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Original article

Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States

Anthony R. Musante, Peter J. Pekins & David L. Scarpitti

Abundance indices suggested that the moose *Alces alces* population in northern New Hampshire was stable despite favourable habitat and conservative harvest. Causes and rates of mortality were unknown because moose reproduction and survival was unstudied in the region. Our study was designed to investigate the dynamics of the regional population in 2002-2005. A total of 92 moose (33 cows and 59 calves) were captured and fitted with radio-collars (VHF = 83, GPS = 9). Parturition ranged from 8 May to 13 July (median = 19 May) with 78% of births occurring during 13-27 May. Calving rate of yearlings and adults (> 2 years old) averaged 30 and 85%, respectively; twinning rate was 11%. Analysis of reproductive data from harvested cows (1988-2004) indicated that the average weight of adult cows increased but their *corpora lutea* count declined from ~ 1.4 to 1.2/cow. Both ovulation rate and average weight of yearling cows declined about 25 and 4%, respectively. There were 39 mortalities (49% calves) with winterkill/parasite (41%), vehicle collision (26%) and hunting (18%) as the leading causes. Major sources of mortality of radio-marked cows were human-related; survival was 0.87. Annual calf survival was 0.45. Unmarked calf (0-2 months of age) survival was 0.71 with 76% of mortality in the first month of life. Radio-marked calves (~ 7-12 months of age) had a survival rate of 0.67; 74% of the mortality was winterkill/parasite related. Calf mortality was concentrated (88%) in late winter-early spring. The unseasonably warm and snowless fall in 2001 probably favoured high tick transmission and increased tick loads on moose that resulted in high calf mortality (0.51) and measurable cow mortality (10%) in mild winter-spring 2002. Documentation of substantial tick-related mortality of radio-marked moose calves was unique to this study. The stability of the moose population probably reflects the variation in annual recruitment and lower fecundity of yearling cows associated with heavy infestations and epizootics of winter tick. Given that fertility, calving rate and body condition of adult cows, and summer calf survival are annually high, the population should recover from tick epizootics that periodically inhibit population growth.

Key words: Alces alces, corpora lutea, epizootic, moose, mortality, parturition, survival, winterkill, winter tick

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A once abundant moose *Alces alces* population was nearly extirpated in New Hampshire, USA, by the beginning of the 20th century due to unregulated hunting and loss of habitat, which compelled the state to legally protect moose in 1901 (Silver 1957). The succession of farmlands to forest in the early 1900s, extensive clear-cutting in the 1960s and 1970s, severe winters reducing white-tailed deer *Odocoileus virginianus* numbers and the continued legal protection of moose all contributed to a

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population rebound (Bontaites & Gustafson 1993). As moose populations continue to expand their range in New England (Franzmann 2000) approximately 7,000 moose now occupy their historic range within New Hampshire; however, knowledge of moose population dynamics in New Hampshire and the Northeastern United States is limited. Population parameters including size, growth rate, fecundity and mortality must be known to predict the dynamics of a wildlife population (Caughley 1977), and to identify and possibly influence factors regulating regional population density.

The status and trend of the moose population in northern New Hampshire is monitored by assessing annual vehicular collision rates, deer hunter observation reports, aerial infrared censuses, and analysis of biological information (e.g. field-dressed body weight and *corpora lutea* counts) from harvested moose (Adams & Pekins 1995, Bontaites et al. 2000). These abundance indices suggested that the northern moose herd was no longer growing and below biological carrying capacity despite perceived optimal moose habitat and a conservative annual harvest; substantial natural mortality of unknown cause was suspected. Disease, parasites, predation, human-related activities, weather and population density are factors which can account for the demographic variation observed among years within a population or among populations within a species (Gaillard et al. 1998). Therefore, investigation of this population was important due to the ecological, recreational, aesthetic and economical values that moose represent to New Hampshire.

While many agencies use harvest data to assess wildlife populations, these data alone are often insufficient because other mortality factors influence a population (Bender & Hall 2004). Therefore, marked populations can greatly aid in efforts to understand and predict moose population dynamics (Modafferi & Becker 1997), and also identify parameters and mechanisms that induce population response. Radio-telemetry studies of moose have demonstrated that fecundity, survival and cause-specific mortality rates vary regionally and seasonally with age, sex and density of moose (Van Ballenberghe & Ballard 1998); these rates had not been previously documented in New Hampshire. Our research with radio-marked moose focused on and assessed factors influencing these parameters and their effect on the population which will be used to assist in the development of informed management strategies. Our first objective was to determine how parturition, yearling and adult fecundity, and twinning rates influence productivity. Our second objective was to identify the timing, magnitude and cause of age-specific mortality occurring in the study population.



Figure 1. Study area of the moose project in Coos County New Hampshire, during 2002-2005.

Material and methods

Study area

Our study area was located in the eastern portion of Coos County in northern New Hampshire where the majority of forestland was privately owned and commercially harvested (Fig. 1). It encompassed roughly 1,000 km^2 and included most of wildlife management units (WMU) B, C1 and C2 as designated by the New Hampshire Fish and Game Department (NHFG). The eastern edge of WMU C2 along the Mahoosuc Mountain Range bordered the state of Maine. The core of the study area was located within the Androscoggin River watershed in the town of Milan. The primary land use was harvesting of pulp and saw logs with recreational activities such as hunting, fishing, trapping and snowmobiling common in the area. Maintained logging roads and off-highway recreational vehicle (OHRV) trails intersected much of the study area providing year-round accessibility (e.g. 4WD truck, ATV and snowmobile).

The region was dominated by mountainous

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terrain bordered by lowland valleys containing a myriad of lakes, ponds and river systems; elevation ranged from 300 to 1,200 m. The dominant cover type was northern hardwood forest (36%) consisting of American beech *Fagus grandifolia*, sugar maple *Acer saccharum* and yellow birch *Betula alleghaniensis*. Spruce-fir forests (21%) thrived in less drained sites and higher elevation areas were dominated by red spruce *Picea rubens* and balsam fir *Abies balsamea*. Mixed forests (23%) consisted of northern hardwood and spruce-fir, whereas, clearcuts and regenerating stands of quaking aspen *Populus tremuloides*, paper birch *Betula papyrifera* and pin cherry *Prunus serotina* were 16% of the forest cover (Degraaf et al. 1992, Sperduto & Nichols 2004).

Monthly precipitation, mean ambient temperature, precipitation, snow depth and other weather variables were available at the National Climatic Data Center (44°27'N, 71°11'W) weather station in Berlin, New Hampshire (#270690/99999) located centrally in the study area at an elevation of 283 m. Annual ambient temperature ranged from 30 to -30°C, annual precipitation ranged from 91 to 123 cm, and maximum snow depth ranged from 50 to 70 cm. Mean annual snowfall was 191.8 cm and maximum recorded snow depth was 35.6, 71.1, 88.9 and 104.1 cm in 2002-2005, respectively. During December-April 2002-2005, the average weekly snow depth measured at open sites ranged from 25 to 50 cm and did not exceed 70 cm.

The estimated moose density within the management units B, C1 and C2 was 0.78 moose/km^2 or approximately 1,500 moose, one of the highest concentrations of moose in New Hampshire (NHFG, unpubl. data). Moose of both sexes were hunted annually through a permit-lottery during a nine-day period in October. An average of 115 either sex permits were assigned to the area with hunter success $>$ 85% (NHFG 2004). Known carnivores and possible predators of moose included black bear *Ursus americana*, coyote *Canis latrans* and bobcat *Lynx rufus*. Bear densities ranged from 0.23 to 0.34 bear/km^2 in the region and white-tailed deer existed throughout the study area in density of 2.3-3.1 deer/km^2 (NHFG, unpubl. data).

Capture and marking

All but two moose were captured in cooperation with Hawkins and Powers Aviation, Inc. (Greybull, Wyoming, USA) by helicopter (Bell Long Ranger L-3) net-gunning (Carpenter & Innes 1995). When capture was not conducive to net-gunning, moose were darted and immobilized using a mixture of carfentanil citrate and xylazine hydrochloride. Captures occurred each December 2001-2003 and were completed in 1-2 weeks each year. The study area was surveyed from a fixed-wing aircraft (Cessna 172, Hamel Air, Milan, New Hampshire, USA) for moose abundance and favourable capture sites (e.g. clearcuts, log landings or forest openings) 1-2 weeks prior to captures. After the first year, primary capture sites were based on the location of marked moose; an observer in a Cessna was used as a 'spotter' to locate radio-marked cows to attempt capture of their calves.

Both cows and calves were targeted each year. Calves were distinguished by relative size, and non-calves were considered adults ($\geq$ 2.5 years) due to the difficulty of aging moose without observing tooth wear (Peterson et al. 1983). Capture effort per age class was dictated by the objective to maintain 25 marked adult cows each summer. Moose were fitted with VHF (N = 83) or breakaway GPS (N = 9) radio-collars (VHF: Model 600, GPS: Model TGW-3700, Telonics, Inc., Mesa, Arizona, USA) in the 150-MHz range and with a 4-hour mortality delay. Collars were sized at 96 cm circumference for cows and were modified for calves with duct tape and medical latex cord; calf collars eventually opened to 114 cm for bulls and 96 cm for cows after deterioration of the latex and tape ($\sim$ 1 year). Each moose received a numbered ear tag with capture year differentiated by tag color (ALLFLEX USA Inc. Dallas, Texas, USA). Pregnancy at capture was determined from blood samples with an assay of the pregnancy-specific protein B (PSPB, BioTracking, Moscow, Idaho, USA; Huang et al. 2000) or portable ultrasound device (Stephenson et al. 1995).

Productivity

To estimate calving date and fecundity rate, radio-marked cows were approached on foot and observed at regular intervals 2-3 times weekly from 1 May to 1 July and weekly thereafter until 15 August, during 2002-2005. Age class was categorized as calves $<$ 1 year, yearlings $\geq$ 1 year but $<$ 2 years, and adults $\geq$ 2 years at the time of breeding. The yearling sample size was unknown in 2002 (first capture year) because age could only be determined after mortality; thereafter, known yearlings were recruited as radio-marked calves. Attempts were made at least once weekly to observe yearlings possibly bred as calves.

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Cows were stalked within sighting distance using telemetry homing techniques (Mech 1983); dense canopy and thick vegetation typical of calving habitat in New Hampshire hindered aerial observation. Parturition dates were assigned by backdating from the estimated age of neonates; calves were aged as $<$ 1 day (0 days), 1 day, 2 days, 3-7 days (5 days) or $>$ 7 days based on coordination, mobility, wet or dry appearance, and presence of an umbilicus (Larsen et al. 1989). We also considered evidence of the birth site (e.g. birthing membranes), calf beds, tracks or fecal matter, and behaviour and posture of cows associated with protection or leading calves at heel.

Harvest reproductive data

Ovaries from harvested cows at New Hampshire moose check stations (1988-2004) were used to measure ovulation rate and test age-specific relationships of harvested moose. Two age classes were considered; yearlings ($\geq$ 1 year but $<$ 2 years) and adults ($\geq$ 2 years). Ovulation rate was calculated for each age class within the study area and statewide during 1988-2004. We analysed these data to detect difference in distribution for all harvest years and between 1988-1998 and 1999-2004. Categories were 0 and $\geq$ 1 *corpora lutea* (CL) for yearlings and 0, 1 and $\geq$ 2 CL for adults. We also examined mean field-dressed body weights for cows harvested within the study area and statewide during 1988-1998 and 1999-2004; the age classes were 1.5 - $\geq$ 6.5 years.

Monitoring of unmarked calves

We measured calf survival during summer (8-10 week postpartum period of 1 May - 15 August) and post-summer periods. Observation of cow behaviour and evidence of a calf present (e.g. tracks, beds and fecal matter) at location sites aided to establish fate of the calf. Cows were observed $\geq$ 3 separate times over a 1-2 week period after initial absence of their calf; the mortality date was set as the midpoint between the last observation and the initial date of absence. An unmarked calf was considered a mortality if the cow died $\leq$ 2 months after birth; the mortality date of the cow was assigned to the calf. Cause-specific mortality was never determined due to elapsed time between relocations, movement of cows and dense vegetation.

The post-summer period was 16 August - 1 May the following year. Ground observations of each marked cow and calf occurred $\geq$ 3 times during this period with additional observations during aerial telemetry flights. Unmarked calves were considered a mortality if a cow was observed alone; subsequent direct observations on foot were performed $\geq$ 3 times over a 1-2 week period to confirm absence. Because monitoring was less intensive during the post-summer period than in summer, a mortality date was only assigned when cause and date were positively known.

Mortality assessment of radio-marked moose

Moose were relocated 1-3 times weekly with a combination of aerial telemetry, ground-based telemetry and direct observation. The animal was located within 24 hours of a mortality signal to confirm mortality vs a dropped collar. The site was examined for evidence of cause of death (e.g. predation and struggle). Necropsies (Wobeser & Spraker 1980) were primarily performed in the field, and when feasible, with veterinarian assistance (Dr. Richard Kingston, DVM, New Hampshire Technical Institute, Concord, New Hampshire, USA).

Tissue and organ samples were collected for gross and histological examinations. An estimate of overall body condition was based on carcass fat at the cardiac, omental, perirenal and subcutaneous (tail, head and brisket) regions (Kistner et al. 1980). Fat deposits were classified as no visible fat, slight fat, moderate fat or heavy fat. Femur marrow was graded visually (Cheatum 1949) and a $>$ 30 g plug of marrow was extracted from the middle third of the femur to measure percent fat content oven dry weight (% FMF; Neiland 1970). Winter tick *Dermacentor albipictus* associated hair loss/damage (Samuel & Barker 1979, Samuel 2004) and degree of lungworm *Dictyocaulus viviparus* infestation and associated lung tissue damage (e.g. emphysema and congestion) was described visually and subjectively as light, moderate, severe or very severe. The dorsal portion of the cranium was removed and the meninges throughout the cranium and brain were inspected for meningeal worms *Parelaphostrongylus tenuis* (Anderson 1965, Lankester & Samuel 1998). First incisors were removed to determine age by counting *cementum annuli* on a tooth section (Matson's Laboratory, LLC. Milltown, Montana, USA; Sergeant & Pimlott 1959, Wolfe 1969). Depending on carcass condition, the mortality date was assumed to be the day the mortality pulse mode was first detected. Probable cause of death was assigned categorically as: vehicle collision, hunting, winter kill/parasite or undetermined. Winterkill/

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parasite mortality was classified by time of year (March - April), obvious winter tick infestation, combination of tick and lungworm parasitism, low % FMF and no other indicators of cause of mortality.

Survival analysis

Radio-marked moose

Known-fate modeling was implemented in program MARK version 4.2 (White & Burnham 1999, Cooch & White 2004) to estimate survival rates of radio-marked adult cows and calves and to evaluate candidate models relative to survival. These survival estimates are analogous to rates calculated by the Kaplan-Meier product-limit estimator allowing for staggered entry of new subjects to a study (Kaplan & Meier 1958, Pollock et al. 1989). The fate of each radio-marked animal is assumed known at the beginning and end of each encounter occasion; therefore, survival probabilities are estimated with high precision and require fewer assumptions than apparent survival estimates (White & Burnham 1999).

Known-fate data were separated into two sets of analyses, survival of yearling and adult cows and survival of calves. Adult and yearling males were omitted from the analysis due to the limited sample size (19 individuals with six collar losses). Analysis of radio-marked animals began three weeks after capture to exclude capture-related mortality and bias; five animals were excluded due to capture injury (3), capture myopathy and vehicle collision. Adult annual survival was considered during 1 January - 31 December to coincide with captures that occurred in December each year. Winter survival of calves was calculated from 1 January to 18 May and included animals marked at approximately seven months of age. Calves entered the next age class on 19 May, the median birth date in the study. Adults and calves were classified into four (2002-2005) and three (2002-2004) year groups, respectively. Telemetry locations were collapsed into 52 weekly intervals for adults and 20 weekly intervals for calves. Moose were classified as alive, dead or censored due to collar loss, removal or emigration at the beginning of each sampling interval. The 2005 adult analysis censored animals after 3 September due to termination of the regular monitoring schedule.

We developed 26 models to examine adult/yearling survival and six of calf survival (Burnham & Anderson 2002). These included models that considered constant survival, weekly categorical time, year, season, interactions of year and weekly time, and year with seasons. The four seasons were early winter (weeks 1-7; 1 January - 17 February), late winter (weeks 8-18; 18 February - 4 May), summer (weeks 19-37; 5 May - 15 September) and fall (weeks 38-50; 18 September - 16 December). Weeks 51-52 were not considered part of fall or included in seasonal analysis, but were used in calculating annual rates. Data from 2005 were not used in year models and weeks 36-52 in 2005 (no monitoring) were censored or fixed in remaining models; however, apparent survival was 1.0 through 35 weeks in 2005.

Unmarked calves

We used the nest-survival model in program MARK to estimate survival rates of unmarked calves and to evaluate relative support for covariate candidate models. This model is a type of known-fate analysis that generates point estimates of daily survival rates (DSR) and is appropriate for known-fate data where the encounter occasions are not clearly delineated; the key difference between known-fate and nest-survival data types is that the exact day of animal disappearance is not known (Cooch & White 2004).

We standardized the four calving seasons (2002-2005) to 98 days by assuming 10 May as the first day of data collection (earliest date a calf was observed) and 15 August as the last day (end of the neonatal monitoring season). For calves with fate unknown at 60 days (e.g. late-born calves), data were only included to the day that fate was certain. The nest-survival model provides an estimation of total calf survival from day one to 60 days as a product of DSR over that period. Six models incorporated constant survival, year, calf age and birth date to test calf survival.

We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to evaluate and rank all models for radio-marked moose and unmarked calves, select the model that best described survival and report survival rates and log-normal 95% confidence intervals (CI) generated by MARK (Burnham & Anderson 2002).

Statistical analysis

We analysed median parturition dates among years using a Tukey-type multiple comparison median test, and results were considered statistically signif-

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icant at $\alpha = 0.05$ (Zar 1999). We used χ^2 tests of independence to compare CL counts, and mean cow weights were examined using a general linear model (GLM) followed by Tukey's test for multiple comparison of means as part of the annual New Hampshire moose harvest data (1988-2004) statewide and in management units B, C1 and C2 (Zar 1999). We compared intraspecific variations in sources of mortality among age classes using χ^2 goodness-of-fit tests. A χ^2 goodness-of-fit test was used to determine variation in timing of unmarked neonatal losses. Analysis was performed using SYSTAT version 10 (SPSS Inc. 2000) with results considered statistically significant at $P < 0.05$.

Results

In total, 96 moose were captured (81 were net-gunned and 15 darted) of which 92 (33 cows and 59 calves) were successfully radio-marked. In 2001, 15 of 24 cows (63%) were tested pregnant by blood assay (PSPB), and 13 of the 15 (87%) were subsequently observed with a calf in spring 2002. Of the nine that tested negative, four were winter mortalities aged 1.5, 6.5, 12.5 and 15.5 years and without fetus, one was observed with a calf, and three were later identified as yearlings. The four cows identified as pregnant by ultrasound in 2002 were all observed with a calf the following summer. The overall pregnancy rate was 68%; i.e. 78% in adult cows and 20% in yearlings.

Parturition dates

Based on estimated birth dates (N = 77), parturition ranged from 8 May to 13 July with a median date of 19 May. The same cow had two July births; no other births were recorded beyond June. The annual median parturition date ranged from 17 to 22 May and birthing was highly synchronous with 78% of births occurring during 13-27 May, and 10% beyond 31 May. The annual calving season averaged 42 days in length ranging 22-62 days long. Timing of parturition was similar among years (Tukey-type multiple comparison median test: $\alpha = 0.05$). The mean estimated age at first observation (N = 86) was 2.1 days (SD = 1.9); only one calf was aged initially at > 1 week old.

Productivity

The overall calving rate (cows observed with a calf/total cows) was 75% (79 of 106) for yearling and adult cows combined in 2002-2005 (Table 1). Annual calving rates of yearlings and adults averaged 30 and 85%, ranging from 0 to 100% and 77 to 92%, respectively; no calves were known to reproduce. Average fecundity (total calves/total cows) was 0.35 and 0.94 for yearlings and adults, respectively. Of the adult cows, 28 were observed > 1 calving season; 21 (75%) had a calf in consecutive years. Of the adult cows, 14 were observed each calving season and seven had a calf each of the four years; the annual production for these 14 cows averaged 0.96 calves/cow. The overall twinning rate (cows observed with twins/cows observed with at least one calf) was 11% ranging from 9 to 20% annually. Of the nine sets of twins observed, two adult cows had twins in multiple years (two and three years), and one yearling was observed with twins.

Table 1. Annual and total observed reproduction of radio-marked yearling and adult cow moose in northern New Hampshire, during 2002-2005. Sample sizes are given in parentheses.

	Calving rate %			Twinning rate %		
Year	Yearling	Adult	All	Yearling	Adult	All
2002	20 (5)	82 (17)	68	0	21	20
2003[a]	100 (1)	77 (26)	88	0	10	10
2004	0 (5)	92 (24)	78	0	9	9
2005[a]	44 (9)	89 (19)	74	25	6	10
All years	30 (20)	85 (86)	75	17	11	11

[a] Both 2003 and 2005 include a yearling that dropped its collar but was observed with a calf.

Harvest reproductive data

The yearling ovulation rate declined from 56 to 42% in the study area from 1988-1998 (N = 55) to 1999-2004 (N = 38), but there was no difference in the distribution of CL counts (0 and ≥ 1) in the two time periods ($\chi^2 = 1.83$, df = 1, P = 0.176). The CL count per yearling declined from 0.62 (SD = 0.62) to 0.42 (SD = 0.50). The statewide ovulation rate of yearlings declined similarly from 56 to 41%, but we observed a difference in the CL distribution ($\chi^2 = 9.48$, df = 1, P = 0.002); the related CL count per yearling declined from 0.65 (SD = 0.65) to 0.42 (SD = 0.52).

There was also no difference detected in the distribution of CL counts (0, 1 and ≥ 2) for adults in our study area in 1988-1998 (N = 104) and 1999-2004 (N = 134; $\chi^2 = 1.77$, df = 2, P = 0.412). Adult ovulation rates remained similar at 93 and 91%, although the proportion of cows with ≥ 2 CL de-

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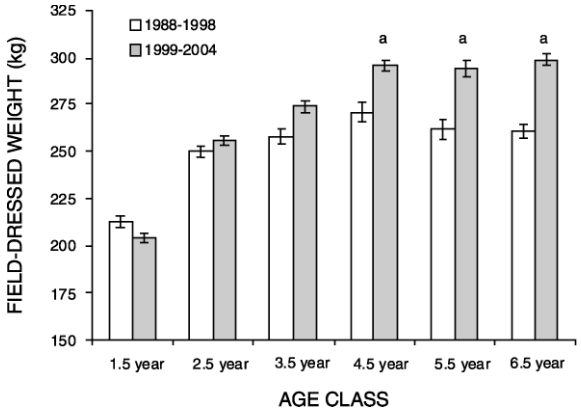


Figure 2. Mean (± SE) field-dressed body weight (in kg) of harvested cow moose in New Hampshire, during 1988-1998 and 1999-2004; a above bars denotes a significant difference between the two time periods.

clined slightly from 46 to 39%. The number of CL per adult declined from 1.44 (SD=0.74) to 1.24 (SD= 0.61). Statewide, adult cows had an ovulation rate of 92% in both time periods; CL per adult declined from 1.36 (SD = 0.67) to 1.22 (SD = 0.59). A difference occurred in CL count distribution (χ^2 = 13.38, df = 2, P = 0.001) as the proportion of cows with $\geq$ 2 CL fell from 44 to 33%.

Field-dressed body weight of cows in our study area and statewide were not different between the time periods ($P < 0.05$); therefore we counted and analysed all weights statewide. The mean field-dressed weight was different for like age classes between the time periods 1988-1998 and 1999-2004 ($P < 0.05$), with most higher in the latter period (Fig. 2). Mean weight of 4.5 year, 5.5 year and $\geq$ 6.5 year old cows were higher in 1999-2004 ($P \leq 0.018$). Mean weight of yearling cows declined about 4% statewide (from 213 to 204 kg) in 1999-2004. The percentage of yearlings $\geq$ 200 kg was similar in our study area (75-77%) and statewide (64-68%). Mean body weights increased between time periods in the study area and statewide for each age class $\geq$ 2.5 years (see Fig. 2).

Unmarked calf survival

A total of 86 calves were monitored during four calving seasons (18-24/season); 71% survived for approximately 60 days to 15 August. The apparent summer survival (calves surviving/calves born) ranged within 0.55-0.81. Most mortality (76%) occurred $\leq$ 28 days post-parturition; mortality was higher at 0-28 days (N=19) than at $\geq$ 29 days (N=6; χ^2=6.76, df=1, P=0.009). One set of twins was lost and four of the nine sets of twins had one loss. Four cows lost a calf in more than one summer season. Thirty calves monitored in three post-summer periods (2002-2004) had an overall apparent survival rate of 0.80, ranging within 0.67-0.91 annually; one death by vehicle collision was confirmed. The estimated annual survival based on summer and post-summer estimates was 0.57.

Cause-specific mortality of radio-marked moose

The status of all but one of the 92 radio-marked moose was known at the project termination. There were 39 mortalities (19 calves, six yearlings and 14 adults) with 41% occurring in April and 21% in October. Calves, yearlings and adults comprised 49, 15 and 36% of mortalities, respectively. The mortality rate of female calves (30%) was lower than the mortality rate of males (44%). Yearling and adult bulls represented, on average, six individuals (~ 20%) in the annual marked population and comprised only 10% of the overall mortality. Cause-specific mortality of calves was associated with winterkill/parasite (74%) (χ^2 = 24.58, df = 3, $P < 0.001$). There was no predominant cause of yearling and adult mortality (χ^2 = 7.26, df = 3, P = 0.064).

Winterkill/parasite was the most common cause of mortality (41%); 12 deaths (75%) occurred in April and 1-2 in February, March and May. Calves represented most of this mortality (88%) with 57, 25 and 27% of calves dying in successive years. Two adult cows (6.5 and 15.5 years) and 14 calves were necropsied and documented as malnourished (slight - no body fat measured), infested with winter ticks, and with varying degrees of hair loss/damage; nine of the 14 calves had lungworm infestations. The mean % FMF for this mortality source was 15.6% (SD = 8.1, range: 10.1-41.1%); however, 13 of 15 were $\leq$ 15.5% (N = 15).

Vehicle collisions (N = 10) accounted for 26% of mortality with 1-3 deaths annually; 50% occurred in May - June and 60% occurred proximate to roadside salt licks. Two, 2-year old cows were struck and killed in Maine approximately 160 km from the core of the study area. Hunting accounted for 18% of the overall mortality with five adult cows, one adult bull and one yearling bull harvested within the study area. One adult cow was harvested in Maine along the fringe of the study area. Hunting represented 31% of all yearling and adult cow mortalities and 50% of yearling and adult bulls. Five (13%) mortalities were classified as undetermined includ-

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ing a calf that died in April 2004 with 13.4% FMF but which was heavily scavenged and likely a winterkill/parasite mortality.

Survival analysis

Radio-marked cows

The best-fitting model out of the 25 models for adult cows was S(year 2002-2004; AIC_c weight = 0.249) which indicated that survival was year dependent or had annual variation (Table 2). Derived annual survival estimates were 0.74 (SE = 0.08; 95% CI = 0.55-0.87) in 2002, 0.87 (SE=0.06; CI=0.70-0.95) in 2003 and 0.91 (SE = 0.05; CI = 0.74-0.97) in 2004. The model S(year*early winter*late winter) was the second best-fitting model, which suggested that variation in survival was related to the interaction between the time periods of early winter (1 January - 17 February), late winter (18 February - 4 May) and year (Δ AIC_c = 1.374 and AIC_c weight = 0.125). Variation was most likely due to no mortality observed in the early winter season and that late winter of 2002 had the lowest seasonal survival observed in the study. The remaining models received less support which incorporated effects of constant survival, week, season and combinations of covariates (see Table 2). Adult seasonal survival estimated as a product of weekly estimates ranged from 0.94 (SE=0.03) in fall to 1.0 (SE=0.00) in early

Table 2. Ranking of known-fate models in program MARK for radio-marked yearling and adult moose survival in northern New Hampshire, during 2002-2005.

Adult known-fate model	Model description	AIC_c[a]	AIC_c weight[b]	K[c]
S(year 2002-2004)	Survival varies between years	0.000	0.249	3
S(year*early winter*late winter)	Survival varies between years and among early and late winter	1.374	0.125	9
S(year*fall)	Survival varies between years and fall	2.054	0.140	6
S(early winter)	Survival varies through early winter	2.420	0.074	2
S(year*late winter*fall)	Survival varies between years and among late winter and fall	2.714	0.064	9
S(year*late winter)	Survival varies between years and late winter	3.029	0.055	8
S(early winter*fall)	Survival varies between early winter and fall	3.302	0.048	3
S(year*summer*fall)	Survival varies between years and among summer and fall seasons	3.758	0.039	9
S(early winter*late winter* summer*fall)	Survival varies between seasons	4.205	0.038	4
S(year*early winter*fall)	Survival varies between years and among early winter and fall	4.379	0.030	9
S(early winter*late winter)	Survival varies between early and late winter	4.390	0.028	3
S(constant)	Survival constant over time	4.811	0.028	1
S(fall)	Survival varies through fall	4.894	0.022	2
S(year*early winter*late winter* summer*fall)	Survival varies between years and among seasons	4.985	0.022	12
S(late winter*fall)	Survival varies between late winter and fall	5.819	0.021	3
S(year*early winter)	Survival varies between years and early winter	5.890	0.014	8
S(late winter)	Survival varies through late winter	6.543	0.013	2
S(summer)	Survival varies through summer	6.698	0.009	2
S(summer*fall)	Survival varies between summer and fall	6.810	0.009	3
S(year*early winter*summer)	Survival varies between years and among early winter and summer	7.169	0.007	9
S(late winter*summer)	Survival varies between late winter and summer	8.531	0.004	3
S(year*summer)	Survival varies between years and summer	9.638	0.002	8
S(year*late winter*summer)	Survival varies between years and among late winter and summer	10.202	0.002	12
S(time)	Survival varies through weekly time	50.815	0.000	52
S(year*time)	Survival varies through weekly time and between years	315.841	0.000	191

[a] Difference between $AIC_{c(i)}$ and minimum AIC_c observed.
[b] Akaike's model weight.
[c] Number of estimable parameters.

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Table 3. Survival rates generated from weekly estimates in known-fate analysis of program MARK, for radio-marked calves (~ 7-12 months of age), and yearling and adult cows in northern New Hampshire, during 2002-2005.

	Adult			Calf		
Season	S[a]	SE	95% CI	S[a]	SE	95% CI
Early winter, 1 January-17 February	1.000	0.000	1.000 - 1.000	0.983	0.017	0.888 - 0.998
Late winter, 18 February-4 May	0.963	0.018	0.906 - 0.986	0.701	0.065	0.561 - 0.811
Summer, 5 May-17 September	0.957	0.019	0.902 - 0.982	-	-	-
Fall, 18 September-16 December	0.940	0.026	0.864 - 0.975	-	-	-
Overall[b]	0.866	0.033	0.786 - 0.920	0.668	0.066	0.550 - 0.800

[a] Seasonal survival rates are a product of weekly estimates.
[b] A total of 52 weeks for adults and 20 weeks for calves.

winter; overall adult survival for the study was 0.87 (SE = 0.03; Table 3). Adult weekly survival rate was the lowest (0.88) in late winter 2002. Other period trends with lower weekly survival for all years occurred in weeks 24-25 in June (summer), and weeks 41-43 in October (fall; Fig. 3).

Radio-marked calves (~ 7-12 months of age)

The best-fitting model for calves was S(late winter) which indicated variation in survival for all years between late winter (18 February - 4 May) and the remaining weeks of early winter (1 January - 17 February) and the first two weeks of summer (5 May - 15 September) prior to entering the yearling age class (AIC_c weight = 0.848; Table 4). This model estimated the probability of surviving the 20-week monitoring period (1 January - 18 May) as 0.70 (SE = 0.06; 95% CI = 0.57-0.81). The remaining five models

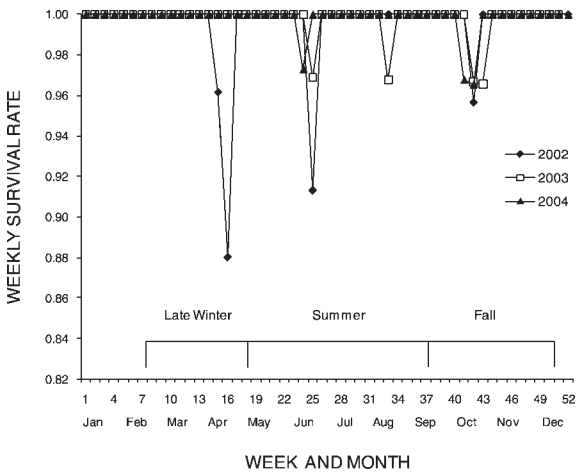


Figure 3. Weekly survival rates generated in program MARK for radio-marked cow moose in northern New Hampshire, during 2002-2004. Weeks begin on 1 January and the survival rate was 1.0 for weeks 1-35 in 2005.

that incorporated effects of constant survival, week, year and combinations of covariates were inferior. Although no relationship was detected in survival rates of calves in model analysis between years, the derived estimate in 2002 was 0.49 (SE = 0.19; CI = 0.18-0.82), 0.71 (SE = 0.10; CI = 0.49-0.87) in 2003 and 0.68 (SE = 0.10; CI = 0.47-0.84) in 2004. The highest percentage of calves died in 2002, but high collar loss that year weakened the precision of the estimates. There was a trend in weekly survival among years where weeks 13-18 (25 March - 4 May) had the lowest survival, and only one mortality was observed during the early winter (Fig. 4). Overall, calf survival (N = 57) from ~ 7-12 months of age as a product of the 20 weekly estimates (1 January - 18 May) was 0.67 (SE = 0.07; see Table 3).

Unmarked calves (0-2 months of age)

Constant daily calf survival (i.e. Mayfield estimator) was 0.9943 from model S(constant) and assuming constant DSR, overall calf survival was 0.71 (SE = 0.05; 95% CI = 0.61-0.80) to 60 days for all years pooled. Annual rates calculated by model S(year) were 0.73 (SE = 0.10; CI = 0.47-0.88) in 2002, 0.75 (SE = 0.09; CI = 0.53-0.88) in 2003, 0.81 (SE = 0.08; CI = 0.58-0.93) in 2004, and 0.55 (SE = 0.10; CI = 0.33-0.73) in 2005; no annual difference in DSR was found. Other candidate models better explained the variation in calf survival (Table 5). The best-fitting model, S(calf age), indicated variation in DSR with calf age (AIC_c weight = 0.584). This model displayed a linearly increasing trend in calf survival as a calf ages with a positive slope for logit DSR; $\beta = 0.025$ (SE = 0.01; Fig. 5). The remaining five models that incorporated effects of constant survival year, birth date and combinations of covariates performed poorly in comparison.

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Table 4. Ranking of known-fate models in program MARK for radio-marked calf (~ 7-12 months of age) moose survival in northern New Hampshire, during 2002-2004.

Calf known-fate model	Model description	Δ AIC_c[a]	AIC_c weight[b]	K[c]
S(late winter)	Survival varies through late winter	0.000	0.848	2
S(time)	Survival varies through weekly time	4.387	0.095	20
S(year*late winter)	Survival varies between years and late winter	6.319	0.036	6
S(constant)	Survival constant over time	7.673	0.018	1
S(year)	Survival varies between years	11.451	0.002	3
S(year*time)	Survival varies through weekly time and between years	73.322	0.000	60

[a] Difference between $AIC_{c(i)}$ and minimum AIC_c observed.
[b] Akaike's model weight.
[c] Number of estimable parameters.

Discussion

Productivity

Excluding the July births of one cow, the calving period (8 May - 11 June) occurred earlier and was two weeks longer than measured in Quebec, Canada (18 May - 8 June; Laurian et al. 2000) and worldwide (19 May - 8 June; Sigouin et al. 1997). The median parturition dates (17-22 May) were similar to those documented by Addison et al. (1993) in central Ontario (18-20 May), but earlier than most of those reported in the interior of Alaska, USA (20-27 May; Bowyer et al. 1998, Testa et al. 2000, Bertram & Vivion 2002). Synchrony of parturition was evident with 80% of births occurring within 10-14 days each year, which was also observed in Alaska (80% in 11-17 days; Bowyer et al. 1998, Keech et al. 2000, Testa et al. 2000).

Timing and synchrony of birthing in moose is hypothesized to be adaptive to climatic patterns that provide optimal conditions such as maximum forage availability during summer (Bowyer et al. 1998, Keech et al. 2000), although little evidence exists of a proximal relationship between environmental conditions (e.g., snow depths and temperatures) and timing or synchrony of calving (Sigouin et al. 1997, Bowyer et al. 1998). Others propose that parturition is timed to avoid predation (Adams et al. 1995, Testa et al. 2000). If predation influences timing of parturition in moose, calves born during the peak of the birthing period should experience increased survival (Bowyer et al. 1998, Keech et al. 2000). However, summer survivorship was not higher for calves born during peak parturition, nor was survival dependent on birth date. The relatively high calf survival (0.71) in the first two months suggests that moose predators present in northern New Hampshire, which are likely limited to black bear, probably do not limit or influence the timing of calving. Presumably, forest harvest practices in New Hampshire, which produce high habitat heterogeneity, provide adequate habitat for parturient moose; > 75% of neonatal sites were in mixed or coniferous forest habitat with little affinity for water features (Scarpitti et al. 2007). The annual consistency of parturition dates most likely reflects the relationship of abundant forage resources and high energetic requirement associated with lactation and optimal growth rate of calves.

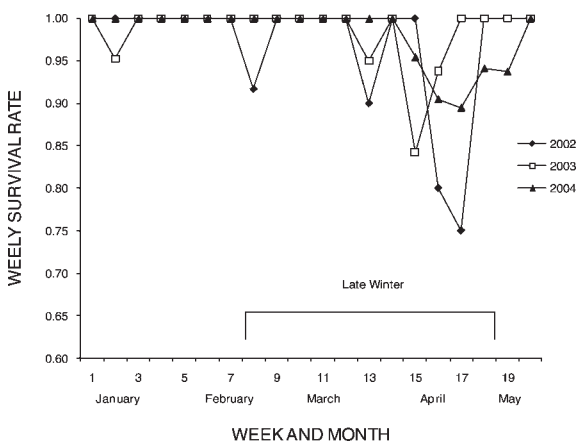


Figure 4. Weekly survival rates (1 January - 18 May) generated in program MARK for radio-marked moose calves (~ 7-12 months of age) in northern New Hampshire, during 2002-2004.

Reproductive status of yearling cows is an indicator of population condition, can be highly variable (Schwartz 1998) and was assessed previously in New Hampshire (Adams & Pekins 1995). The pregnancy (20%) and calving rates (30%) of yearlings were lower than the mean pregnancy rate in North America (49%; Boer 1992), but similar to the rate measured in Michigan, USA (10-30%; Dodge 2002). Yearling fecundity rates in moose populations above, near and below carrying capacity were

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Table 5. Ranking of nest-survival models in program MARK for unmarked calf moose survival to 60 days of age in northern New Hampshire, during 2002-2005.

Nest-survival model	Model description	AIC_c[a]	AIC_c weight[b]	K[c]
S(calf age)	Survival varies between age of calf	0.000	0.584	2
S(year*calf age)	Survival varies through calf age with a constant difference between years	2.269	0.188	5
S(constant)	Survival constant over time	3.272	0.114	1
S(birth date)	Survival varies between birth date of calf	4.928	0.050	2
S(year)	Survival varies between years	5.283	0.042	4
S(year*birth date)	Survival varies though birth date with a constant difference between years	6.406	0.024	5

[a] Difference between $AIC_{c(i)}$ and minimum AIC_c observed.
[b] Akaike's model weight.
[c] Number of estimable parameters.

18, 41 and 64%, respectively (Boer 1992); the fecundity rate (calves/cow) in our study was 35%.

Nutritional status and body size determine whether a yearling cow breeds and produces young (Sæther & Haagenrud 1985, Schwartz & Hundertmark 1993), and ovulation rates provide indirect evidence of reproductive condition (Schwartz 1998). The New Hampshire yearling ovulation rate was 56% in 1988-1998 and 42% in 1999-2004 compared to the average in North America (49%; Boer 1992). The decline in ovulation rate and field-dressed weight of yearling cows since 1988-1998 in New Hampshire suggests a relative change in body condition. On poor habitat, yearlings have low ovulation and pregnancy rates (Schwartz 1998), and adult cows should express similar declines as well, however, these parameters increased in adult cows during the same time period, making it unlikely that habitat quality was an influencing factor. Of importance to productivity of local and regional populations is that the field-dressed weight of yearlings declined to 204 kg statewide and 210 kg in our study area, and yearlings < 200 kg are not reproductive (Adams & Pekins 1995).

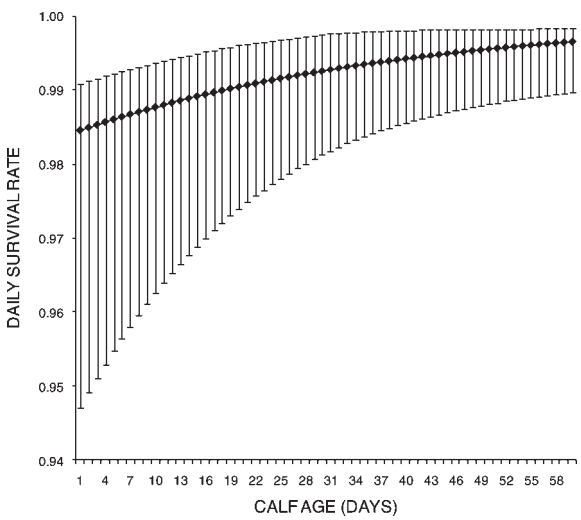


Figure 5. Estimates of daily survival rate (DSR) in nest-survival analysis of program MARK for unmarked calves in northern New Hampshire, 2002-2005. Pooled data from best-fitting model {S(age)} for calf age to 60 days and error bars represent 95% confidence intervals.

Lower ovulation rates and productivity of yearling cows could be related to the impact of tick infestations endured as calves the previous winter. Addison et al. (1994) reported that captive calves heavily infested with winter ticks in fall had lower weight gain than moderately infested or uninfested calves, and those with extensive hair loss had less visceral fat stores (McLaughlin & Addison (1986). Yearling cows need to maintain high fat reserves for both successful pregnancy and winter survival (Heard et al. 1997). Ticks are not known to cause anorexia in captive moose fed quality diets (Addison & McLaughlin 1993, Samuel 2004), but anorexia and weight loss were observed in cattle experimentally infested with the southern cattle tick *Boophilus microplus* (Seebeck et al. 1971). Musante et al. (2007) constructed physiological models which predicted that blood loss to winter ticks alters protein and energy metabolism of moose calves substantially, and likely influences their fitness and survival.

Adult ungulates normally exhibit compensatory growth after nutritional stress of winter (Watkins et al. 1990), whereas young ungulates are unable to compensate under certain conditions (Schwartz et al. 1994, Schultz & Johnson 1995, Keech et al. 1999). Female elk *Cervus canadensis* calves that experienced a harsh winter were less likely to breed as yearlings (Hancock 1957), and much of the variation in yearling pregnancy was attributed to previous winter severity (Houston 1982). Pimlott (1959) proposed that calf nutrition the first winter

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determines if puberty is reached the following breeding season. Excessive winter weight loss in calves due to tick infestation may influence their breeding as yearlings because summer nutrition is allocated to recovery more than growth. We suggest that the decline in CL counts and calving rate of yearlings may be related to lower body condition and growth. This could possibly be influenced by winter ticks that may reduce their winter survival and fitness as calves and their compensatory growth prior to fall as a yearling, effectively increasing the age of first breeding. Annual monitoring of body weight and productivity of yearling cows is warranted given their declining trend, the importance of yearlings as an indicator of population status (Adams & Pekins 1995) and that yearling productivity is a key to maintain population stability and growth.

The adult pregnancy rate (78%) was slightly lower than the mean adult calving rate (85%). These rates were higher than the pregnancy rates measured in the Upper Peninsula of Michigan, USA (74%; Dodge et al. 2004) and northwest Minnesota, USA (48%; Murray et al. 2006), but lower than the rate measured in Ontario, Canada (97%; Bergerud & Snider 1988). While the annual adult calving rate varied from 77 to 92%, the mean was similar to the mean across North America (84%; Boer 1992; 74-100%; Gasaway et al. 1992). Even though the mean calving rate was relatively high and the mean calf age was 2.0 days at first detection, the calving rate could have been slightly biased by neonatal mortality at < 2 days.

The average twinning rate was 11% (range: 9-20%) and fell within the range (5-25%) of a population near carrying capacity (Gasaway et al. 1992), although an average rate of 49% (range: 4-90%) was cited for 25 North American populations (Franzmann & Schwartz 1985, Boer 1992, Gasaway et al. 1992, Heard et al. 1997). Although twinning may have been underestimated, the annual rate was similar among years and was primarily observed in cows that gave birth to twins in previous years (67%). Variation in twinning has been associated with body condition of moose (Testa & Adams 1998, Keech et al. 2000), habitat quality and population density (Franzmann & Schwartz 1985, Gasaway et al. 1992). Neither adult field-dressed weight nor habitat quality within the study area was considered low or inferior.

While annual ovulation rates remained similar, the number of CL per animal declined between the periods of 1988-1998 and 1999-2004 despite an increase in mean weight of adults in each age class (see Fig. 2). Testa & Adams (1998) found a relationship between fall body condition of cows and pregnancy but not between condition and ovulation or twinning; multiple ovulations were lower than the rates of twins in other Alaskan populations (Boer 1992, Gasaway et al. 1992). Their results suggest that low potential for twins could reflect nutritional or genetic constraints (Testa & Adams 1998, Testa 2004).

Adult twinning rate is highly correlated with yearling pregnancy rate signifying that each may be influenced by similar factors (Boer 1992). Variation in reproductive strategies may be an adaptive response to the environment and stress (Sand 1996, 1998). In Sweden, cows that experienced more severe climatic conditions had to attain 22% higher body mass to achieve the same probability of multiple ovulations compared to cows in less harsh environments (Sand 1996). Winter tick infestations that reduce overall condition may also influence fecundity of adults as reflected in reduced CL counts and twinning rate. Larger body size should be an advantage to compensate for the negative influence of tick infestations on gestation and lactation.

Another possible explanation for the low twinning rate and the decline of multiple ovulations and yearling fecundity is higher population density. Both twinning rate and calving rate of yearlings were comparable to a population near carrying capacity. Moose density within the study area appeared stable to declining based on annual moose observation rates (moose observed/100 deer hunter hours) used to set the State's population goals. Moose density was also below the desired management level (NHFG 2002-2005) which is determined on a 10-year cycle through a public working group of stakeholders, direction from the board of wildlife commissioners and public hearings. Moose density had been estimated at 0.78 moose/km^2 within the study area during the project (NHFG, unpubl. data) and was consistent with previous estimates in the area but lower than densities to the north in Pittsburg, New Hampshire (1.6/km^2) located along the Canadian border (Adams et al. 1997). Cederlund & Sand (1991) estimated 1.5 moose/km^2 in south central Sweden for a hunted population with no predators, and Crête (1987) reported a density of 2.0 moose/km^2 as the North American average food carrying capacity in a predator-free environment. Dussault et al. (2005) estimated the moose popula-

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tion in a conservation area of southern Quebec at a moderate density of < 0.5 moose/km^2 as compared to similar habitats in eastern Quebec where 2.0 moose/km^2 was observed (Crête 1989).

Various studies have reported density-dependence effects on adult fecundity and increasing age of first reproduction of ungulates (Kie & White 1985, Clutton-Brock et al. 1987, Festa-Bianchet et al. 1995, Stewart et al. 2005), although density-dependence effects are generally less evident in adult fecundity (Gaillard et al. 2000). In red deer *Cervus elaphus* an increasing body mass threshold for fecundity occurred at higher densities and was an adaptive strategy to increase calf survival and reduce risk of late winter mortality of cows (Albon et al. 1983). However, the twinning rate of moose in Scandinavia did not decline with increasing density and no density-dependent decline in body weight was detected (Sand 1998, Solberg et al. 1999). The reasons for low twinning rates and decline in number of CL per adult cow in northern New Hampshire are uncertain, however, moose habitat in northern New Hampshire appears to be of high quality (Scarpitti 2006) and does not seem implicated because field-dressed weights and reproductive data collected at hunter check stations since 1988, as well as more recently survival data (2001-2005) of adults, were not representative of a habitat limited population.

Cause-specific mortality of radio-marked moose

Winterkill/parasite

Mortality of most individuals was attributed to winterkill/parasite because snow conditions throughout the study were not considered severe or the direct cause of mortality. Whereas a snow depth of 90 cm is known to confine moose movements and increase mortality (Coady 1974), this was exceeded only once, but did not persist and was measured in 2005 when no adult winter mortality occurred; however, no calves were radio-marked that winter. The only winter mortality of cows > 1.5 years old ($N = 3$) occurred in 2002 when the maximum snow depth was < 36 cm, and the mean ambient temperature in January - March (-3.7°C) was above normal and the highest recorded in any year of the study. Calves and adult cows categorized as winterkill/parasite had a mean % FMF of 16.5 and 11.6%, respectively, and were classified as poor body fat and poor condition. Femur fat content $< 10.0\%$ in calves and $< 20.0\%$ in adults is representative of moose starving or approaching starvation (Franzmann & Arneson 1976, Peterson et al. 1984); Murray et al. (2006) considered moose with $< 30\%$ as suffering from acute malnutrition. Given the high quality and heterogeneous forest habitats created by commercial harvesting within the study area (Scarpitti 2006) and the lack of winter severity, poor body condition and winter nutritional stress were most likely related to the influence of winter ticks. All calf mortalities had measurable winter tick infestations, many were infested with lungworms and 75% of winter tick-related mortality occurred in April.

Mortality factors rarely act alone to influence animal populations and the impact of parasitism is heightened when an animal is nutritionally stressed (Lankester & Samuel 1998). Certain data suggest that smaller cows and calves may be more susceptible to winterkill/parasite. None of the four cow mortalities in 2002 were pregnant, and of 11 calves monitored since birth and later collared, two of three that died were born after 11 June, nearly a month past peak parturition. Late-born calves are often unable to attain optimal body condition prior to winter (Clutton-Brock et al. 1982), and cows with higher rump fat have high rates of pregnancy and heavier calves (Keech et al. 2000). Although birth date did not influence summer survival of calves, it may influence winter survival and long-term life history traits.

Moose do not appear to be efficient groomers and presumably carry a high density of winter ticks and suffer greater consequences than other ungulate hosts (Samuel 2004). Moose average about 35,000 ticks, commonly have $> 50{,}000$, and in rare cases may have $> 80{,}000$ ticks (Welch & Samuel 1989, Welch et al. 1991, Mooring & Samuel 1998, Samuel 2004). Moose calves infested with approximately 30,000 ticks lose about eight liters of blood (58% blood volume) to engorging adult females in March - April; adult cows lose about 3.2 liters (11% blood volume) due to differences in age and sex composition of ticks. Because moose, and particularly calves, are in negative energy balance in late winter (Schwartz & Renecker 1998), the energetic cost associated with compensating for blood loss further exacerbates their steadily declining condition (Lankester & Samuel 1998, Samuel 2004). Although cows in the last trimester are at risk, prime bulls suffering from high-energy expenditure and decreased foraging during the rut may be as vulnerable to mortality as calves.

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Grooming relieves irritation from feeding ticks, but also reduces time spent feeding and resting (Mooring & Samuel 1999) and can result in severe alopecia (McLaughlin & Addison 1986). Hypothermia probably has minor influence on moose mortality because hair loss is greatest in March - April at the end of winter (Welch et al. 1990, Samuel 2004), however, hair loss can contribute to the negative energy balance of calves through heat loss and reduction in visceral fat and weight gain which has been observed in captive calves (McLaughlin & Addison 1986). Although weather is normally less severe at this time of the year, unusually wet and cold weather probably increases thermoregulatory costs of calves in April. Captive calves that were heavily tick-infested gained less weight in fall than uninfested or moderately infested calves (Addison et al. 1994).

Musante et al. (2007) modeled the potential metabolic impact on protein and energy balance of moose calves associated with blood loss to winter tick; conservative estimates indicated that daily protein losses of $\sim 30 - > 100\%$ of the daily protein requirement occurred during peak female tick engorgement. Such losses suggest that acute anemia and mortality should be expected, particularly in malnourished calves that have minimal protein intake at the end of winter. Energy costs associated with compensating for blood loss would also elevate the daily energy deficit which is normal at the end of the winter, accelerate nutritional decline and weight loss, and cause increased physiological stress related to concurrent anemia. Severely infested calves are obviously susceptible to late winter mortality, and the impact of moderate infestations would be exacerbated by secondary parasitic infestations, severe winters and poor body condition.

Most mortality (calves and adults) in winter 2002 was attributed to winterkill/parasite, whereas, calf survival was higher and no adult mortality occurred in the winters of 2003 and 2004. Hair loss and damage was also more severe in 2002 than in 2003 and 2004. A high incidence of dead, tick-infested moose was noted throughout northern New England, Michigan and Canada the same year (Samuel & Crichton 2003). Mortality associated with winter ticks combined with other factors (e.g. lungworms) is probably an annual event for moose calves, however, elevated calf mortality and some mortality of yearlings and adults should be expected in years of tick epizootics. Although April conditions are important in the tick life cycle, unseasonably warm and snowless conditions in November and December probably best forecast potential tick epizootics and abnormal winter mortality of moose. Samuel (2007) confirmed during a 12-year period in Alberta, Canada, that shorter, warmer winters with less precipitation than usual result in increased winter tick numbers the following year. Consequently, long-term climatic fluctuations may prove detrimental to moose populations in New England if tick-related mortality continually reduces productivity and survival. The frequency of winter tick epizootics is the most important factor of winter tick ecology for concern to moose managers. With the possibility of future climate change, predictions of warmer mean temperature increases the probability of extreme warm days and decreases the probability of extreme cold days in northern latitudes (Intergovernmental Panel on Climate Change 2003). Murray et al. (2006) concluded that climate acted in tandem with pathogens and chronic malnutrition leading to a moose population decline in northwestern Minnesota, USA.

Human-related mortality

Overall, vehicle collisions and hunting represented 69% of yearling and adult radio-marked cow mortality ($N = 16$). The average annual vehicular mortality rate of 0.06, when applied to the estimated moose abundance ($N = 1{,}500$) in the study area, predicts 90 deaths, a reasonable estimate relative to the 3-year average of 78 (Bontaites 2004). On average 390 animals are harvested in New Hampshire annually from an estimated population of 6,000-7,000 moose for a harvest rate of 7-8%; about 7% of the study area population, including 1% cows, was harvested in 2004 (Bontaites 2004, NHFG 2004). Although these human-related causes were the highest source of mortality in a potentially biased sample, their effect is minor because annual cow survival is high (0.87). Summer vehicle collisions and fall harvest were basically stable each year, and measurable late winter mortality occurred only in 2002. Likewise, the survival analysis indicated that yearling and adult survival were more dependent on year than on season. Therefore, under the current harvest management strategy, survival of cows may be most influenced by natural mortality factors, notably annual fluctuations in winter tick; however, hunter harvest represents the primary mechanism to influence productivity and abundance.

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Survival analysis

Radio-marked cows

Annual cow survival rate (0.74-0.91) and overall cow survival (0.87) were similar to those in hunted populations with little to no predation in Norway (0.83-0.93; Stubsjøen et al. 2000) and an unhunted population in the Upper Peninsula of Michigan (0.88; Dodge et al. 2004), and higher than a population in northwest Minnesota severely affected by parasites (liver fluke *Fascioloides magna* and brain worm *Parelaphostrongylus tenuis*) and disease/malnutrition (0.79; Murray et al. 2006). Survival rates in Alaska and northwestern Canada varied from 0.75 where hunting was the main source of mortality (Hauge & Keith 1981) to 0.85-0.95 where predators accounted for most mortality (Larsen et al. 1989, Ballard et al. 1991, Gasaway et al. 1992, Stenhouse et al. 1995, Keech et al. 2000, Bertram & Vivion 2002, Testa 2004). The variation in survival between years (2002-2004) was due to late winter mortality from winterkill/parasite and undetermined causes in April 2002. The only late winter (18 February - 4 May) adult mortality occurred in 2002, suggesting that tick epizootics may cause periodic adult cow mortality. Adult female survival of large herbivores appears to be normally buffered against temporal variation, and is always less variable than juvenile survival, although epizootics have caused substantial differences in annual survival of adults (Cransac et al. 1997, Gaillard et al. 1998). The high survival of adult cows in New Hampshire can be attributed to lack of predation, a conservative cow harvest, moderate winter conditions and good body condition in fall (see Fig. 2).

Radio-marked calves (~ 7-12 months of age)

Winter survival rate of calves ~ 7-12 months of age (0.67) was lower than those in populations with little to no predation in Michigan (0.84; Dodge 2002), Norway (0.83-0.98; Stubsjøen et al. 2000) and Sweden (~ 0.89; Ericsson et al. 2001). Most Alaskan populations experience higher winter survival than summer survival; > 85% calf survival occurred after the first month of life in a high-density moose population (Keech et al. 2000). Winter calf survival in Yukon, Canada and Alaska ranged from 0.77-0.78 (Larsen et al. 1989, Testa 2004) to 0.85-0.94 (Ballard et al. 1991, Gasaway et al. 1992, Bertram & Vivion 2002). Contrary to Alaska, calves in our study were not influenced by winter predation or winter severity (winters were mild); instead, mortality was attributed to parasite infestations and related malnutrition. There was a consistent trend of among- and within-winter variation of calf survival; survival was high in early winter in comparison to late winter when mortality risk increased and 88% of winter mortality occurred. Survival in 2002 was lower than in 2003-2004 but no variation in weekly survival was detected between years; precision of weekly survival estimate was likely influenced by collar loss (small sample size) in 2002. Documentation of substantial tick-related mortality of radio-marked moose calves was unique to our study. When epizootics occur, ticks can dramatically reduce calf survival and recruitment, and in combination with severe winter weather, could probably cause > 50% calf mortality.

Unmarked-calves (0-2 months of age)

Despite summer survival ranging from 0.55 to 0.81, overall survival rate in the first 60 days (0.71) was higher than in most Alaskan populations experiencing substantial predation (range: 0.24-0.49; Larsen et al. 1989, Osbourne et al. 1991, Gasaway et al. 1992, Bertram & Vivion 2002, Testa 2004). High survival was observed where predation was limited in Northwest Territories, Canada (0.86; Stenhouse et al. 1995) and in Sweden (~ 0.87; Ericsson et al. 2001). In a review of northern temperate ungulates, mean survival of neonates was 0.53 where predators occurred, and 0.81 in predator-free populations (Linnell et al. 1995).

Most calf mortality occurs within the first six weeks of life (Ballard & Van Ballenberghe 1998), and we observed similar results (84%). Predation is the main source of neonatal mortality in moose calves, although accidents such as drowning can account for 15% of deaths (Gasaway et al. 1992). Black bears are a principle predator of moose calves and radio-telemetry studies have revealed that they kill large numbers of calves (Franzmann et al. 1980, Osborne et al. 1991, Ballard 1992, Bertram & Vivion 2002). We did not mark neonates, so the cause of death remained unknown, but a similar timing (76% in first 28 days of life) of most mortality each year suggests that the cause was consistent. Predation was expected because black bears account for substantial calf mortality where they outnumber other large predators and their density exceeds 0.20/km^2 (Ballard 1992); bear density in our study area was estimated at 0.23-0.34 bear/km^2 (NHFG 2004).

Models suggested that age-specific survival in-

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creased as the calves aged (0-60 days), which is similar to the results obtained by Testa et al. (2000) who found that age-specific, daily mortality rate of calves declined in a linear trend from 0.04 to 0.0/day at 65 days of age. Survival of calves in our study was not higher for calves born during peak parturition (15-21 May; 51% of births occurred), and the models also suggested that survival was not dependent on date of birth. Several studies have demonstrated that calf survival was not influenced by timing and synchrony of births (Bowyer at al. 1998, Keech et al. 2000), whereas, other research suggests poor summer survival of early and/or late-born calves (Adams et al. 1995, Testa et al. 2000). The relatively high summer survival of calves in our study suggests that predation and incidental mortality are moderate in northern New Hampshire, and that summer mortality of calves is probably not a limiting factor of population abundance in our study area.

Annual calf survival

Unmarked calves survival during August-December was estimated at 0.93 although calves were not monitored as frequently at ~ 3-6 months of age. This rate is comparable to those of areas in Alaska with little to no calf harvest (0.90; Keech et al. 2000, Bertram & Vivion 2002, Testa 2004). Therefore, survival was conservatively estimated at 0.95. The survival rates of unmarked calves at 0-2 months of age (0.71), ~ 3-6 months (0.95) and survival of marked calves at ~ 7-12 months (0.67) were used to calculate an annual survival rate of 0.45 (i.e. $0.71 \times 0.95 \times 0.67 = 0.45$).

In Michigan, annual calf survival was 0.71 (Dodge et al. 2004), and in areas of Scandinavia with few to no predators, the annual survival was high excluding deaths during the hunting season (~ 0.75; Stubsjøen et al. 2000, Ericsson et al. 2001). Annual calf survival in predator-rich environments in Canada and Alaska ranged from 0.18 to 0.33 (Hauge & Keith 1981, Larsen et al. 1989, Ballard et al. 1991, Osborne et al. 1991, Gasaway et al. 1992, Bertram & Vivion 2002, Testa 2004), whereas, areas with lower predation had survival rates > 0.44 (Mytton & Keith 1981, Stenhouse et al. 1995, Keech et al. 2000). Juvenile survival and recruitment are highly sensitive to limiting factors regardless of whether variation is related to population density or stochastic environmental factors, and the high variability in survival may be a primary influence in population dynamics (Gaillard et al. 1998). Survival in our study area was lower than in populations with little predation and appears to be related to winter mortality associated primarily with winter ticks absent in many populations.

Conclusions

Moose have high economic value in New Hampshire because they are an important source of revenue related directly to hunting and ecotourism. Our study presented the first assessment of the dynamics and potential limiting factors of the moose population in northern New Hampshire and yielded important, undocumented and novel information concerning population dynamics of moose. Our data revealed that habitat quality, winter severity and predation were not limiting factors of the population, however, population stability was likely parasite related. Winter ticks had the most influence on the population dynamics, through reductions in winter calf survival and juvenile recruitment. We suggest that other related impacts include reduced fertility, low yearling productivity, increased age of first reproduction and low twinning rates. The impact of winter ticks in our study was probably low on a relative scale because winter conditions were moderate to mild. Higher mortality rates of all sex and age classes should be expected during tick epizootics occurring in long and severe winters due to additive impacts of extended malnutrition, and other pathogens and parasites. The temporal variation of winterkill/parasite-related mortality is certainly an influencing factor in population dynamics in our study area, and likely throughout New Hampshire. However, current conditions suggest that the high fertility, calving rate and body condition of adult cows, and high summer survival of calves, should ensure local moose population recovery following tick epizootics that periodically inhibit population growth.

The frequency of winter tick epizootics is likely the most important factor for moose management in the Northeastern United States where harvest rates are conservative. The mechanisms influencing tick-related mortality are not adequately understood, and likely impossible to manage, but their impact could be predictable. Long-term climatic fluctuations leading to extended periods of warm weather and shorter winters could have substantial impacts on moose populations throughout New England due to increased epizootics and tick-related

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mortality. Continuous reduction in survival and productivity of yearlings and calves can negatively influence population growth and stability of regional populations. Monitoring winter tick epizootics, fall and spring weather, degree of winter mortality, field-dressed harvest weights and age-specific ovulation rate would provide a basis for understanding the relationships among these factors. Research foci on the effect of winter ticks on moose population dynamics include: 1) what effect does an infestation have on yearling productivity and adult twinning, 2) are birth weight and body condition of calves affected by tick infestations of cows, and 3) can tick epizootics be accurately forecasted from moose density, snow cover, and fall and spring weather conditions? Our study indicates that further research of the annual and long-term role and influence of the winter tick on moose populations is warranted, not only in the Northeastern United States, but wherever winter ticks influence moose.

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