Management and Conservation Article

Living on the Edge: Viability of Moose in Northeastern Minnesota

MARK S. LENARZ,[1] *Minnesota Department of Natural Resources, Forest Wildlife Populations and Research Group, 1201 E Highway 2, Grand Rapids, MN 55744, USA*

JOHN FIEBERG, *Minnesota Department of Natural Resources, Biometrics Unit, 5463-C W Broadway, Forest Lake, MN 55025, USA*

MICHAEL W. SCHRAGE, *Fond du Lac Resource Management Division, 1720 Big Lake Road, Cloquet, MN 55720, USA*

ANDREW J. EDWARDS, *1854 Treaty Authority, 4428 Haines Road, Duluth, MN 55811, USA*

ABSTRACT North temperate species on the southern edge of their distribution are especially at risk to climate-induced changes. One such species is the moose (*Alces alces*), whose continental United States distribution is restricted to northern states or northern portions of the Rocky Mountain cordillera. We used a series of matrix models to evaluate the demographic implications of estimated survival and reproduction schedules for a moose population in northeastern Minnesota, USA, between 2002 and 2008. We used data from a telemetry study to calculate adult survival rates and estimated calf survival and fertility of adult females by using results of helicopter surveys. Estimated age- and year-specific survival rates showed a sinusoidal temporal pattern during our study and were lower for younger and old-aged animals. Estimates of annual adult survival (when assumed to be constant for ages >1.7 yr old) ranged from 0.74 to 0.85. Annual calf survival averaged 0.40, and the annual ratio of calves born to radiocollared females averaged 0.78. Point estimates for the finite rate of increase (λ) from yearly matrices ranged from 0.67 to 0.98 during our 6-year study, indicative of a long-term declining population. Assuming each matrix to be equally likely to occur in the future, we estimated a long-term stochastic growth rate of 0.85. Even if heat stress is not responsible for current levels of survival, continuation of this growth rate will ultimately result in a northward shift of the southern edge of moose distribution. Population growth rate, and its uncertainty, was most sensitive to changes in estimated adult survival rates. The relative importance of adult survival to population viability has important implications for harvest of large herbivores and the collection of information on wildlife fertility.

KEY WORDS *Alces alces*, fertility, growth rate, matrix model, Minnesota, moose population dynamics, species distribution, survival.

It is well established that the global climate is warming (Intergovernmental Panel on Climate Change 2007). In the Great Lakes region of North America, predictions call for an increase of 1.5° to 2° C in spring and summer temperatures as early as 2025–2035, and as much as 5° to 8° C in fall and winter temperatures over the next century (Union of Concerned Scientists 2003). Wildlife species throughout this region will be affected indirectly by changes to habitats in which those species have evolved. More direct effects of this warming may include altered survival and reproductive rates, which ultimately result in a change to the growth rate of a population and perhaps a shift in species distribution (Humphries et al. 2004). North temperate wildlife species on the southern edge of their distribution are especially at risk and may experience a northward shift (Parmesan and Yohe 2003, Humphries et al. 2004). A more thorough understanding of how wildlife species on the edge of their distribution are responding to changes in environmental conditions is essential to their management.

One species that may ultimately experience such a shift is the moose (*Alces alces*), whose continental United States distribution is restricted to northern states or northern portions of the Rocky Mountains cordillera. The moose is particularly vulnerable, because it is superbly adapted to cold temperatures but intolerant of heat (Renecker and Hudson 1986, 1990). Based on metabolic research, when ambient winter temperatures exceeded −5° C or summer temperatures exceeded 14° C, moose experienced an increase in metabolism and heart and respiration rates, reduced feed

intake, and lost body weight (Belovsky and Jordan 1978; Renecker and Hudson 1986, 1990). These upper critical temperatures were substantially lower than those reported for the ubiquitous white-tailed deer (*Odocoileus virginianus*), where the winter threshold was 25° C and heat stress in other seasons did not cause a perceptible rise in energy expenditure (Holter et al. 1975).

Until recently, moose occurred in 2 disjunct populations in Minnesota, USA: one population in the boreal forest of the northeast and a second population in the aspen parklands of the northwest (Fuller 1986). Moose were common in the northwestern range in the 1980s but declined dramatically in the 1990s and now number <100 moose (Murray et al. 2006, Lenarz 2007). Warming temperatures were implicated as an ultimate cause of mortality in this population (Murray et al. 2006). Moose remain common throughout much of northeastern Minnesota, but recent research indicated that temperature metrics explained a high proportion of variation in seasonal or annual moose survival (Lenarz 2009, Lenarz et al. 2009). Mean annual adult survival in the northeastern population was similar to that for moose in northwestern Minnesota, but pregnancy rates of adult female moose in the northwest were substantially lower (Murray et al. 2006; Lenarz et al. 2009; M. S. Lenarz, Minnesota Department of Natural Resources [MNDNR], unpublished data).

Temperature-mediated survival observed by Lenarz et al. (2009) raised concerns regarding long-term viability of the northeastern population, particularly given the abrupt decline of the northwestern population and also current climate change projections (Intergovernmental Panel on

Climate Change 2007). We sought to build on the analyses in Lenarz et al. (2009), in hopes of furthering our understanding of the potential risks for this population. Our objectives were to 1) estimate age-specific survival and fertility rates, 2) construct a series of Leslie matrices from which we could estimate deterministic and stochastic long-term population growth rates, 3) evaluate the relative importance of survival and fertility to population growth rates, 4) quantify the effect of parameter uncertainty on our ability to estimate these rates, and 5) examine long-term weather records from northeastern Minnesota to better understand and put in a historical context the observed relationships between temperature and survival noted by Lenarz et al. (2009).

STUDY AREA

We defined our 3,780-km^2 study area by capture locations for moose in northeastern Minnesota (47°30′N, 91°21′W; Lenarz et al. 2009). The area contained a variety of wetlands, including bogs, swamps, small- to medium-sized lakes, and small streams, which were interspersed on a low plateau that rose abruptly from Lake Superior to a crest approximately 700 m above sea level (Heinselman 1996). A continental divide runs northeast–southwest down the middle of the plateau, with water flowing northwest into the Hudsonian watershed or southeast into Lake Superior.

The study area was a mosaic of conifer communities classified as the Northern Superior Upland section (MNDNR 2007). The landscape was characterized by northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*) on the lowlands and balsam fir (*Abies balsamea*) and jack (*Pinus banksiana*), white (*Pinus strobus*), and red pines (*Pinus resinosa*) on the uplands. Deciduous species intermixed with the conifers on uplands and included quaking aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*).

The majority of our study area occurred within the Superior National Forest with the balance in state, county, or private ownership. The area was sparsely inhabited and communities within the study area contained <100 permanent residents. Few paved roads existed, and much of the area was accessible only from logging roads or snowmobile and all-terrain vehicle trails.

State and tribal hunters harvested an average of 197 moose annually between 2002 and 2008 (M. S. Lenarz, unpublished data). Beginning in 2007, state-licensed hunters were restricted to harvesting adult males, and in the past 2 years ≤8 adult females were harvested annually by tribal hunters. Since 2007, the combined state and tribal harvest represented approximately 2% of the estimated fall population (M. S. Lenarz, unpublished data).

METHODS

Field Procedures

We provide only a general description of capture, handling, and monitoring of moose (see Lenarz et al. 2009 for greater detail). Between 2002 and 2008, we captured adult male and female moose (≥1.7 yr old) in early February or March by net-gunning (2002, Wildlife Capture Services, Marysvale, UT) or darting (2003–2005 and 2008, Quicksilver Air, Inc., Fairbanks, AK) from helicopters. Beginning in 2003, we extracted a last incisor (I$_4$) following procedures similar to those in Nelson (2001). We aged adult moose by counting cementum annuli (2003–2005, Matson's Laboratory, Milltown, MT; 2008, Wyoming Game and Fish Department Laboratory, Laramie, WY) of incisors (I$_4$) extracted at capture or I$_1$ postmortem.

We fitted each moose with a very high frequency radiocollar (Advanced Telemetry Systems, Isanti, MN) equipped with motion-sensing-mortality detectors, which increased the pulse rate when the collar was motionless for >6 hours. We monitored mortality of radiocollared moose each week from fixed wing aircraft during February 2002 to June 2008. If a radiocollar emitted a mortality signal, we located the collar on the ground in an attempt to determine the cause of mortality. Our data were interval censored (i.e., dates of death were only known to occur between observation intervals that ranged from 2 to 24 days; $\bar{x} = 7.8$ days, SE = 0.194, $n = 280$). Interval censoring can be accounted for using the nest survival module in Program MARK (e.g., Dinsmore et al. 2002) or by writing code to directly maximize likelihood of the observed data (Heisey et al. 2007, Fieberg and DelGiudice 2008). Accounting for interval censoring can be important when trying to link time-dependent environmental covariates to event times (e.g., death), but estimates of survival are frequently robust to interval censoring (Odell et al. 1992, Lindsey 1998, Fieberg and DelGiudice 2008).

We estimated date of death based on the condition of remains or by the midpoint between telemetry locations, which allowed us to use generalized linear models software to estimate survival rates as a smooth function of age and calendar time. Using custom written R code, we verified that survival rates estimated by maximizing the exact likelihood (i.e., accounting for interval censoring) agreed to ≥2 decimal places with estimates obtained by assuming known death times. Animal capture and handling protocols met the guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

Estimation of Demographic Rates

Peak birthing for moose occurs during a 1–2-week period, normally ending by 1 June (Schwartz 1997). Between late May and early June (M–J, 2004–2007), we used a helicopter to locate all radiocollared females (≥24 months) ≥1 time to determine whether females were accompanied by newborn calves; females with newborn calves tended to remain stationary and did not flee, whereas females without calves immediately ran when they heard the helicopter. We also sporadically observed radiocollared females ($\bar{x} = 1.8$ observations/ad F/yr, range = 1–11) during the following year to document whether calves had been born subsequent to the M–J survey; we missed 6 calves during the first year of the M–J survey (2004) but only 2 calves in the remaining 3 years, reflecting greater observer experience at observing newborns. We estimated annual fertility rates as calves

observed per radiocollared female. We used the term fertility to describe actual reproductive performance (Caswell 2001).

We modeled the number of calves born per adult female as a function of age by using a Poisson regression model. We used regression splines with 2 degrees of freedom, constructed using the ns function in Program R (Bates and Venebles 2004, R Development Core Team 2008) to allow the effect of age to be nonlinear (on the log scale; Harrell 2001). The ns function creates the basis (i.e., predictors of dimension df) for fitting a piecewise cubic polynomial function with continuous first and second derivatives between (df-1) interior points, called knots (chosen using quantiles of the data), while constraining the fit to be linear outside of the range of 2 boundary knots (placed at the extremes of the data). Initially, we fit a model that allowed fertility rates to vary from year to year. Estimated year-effects were similar, except for 2007, when rates were lower. Thus, we modeled temporal variability in fertility rates by including an indicator variable (equal to 1 for 2007 and 0 otherwise).

Recognizing that our female-calf observations represented minimum productivity estimates, we conducted a sensitivity analysis to determine the extent to which undetected calves may have biased our results. For each female observed without calves, we generated a binomial random variable with probability of success equal to 0.1 (thus, assuming calves went undetected 10% of the time). For each success, we randomly generated 1 or 2 calves (with probability of twins given by the twinning rate observed in our data). We then refit our Poisson regression model to these simulated data to estimate new rates. We repeated this process 1,000 times.

In late April or early May (A–M) the following year, we relocated all radiocollared females that had been accompanied by calves during the previous year to determine first-year (calf) survival. Calves remain with their mother until driven away in preparation for the next birthing and are readily observable prior to leaf-out (Bubenik 1997). We estimated first-year survival each year as the proportion of known calves born to radiocollared females that survived until the following spring (Van Ballenberghe 1979, Hauge and Keith 1981, Gasaway et al. 1983).

Survival Estimation (Ages >1 yr)

We estimated age-specific annual survival rates (under a no-hunting regime) using a semi-parametric age-period model, where we modeled effects of both age and Julian date (i.e., period) by using cubic regression splines, under the assumption that risk of mortality varied smoothly with respect to both age and time (Carstensen 2006a, b; Fieberg and DelGiudice 2009b). We censored those individuals that died from hunting at the time of their death to evaluate growth rate in the absence of hunting under the assumption that removing hunting pressure would not change the instantaneous risk of dying from other causes. We included both adult male and female moose in our analysis because we did not detect a difference in survival between sexes

when we added gender to the model (relative risk for M:F = 0.8, with 90% CI = 0.51–1.24). We divided the follow-up time for each individual into daily intervals by using the split-Lexis function of the Epi R package (Carstensen et al. 2008). The split-Lexis function uses the ages and dates at capture and (death or censorship) to automatically create records with appropriately updated values (of age and date) at specific time points (in this case each day we followed the animal during the study).

We modeled daily (non-hunting) hazard as a function of age and Julian date by using a complementary log-log link function (Fieberg and DelGiudice 2009b). The log-log link function follows naturally from processes that follow proportional hazards in continuous time but are modeled in discrete time (Heisey et al. 2007). We fit models using cubic regression splines with 2, 3, and 4 degrees of freedom and 2, 3, 4, and 5 degrees of freedom for age (f) and period (g) effects, respectively, and determined the appropriate amount of smoothing by comparing Akaike's Information Criterion for the fitted models. For comparison with other studies, we also fit a model that assumed survival was constant for adults (>1.7 yr) by dropping age (i.e., f) from the best-fit age-period model. We estimated annual adult survival rates (constant across age classes; AC) and annual age-specific survival rates (AS) by taking the product of estimated daily survival rates from the fitted model over the appropriate daily time and age intervals. Annual survival spanned 2 calendar years, and for the sake of clarity we used the earlier year for identification purposes (e.g., 1 Jun 2002 to 31 May 2003 = 2002).

Matrix Calculations

We created 2 sets of projection matrices for 6 consecutive years (1 Jun to 31 May) using a postbreeding model (Caswell 2001). We combined the first-year survival estimates with AC or AS survival estimates (ages 1–20 yr), and age-specific fertility rates from the Poisson regression model. We did not conduct helicopter surveys during 2002 or 2003 to estimate first-year survival, so we set first-year survival rates in these years to the mean rate estimated in the other 4 years. We assumed a 50:50 sex ratio at birth and determined the dominant eigenvalue of each matrix λ, using the popbio package in Program R (Stubben and Milligan 2007, R Development Core Team 2008). We estimated uncertainty in λ using a nonparametric bootstrap, which required re-estimating each set of vital rates (survival, fertility) for each of 2,000 bootstrap samples (resampling individuals). We used percentile-based 90% confidence intervals to characterize the uncertainty in the survival rates and yearly λs.

We calculated sensitivity and elasticity of λ to changes in survival and fertility rates by using the popbio package in Program R (Stubben and Milligan 2007, R Development Core Team 2008). Elasticity represents the proportional response to a proportional perturbation and is generally interpreted as the contribution of each estimate of age-specific survival and fertility to λ (Caswell 2001). We calculated elasticity with respect to individual demographic

Table 1. Annual survival (when assumed to be constant for ages >1.7 yr old) and 90% bootstrap confidence intervals, mean age, standard error, and sample size of each modeled year in northeastern Minnesota, USA, 2002–2007. Years represent time periods from 1 June to the following 31 May (i.e., 2002 reflects the time period from 1 Jun 2002 to 31 May 2003). Annual survival based on non-hunting mortality including wolf predation, poaching, disease, vehicle collisions, or unknown.

Yr	Survival	90% CI	Mean age (yr)	SE	n^a
2002	0.77	0.69–0.85	6.8	1.0	10
2003	0.85	0.79–0.90	6.8	0.6	43
2004	0.84	0.79–0.89	6.9	0.5	49
2005	0.77	0.71–0.83	6.6	0.3	68
2006	0.74	0.67–0.81	7.4	0.4	45
2007	0.78	0.69–0.87	8.7	0.4	28
Mean	0.79				

[a] Sample size only includes moose with cementum ages. We did not extract tooth samples in 2002 captures, and n underestimates total no. of radiocollared moose alive.
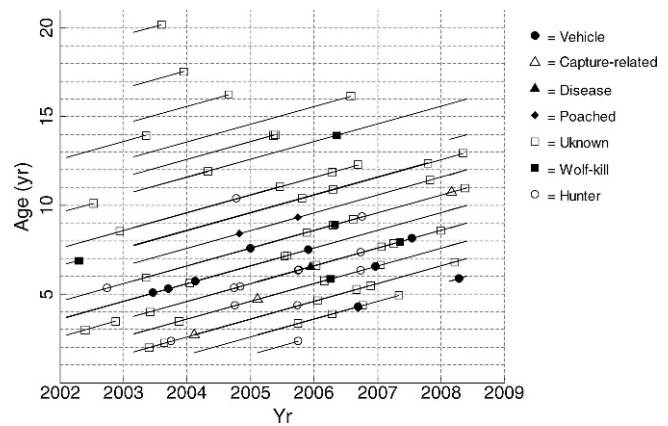

Figure 1. Lexis Diagram illustrating the sample coverage across 2 time scales (Julian date and age) for each of the adult moose from each of the 17 birth cohorts represented in our study in northeastern Minnesota, USA, 2002–2007. Each line represents an individual we followed from capture until death or censorship.

rates rather than matrix elements because the top row elements in a postbreeding model are the product of fertility and survival.

We calculated an estimate of the stochastic growth rate, λ_s, using Tuljapurkar's (1990) small noise approximation, under the assumption that each of the estimated matrices were equally likely to occur in future years (Fieberg and Ellner 2001). This approximation provided an estimate of the stochastic growth rate that was nearly identical to rate obtained by projecting the population using randomly chosen matrices, with considerably less computing effort (J. Fieberg, MNDNR, unpublished data). We used the bootstrap samples of our vital rate estimates to calculate a confidence interval for λ_s. Importantly, this interval accounts for sampling uncertainty associated with the estimated vital rates in the 6 matrices but does not account for uncertainty in our characterization of future temporal dynamics (i.e., these 6 yr only provide an estimate of the distribution of matrices that might occur in future years; Fieberg and Ellner 2001).

We also used Sobol' sensitivity indices to examine the relative importance of parameter uncertainty associated with each set of vital rates when estimating λ_s (Sobol' 1993, Ellner and Fieberg 2003, Fieberg and Jenkins 2005). Sobol' indices decompose the variance (i.e., uncertainty) in model predictions (here, λ_s) into main effects of independent sets of model parameters and their higher order interactions. We calculated first order and total Sobol' sensitivity indices associated with (first-yr survival, survival of all other age classes, and age-specific fertility rates), using methods described in Fieberg and Jenkins (2005). First-order sensitivity indices account for main effects of the parameters, and total sensitivity indices account for main effects and all higher order interactions involving each parameter (Sobol' 1993, Fieberg and Jenkins 2005).

Temperature Trends
We downloaded daily minimum and maximum temperatures at Ely, Minnesota (37 km NW of study area), for 1960 to 2007 (Minnesota Climatological Working Group 1960–2007). To characterize long-term temperature trends, we fit generalized additive models containing separate terms for seasonal (within-yr) and long-term trends, both modeled using smoothing splines. We constrained estimates of within-year trends to have the same value and first 2 derivates at the upper and lower boundaries (i.e., 31 Dec and 1 Jan; Wood 2006:323–324). We fit models using the gam function in the mgcv library of the R programming language (R Development Core Team 2008), which determines an appropriate level of smoothing using a generalized cross-validation score (for details, see Wood 2006).

RESULTS

We captured and radiocollared 150 adult moose (95 F, 55 M) between 2002 and 2008. Of these, 90 (60%) died before 1 June 2008. Sex ratio (M:F) of collared animals at the beginning of each year (1 Jun) varied from 0.45 to 0.86 ($\bar{x}$ = 0.65, SE = 0.07, n = 6). We determined ages for 88% of radiocollared moose, and mean age at the beginning of each year ranged from 6.6 years to 8.7 years (SE = 0.3, n = 6; Table 1). See Lenarz et al. (2009) for details on specific causes of mortality. We monitored survival of individual radiocollared animals in 17 birth cohorts during a mean of 717 days (SE = 54, n = 150) between February 2002 and June 2008 (Fig. 1).

Between 2004 and 2007, 114 observations of 43 radiocollared adult females (not including ad F radiocollared in 2008) indicated the birth of ≥92 calves (59 singles, 15 twins, and 1 set of triplets). Annual ratio of calves:radiocollared female in late May ranged from 0.53 to 0.96 ($\bar{x}$ = 0.78, SE = 0.09, n = 4). The estimated relationship between age and expected number of calves (Fig. 2) indicated reduced reproduction for younger and older animals. Decreased precision at the extremes of the curve reflect the low number of radiocollared females in these age classes. Eight of 114 observations of radiocollared females were not accompanied by calves during M–J surveys, but we subsequently observed them accompanied by one calf and
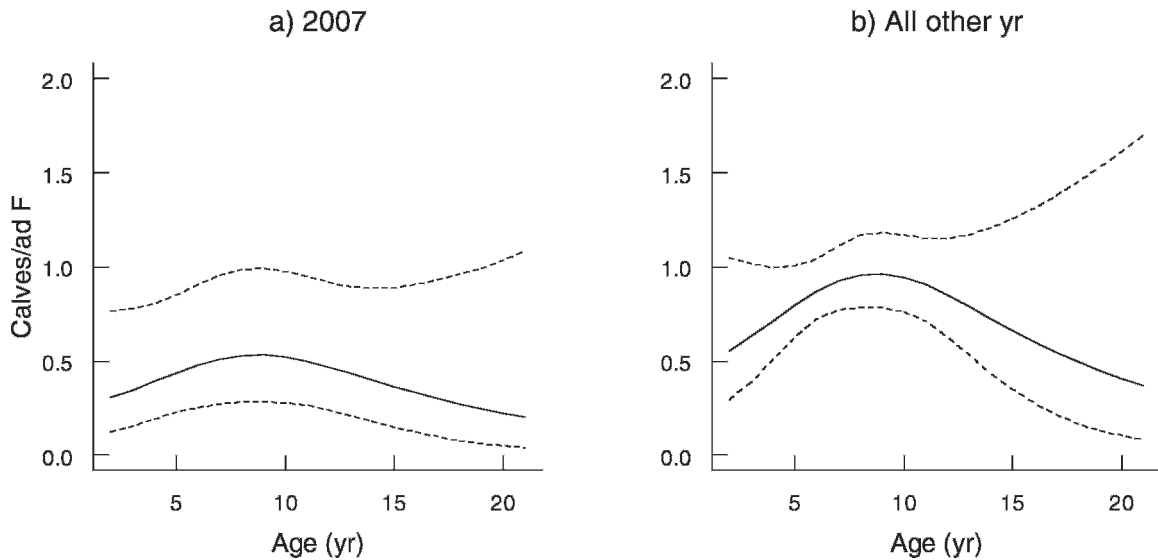
a) 2007

b) All other yr

Figure 2. Estimates of the expected number of calves/adult female (a = spring 2007; b = all other yr) from a log-linear Poisson regression model fit to data from moose in northeastern Minnesota, USA, 2002–2007. Dashed lines in both cases correspond to 90% pointwise confidence bands.

included them in the calculation of fertility and first-year survival. First-year survival varied according to year and averaged 0.404 (0.238–0.556, SE = 0.066, $n = 4$). We never observed lone calves <11 months old during flights within the study area and assumed that calves did not survive if their mother died (Testa 2004).

When we allowed risk to vary with age (AS), we found risk of death was highest for young and old-aged animals (Fig. 3). The estimated risk of mortality also showed a

sinusoidal pattern during our study, with high initial and end values. As a result, age-specific survival varied substantially among years (Fig. 3) and estimates of annual survival (AC) ranged from 0.74 to 0.85 (Table 1).

Estimates of λ and its precision varied according to whether we used AC or AS survival (Fig. 4). Values of λ based on the AC model tended to be higher and were more precise than values based on the AS approach. Point estimates in all cases were <1, indicative of a long-term
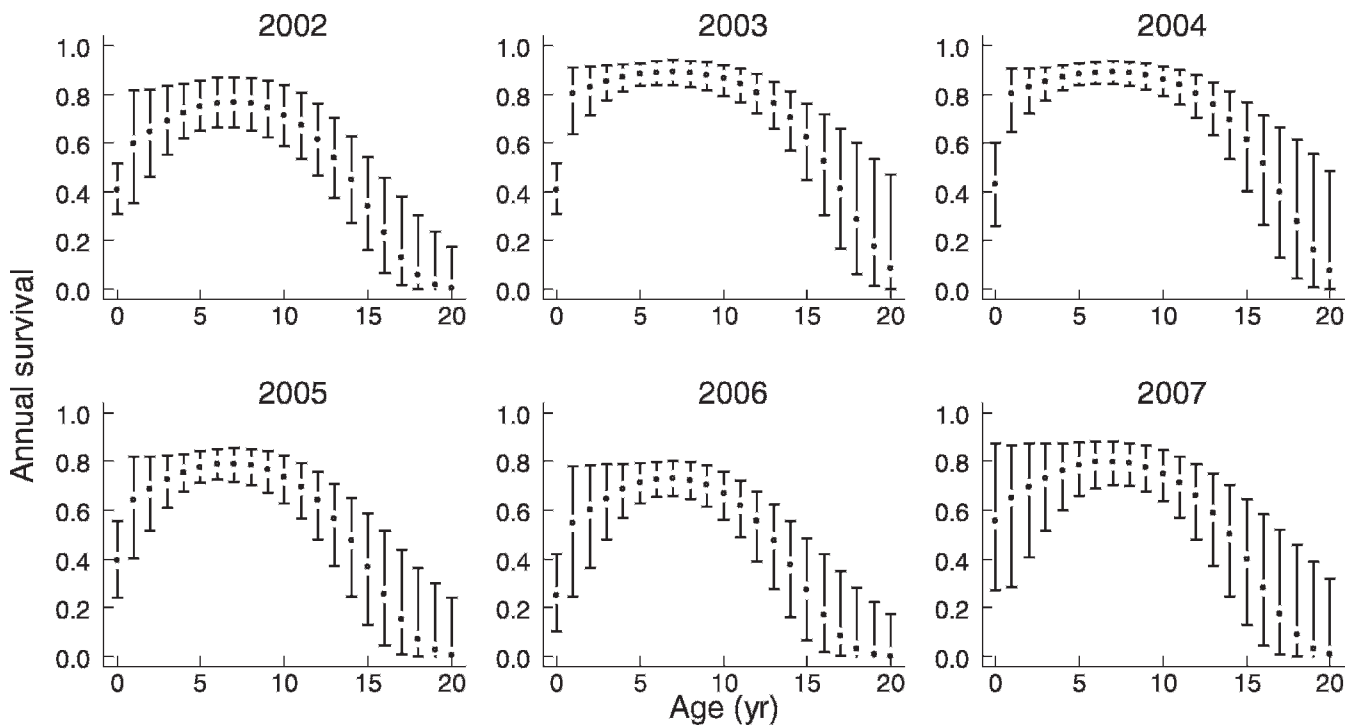

Figure 3. Annual age-specific estimates of survival and pointwise 90% confidence intervals for moose in northeastern Minnesota, USA, 2002–2007. We estimated first-year survival (age 0 yr) by using helicopter surveys. We estimated survival for other ages by fitting a semi-parametric age-period model to telemetry data, where we modeled effect of age and Julian date (i.e., period) by using regression splines, under the assumption that risk of mortality varied smoothly with respect to both age and time. Years represent time periods from 1 June to the following 31 May (i.e., 2002 reflects the time period from 1 Jun 2002 to 31 May 2003).
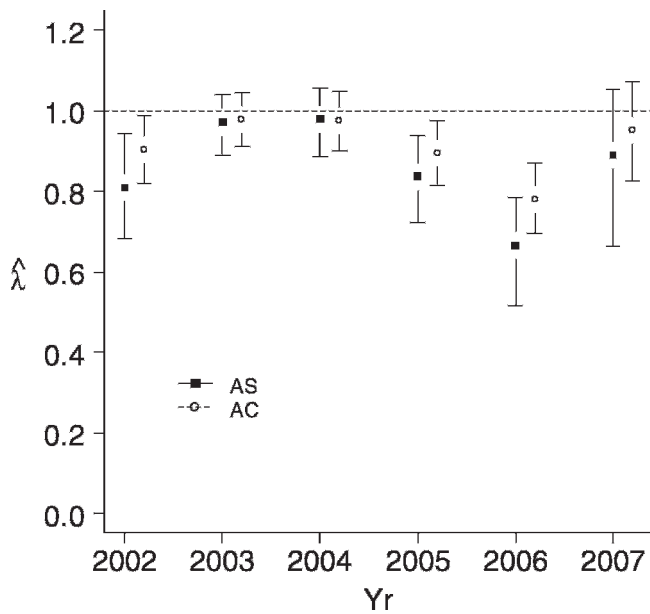
Figure 4. Estimates of finite rate of increase (λ) and 90% bootstrap confidence intervals for moose population in northeastern Minnesota, USA, 2002–2007. Closed squares and open circles give point estimates from models with age-specific survival rates (AS) and constant adult (age >1 yr) survival rates (AC), respectively. We calculated bootstrap confidence intervals by resampling individuals with replacement.

declining population. Confidence interval widths (relative to points estimates) for yearly λs averaged 19% (range = 14–26%, SE = 1.9%, n = 6) and 29% (range = 15–44%, SE = 4.8%, n = 6) when based on AC and AS, respectively. The yearly λs increased only slightly (median increases of 0 to 0.01 units) when we replaced original fertility rates with new rates estimated under the assumption that 10% of calves went undetected in the M–J survey.

Age-specific elasticities and sensitivities were higher for survival than fertility rates (until age 15–17 yr, elasticities;

12–16 yr, sensitivities; depending on yr), and except for fertility rates in the 2006 matrix (estimated in spring of 2007), both sets of values tended to decrease with age (Fig. 5). It is important to note that estimates of elasticities and sensitivities apply only to female moose. Although we included males in our estimation of survival, our models tracked only females under the assumption that sufficient males were available to breed females. Thus, changes to male survival (e.g., hunter harvest) would have no effect on λ unless it affected fertility of females. Using AS survival estimates, and assuming each matrix to be equally likely to occur in the future, we estimated a long-term stochastic growth rate of exp(−0.16) = 0.85 (90% CL = 0.76–0.93), close to the mean λ = 0.86 using AS rates. Sobol' sensitivity indices suggested that most uncertainty associated with $\hat{\lambda}_{s}$ was due to estimating survival rates (Table 2). Specifically, 11% and 78% of the variance of $\hat{\lambda}_{s}$ was attributable to main effects associated with first-year survival and survival rates for ages 1–20 years, respectively, whereas all fertility parameters combined accounted for only 5% of the variance. Large Sobol' indices for survival parameters reflect the combined effect of sampling uncertainty associated with these estimates (Fig. 3) and the sensitivity of population growth rate to these parameters (Fig. 5).

Maximum daily temperature at Ely, Minnesota, increased between 1960 and 2007 (Fig. 6a) but displayed several short-term fluctuations during that period. Minimum daily temperature also fluctuated over this period but demonstrated no apparent long-term trend (Fig. 6b). It is noteworthy that telemetry data we used to calculate survival were collected during a period with the highest maximum temperatures.

DISCUSSION

Our estimates of survival and fertility suggest the moose population in northeastern Minnesota is probably declining.
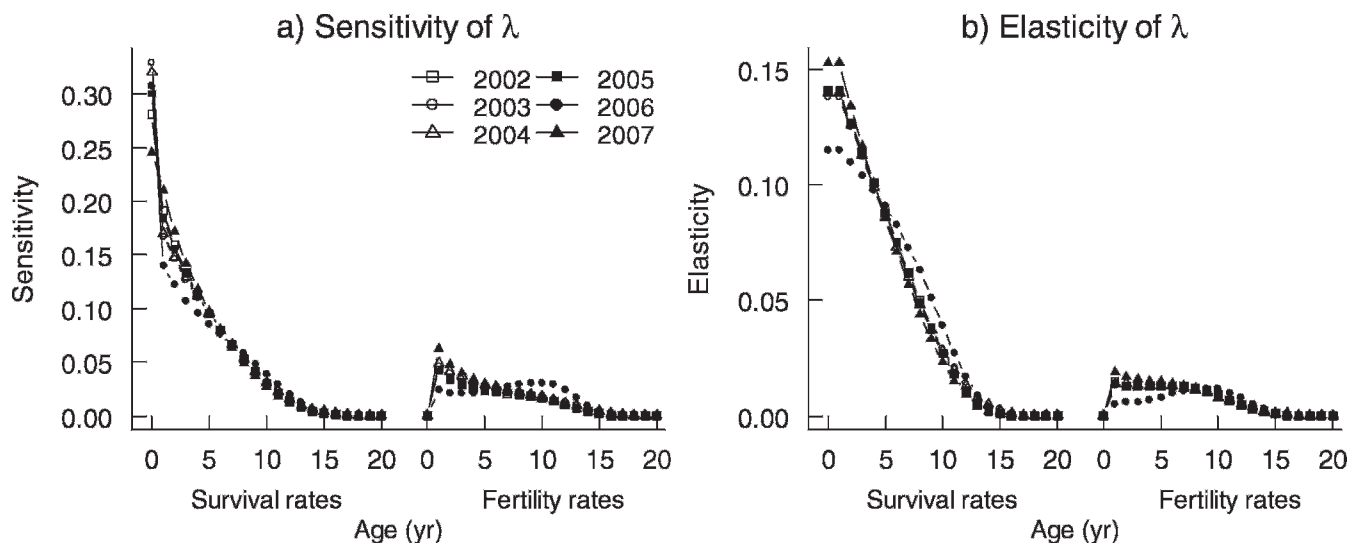

Figure 5. Sensitivity and elasticities of finite rate of increase (λ) to changes in survival and fertility rates. Sensitivities reflect absolute changes in λ resulting from a change in one vital rate, whereas elasticities reflect proportional changes in λ after a proportional change in one vital rate. Sensitivities and elasticities were generally higher for survival than fertility rates and, except for fertility rates in the 2006 matrix (measured in spring of 2007), both sets of values tended to decrease with age.

Table 2. First-order and total Sobol' sensitivity indices for the effect of vital rate uncertainty on the long-term stochastic growth rate, λ_s, for moose in northeastern Minnesota, USA, 2002–2007. We calculated indices assuming each of the 6 yearly matrices to be equally likely to occur in future years. First-order sensitivity indices account for main effects of the parameters, whereas total sensitivity indices account for main effects and all higher order interactions involving each parameter (Sobol' 1993, Fieberg and Jenkins 2005).

Vital rate	First-order sensitivity index	Total sensitivity index
First-yr survival	0.11	0.17
Survival (ages 1–20 yr)	0.78	0.83
Fertility rates (ages 2–20 yr)	0.05	0.11

Point estimates of λ were <1 in all years whether we used AS or AC survival and confidence intervals for λ spanned one (a value of one implies stable population size) in only 3 of 6 years (Fig. 4). The magnitude of λ varied considerably among years and reflected temporal variability in survival risk during the study (Fig. 4). Point estimates of λ were as low as 0.67, which implies a long-term annual decline of as much as 33%. Point estimates of λ averaged 0.86 using AS survival or 0.92 using AC survival over the 6-year period. Similarly, we estimated a long-term stochastic growth rate of 0.85 from the AS matrices. Our data were collected over a short time interval when maximum daily temperatures were warmer than normal (Fig. 6a). If our results are representative of a longer term pattern, the moose population in northeastern Minnesota is in serious jeopardy.

Eberhardt (1977, 2002) proposed that when confronted by reduced resources, vital rates would change in a specific order. Juvenile survival would change first, followed by age at first reproduction, and then reproductive rates of prime-aged animals. Adult survival would be the last to change. Most long-term studies of large herbivorous mammals, in fact, suggest that adult survival is high and varies little from year to year and across populations (Gaillard et al. 1998, 2000). Several demographic analyses have also demonstrated

that based on elasticity, adult survival had the greatest impact on population viability, whereas juvenile survival and fertility had the lowest (Table 2; Fig. 5; Gaillard 1998, 2000; Heppell 2000; Caswell 2001). Presumably, high, stable adult survival results in greater population stability, although Gaillard (1998, 2000) suggested that high annual variability in juvenile survival may also play a major role in population dynamics. Estimates of adult non-hunting mortality from studies of radiocollared moose in the core distribution in North America have, without exception, ranged from 8% to 12% (88–92% survival; e.g., Mytton and Keith 1981 [AB, Canada], Larsen et al. 1989 [YT, Canada], Ballard et al. 1991 [AK, USA], Stenhouse et al. 1995 [NT, Canada], Modafferi and Becker 1997 [AK]). These values are substantially lower than the 21% mean annual mortality observed in both northeastern and northwestern Minnesota (Table 1; Murray et al. 2006). Adult survival in our study also varied considerably among years (Table 1; Fig. 3), which further implies that the northeast moose population is unstable and under considerable stress.

Uncertainty in our estimate of population growth was mainly attributed to estimated survival parameters, with 78% and 11% of the variance of $\hat{\lambda}_s$ attributable to main effects associated with adult survival (ages 1–20 yr) and first-year survival, respectively. Our estimates of first-year survival were based on following survival of calves born to radiocollared female moose and in some years the sample size was small (8 to 28). These calf survival estimates (0.238–0.556) were consistent, however, with estimates from other moose populations, where gray wolves (*Canis lupus*) and black bear (*Ursus americanus*) were common (Hauge and Keith 1981), and generally higher than areas that also contained brown bear (*Ursus arctos*, Gasaway et al. 1983, Ballard et al. 1991, Keech et al. 2000, Testa et al. 2000, Bertram and Vivion 2002). Our estimates assume no postnatal mortality prior to the M–J survey; if postnatal mortality did occur during this time period, our estimates of
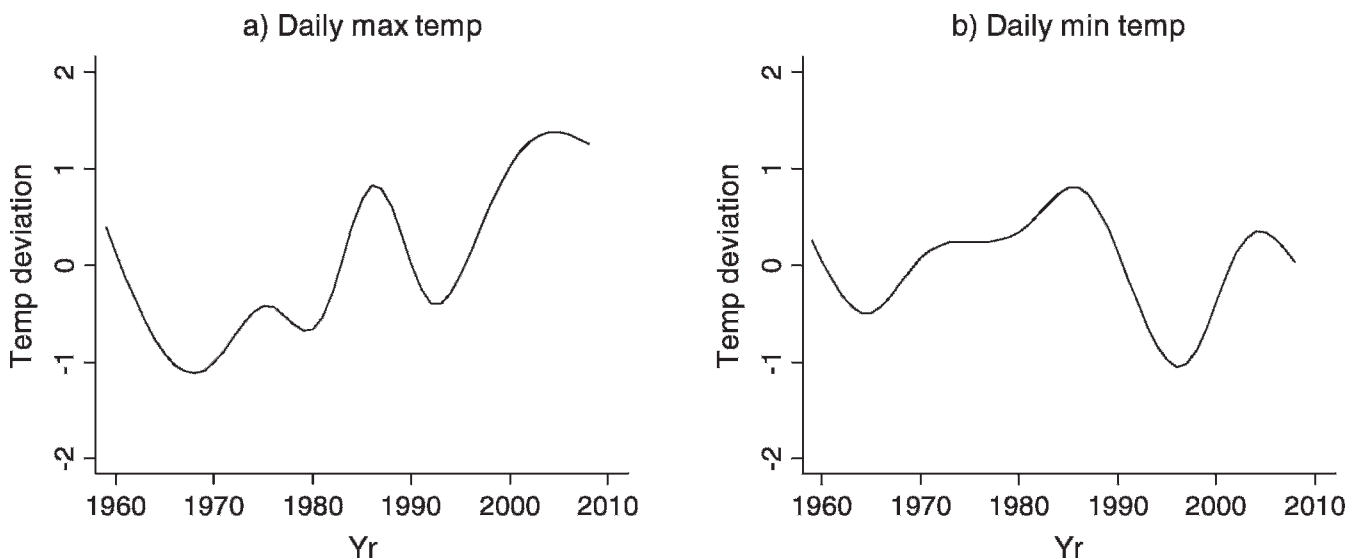

Figure 6. Long-term trends in (a) daily minimum and (b) daily maximum temperatures at Ely, Minnesota, USA, 1960–2007, estimated using generalized additive models containing separate terms for seasonal (within-yr) and long-term trends, both modeled using smoothing splines.

fertility were too low and estimates of first-year survival were too high. The AS approach indicated reduced survival in younger age classes but suffered from reduced precision because of low numbers of young radiocollared moose (Fig. 3). Large mammals typically show a pattern of reduced survival during a juvenile phase (Cauglèy 1966), and this assessment of reduced survival (increased hazard) in the youngest age classes is consistent with other studies of large mammals (Deevey 1947; Siler 1979; Eberhardt 1985; DelGiudice et al. 2002, 2006). Importantly, estimation of survival from age 1–2 yr required extrapolating outside of the range of observed data, using the estimated relationship between age and mortality risk. Similar to pooling, smoothing borrows information from similarly aged individuals. Smoothed survival estimates for early age classes may be biased high when the risk of mortality decreases rapidly after birth (Fieberg and DelGiudice 2009a). Thus, our estimates of survival from age 1–2 yr may be too high. Similarly, in the AC model, we assumed survival to be constant for all ages, which resulted in higher estimates of survival in the younger age classes. Despite this apparent bias, point estimates of λ from the AC model remained <1 in all years of the study.

Matrix elasticities and sensitivities of λ to perturbations in fertility rates were small (Fig. 5); so, too, were Sobol' indices for fertility parameters (Table 2). These results suggest that fertility rates are likely to play a lesser role in determining population trends (under current demographic schedules), and uncertainty in their values also has less impact on our ability to estimate these trends. Log linear models we used to smooth our age-specific fertility reflect decreased fertility in both young and older age classes, a pattern found in other moose populations where reproductive output is a function of age and body condition (Sæther and Haagenrud 1983, Heard et al. 1997, Ericsson et al. 2001). Our annual estimates of fertility for northeastern Minnesota ranged from 0.53 to 0.96 calves/adult female, substantially below levels reported for other moose populations. Boer (1992), for example, reported estimates ranging from 0.88 calves to 1.24 calves/adult female, in moose populations above and below K carrying capacity, respectively. Boer (1992) based his data on rectal palpation during the last trimester or intrauterine counts during pregnancy, so his data were less likely to be affected by observation bias. At least 7% (8/114) of radiocollared females gave birth subsequent to the M–J survey, with 6 of these occurring in the first year of the survey. Although we included these calves in our estimates of fertility, it is possible that we did not detect additional late born calves. However, we found that estimates of λ increased only slightly when we inflated fertility rates to account for undetected calves in our simulations (assumed to occur with probability 0.1).

Although our matrix models are suggestive of a declining population, aerial survey estimates in northeastern Minnesota do not corroborate these results and suggest the population was stable from 2004 to 2009 (Lenarz 2009). Precision of annual estimates was poor (90% CI = ±23 to 30%) and may explain the absence of a downward trend in recent years. Even with precise survey estimates, a change of 20% may be required to detect a statistically significant change in population size (Gasaway and Dubois 1987). The proportion of calves observed during the aerial survey has steadily declined over the past 12 years ($r^2 = 0.47$, $P = 0.015$; Lenarz 2009), suggestive of a population decline. Although fertility has little contribution to λ, the proportion of calves observed during the survey integrates annual fertility and calf survival to 7 months, the latter a more important determinant of λ. In addition, the proportion of hunters successful at harvesting a male moose has steadily declined in the last 8 years ($r^2 = 0.92$, $P > 0.001$; Lenarz 2009), and anecdotal reports from local residents support the inference of a declining population.

That maximum daily temperatures at Ely, Minnesota, have been increasing over the past 47 years, which was expected considering global patterns of temperature increase, and it is likely that temperatures will continue to increase over the next century (Intergovernmental Panel on Climate Change 2007). It is important to note, however, that this statistic has fluctuated over time (Fig. 6a), and we collected survival data during a period with the warmest temperatures. Daily minimum temperatures have apparently not increased during this period (Fig. 6b), suggesting greater variation over the diel cycle. The implications of these trends are especially important to species such as moose, which suffer increased thermoregulatory costs and potential disruption of their energy balance that ultimately would decrease their fitness (Renecker and Hudson 1986, Murray et al. 2006). After identifying a negative association between the population rate of change and summer temperatures in northwestern Minnesota moose, Murray et al. (2006) suggested that a direct link may exist between summer heat stress and body condition deterioration that could translate into energy loss, general malnutrition, and immunosuppression. Eventually, such changes would lead to reduced productivity, higher mortality, and ultimately population decline.

Although it is premature to conclude that climate change is ultimately responsible for the decline of moose in northeastern Minnesota, it is clear that proximate sources of mortality, independent of climate change, probably played a minor role in their decline. Moose harvest in northeastern Minnesota, for example, represented only 2% of the fall population. We censored harvested moose from our analysis, yet λ remained <1. Wolf numbers have remained constant and black bear have declined in the last 10 years (Erb 2008, Garshelis and Noyce 2009). Moreover, wolves were considered the cause of mortality in only 6% of radiocollared moose that died during our study (Lenarz et al. 2009). White-tailed deer, a potential competitor, occurred at approximately 4 deer/km^2 within the study area and have been declining in recent years (M. S. Lenarz, unpublished data). Deer may be more important as a reservoir for several parasites fatal to moose (e.g., meningeal worm [Parelaphostrongylus tenuis] and liver fluke [Fascioloides magna]; Murray et al. 2006).

Estimates of growth rates and extinction probabilities from demographic models are often difficult to interpret because of the large uncertainties associated with population projections (Ludwig 1999, Fieberg and Ellner 2000). Estimates of risk metrics can be improved by linking demographic patterns to environmental data (Fieberg and Ellner 2001). Recently, Lenarz et al. (2009), working with the same moose in northeastern Minnesota, identified inverse relationships between heat stress, as indicated by various temperature metrics, with annual and seasonal survival and found that heat stress as measured in January and in late spring (Apr–May) was most important in explaining variation in survival. Although important in an exploratory context, these relationships were based on a small sample size that occurred during a period of warm weather (Fig. 6a). Rather than model seasonal or annual survival, we estimated a smooth temporal trend in mortality risk that followed a sinusoidal pattern during our study. Although it was not readily apparent if or how much of this temporal trend was mediated by temperature, one might expect even greater fluctuations to have occurred historically (given the wide range of temperatures experienced this century compared to our relatively homogenous study period).

To make a stronger link between temperature and survival, it would be desirable to collect data over a much longer time period with greater temperature swings. Such long-term data are essential, particularly because the relationship between temperature and survival is likely to be complex, involving lagged and cumulative responses, and therefore difficult to model. Nevertheless, literature on the effects of heat stress on cattle indicate hot weather can reduce food intake, body growth, milk production, and reproduction (Hahn 1999), as well as impair immune system of those animals (Kelley et al. 1982, Morrow-Tesch et al. 1996). In a large wild ungulate, such as moose, that is dependent on accumulation of fat reserves for survival, any decrease in body condition will ultimately result in reduced fitness (Mautz 1978, Verme and Ullrey 1984, Murray et al. 2006). Regardless of the existence of a causal relationship, unless moose survival and fertility increase above levels measured between 2002 and 2008, the moose population in northeastern Minnesota will probably decline and ultimately the southern edge of moose distribution will shift northward out of northern Minnesota.

MANAGEMENT IMPLICATIONS

In general, the growth rate of wildlife populations on the edge of their range will probably be more variable than in established populations in the core of their distribution. As species pioneer new range, populations may grow rapidly (McCullough 1979, Klein 1968); when conditions become marginal, populations decline or disappear. Our results suggest moose numbers in northeastern Minnesota may decline, in which case the southern edge of moose range will shift northward. The proximate causes of mortality in this population are largely unknown (Lenarz et al. 2009), and until ultimate and proximate causes are better understood, it will be difficult to identify management that will benefit the population. Our results also illustrate the relative importance of survival to λ, a pattern common to species ranging from flour beetles (*Calandra oryzae*) to killer whales (*Orcinus orca*; Gaillard 1998, 2000; Heppell et al. 2000; Caswell 2001), which is not widely understood by wildlife ecologists. The relative importance of survival to population viability implies that harvest of females in large herbivorous mammals, especially if it represents additive mortality, may have a much greater impact on population growth than management focused to change fertility. Finally, whereas surveys designed to measure fertility of a wildlife species (e.g., pregnancy rates, newborn:ad F ratios) may in many cases be easier and less expensive to conduct, such surveys provide less information about population growth rate than do estimates of survival.

ACKNOWLEDGMENTS

LITERATURE CITED

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs 114.

Bates, D. M., and B. W. N. Venables. 2004. Splines version 1.9.0. R package. <http://cran.R-project.org>. Accessed 29 Jun 2009.

Belovsky, G. E., and P. A. Jordan. 1978. The time-energy budget of a moose. Theoretical Population Biology 14:76–104.

Bertram, M. R., and M. T. Vivion. 2002. Moose mortality in eastern interior Alaska. Journal of Wildlife Management 66:747–756.

Boer, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces (Supplement) 1:1–10.

Bubenik, A. B. 1997. Behavior. Pages 173–221 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.

Carstensen, B. 2006a. Demography and epidemiology: age-period-cohort models in the computer age. Technical Report 06.1. Department of Biostatistics, University of Copenhagen, Denmark. <http://biostat.ku.dk/reports/2006/ResearchReport06-1.pdf/>. Accessed 5 May 2009.

Carstensen, B. 2006b. Demography and epidemiology: practical use of the Lexis diagram in the computer age. Or: Who needs the Cox-model anyway? Technical Report 06.2. Department of Biostatistics, University of Copenhagen, Denmark. <http://biostat.ku.dk/reports/2006/rr-06-2.pdf/>. Accessed 5 May 2009.

Carstensen, B., M. Plummer, E. Laara, and M. Hills. 2008. Epi: a package for statistical analysis in epidemiology. R package version 1.1.7. <http://cran.at.r-project.org/web/packages/Epi/index.html>. Accessed 30 Jul 2008.

Caswell, H. 2001. Matrix population models, construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Caugley, G. 1966. Mortality patterns in mammals. Ecology 47:906–918.

Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22:283–314.

DelGiudice, G. D., J. Fieberg, M. R. Riggs, M. Carstensen-Powell, and W. Pan. 2006. A long-term age-specific survival analysis of female white-tailed deer. Journal of Wildlife Management 70:1556–1568.

DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause specific mortality of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66:698–717.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Eberhardt, L. L. 1977. "Optimal" management policies for marine mammals. Wildlife Society Bulletin 5:162–169.

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

Ellner, S. P., and J. Fieberg. 2003. Using PVA for management despite uncertainty: effects of habitat, hatcheries, and harvest of salmon. Ecology 84:1359–1369.

Erb, J. 2008. Distribution and abundance of wolves in Minnesota, 2007–2008. Minnesota Department of Natural Resources, St. Paul, USA. <http://files.dnr.state.mn.us/fish_wildlife/wildlife/wolves/2008_survey.pdf>. Accessed 8 Oct 2009.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology 82:1613–1620.

Fieberg, J., and G. DelGiudice. 2008. Exploring migration data using interval-censored time-to-event models. Journal of Wildlife Management 72:1211–1219.

Fieberg, J., and G. D. DelGiudice. 2009a. Estimating age-specific hazards from wildlife telemetry data. Environmental and Ecological Statistics DOI 10.1007/s10651-009-0128-x. <http://www.springerlink.com/content/30647140053608v7/>. Accessed 14 Apr 2010.

Fieberg, J., and G. D. DelGiudice. 2009b. What time is it? Choice of time origin and scale in extended proportional hazards models. Ecology 90:1687–1697.

Fieberg, J., and S. P. Ellner. 2000. When is it meaningful to estimate an extinction probability? Ecology 81:2040–2047.

Fieberg, J., and S. P. Ellner. 2001. Stochastic matrix models for conservation and management: a comparative review of methods. Ecology Letters 4:244–266.

Fieberg, J., and K. J. Jenkins. 2005. Assessing uncertainty in ecological systems using global sensitivity analysis: a case example of simulated wolf reintroduction effects on elk. Ecological Modeling 187:259–280.

Fuller, T. K. 1986. Observations of moose, *Alces alces*, in peripheral range in northcentral Minnesota. Canadian Field Naturalist 100:359–362.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gannon, W. L., R. S. Sikes, and Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Garshelis, D., and K. Noyce. 2009. Status of Minnesota black bears, 2008. Minnesota Department of Natural Resources, St. Paul, USA. <http://files.dnr.state.mn.us/outdoor_activities/hunting/bear/2008bear_report.pdf>. Accessed 8 Oct 2009.

Gasaway, W. C., and S. D. DuBois. 1987. Estimating moose population parameters. Swedish Wildlife Research (Supplement) 1:603–617.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84.

Hahn, G. L. 1999. Dynamic responses of cattle to thermal heat loads. Journal of Animal Science 77:10–20.

Harrell, F. E., Jr. 2001. Regression modeling strategies, with applications to linear models, logistic regression, and survival analysis. Springer Science+Business Media, New York, New York, USA.

Hauge, T. M., and L. B. Keith. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management 45:573–597.

Heard, D., S. Barry, G. Watts, and K. Child. 1997. Fertility of female moose (*Alces alces*) in relation to age and body composition. Alces 33:165–176.

Heinselman, M. 1996. The boundary waters wilderness ecosystem. University of Minnesota Press, Minneapolis, USA.

Heisey, D. M., T. L. Shaffer, and G. C. White. 2007. The abcs of nest survival: theory and application form a biostatistical perspective. Studies in Avian Biology 34:13–33.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Holter, J. B., W. E. Urban, Jr., H. H. Hayes, H. Silver, and H. R. Skutt. 1975. Ambient temperature effects on physiological traits of white-tailed deer. Canadian Journal of Zoology 53:679–685.

Humphries, M. M., J. Umbanhowar, and K. S. McCann. 2004. Bioenergetic prediction of climate change impacts on northern mammals. Integrative and Comparative Biology 44:152–162.

Intergovernmental Panel on Climate Change. 2007. Climate change 2007: synthesis report. <http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr_spm.pdf>. Accessed 5 May 2009.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

Kelley, K. W., R. E. Greenfield, J. F. Evermann, S. M. Parish, and L. E. Perryman. 1982. Delayed-type hypersensitivity, contact sensitivity, and phytohemagglutinin skin-test responses of heat- and cold-stressed calves. American Journal of Veterinary Research 43:775–779.

Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthews Island. Journal of Wildlife Management 32:350–367.

Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in southwest Yukon. Journal of Wildlife Management 53:548–557.

Lenarz, M. S. 2007. 2007 Aerial moose survey. Minnesota Department of Natural Resources, St. Paul, USA. <http://files.dnr.state.mn.us/outdoor_activities/hunting/moose/moose_survey_2007.pdf>. Accessed 5 May 2009.

Lenarz, M. S. 2009. 2009 Aerial moose survey. Minnesota Department of Natural Resources, St. Paul, USA. <http://files.dnr.state.mn.us/outdoor_activities/hunting/moose/moose_survey_2009.pdf>. Accessed 5 May 2009.

Lenarz, M. S., M. E. Nelson, M. W. Schrage, and A. J. Edwards. 2009. Temperature mediated moose survival in northeastern Minnesota. Journal of Wildlife Management 73:503–510.

Lindsey, J. K. 1998. A study of interval censoring in parametric regression models. Lifetime Data Analysis 4:329–354.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80:298–310.

Mautz, W. W. 1978. Nutrition and carrying capacity. Pages 321–348 *in* J. L. Schmidt and D. L Gilbert, editors. Big game of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

McCullough, D. R. 1979. The George Reserve deer herd, population ecology of a K-selected species. University of Michigan Press, Ann Arbor, USA.

Minnesota Climatological Working Group. 1960–2007. Historical climate data, Station 212543, Ely, MN. <http://climate.umn.edu/HIDradius/radius.asp>. Accessed 5 May 2009.

Minnesota Department of Natural Resources [MNDNR]. 2007. Ecological Classification System. Minnesota Department of Natural Resources, St. Paul, USA. <http://www.dnr.state.mn.us/ecs/index.html>. Accessed 5 May 2009.

Modafferi, R. D., and E. F. Becker. 1997. Survival of radio collared adult moose in lower Susitna River valley, south central Alaska. Journal of Wildlife Management 61:540–549.

Morrow-Tesch, J., N. Woolen, and L. Hahn. 1996. Response of gamma delta T-lymphocytes to heat stress in *Bos taurus* and *Bos indicus* crossbred cattle. Journal of Thermal Biology 21:101–108.

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs 166.

Mytton, W. R., and L. B. Keith. 1981. Dynamics of moose populations near Rochester, Alberta, 1975–1978. Canadian Field Naturalist 95:39–49.

Nelson, M. E. 2001. Tooth extraction from live-captured white-tailed deer. Wildlife Society Bulletin 29:245–247.

Odell, P. M., K. M. Anderson, and R. B. D'Agostino. 1992. Maximum likelihood estimation for interval-censored data using a Weibull-based accelerated failure time model. Biometrics 48:951–959.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Version 2.6.2, ISBN 3-900051-07-0. <http://www.R-project.org>. Accessed 18 Aug 2008.

Renecker, L. A., and R. J. Hudson. 1986. Seasonal energy expenditure and thermoregulatory response of moose. Canadian Journal of Zoology 64:322–327.

Renecker, L. A., and R. J. Hudson. 1990. Behavioral and thermoregulatory responses of moose to high ambient temperatures and insect harassment in aspen dominated forests. Alces 26:66–72.

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

Schwartz, C. C. 1997. Reproduction, natality and growth. Pages 141–171 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.

Siler, W. 1979. A competing-risk model for animal mortality. Ecology 60:750–757.

Sobol', I. M. 1993. Sensitivity analysis for non-linear mathematical model. Mathematical Modeling and Computational Experiments 1:407–414.

Stenhouse, G. B., P. B. Latour, L. Kutny, N. MacLean, and G. Glover. 1995. Productivity, survival, and movements of female moose in a low density population, Northwest Territories, Canada. Arctic 48:57–62.

Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:1–23.

Testa, J. W. 2004. Population dynamics and life history trade-offs of moose (*Alces alces*) in southcentral Alaska. Ecology 85:1439–1452.

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

Tuljapurkar, S. D. 1990. Population dynamics in variable environments. Lecture Notes in Biomathematics. Volume 85. Springer-Verlag, New York, New York, USA.

Union of Concerned Scientists. 2003. Confronting climate change in the great lakes regions: impacts on our communities and ecosystems. <http://www.ucsusa.org/greatlakes/glchallengereport.html>. Accessed 5 May 2009.

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

Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91–118 *in* L. K. Halls, editor. White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, New York, New York, USA.

Associate Editor: White.