage, and length of the face; we made final determination following capture based on tooth eruption (Peterson et al. 1983, Boertje et al. 2009). We captured and immobilized moose as described by Boertje et al. (2007), and we attempted to capture moose proportionate to the geographic distribution of the March moose population. We considered 1 (2.5%) adult and 5 (4.8%) short-yearling moose to be study-induced mortalities because they died within 3 weeks of capture and moved little beyond capture sites.

We extracted a canine tooth from adult moose to determine age from cementum annuli (Gasaway et al. 1978, Boertje et al. 2009) and weighed short-yearling moose with a 450-kg capacity dynamometer (Dillon, Fairmont, MN) attached below a helicopter or a portable tripod and winch. We deployed very high frequency (VHF) radiocollars (Telonics model 600NH) on all 25 adult moose captured in 2001 and 5 of 15 captured in 2002. We also deployed

radiocollars (CB-8 collars with 600NH transmitters) on all 15 short-yearling moose captured each year during 2001–2004, 9 of 15 captured in 2005, and 11 of 15 captured in 2006. Collars were equipped with motion-sensitive mortality sensors.

We monitored radiocollared short-yearling and yearling moose monthly to detect mortalities and movements. We monitored radiocollared adults ($\geq$3 yr of age) daily in May and early June to detect newborn calves and approximately monthly for the remainder of the year. During May and early June radiotracking flights (2002–2007) we also recorded observations of twin and single calves of uncollared females (Boertje et al. 2007) to determine twinning rates (i.e., the percentage of twins among parturient females). We conducted all aspects of our study in accordance with acceptable methods for field studies adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998) and Alaska Department of Fish and Game (Protocols 04–005, 04–007, 08–13).

Capture and Monitoring of Newborn Moose
To locate newborn moose calves for capture from mid-May through early June 2001–2007, we radiotracked adult females and opportunistically searched for calves of uncollared females. We captured newborns as soon as practical, typically within 1 day of observation. We captured 422 calves: 220 from radiocollared females and 202 from uncollared females. We considered 32 (7.6%) calves to be study-induced mortalities or abandonments and removed them from calculations of mortality sources and modeling analysis. We also censored 4 calves from calculations of mortality sources and modeling analysis because of loss of radio signal prior to the end of the first survival interval, and we censored an additional 6 calves from modeling analysis alone because either sex or mass was unknown. We included 21 calves captured <17 km outside the study area during 2001 and 2002 because survival did not differ between those calves and ones captured within the study area and we had no reason to expect survival would vary between areas prior to predator treatments. We also included some newborns (2 in 2003, 2 in 2004, 2 in 2005, and 1 in 2007) of radiocollared females known to live primarily within the study area that we captured <3.5 km outside the study area.

We captured newborns using helicopter techniques described by Ballard et al. (1979), Keech et al. (2000), and Bertram and Vivion (2002a). We released calves in <5 min (even if data collection was incomplete) to minimize their separation from the dam. When twins were present, the 2-person crew captured, processed, and released both calves together. During processing we determined sex of calves and weighed calves by placing them in a bag and suspending them with a calibrated 25- or 50-kg Chatillon spring scale (Kew Gardens, NY). To estimate age, we recorded posture, umbilicus condition, and hoof hardness (Haugen and Speake 1958, Adams et al. 1995).

We deployed VHF radiocollars weighing approximately 180 g and constructed from 4 layers of 10-cm wide elastic bandage with a diameter of 14 cm when sewn (Telonics

model 335; PEG elastic bandage, Franklin Lakes, NJ). Collars expanded with neck growth and detached after approximately 2 yr (Osborne et al. 1991, Keech et al. 2000). Pulse rate of collars doubled after remaining motionless for 1 hour. We visually located calves within 24 hr post-capture to determine if they rejoined the dam, were separated from the dam, or had died. Thereafter, we monitored radio-signals of calves approximately daily until mid-June and every other day until early July, after which tracking interval increased to every 5 days until mid-August, every other week until November, thereafter to once per month (Keech et al. 2000).

We accessed mortality sites within 24 hr of mortality detection in most instances. We examined carcasses and mortality sites using criteria and techniques described by Ballard et al. (1979) and Adams et al. (1995). We collected hair samples of suspected predators for species-specific DNA analysis (University of Idaho laboratory, Moscow, ID; Farrell et al. 2000, Murphy et al. 2000, Onorato et al. 2006). We included mortalities of all collared moose in analyses even if they occurred outside of the study area.

Estimating Moose Density, Composition, and Harvest
During late October–early December 2001–2007, except 2002, we surveyed moose in the study area to estimate abundance and composition. We divided the study area into 87 sample units (2 min latitude × 5 min longitude; each approximately 15.7 km^2, Kellie and DeLong 2006). Pilot–observer teams in small aircraft searched for moose at approximately 3.1 min/km^2 using techniques described by Gasaway et al. (1986) and Kellie and DeLong (2006). During 2001 and 2004–2007 we surveyed 100% of the 87 sample units. In 2003 we defined high- and low-density strata (using results from previous surveys) and surveyed 45 of the 87 sample units, of which 60% were in the high-density stratum. We recorded total moose numbers, sex, and number of calves and yearling males (Boertje et al. 2009), as well as search effort and survey conditions. We employed analytical methods and followed procedures described in Gasaway et al. (1986), DeLong (2006), and Ver Hoef (2008).

Because some moose in a surveyed unit may not be observed, we estimated a sightability correction factor (SCF) and its variance for each survey based on observations of radiocollared moose (Boertje et al. 2009). Unlike Boertje et al. (2009) we estimated the SCF annually, except in 2004 when we used the average SCF recorded for 2001, 2003, and 2005–2007 and the largest variance recorded flying 100% coverage of the study area. Also, we improved our estimates of SCFs by adding the second term of the delta-method (Seber 1982) derived estimator for the SCF:

$$\text{SCF} \approx \frac{1}{\hat{p}} + \frac{\text{V}\hat{\text{a}}\text{r}[\hat{p}]}{\hat{p}^3}$$

where $\hat{p}$ represents the proportion of moose observed, which corrects for nonlinearity in the expectation of $1/\hat{p}$ (Rice 1995). We multiplied our counts of observable moose by the respective SCFs to estimate total moose abundance and

estimated the associated sampling variance (Goodman 1960). We similarly adjusted composition ratios for sightability and used the delta method to estimate the sampling variance of these ratios (Rice 1995).

We analyzed moose population abundance estimates for trend (lambda) and obtained smoothed estimates using a linear mixed effects model (Zhang et al. 1998, McCulloch and Searle 2001, DeLong and Taras 2009). The mixed effects model includes a parameter that accounts for random deviations of estimates from the linear trend and yields smoothed estimates based on information from both combined surveys (trend) and individual surveys. Resulting smoothed estimates of abundance lie closer to the trend line and have tighter confidence intervals.

We estimated lambda for 2002–2007 because that time period best represented population change in the study area. We lacked a 2002 abundance estimate. However, because vital rates indicated moose abundance likely changed little prior to predator treatments, we used the 2001 abundance estimate as a substitute for 2002.

Hunting for moose was legal during 1–20 September 2001–2003 in the entire study area. A partial hunting closure (68% of the accessible study area) existed during 2004–2007; hunting season was 1–25 September in the portion that remained open. During all years hunters were allowed to harvest 1 male moose and were required to report harvested moose within 15 days of the close of season.

Because partial moose hunting closures occurred simultaneous with predator treatments and contributed to population growth via decreased harvest of males, we also calculated lambda assuming no closures. To model a sustained hunt, we first assumed harvest was additive and subtracted a range of hypothetical additional moose that would have been harvested (if partial closures had not occurred) from the 2004–2007 yearly population estimates. We derived this range of hypothetical moose by subtracting the annual reported harvest during 2004–2007 from both the annual minimum and maximum reported harvests during 2001–2003 (pre-closure yr), which provided us with both liberal and conservative approximations of harvest, and thus additional moose. Second, we adjusted the additional moose numbers for cumulative age-specific survival (e.g., additional moose in 2004 were those not harvested in 2004; additional moose in 2005 were those not harvested in 2005 plus those not harvested in 2004 multiplied by annual survival rates for yearlings and adults).

Assessing Characteristics of Calf Mass, Twinning, and Moose Mortality

We used general linear models to estimate the effects of year, twin status, and sex on calf mass and compared these models using AIC_c. We used generalized linear models to assess the effect of year and collar status (i.e., radiocollared or uncollared) on twinning rates of adult moose and compared these models using quasi-AIC_c ($QAIC_c$; Lebreton et al. 1992).

We used chi-square tests, and when any cell count was <5, we used Fisher's exact tests (FET) on 2 × 2 contingency tables (Agresti 2007) to identify differences in cause specific-

rates of moose mortality. To test for differences in mortality rates within a treatment period, we followed the method specified by Scott and Seber (1983), which accounts for the covariance associated with sampling a multinomial distribution.

Modeling Moose Survival Probability

Our objective was to estimate the effects of predator treatments on moose by investigating changes in seasonal (calf and yearling) and yearly (adult) survival while evaluating potential covariates that may influence results such as weather and individual moose traits. As a first step in modeling moose survival, we described patterns of calf and yearling moose mortality at 15- and 30-day intervals using the Kaplan–Meier estimator (Pollock et al. 1989). We then created a priori models of survival that included combinations of variables describing predator treatments and covariates that could further influence survival using known-fate models in Program MARK (White and Burnham 1999). We used a logit-link function, selected among competing models using an information-theoretic approach, and obtained maximum likelihood estimates of survival of radiocollared moose calves ($n = 380$), yearlings ($n = 175$), and adult females ($n = 90$) from mid-May 2001 to mid-May 2008.

We modeled survival probability of moose calves and yearlings by dividing the year into 3 intervals; summer (marking date–31 Aug [calves] or 16 May–31 Aug [yearlings]), autumn (1 Sep–15 Nov), and winter (16 Nov–15 May). These intervals represented seasonal changes in the environment, calf development, and forms of predation risk. The start date for summer for calves was variable because we marked calves over about a 2-week period, and we included marking date in some models to examine if interval length influenced calf survival. All years and winters were referenced by the starting year (i.e., yr t not yr $t + 1$).

We modeled potential effects of predator treatments by examining survival during 3 distinct periods: 1) prior to any treatments (summer 2001–winter 2002), 2) intervals when only bears were treated (summer and autumn 2003), and 3) intervals and years with both bear and wolf treatments (winter 2003–2007). Because bears hibernated during the winter, we modeled bear-treatment effects only during summer and autumn. We included 2005–2007 as treatment years for bears because repopulation of the study area did not occur immediately. We considered the potential effects of wolf treatment for all intervals encompassing winters 2003–2007 because some active form of wolf treatment occurred during this entire period. However, in some models we restricted effects to just winter or summer and winter, reflecting those times when wolf predation may be more important.

Additional covariates potentially affecting calf survival that we included were: calf marking date, number of siblings, sex, depth of snow in the winter prior to birth, and capture age and mass. The number of siblings in our models represented the number of siblings at the time of an individual's death because number of siblings may affect the probability of detection by predators and the female's ability to protect calves from predators. We included mass as the mass unad-

justed for capture age because capture age was also included as a covariate. We averaged snow depth from 15 January, 15 February, and 15 March of each winter (Ballard et al. 1991) for our relative measure of snow depth. For winter, we added as covariates the average snow depth during the current winter of each year and the number of days $<-28°$ C (Renecker et al. 1978). We obtained weather records (National Weather Service 2000–2007) from the McGrath airport located in the center of our study area (Fig. 1). We also modeled the potential effects of moose density during the previous or current year on survival. We substituted moose density from 2001 for 2000 and 2002.

In models of yearling survival, we used the same strategy described for calf survival, except we included only sex, moose density, and weather covariates. We modeled the potential effects of sex on yearling survival separately for the 2002 and 2003 autumn intervals because hunting for male moose occurred throughout the study area (no males were marked during 2001).

Our modeling strategy was to first consider single-variable models of calf survival while allowing yearling survival to vary by interval and year (i.e., unconstrained). We then created multiple-variable models with additive and interactive relationships based on a priori reasoning and supported by results from single-variable models. We only considered 2-way interactions because we could not easily explain the biological rationale for 3-way interactions. After completing multiple-variable models of calf survival, we modeled yearling survival by modifying the top ($\Delta AIC_c < 3$) calf survival models. Our hierarchical approach to modeling resulted in 65 models, all of which were constructed based on a priori reasoning to avoid data dredging (Burnham and Anderson 2002).

We modeled survival of adult females annually because few died during any given seasonal interval. We defined the annual interval as 16 May to 15 May. These models examined the potential effects of predation by contrasting 1) years with no treatments of either predator versus years with treatments of both bear and wolves or 2) years with either no treatments or predominately bear-only treatment versus years with treatment of both bears and wolves, to examine the potential differences in the effects of bear versus wolf treatments. For example, we examined only the effects of bear treatment (difference between 2001–2002 survival and 2003–2007 survival) or the combined effects of bear treatment and wolf treatment on survival (difference between

2001–2003 survival and 2004–2007 survival). In addition to predator treatment effects, we considered the potential effects of age, moose density, temperature, and snow depth in the current and previous winter. We removed human-caused mortalities ($n = 4$) from the adult-modeling analysis to separate the effects of predator treatments on survival.

RESULTS

Predator Treatments and Bear Recovery

The untreated population of independent black bears was reduced approximately 96% immediately following the 2004 treatments. Approximately 96 (SE = 6.4) independent black bears used the study area in early May 2003 prior to our treatments, approximately 29 (SE = 6.4) bears immediately following the 2003 treatments, and 4 (SE = 4.5) bears immediately following the 2004 treatments (Table 1). The top removal model for black bears during both years invoked a constant probability of encounter. Models that included individual heterogeneity, those with bears grouped by sex, and those including relative effort as a covariate were not supported by the data. These models had ΔAIC_c of 1.4–1.9 but differed from the top model by one additional parameter, had small ≤0.85 differences in deviance, and resulted in nearly identical abundance estimates.

We estimated 70 (SE = 6.9) independent black bears used the study area during our 2007 survey (27% fewer than the 2003 estimate prior to treatment). The top model (AIC_c wt = 0.63) indicated a constant abundance of bears across occasions (days) within the study area, resighting probabilities consistent with an increasing linear trend by group (females with young or others) interaction, and no individual heterogeneity. The top 4 models, which comprised 95% of AIC_c weight, differed only in terms of individual heterogeneity with the latter 3 models supporting heterogeneity for one or both groups. Despite these differences, the top 4 models yielded the same point estimates (to nearest integer) and similar estimates of standard error.

Approximately 12 independent brown bears used the study area prior to treatments, and approximately 6 bears remained immediately following the 2004 treatment. Brown bears may have recovered by 2007, as indicated by elevated take of moose calves by brown bears in 2007 (Fig. 2).

During February 2001, we estimated a density of 5.1 wolves/1,000 km² ($n = 42$) in the wolf treatment area,

Table 1. Estimated independent black bear abundance prior to and following treatment efforts to increase moose survival, and number of independent black bears removed, western Interior Alaska, USA, 2003–2007. Abundance estimates for 2003 and 2004 based on removal estimators, and 2007 abundance based on mark–resight estimators.

	Untreated								Treated		
	Removal estimator			Females not removed	Total independents			No. removed	No. independents		
Year	Abundance	SE	95% CI		Abundance	SE	95% CI		Abundance	SE	95% CI
2003	77	6.4	64–90	Approx. 19[a]	Approx. 96	6.4[b]	83–109	67	Approx. 29	6.4[b]	26–42
2004	30	4.5	21–39	0	30	4.5	21–39	26	4	4.5	0–13
2007									70	6.9	56–84

[a] Calculated as 16 bears purposely not translocated divided by an estimated average probability of encounter based on the removal estimate (0.87).
[b] This estimate of SE does not include a small increase in uncertainty related to estimating the number of adult females not removed.
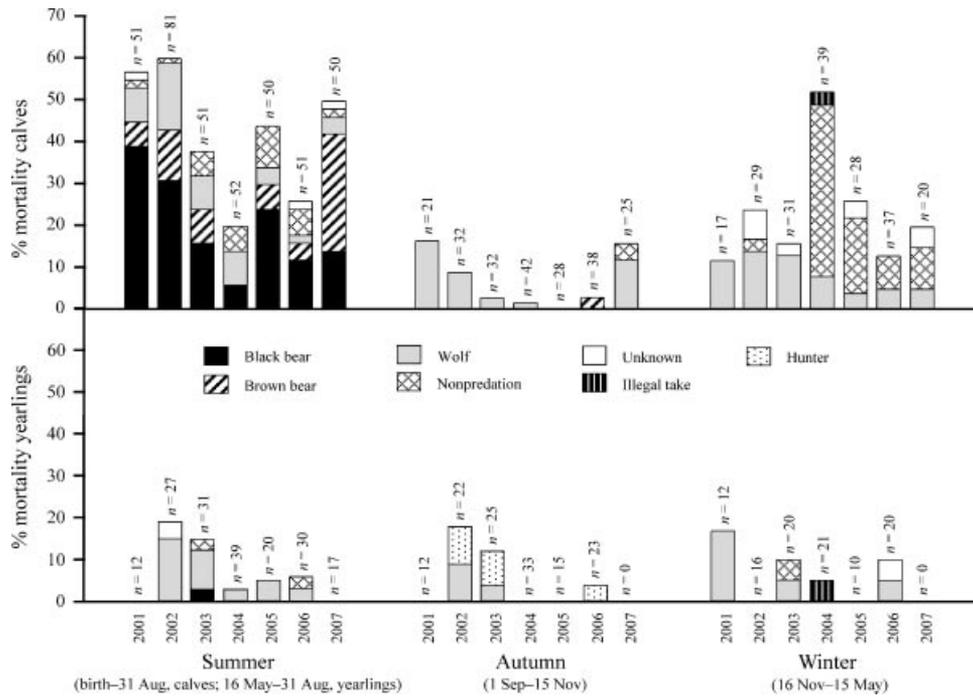
Figure 2. Cause-specific mortality rates for radiocollared moose calves (birth to 12 months of age) and yearlings (12–24 months of age), western Interior Alaska, USA, 2001–2007. Sample sizes represent the number of moose monitored each interval.

whereas in both March 2005 and 2006, we estimated 1.3 wolves/1,000 km^2 ($n = 11$). Reduced overall take of wolves during winters 2005–2006 and 2006–2007 (Table 2) was supportive evidence that wolf density declined and remained low.

Characteristics of Moose

Calves of radiocollared moose were born between 11 May and 7 July, with a median parturition date for all years of 22 May. We observed 3 (6%) radiocollared 2-year-old female moose with single calves ($n = 54$), and 81% of 3-year-old female moose produced calves (Table 3). The rate of parturition for radiocollared female moose ≥ 3 yr of age averaged 89% (Table 3). Annual twinning rates for radiocollared female moose ≥ 3 yr old ranged 0.24–0.59 and were similar to those for uncollared females (Table 3). The top model (QAIC$_c$ wt = 0.44) indicated an overall twinning rate of

Table 2. Number of wolves taken in the 8,314-km^2 wolf treatment area to reduce predation on moose, western Interior Alaska, USA, during 2000–2007 harvest seasons (e.g., harvest season 2000 = Aug 2000–May 2001). Categories include wolves taken by private permittees using aircraft-assisted take and total take by all methods.

	No. wolves taken	
Year	Aircraft-assisted take	Total take all methods
2000	0	28
2001	0	18
2002	0	33
2003	17	27
2004	14	22
2005	4	11
2006	2	12
2007	17	19

0.42 (95% CI = 0.38–0.47) with no year or collaring effects. Mass of short-yearling female moose averaged 180.2 kg (Table 4) and individuals ranged 129.5–226.8 kg. Annual average mass of short-yearling female moose varied from 167.5 kg in 2006 to 191.4 kg in 2002 (Table 4).

Estimated mean age of newborns at capture ($n = 422$) was 2.6 days (range: 0.5–11 days). Average capture date for all years was 24 May (range: 14 May–4 Jun), 2 days after the observed median birth date. Mass of sampled calves estimated to be $\leq$3-days old at capture ranged 7.7–25.9 kg with an average of 17.4 kg (Table 4). The top model (yr, twin status, and sex as main effects; AIC$_c$ wt = 0.64) indicated that on average males were 0.7 kg (SE = 0.28) heavier than females and singletons were 2.8 kg (SE = 0.29) heavier than twins.

Moose Abundance and Harvest

Early winter moose abundance estimates ranged from 525 (95% CI = 452–598) in November 2001 to 883 (95% CI = 729–1,037) in November 2007 (Table 5). The linear mixed model produced smoothed population estimates of 521 moose (95% CI = 456–586, 0.38 moose/km^2) for November 2002 and 766 moose (95% CI = 690–842, 0.56 moose/km^2) for November 2007 (Table 5). During 2002–2007, lambda was 1.08 (SE = 0.018) corresponding to an annual increase of 49 moose (SE = 11.76, $P = 0.014$). The calf:100 adult females ratio increased from 34 calves:100 adult females ($\geq$17 months of age) during the 2001 survey to 51–63 calves:100 adult females during 2003–2007 surveys (Table 5).

Hunting closures reduced harvests of male moose by an average of 60% in the study area. Reported harvests of 27 (2001), 45 (2002), and 32 (2003) moose occurred annually

Table 3. Observed parturition and twinning rates for female moose, western Interior Alaska, USA, 2001–2007.

| | Observed parturition (collared) | | | | | | Observed twinning | | | | | |
| | 3 yr of age | | | ≥3 yr of age | | | ≥3 yr of age (collared) | | | Uncollared | | |
Year	n	Rate	SE	n	Rate	SE	n	Rate	SE	n	Rate	SE
2001	3	1.00		22	0.73	0.097	16	0.25	0.112			
2002	1	0.00		25	0.88	0.066	22	0.59	0.107	46	0.39	0.073
2003	9	0.56	0.175	31	0.84	0.067	25	0.24	0.087	39	0.36	0.078
2004	10	0.70	0.153	40	0.80	0.064	31	0.32	0.085	31	0.39	0.089
2005	11	1.00		51	0.92	0.038	45	0.44	0.075	40	0.50	0.080
2006	13	1.00		62	0.97	0.022	60	0.40	0.064	29	0.35	0.090
2007	7	0.71	0.185	59	0.95	0.029	56	0.52	0.067	30	0.50	0.093
All yr	54	0.81	0.054	290	0.89	0.018	255	0.42	0.031	215	0.41	0.034

Table 4. Mean mass (kg) of newborn moose calves and short-yearlings captured, western Interior Alaska, USA, 2001–2007. We included only newborn calves known or estimated to be ≤3 days old.

| | Newborn calf mass (kg) | | | | | | | | | Short-yearling mass (kg) | | |
| | Singletons | | | Twins | | | All calves | | | | | |
Year	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
2001	19	19.6	0.68	13	17.4	0.48	32	18.8	0.48	14	178.1	4.67
2002	16	18.9	0.47	38	17.4	0.26	54	17.8	0.25	15	191.4	5.47
2003	23	19.4	0.44	18	16.4	0.70	41	18.1	0.46	15	179.5	4.62
2004	23	20.2	0.51	26	16.2	0.43	49	18.1	0.44	15	184.9	3.75
2005	20	18.3	0.59	32	15.4	0.57	52	16.5	0.46	15	174.8	3.95
2006	15	17.5	0.76	30	15.2	0.48	45	16.0	0.44	15	167.5	3.79
2007	14	18.8	0.71	23	16.4	0.37	37	17.3	0.40	15	185.3	5.39
All yr	130	19.1	0.23	180	16.3	0.19	310	17.4	0.16	104	180.2	1.82

($\bar{x} = 35$ moose/yr) in the study area prior to hunting closures. Following hunting closures, hunters refocused efforts in those portions that remained open, and reported harvesting 9 (2004), 14 (2005), 16 (2006), and 16 (2007) moose annually ($\bar{x} = 14$ moose/yr) within the study area. Assuming no hunting closures, we estimated lambda would have been 1.04–1.06 during 2002–2007.

Moose Mortality

Mortality of radiocollared moose calves was lower in treated years than untreated years (Fig. 3). However, combined predation by black bears, brown bears, and wolves accounted for most annual mortality of moose calves during both untreated (94%, $n = 93$, 2001–2002) and treated (65%, $n = 137$, 2003–2007) years (Fig. 2). In all years except 2004, most calf mortality (68–85%) occurred during summer with few calf deaths observed in autumn or winter during either untreated or treated years (Figs. 2 and 3). In 2004, only 32% of calf mortality occurred during summer, presumably because combined predator densities were lowest and non-predation deaths from deep late-winter snow were greatest.

Cause-specific mortality rates varied between untreated and treated years, yet black bears were the dominant source of predation mortality during all years except 2007 (Fig. 2). During summer of untreated years, we attributed the deaths of 34% ($n = 45$) of radiocollared calves to black bear preda-

Table 5. Observable moose numbers, sightability, and estimated total numbers and composition in the 1,368-km² study area with untreated (2001) and treated (2003–2007) predators, western Interior Alaska, USA, 2001–2007.

| | Survey sightability | | | | Total estimated abundance (SCF applied) | | Moose population composition (age or sex class:100 females ≥17 months of age) | | | | | | Linear mixed effects (smoothed) population estimates | |
Year	Moose obs[a]	Collars obs	Collars present	SCF[b]	Estimate	95% CI	Calves	95% CI	Male > calves	95% CI	17-month males	95% CI	Estimate	95% CI
2001	440	32	38	1.19	525	452–598	34	27–41	18	14–22	8	6–10		
2002													521	456–586
2003	424	21	28	1.35	573	413–733	56	33–79	18	9–27	5	2–8	570	520–620
2004	531			1.27	674	550–798	63	47–79	13	9–17	6	4–8	619	578–660
2005	479	38	49	1.30	621	527–715	51	40–62	18	14–22	9	7–11	668	624–712
2006	591	42	49	1.17	692	612–772	58	49–67	25	21–29	14	12–16	717	659–775
2007	662	31	41	1.33	883	729–1037	56	42–70	39	29–49	16	12–20	766	690–842

[a] All years, except 2003, were census counts, therefore SE = 0. In 2003 we estimated number of moose (SE = 39.0).
[b] Sightability correction factor (SCF) for 2004 calculated as the average SCF for 2001 and 2003–2007.
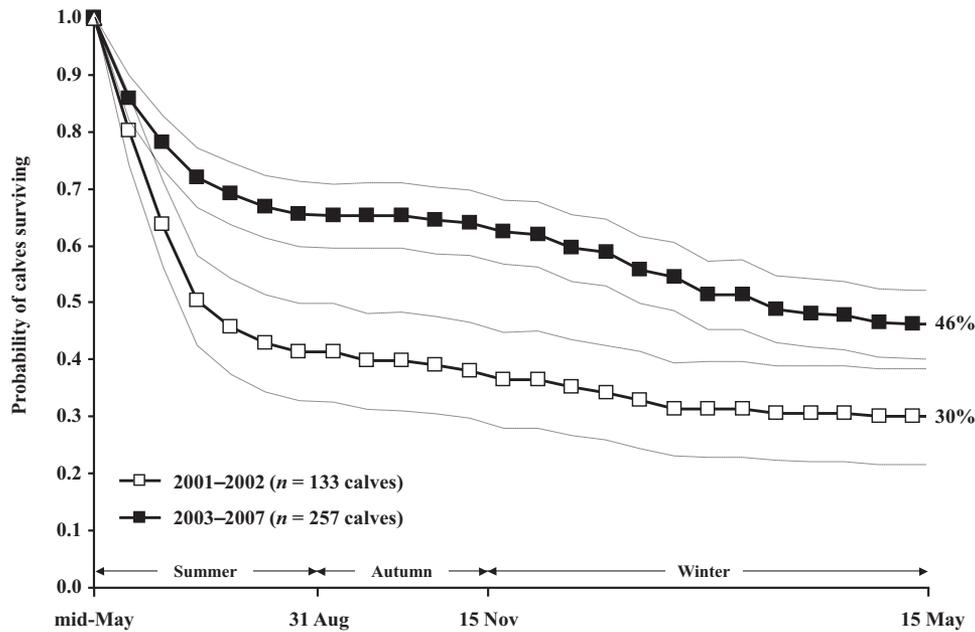
Figure 3. Average annual survival functions and 95% confidence intervals for radiocollared calf moose using Kaplan–Meier analysis (15-day increments), western Interior Alaska, USA, untreated predators (2001–2002) and treated predators (2003–2007).

tion versus 14% ($n = 36$) during treated years, a significant ($\chi_1^2 = 20.78$, $P < 0.001$) decrease. Wolves and brown bears were largely secondary predators compared to black bears. However, comparing years with untreated wolves (2001–2003) to years with treated wolves (2004–2007), we also observed a significant reduction in wolf-induced calf mortality during summer (12% vs. 4%, $\chi_1^2 = 6.66$, $P = 0.010$). Mortality attributable to brown bear predation varied, accounting for few deaths ($\leq12\%$) except in 2007 (28%, Fig. 2).

We observed an increase in the proportion of nonpredation mortality of calves in treated years. During summer, deaths from nonpredation increased from 2% ($n = 2$) of all radiocollared calves during untreated years 2001–2002 to 6% ($n = 15$) during treated years 2003–2007 (FET, $P = 0.064$). However, this elevated nonpredation mortality rate (6%) was still substantially less than the predation-caused mortality rate (28%, $n = 72$) during treated years ($p_{nonpred} - p_{pred} = -0.22$; 95% CI = -0.29 to -0.16; $n = 254$). During winter, nonpredation deaths increased from 2% ($n = 1$) of all radiocollared calves during untreated years to 17% ($n = 26$) during treated years (FET, $P = 0.012$) as a result of winter kill in 2004, when snow depths were severe. With 2004 removed, comparable values were 2% versus 9% (FET, $P = 0.182$), respectively. Besides winterkill, nonpredation mortality of calves included drowning, undetermined nontraumatic causes, and a congenital defect. We also observed one illegal take resulting from accidental capture in a snare set for furbearers (Fig. 2). We observed an increase in study-induced mortalities in the latter years of the study. Of 32 study-induced mortalities or abandonments 31 occurred during 2004–2007 (2001 = 1, 2002 = 0, 2003 = 0, 2004 = 4, 2005 = 8, 2006 = 8, and 2007 = 11).

Excluding hunting-caused deaths, mortality of radiocollared yearling moose was lower in years with treated wolves than years with untreated wolves (Fig. 4), with wolves accounting for most yearling mortality during both periods. During years with untreated wolves (2001–2003), wolves were the cause of death for 10% ($n = 7$) of yearlings in summer, 5% ($n = 3$) in autumn, and 6% ($n = 3$) in winter. During years with treated wolves (2004–2007), wolves were the cause of death for 3% ($n = 3$) of yearlings in summer and 2% ($n = 1$) in winter (Fig. 2). Legal harvest was the largest cause of yearling mortality during autumn and we also observed 1 illegal take resulting from accidental capture in a snare set for furbearers (Fig. 2). Other causes accounted for few yearling deaths (Fig. 2).

We observed few adult mortalities. Excluding human causes, wolves accounted for most adult moose mortality ($n = 4$) prior to wolf treatments, 2001–2003 ($n = 100$ adult-yr monitored; Fig. 5). During wolf treatment (2004–2007), we observed no predation mortalities among radiocollared adult moose ($n = 239$ adult-yr monitored; Fig. 5). Nonpredation mortalities ($n = 5$) occurred throughout the study and included 3 undetermined nontraumatic causes, 1 ice-bound, and 1 birthing complication. Mortalities attributed to illegal take were also an important source of adult female deaths ($n = 4$) and include 2 moose accidentally captured in furbearer snares, 1 moose accidentally shot during autumn hunting season, and 1 death of unknown human cause.

Modeling Factors Affecting Moose Survival
For calves ($n = 380$) we focused on interpreting parameter estimates from the top model (AIC$_c$ wt = 0.37), because ΔAIC$_c$ for the top 4 models of survival was <2.4 (ΣAIC$_c$
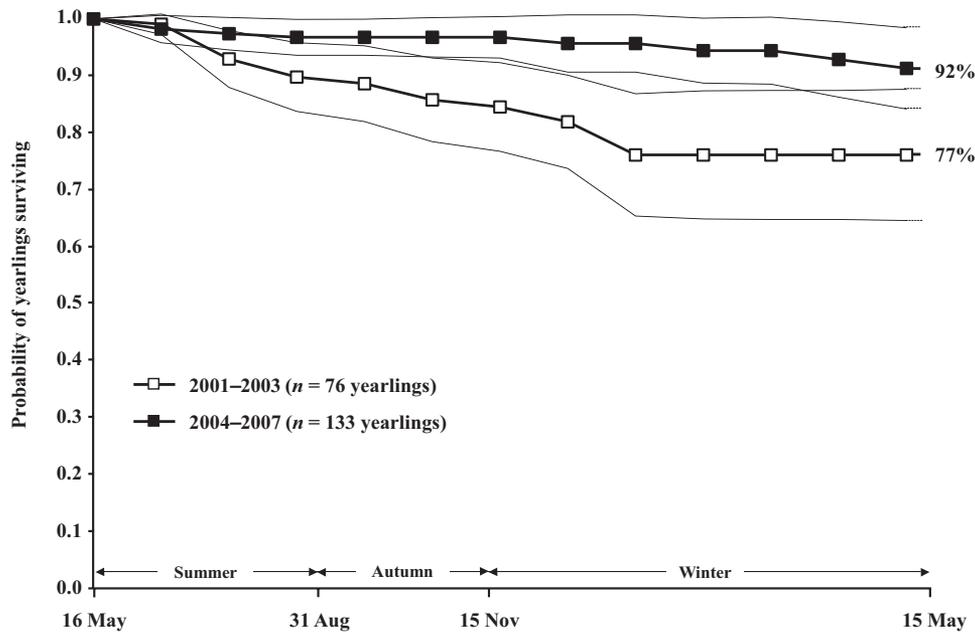
Figure 4. Average annual survival functions and 95% confidence intervals for radiocollared yearling moose using Kaplan–Meier analysis (30-day increments), western Interior Alaska, USA, untreated wolves (2001–2003) and treated wolves (2004–2007). We censored hunter-caused mortality.

wt $= 0.93$; Table 6). Also, all models up to $\Delta AIC_c = 33$ had the same structure for calf survival as one of these top 4 models. Furthermore, the top 4 models included nearly the same subset of variables (Table 6). In the top model, calf survival was most affected by number of siblings (constant all yr; Figs. 6 and 7), mass (yr-specific; Fig. 7), and capture age (yr-specific) in summer and autumn, and by snow depth (constant all yr) and temperature (constant all yr) during winter (Fig. 8).

When controlling for mass and capture age during summer, survival differed by number of siblings and was year-specific (Tables 6 and 7) in a manner consistent with the prediction that survival would be higher in treated years (2003–2007) than untreated years (2001–2002; Fig. 6a). In autumn, survival was higher during all treatment years, except 2007, for both singletons and twins at the mean values of mass and

capture age (Fig. 6b), although we did not observe a difference in intercepts. Survival during winter was constant across years after controlling for the influence of covariates (i.e., snow depth and temperature).

Across years, summer and autumn survival of calves with siblings was lower ($\beta = -0.82$, SE $= 0.247$) than calves without siblings, even after controlling for difference in mass and capture age (Fig. 6). However, during summer and autumn, the effects of calf mass varied among years with weak effects ($\beta < 0.06$) in untreated years and stronger effects ($\beta > 0.06$) in treated years (Fig. 7). In contrast, the effects of capture age varied and ranged from -0.49 (SE $= 0.242$) in 2007 to 0.29 (SE $= 0.323$) in 2006. In the model without year-specific effects of age (second model), the relationship between capture age and survival was negative ($\beta = -0.18$, SE $= 0.089$; Table 7).

Calf survival during winter was negatively related ($\beta = -0.05$, SE $= 0.017$) to snow depth and positively related ($\beta = 0.03$, SE $= 0.014$) to number of days $< -28°$ C (Fig. 8). Several factors reduced our ability to identify potential effects of predator treatments during winter: 1) the pattern of yearly variation in snow depth and temperature (e.g., no treated yr comparable to winter 2002, an untreated yr with the lowest snowfall and fewest days $< -28°$ C); 2) the lack of replication in weather patterns (i.e., only 2 untreated yr); and 3) the strong effects of both snow depth and temperature on calf survival during winter. However, an exploratory model ($\Delta AIC_c = 1.79$) that had a separate intercept for untreated (2001 and 2002) and treated years (2003–2007) indicated that survival during winter at average yearly snow depth and temperature would have been 0.83 (SE $= 0.057$) in untreated years and 0.76 (SE $= 0.022$) in treated years.
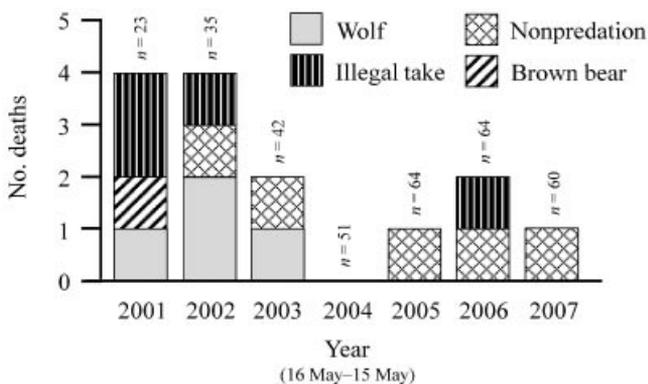

Figure 5. Annual (16 May–15 May) sources of mortality for radiocollared adult ($\geq$24 months of age) moose, western Interior Alaska, USA, 2001–2007. Sample sizes represent the number of moose monitored each year.

Table 6. Top 4 models for survival of calf and yearling moose during summer, autumn, and winter intervals in western Interior Alaska, USA, 2001–2007, based on Akaike's Information Criterion corrected for small sample size (AIC$_c$).

Rank	Component	Model[a]	AIC$_c$	ΔAIC$_c$	AIC$_c$ wt	K	Dev
1	Calf	S(yr, mass, age, sibs, mass × yr, age × yr); A(mass, age, sibs, mass × yr, age × yr); W(temp, snow)	960.1	0.0	0.37	33	892.1
	Yearling	S(yr, sex); A(yr, sex); W(sex)					
2	Calf	S(yr, mass, age, sibs, mass × yr); A(mass, age, sibs, mass × yr); W(temp, snow)	960.3	0.2	0.32	27	905.0
	Yearling	S(yr, sex); A(yr, sex); W(sex)					
3	Calf	S(yr, mass, age, sibs, mass × yr, age × yr); A(mass, age, mass × yr, age × yr); W(temp, snow)	962.1	2.0	0.13	34	892.0
	Yearling	S(yr, sex); A(yr, sex); W(yr, sex)					
4	Calf	S(yr, mass, sibs, mass × yr); A(mass, mass × yr); W(temp, snow)	962.4	2.3	0.11	26	909.2
	Yearling	S(yr, sex); A(yr, sex); W(sex)					

S, summer interval; A, autumn interval; W, winter interval; K, no. of parameters; dev, deviance.

[a] For calf models, year main effect indicates survival differed for each year. For yearling models, year main effect indicates survival differed for untreated (2001–2003) and treated (2004–2007) years.

For yearlings ($n = 175$), all models up to ΔAIC$_c$ = 20 had a similar structure. These models included interval- and sex-specific survival and most models (except one of the top 9 models with a ΔAIC$_c$ = 6.34) had differences in survival among years related to predator treatments. The top 4 models (Table 6) included effects of predator treatments on yearling survival during summer and autumn (models 1, 2, and 4; models 1 and 2 have identical yearling components) or all 3 intervals (model 3). In the top model and in years when we marked both sexes (we monitored only marked females in 2001), survival of males was lower ($\beta = -0.94$, SE = 0.510; Table 7, Fig. 9). Yearling survival was lower during 2001–2003 than during treated years (2004–2007) in both summer and autumn (Fig. 9). Differences in survival between untreated and treated years were greater for males (summer = 0.17, SE = 0.087; autumn = 0.50, SE = 0.144) than females (summer = 0.08, SE = 0.042; autumn = 0.02, SE = 0.021) in both
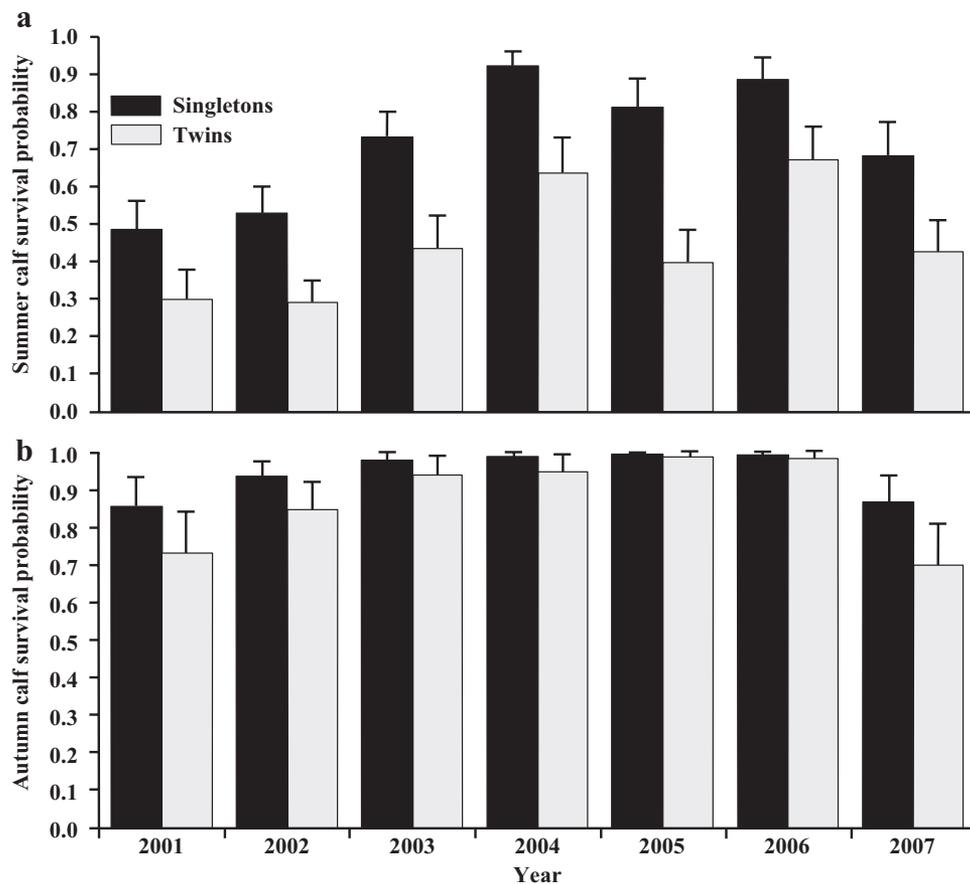

Figure 6. Year-specific estimates of summer (a) and autumn (b) moose calf survival at average mass among years at 3 days of age during years of untreated (2001–2002) and treated (2003–2007) predators, western Interior Alaska, USA.
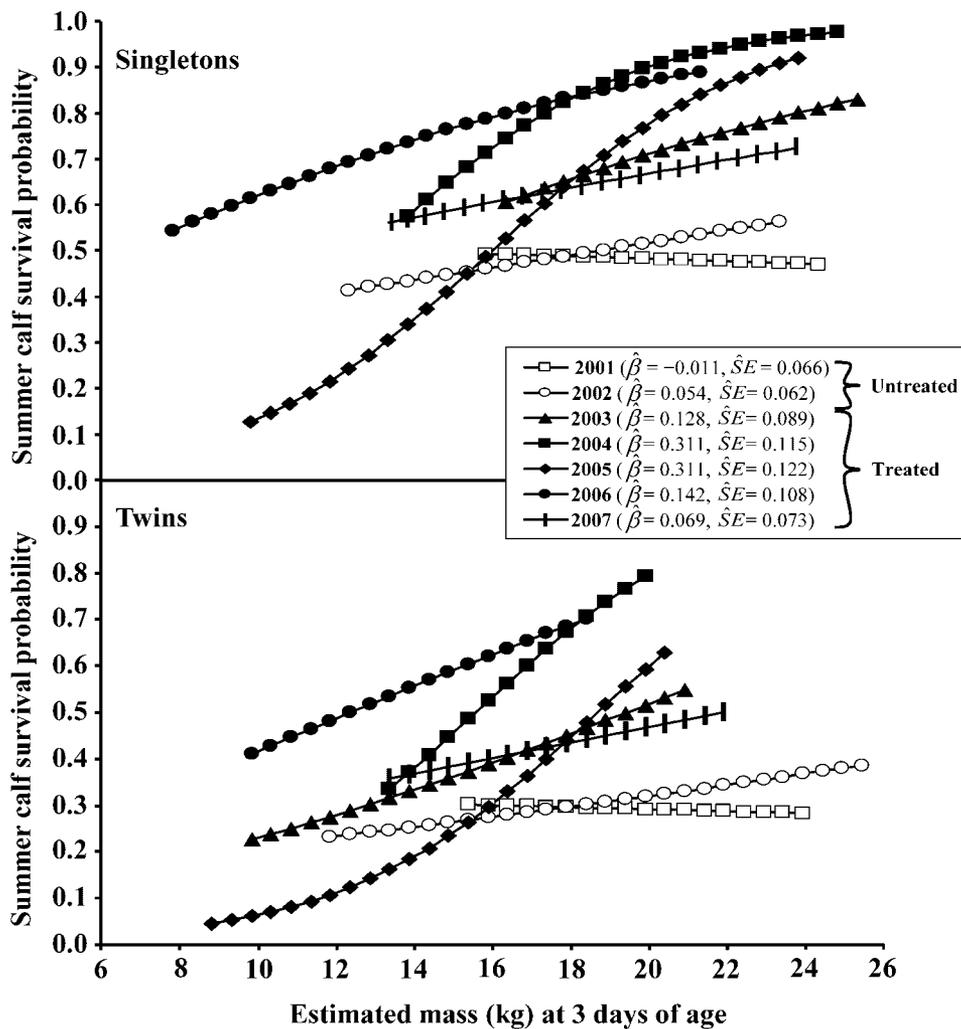
Figure 7. Effects of mass on survival probability of moose calves for mass ranges observed each year, western Interior Alaska, USA, during periods of untreated (2001–2002) and treated (2003–2007) predators. Slopes were the same for both singletons and twins.

intervals, with differences in male survival in autumn mostly the result of male harvest during autumn of 2 of the 3 untreated years (Fig. 9). Lack of support for models that included independent effects of bear treatment (summer and autumn during 2003), as well as cause of mortality data (Fig. 2), indicated wolf treatment was responsible for increases in yearling survival.

For adult females ($n = 334$), all models with a $\Delta AIC_c < 2$ (the top 4 models) had a similar structure and accounted for most of the AIC_c weight (ΣAIC_c wt = 0.67). All 4 models included the effects of age. Effects of predator treatments were included as a difference in survival between the initial 3 yr of the study versus the remaining 4 yr (top and fourth model, $\Delta AIC_c = 1.82$) and as a difference between the initial 2 yr of the study versus the remaining 5 yr (third model, $\Delta AIC_c = 1.47$). The second model received a similar level of support (AIC_c wt = 0.23) as the top model (AIC_c wt = 0.24). The second model included the effects of the current winter's snow and age effects, indicating that the effects of weather were difficult to separate from the effects of predator treatments because of the pattern of snowfall in

untreated and treated years. We summarized estimates from the top 2 models.

In the top adult model (Fig. 10), survival decreased with age ($\beta = -0.21$, SE = 0.078) and was higher in treated (2004 and later) versus untreated years (2001 and 2002) and bear treatment only (2003). In the second model, the effect of age ($\beta = -0.20$, SE = 0.076) on adult survival was similar to that observed in the top model. Adult survival increased ($\beta = 0.12$, SE = 0.061) with snow depth because the effects of predator treatments and snow depth were confounded with deeper snow observed in treated years ($\overline{x}$ monthly depth 2004–2007 = 64.3 cm) than untreated years ($\overline{x}$ monthly depth 2001–2003 = 41.4 cm).

DISCUSSION

The primary effects of reducing predation included increased summer and autumn survival of moose calves and yearlings and increased annual survival of adult female moose. Reduced predation on newborn calves during 2003–2007 resulted largely from the translocation of 70% of the black bears from the study area in May 2003 and 96% by June 2004,
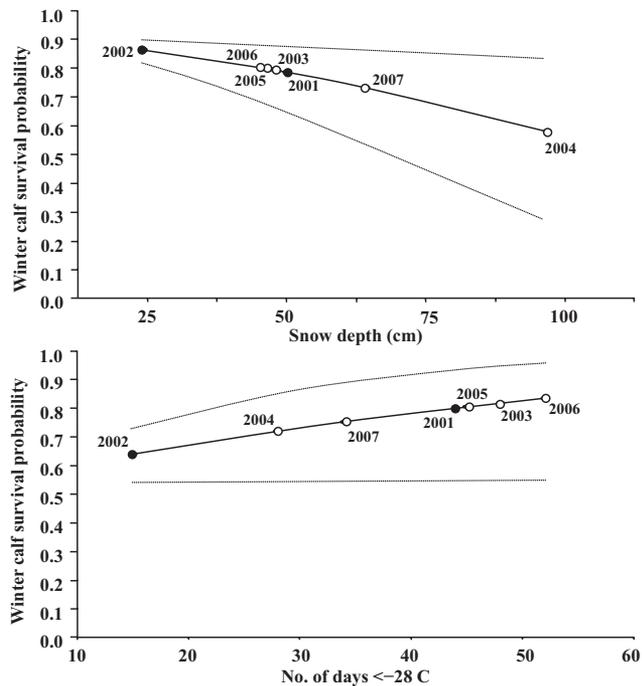
Figure 8. Effects of snow depth at average temperature among years (top) and temperature at average snow depth among years (bottom) on survival of moose calves during winter (16 Nov yr *t*–15 May yr *t* + 1), western Interior Alaska, USA, 2001–2007. We show estimated survival (bold line) and 95% confidence intervals. Predators were untreated during 2001–2002 (solid markers) and treated during 2003–2007 (open markers).

as well as prolonged reduction of black bear numbers through 2007. Likewise, increased survival of yearling and adult moose and fewer wolf-induced mortalities of moose calves during summer and autumn resulted from a 75% reduction in wolf numbers.

We concluded summer predation on moose calves was mostly additive. Given the presence of 3 effective predators and the high nutritional status of our moose population (as measured by reproductive and condition indices), we expected this result (Ballard 1992, Gasaway et al. 1992, Van Ballenberghe and Ballard 1994). However, we confirmed predation mortality was partly compensatory because nonpredation mortalities increased during treated years (Fig. 2), which we also expected because mortality will likely never be totally additive or compensatory (Bartmann et al. 1992, Ballard and Van Ballenberghe 1997). Although the proportion of nonpredation mortalities increased both during treated summers and on an annual basis, the actual number of calves dying from nonpredation causes remained low. Thus, increased nonpredation deaths provided little offset to the decline in the predation-caused rate. A major component of the large increase in annual nonpredation mortality (Fig. 2) was the deep snow winter of 2004, during which 16 of 39 calves died from nonpredation causes. We had no winter with comparable conditions during untreated years.

Although summer and autumn yearling survival clearly increased during treated years, winter survival of yearlings did not change with predator treatments. Our ability to

detect differences in winter survival pre- and post-treatment may have been confounded by conventional wolf hunting and trapping harvest during untreated years (Table 2). We also speculated that high nutritional status in our study area contributed to high winter survival of yearlings. However, in a substantially less-nourished moose population with a high moose/wolf ratio and low snow depths, winter survival of yearlings was similar (0.92 for females and 0.88 for males; Boertje et al. 2007, 2009). This comparison indicates a combination of factors, not solely nutrition, can be important determinants of yearling survival during winter. Snow depth appeared less important to yearlings than calves because snow depth did not enter any of the top models of yearling survival (Table 6). Even during winter 2004 when 51% of radio-collared calves died, we observed no natural mortality of radiocollared yearling moose (Fig. 2). We concluded well-nourished yearlings had a high tolerance for deep snow, as observed by Ballard et al. (1991).

Annual adult survival increased in years with wolf treatment (Fig. 10). However, only 5 adults died from predation during our study; 4 of these died from wolf predation prior to wolf treatments (Fig. 5). As with yearlings, we attributed increased survival to reduced wolf predation rather than reduced bear predation. Gasaway et al. (1983) and Hayes et al. (2003) also reported an increase in survival of radio-collared adult moose following reductions in wolf densities.

Covariates Influencing Survival

In every year of our study, singletons had higher survival than twins from birth to 15 November, even when controlling for calf mass (Fig. 6). This relationship was relatively constant across large changes in calf survival (48–92% [singles] and 29–61% [twins] during summer; Fig. 6), moose densities (0.38–0.55 moose/km^2), and moose/predator ratios (e.g., approx. 525 moose/96 independent black bears in 2001 to 674 moose/4 independent black bears in 2004; Tables 6 and 7). Evidence elsewhere suggests sibling effects may disappear at very high levels of mortality. For example, Testa et al. (2000) and Bertram and Vivion (2002*a*) concluded survival did not differ between singles or twins in environments with very low calf survival (20–22%). In contrast, the lower survival of twins compared to singletons in our study was similar to results of Keech et al. (2000) and Osborne et al. (1991), where total calf mortality was moderate.

Summer calf survival was strongly influenced by capture mass (Fig. 7) and age. In general, survival was positively related to capture mass and negatively related to capture age. The inverse relationship between survival and capture age resulted because survival is relative to age at a given mass (e.g., a 1-day-old calf is healthier than a 5-day-old calf of the same mass). The role of mass in the survival of moose calves changed as survival rate changed. With untreated predators we noted only a weak relationship between summer survival and capture mass ($\beta < 0.06$, SE = 0.062). However, in years of higher calf survival resulting from predator treatments (2003–2007, Fig. 6), we observed strong positive relationships between survival and mass ($\beta > 0.06$,

Table 7. Coefficients for top 4 models of calf and yearling moose survival during summer (S), autumn (A), and winter (W) intervals in western Interior Alaska, USA, 2001–2007. All beta (coeff.) values are on logit scale.

Rank[a]	Component	Yr[b]	Covariate	Coeff.[c]	SE
1	Calf (S)	X	Mass	−0.01 to 0.31	0.06 to 0.12
			Age	−1.18 to 0.29	0.12 to 0.47
			Sibs	−0.82	0.25
	Calf (A)		Mass	−0.01 to 0.31	0.06 to 0.12
			Age	−1.18 to 0.29	0.12 to 0.47
			Sibs	−0.82	0.25
	Calf (W)		Temp	0.03	0.01
			Snow	−0.05	0.02
	Yearling (S)	X	Sex[d]	−0.94	0.51
	Yearling (A)	X	Sex[d]	−3.83	1.16
	Yearling (W)	X	Sex[d]	−0.94	0.51
2	Calf (S)	X	Mass	0.01 to 0.25	0.05 to 0.09
			Age	−0.18	0.09
			Sibs	−0.77	0.24
	Calf (A)		Mass	0.01 to 0.25	0.05 to 0.09
			Age	−0.18	0.09
			Sibs	−0.77	0.24
	Calf (W)		Temp	0.03	0.01
			Snow	−0.05	0.02
	Yearling (S)	X	Sex[d]	−0.94	0.51
	Yearling (A)	X	Sex[d]	−3.83	1.16
	Yearling (W)	X	Sex[d]	−0.94	0.51
3	Calf (S)	X	Mass	−0.01 to 0.31	0.06 to 0.12
			Age	−1.18 to 0.29	0.12 to 0.47
			Sibs	−0.82	0.25
	Calf (A)		Mass	−0.01 to 0.31	0.06 to 0.12
			Age	−1.18 to 0.29	0.12 to 0.47
	Calf (W)		Temp	0.03	0.01
			Snow	−0.05	0.02
	Yearling (S)	X	Sex[d]	−0.95	0.51
	Yearling (A)	X	Sex[d]	−3.83	1.16
	Yearling (W)	X	Sex[d]	−0.95	0.51
4	Calf (S)	X	Mass	−0.06 to 0.19	0.04 to 0.09
			Sibs	−0.81	0.24
	Calf (A)		Mass	−0.06 to 0.19	0.04 to 0.09
	Calf (W)		Temp	0.02	0.01
			Snow	−0.05	0.02
	Yearling (S)	X	Sex[d]	−0.95	0.51
	Yearling (A)	X	Sex[d]	−3.83	1.16
	Yearling (W)		Sex[d]	−0.95	0.51

[a] The model with the lowest Akaike's Information Criterion for small sample sizes (AIC$_c$) score and models within 4 AIC$_c$ scores of the best model; we present only the top models here.

[b] X = year main effect; for calf models survival differed for each year, for yearling models survival differed for untreated (2001–2003) and treated (2004–2007) years.

[c] A range of beta (coeff.) values indicates a variation among year.

[d] Sex effects for yearlings indicate females had higher survival than males, and the effect was stronger in autumns with hunting seasons for males, 2002–2003.

SE = 0.073; Fig. 7). Keech et al. (2000) also reported a positive relationship between birth mass and survival in a moose population with high annual calf survival (53%).

Likewise, research on caribou has shown both positive and no relationships between early survival and birth mass. Where predators were scarce and not limited by available prey biomass, early survival and birth mass were positively related (Whitten et al. 1992). However, in a caribou population limited by neonatal predation, Adams et al. (1995) reported no relationship between early calf survival and birth mass. We acknowledge the interaction between survival and birth mass may change relative to the overall condition of ungulate populations. Indeed, research on elk (*Cervus elaphus*) has demonstrated different relationships between calf survival and birth mass in both low (Barber-Meyer et al. 2008 [no relationship], White et al. 2010 [positive relationship]) and high (Singer et al. 1997 [positive relationship], White et al. 2010 [no relationship]) survival regimes where predation was the major proximate cause of mortality.

We conclude that mortality of moose calves was largely independent of calf condition during periods of high predation (highly competitive environment), presumably because predators had few alternatives. However, during periods of comparatively low predation (less competitive environment), individual calf condition was an important determinant of survival, mediated at least in part through mechanisms such as maternal investment and predators selecting for less fit calves.

Calf survival during winter (15 Nov–15 May) was negatively related to snow depth (Fig. 8) as reported in other
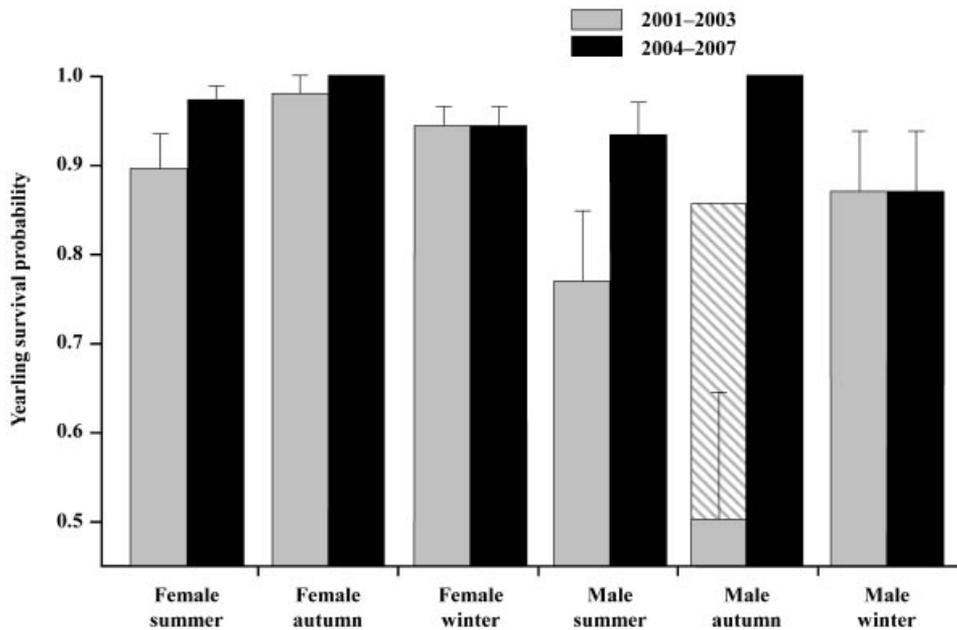
Figure 9. Survival of yearling moose during untreated wolves (2001–2003) and treated wolves (2004–2007), western Interior Alaska, USA, 2001–2007. The hashed bar for males in autumn represents survival in the absence of harvest.

studies (Bishop and Rausch 1974, Coady 1974, Ballard et al. 1991). During 2004 when snow depths exceeded 90 cm for 3 months, 51% ($n = 39$) of calves entering winter died, largely from weather-related causes, not predation (Fig. 2).

We concluded that the positive relationship between survival and number of days $< -28°$ C could be best explained by a post hoc analysis that showed, with the exception of winter 2002, snow depth and number of days $< -28°$ C were highly and inversely correlated ($r = -0.916$ excluding 2002, $r = -0.018$ with 2002). In our study area, snowfall and

accumulation were generally associated with moist warm air, whereas the coldest days were often clear, cloudless, and snow free.

Ballard and Van Ballenberghe (1997) reported predation by wolves often had the greatest impact on calf moose during winter. In our top 4 models, survival of calves in winter was constant across years once we controlled for snow depth and temperature (Table 6), indicating minimal influence of predator treatments on winter calf survival relative to the influence of snow and temperature. However, the pattern of
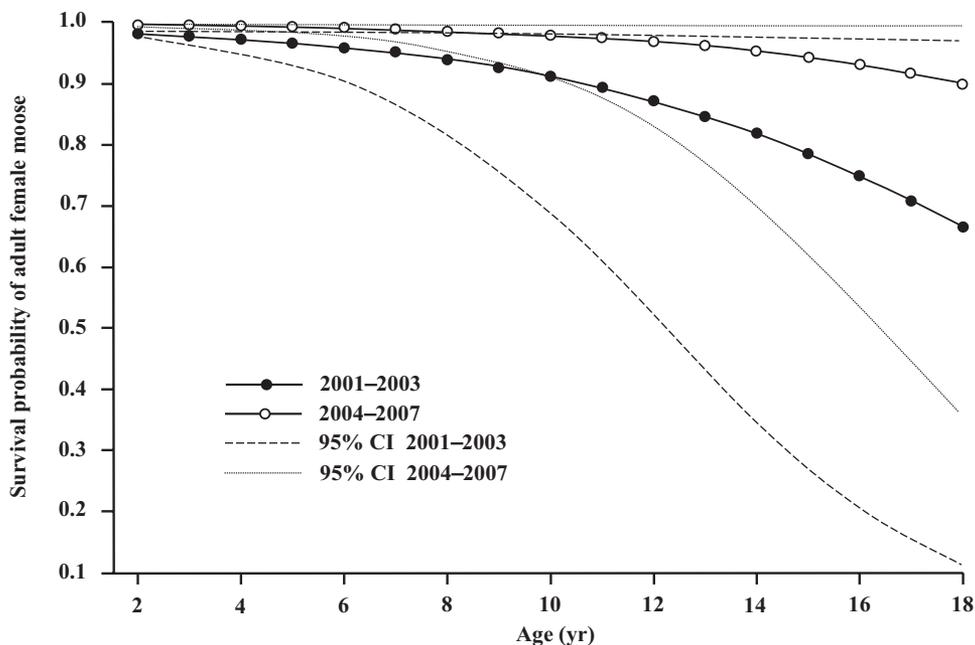
Figure 10. Effects of predator treatment and age on annual survival of adult (≥2 yr old; human-caused mortality censored) female moose for untreated years wolves (2001–2003) and treated wolves (2004–2007), western Interior Alaska, USA, 2001–2007.

yearly variation in snow depth and temperature reduced our ability to identify potential winter effects of predator treatments; in particular we had no untreated deep-snow winters. Another explanation is that wolves were harvested through conventional hunting and trapping before the initiation of wolf treatment in our small study area (Table 2). This level of harvest may have already elevated winter calf survival during 2001–2003, confounding our untreated and treated comparison.

An alternate hypothesis is that winter wolf predation on moose calves was largely compensatory, as evidenced by similar survival rates during untreated and treated years. No comparative data exist for calf moose. However, winter coyote (*Canis latrans*) predation on mule deer (*Odocoileus hemionus*) fawns can have a large compensatory component (Bartmann et al. 1992; Bishop et al. 2005, 2009).

We observed a surprising increase in study-induced neonatal losses during the latter years of the study (31 of 32 study-induced deaths occurred during treated yr 2004–2007), which totaled 11% of captured calves versus 1% prior to treatment. Subjective observations during captures support the hypothesis that females defended calves less vigorously in later years of the study, particularly in 2005 following the severe winter of 2004. Thus, increased study-induced mortalities may have resulted from a nadir in maternal interest, particularly among dams both surviving the severe winter of 2004 and with higher energetic costs associated with treated, high calf survival (Testa and Adams 1998). Lower maternal interest may also explain the increased numbers of nonpredation deaths (Fig. 2) and reduced survival of lightweight calves following predator treatments (Fig. 7). We have no alternate hypothesis for why study-induced losses increased. Methods for capturing calves and classifying mortality sources remained the same throughout the study. Of the 32 study-induced calf losses (all identified within 24 hr of capture), we categorized 15 as abandonments and 17 as immediate deaths. Immediate deaths often exhibited signs of physical trauma inflicted at the capture site consistent with that of an adult moose (e.g., broken bones, bruised organs, and internal injuries with no external punctures or teeth or claw marks).

Female yearlings had higher survival than male yearlings during all 3 untreated intervals and 2 intervals (summer and winter) during treated years (Fig. 9). Higher female survival presumably reflected increased susceptibility of males to mortality through differing movement strategies or more risky behavior compared to females. Male moose often disperse more frequently and have larger home ranges than females (Lynch and Morgantini 1984, Ballard et al. 1991, Cederlund and Sand 1992).

Although adult survival increased in years with wolf treatments, survival was also strongly influenced by age, with survival probability decreasing with age (Fig. 10). This result illustrates that age structure may play an important role in the outcome of predator treatments. For example, young age adults benefit less from predator treatments than older age adults.

We attributed moose population growth to increased survival following treatments, and concluded predation was

limiting moose during untreated years in this population. However, we also recognized that reduction of harvest of male moose in the study area improved the harvest-induced skewed male/female ratio and contributed to the population increase (Table 5). Indeed, the hypothetical population growth had no hunting closures occurred (lambda = 1.04–1.06) was approximately 33% less than we observed with hunting closures (lambda = 1.08). This calculation is simplistic but provides important comparative information, given the lack of an alternative method for calculation and short duration of hunting closures. In reality, the positive contribution of hunting closures on male moose in predator limited populations are ultimately of little consequence to the long-term, beyond balancing sex ratios. For example, other moose populations with high birth rates and bear and wolf predation have remained at low densities even without harvest (Gasaway et al. 1992; Boertje et al. 2007, 2009).

Illegal take of radiocollared adult moose ($n = 4$) was similar to take by predators ($n = 5$). Illegally taken moose were primarily (2 of 4 adults, 4 of 6 of all ages) captured accidentally in snares set for furbearers, as previously documented (Boertje et al. 2009, Gardner 2010). We observed some illegal take in each age class of moose and such take occurred throughout the study (2 in 2001, 1 in 2002, 2 in 2004, and 1 in 2006). We conclude illegal take was a chronic source of mortality rather than a source that changed or diminished during the study. These findings underscore the importance of educating trappers on proper usage of snares and the availability of breakaway or diverter mechanisms (Gardner 2010).

Expectations of Predator Treatments

We demonstrate in our 3-predator, 1-large prey system, substantial predator treatments within a small area was an effective way to increase moose survival and population size. Moose nutritional status was moderate to high based on comparative data on age at first reproduction, birth and twinning rates, and mass of short-yearling moose (Boertje et al. 2007) and was likely an important determinant in the outcome of treatments. Survival of prey should be most responsive to reductions in predation at low densities and least responsive as populations near K and mortality has a greater compensatory component (McCullough 1979).

Reducing predation sufficient to allow moose population growth is a key step toward increasing sustainable harvest densities in much of Interior Alaska where moose occur at low densities and are predator-limited (Gasaway et al. 1992, Boertje et al. 2009). The ultimate goal when reducing predation is to elevate the sustained yield of moose. Our results reflect a short-term response (5 yr) to reducing predators and the duration of elevated moose numbers and future yield of moose remains to be determined. Therefore, whether our treatments will ultimately prove to be a successful management action is unknown.

Reductions of predators in limited areas around human population centers, similar to our study, may be a potential method of increasing local moose harvests. However, our experimental program was too costly to routinely utilize.

Implementing economical and practical ways to initially reduce predator numbers and, presumably, to keep predators at lowered densities is a challenge. Preferably, reductions would be achieved by private citizens using conventional means, but we acknowledge private hunters and trappers have not been successful to date in remote, forested portions of inland Alaska.

MANAGEMENT IMPLICATIONS

A thorough example is now available where 3 predators were treated to successfully increase moose survival and numbers. Given results of this and previous studies, wildlife managers and policymakers may expect similar results from predator treatment programs elsewhere, but use less costly and less thorough study designs. Managers, especially in multi-predator systems, should recognize that a substantial suite of covariates and confounding effects may complicate program results. Consequently, managers should be prepared to adapt study designs as well as treatment methods to increase the likelihood of program success and understanding. To accomplish this, we recommend managers implement programs that include collecting comparative data on 1) the relative abundance and take of moose and predators, 2) basic information on moose nutritional status and population composition, 3) the frequency of deep snowfall winters, and 4) the relative effects of different predators on moose survival, because the effects vary considerably among study areas (Boertje et al. 2009: Tables 4 and 5).

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