

FECUNDITY AND SUMMER CALF SURVIVAL OF MOOSE DURING 3 SUCCESSIVE YEARS OF WINTER TICK EPIZOOTICS

Henry Jones¹, Peter J. Pekins¹, Lee E. Kantar², Matt O'Neil, and Daniel Ellingwood¹

¹Department of Natural Resources and the Environment: Wildlife Program, University of New Hampshire, Durham, NH, 03824, USA; ²Maine Department of Inland Fisheries and Wildlife, Research and Assessment Section: Bangor, Maine, 04401, USA

ABSTRACT: Moose (*Alces alces*) populations in northern New Hampshire and western Maine experienced 3 successive years of high winter tick infestations (epizootics) in 2014–2016 that resulted in late-winter calf mortality rates >70%. To assess productivity in these populations, we measured fecundity rates of yearling and adult cow moose, and neonatal and summer calf survival. Parturition, fecundity, and survival were measured via direct observation by stalking VHF and GPS radio-collared cows (n = 177) in May–August, 2014–2016. Calving rates for yearlings and adults averaged 0 and 57%, respectively; there was no twinning documented. Summer calf survival to August was high overall (83%), with 85% of the mortality occurring in the first week of life. Calving and twinning rates declined since last measured in New Hampshire in 2002–2005 and were below the North American average; conversely, summer survival of calves was considered normal. Given that optimal habitat has increased in the past 15 years in the study area that is dominated by commercial forestry, lower productivity is presumably related to the additive impacts of successive winter tick epizootics on year-round condition of cows.

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Many moose (*Alces alces*) populations along the southern edge of their North American range are declining, including in Minnesota, Manitoba, Nova Scotia, Vermont, New York, and New Hampshire (Murray et al. 2006, Broders 2012). The cause of decline varies regionally, but it is generally associated with the warming climate which likely has an indirect influence through increasing incidence of parasites and disease (Samuel 2004, Murray et al. 2006, Lankester 2010). In northern New England, winter ticks (*Dermacentor albipictus*) are suspected to influence the population through periodic widespread mortality of calves during epizootics (Musante et al. 2010) which have

been occurring at an increasing frequency in the last 15 years (Bergeron et al. 2013). An epizootic event (>50% calf mortality) was documented in northern New Hampshire in 2002 (Musante et al. 2010), and acknowledged to occur in northern New Hampshire and western Maine in 2008 and 2011 by the New Hampshire Fish and Game Department [NHFG] and the Maine Department of Inland Fisheries and Wildlife [MIFW] (Bergeron et al. 2013). In these same areas, epizootics occurred in 3 consecutive years from 2014–2016. Mortality of radio-marked 10–12 month-old calf moose was 60–80% between March and May from blood loss to winter tick parasitism; the average winter

tick infestation on dead calves was 46,800 ticks (range = 34,800–63,600) (Jones 2016, L. Kantar, MIFW, pers. comm.).

The population implications of successive or frequent epizootics with high calf mortality rates are cause for concern among regional moose managers. However, the status and trajectory of a moose population is also dictated by the number of calves recruited into the population, termed here as productivity, which is dependent on fecundity, the number of calves born per cow, and neonate and calf survival. Pregnancy, calving, and twinning rates are parameters that contribute to the fecundity rate of a population (Van Ballenberghe and Ballard 2007). Productivity is influenced by the nutritional condition of cows and calves, and as such, allows for comparison with other populations and overall assessment of health (Schwartz 2007). Where productivity is high, a population is more resilient to mortality factors (Franzmann 2000), hence, an important consideration given the recent decline in the northern New England moose population.

Winter ticks are known to cause population decline in moose through widespread mortality of calves during an epizootic year, and suspected long-term effects due to reduction of adult cow fitness and productivity (Musante et al. 2010, Bergeron et al. 2013). High winter tick infestations presumably exacerbate the negative energy balance of adult cows in late winter and early spring due to the compounding effects of substantial protein deficit from blood loss (Musante et al. 2007) and the nutritional deficiency of late winter browse (Schwartz and Renecker 2007). Optimal condition is relative to season, as moose experience a negative energy deficit during winter resulting in weight loss even on the best range (Schwartz and Renecker 2007). Yet, because gestational and early lactational costs are met prior to spring green-up, availability of tissue energy, or minimizing weight

loss, is paramount to production. Poorer cow condition from the additive effect of blood loss to winter ticks may result in reduced fertility, low yearling productivity, increased age of first reproduction, and low twinning rates (Musante et al. 2010), all of which have been documented in New Hampshire (Bergeron et al. 2013).

Given the increasing frequency of regional epizootics and concurrently declining estimates of productivity (Bergeron et al. 2013), it is critical to measure yearling and adult female fecundity and survival rates of calves to accurately assess the status and trajectory of the regional population. This study was designed to investigate the productivity of two moose populations: one in northern New Hampshire and the second in western Maine. Similar harvest strategies and ecological conditions between these areas provided the opportunity to compare and combine data sets. The specific objectives of this research were to measure: 1) adult cow pregnancy rates and parturition dates, 2) calving and twinning rates of yearling and adult cow moose, and 3) summer calf survival.

STUDY AREA

The 2 study sites were in northern New Hampshire and western Maine, separated by approximately 120 km. The New Hampshire site was located in the eastern portion of Coos County centered on the town of Milan (Fig. 1). This site encompassed ~1,250 km² in NHFG Wildlife Management Unit (WMU) C2 and portions of WMUs A2, B, and C1, and replicated the study area of a comprehensive population dynamics study that occurred from 2002–2005 (Musante et al. 2010). Moose density was estimated as 0.46–0.87 moose/km². The number of moose hunting permits issued in 2013–2015 averaged 28 either-sex and 10 antlerless-only permits. The western Maine site extended north and west of the town of Greenville to the

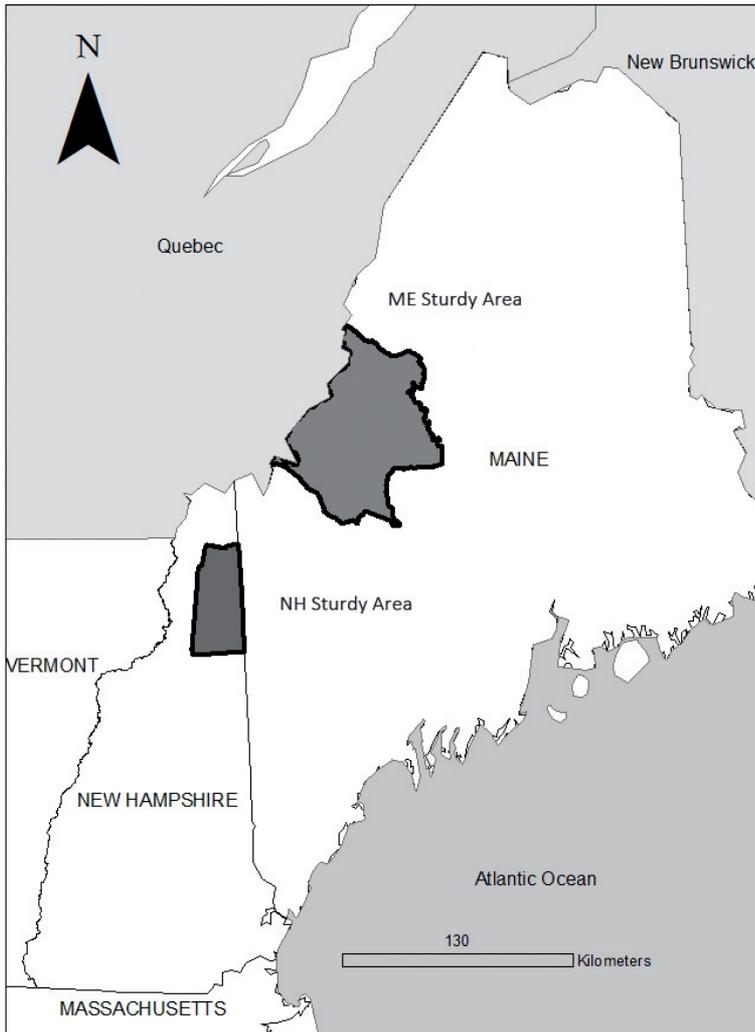


Fig. 1. Study areas located in northern New Hampshire and western Maine, 2014–2016.

Quebec border, including parts of Somerset, Franklin, and Piscataquis Counties (Fig. 1). This site was $\sim 5,620$ km² and encompassed MIFW Wildlife Management District 8. Moose density was estimated as 0.97–1.35 moose/km². The number of moose hunting permits issued in 2013–2015 averaged 175 bull-only and 25 antlerless-only permits. Potential predators of moose calves were black bears (*Ursus americanus*) and coyotes (*Canis latrans*); bear density was estimated as 0.38–0.58 bear/km² in New Hampshire (A. Timmins, NHFG, pers. comm.) and 0.65 bear/km² in Maine (R. Cross, MIFW,

pers. comm.). White-tailed deer (*Odocoileus virginianus*) were sympatric with moose throughout the region and at an estimated density of 6.34 deer/km² in New Hampshire (D. Bergeron, NHFG, pers. comm.) and 0.60 deer/km² in Maine (K. Ravanna, MIFW, pers. comm.).

Both study sites were privately-owned, managed for commercial timber, and considered high quality moose habitat (15–20% of the landscape in 4–16 year-old regenerating forest; Ball 2017). The area was mountainous (max elevation 1220 m) and geographically diverse with lowland valleys, rolling hills,

smaller mountains, and numerous lakes, ponds, and rivers scattered throughout. The dominant cover type was northern hardwood forest consisting of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and paper birch (*Betula papyrifera*). Conifer stands of mostly red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) were common at high elevation, with white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) common in wet lowland sites (DeGraaf et al. 1992). Year-round access was available on logging roads, off highway recreational vehicle (OHRV) trails, and snowmobile trails. Private landowners permitted access during the calving period (May and early June) which typically coincided with road-closures due to mud.

Climate data were available from the National Climatic Data Center weather stations at York Pond, Berlin, New Hampshire (ID: GHCND:USC00279966, Lat/Long: 44.5002, –71.333) and Jackman, Maine (ID: GHCN:USC00174086, Lat/Long: 45.626, –70.246). Annual ambient temperature ranged from 32 to –32 °C in both areas. For New Hampshire and Maine, respectively, annual precipitation ranged from 114.0 to 121.6 cm and 91.0 to 106.0 cm, and maximum snow depth ranged from 17.8 to 66.0 cm and 30.5 to 106.7 cm. The mean annual snowfall of 215.6 cm and maximum recorded snow depths in 2014–2016 (61.0, 66.0, and 35.6 cm) in New Hampshire were generally similar to those in Maine (240.5 cm and 106.7, 53.3, and 43.2 cm). The average weekly snow depth measured at open sites in December–April 2013–2016 ranged from 2.5–26.4 cm in New Hampshire and 5.8–48.7 cm in Maine; average weekly snow depth did not exceed 70 cm at either site.

METHODS

Capture and marking

Animal capture and handling protocols were approved by the Institutional Animal Care and Use Committee at the University

of New Hampshire (IACUC #130805). Cow and calf (both sexes) moose were captured by helicopter net-gunning and helicopter darting (Aero Tech Inc., Clovis, New Mexico, USA in 2014 and 2015; Native Range Capture Services, Elko, Nevada, USA in 2016) with a 4–6 person crew: the pilot, animal handlers, and a veterinarian. Captures occurred in January and were completed in ≤ 7 days at each study site. Concentrations of non-collared moose were identified from helicopter and fixed-wing flights prior to captures. Moose captured via darting were immobilized with 3 mg of Carfentanyl and reversed with 300 mg of Naltrexone. Additional captures in Maine included 6 adult cows collared in water using small boats and a noose in August 2014 (Crossley 1987), and 2 adult cows darted roadside using 2.2 mL of ketamine and reversed with 0.8 mL of medetomidine in December 2014. Moose captured via net gunning were quickly removed from the net and restrained with leg hobbles and blindfolded; the handling process typically lasted < 15 min.

Age classes were categorized as calves (< 1 year old), yearlings (> 1 year but < 2 years old), and adults (> 2 years old) at the time of the fall breeding season. As it can be difficult to differentiate between yearling and adult cow moose without observing tooth wear, all cows were considered adults; the relative size of each was checked with the capture crew in an attempt to identify any obvious yearling. The yearling age class consisted of radio-marked female calves that survived their first winter.

A 30 mL blood sample was taken from the jugular vein to be used for subsequent blood tests including pregnancy. Each moose was fitted with numbered ear tags color-coded by year (Allflex USA, Dallas, Texas, USA) and a very high frequency (VHF) or global positioning system (GPS) radio-collar. Moose in New Hampshire were fitted with either a VHF ($n = 76$; M2610B, Advanced

Telemetry Systems, Isanti, Minnesota, USA; Mod-600, Telonics, Mesa, Arizona, USA) or GPS radio-collar ($n = 54$, GPS Plus Vertex Survey Collar, Vectronic Aerospace GmbH, Berlin, Germany); all moose in Maine were fitted with GPS radio-collars ($n = 142$, GPS Plus Vertex Survey Collar, Vectronic Aerospace GmbH, Berlin, Germany). VHF radio-collars had a motion sensor switch to indicate a 4-h period without movement; collars were continuously monitored with a R4500S datalogger (ATS, Isanti, MN) connected to a large omnidirectional antenna (Cushcraft CRX 150) mounted centrally in the study area. The GPS radio-collars collected 2 GPS fixes daily (0000 and 1200 hr EST) and had a VHF beacon that was active at 0700–1900 hr EST; after 5 h of non-movement, a motion sensor switch triggered a “mortality message” via e-mail and the pulse rate of the VHF signal increased. Adults received collars sized to a standard fit; calves received retrofitted collars that allowed future expansion (see Musante et al. 2010). This research was part of a larger study that also assessed cause-specific mortality of the radio-marked moose.

Fecundity

Pregnancy status of each adult female was determined from the blood samples collected at capture using the pregnancy specific protein-B test (BioPRYN, Moscow, Idaho, USA). Calving and twinning rates were measured principally through direct observation by stalking adult and yearling cows within sighting distance (i.e., walk-ins; Mech 1983, Musante et al. 2010). Calving rates included the annual calving rate or the proportion of cows documented as having a calf each year, and the successive calving rate or the proportion of cows that birthed in consecutive years. In New Hampshire, walk-ins were conducted 2–3x weekly from 1 May–1 July, and weekly thereafter until 1 August. In Maine, movement was monitored through

daily GPS locations and walk-ins were initiated when daily locations became highly localized, indicative of birthing behavior (Testa et al. 2000a, McGraw et al. 2014). If localization did not occur, cows were checked once weekly from mid-May to 1 July.

The age of neonatal calves was estimated from their wet or dry appearance, mobility, and coordination (Larsen et al. 1989, Musante et al. 2010). The time span between the initial calf sighting and the last observation of a cow without its calf was also used to estimate age and birth date. In the absence of direct observation, calves could be identified from tracks, vocalizations, and behavior (mobility and grunting) of cows leading their young. Parturition date and age of the calf at first observation was estimated in New Hampshire because walk-ins occurred multiple times weekly; however, parturition date and calf age at first observation in Maine were assigned to weekly periods because walk-ins occurred $\sim 1x$ weekly which increased the probability of missing some early calf mortality (< 7 days). Direct observation was considered the best method to document births and early survival because it was minimally invasive and reasonable access was available at both locations. Further, because local spring green-up typically occurs ~ 2 weeks after the median birth date (18 May; Musante et al. 2010), observations were ideal during the immediate post-birth period when most calf mortality occurs.

Monitoring of unmarked calves

Calf survival was measured intensively for 60 d post-birth (summer survival) from direct observation or sign (e.g., tracks, beds, fecal matter, vocalizations) observed during walk-ins; we assumed that surviving calves would be near their radio-marked mother. Survival of calves-at-heel was checked 2x and 1x weekly in New Hampshire and Maine, respectively. If a calf was not observed ≥ 3 consecutive times over 2 weeks,

it was considered a mortality on the day midway between the last confirmed observation and the first missing date; specific cause of death was never identified. An unmarked calf was considered a mortality if the cow died during this time period.

Analysis

Fecundity and calf survival rates were compared between years at each study site using a Chi-square independence test and between study sites using Fisher’s exact test. Calf survival was plotted on a Kaplan-Meier survival curve with 95% confidence limits and a Chi-square goodness-of-fit test was used to compare the timing of unmarked calf losses. Analyses were performed using program R (v 3.2.2, Vienna, Austria).

RESULTS

Fecundity

A total of 76 adult cows were monitored for at least one calving season: 46 in New Hampshire and 30 in Maine. The annual pregnancy rate in New Hampshire ranged from 76 to 88%, averaging 78% (n = 45);

there was no difference by year ($\chi^2 = 0.54, P = 0.76$, Table 1). The annual pregnancy rate in Maine ranged from 75 to 90%, averaging 88% (n = 24); there was no difference by year ($\chi^2 = 0.28, P = 0.60$, Table 1). Pregnancy rate did not differ between the study areas ($P = 0.32$), and the combined average was 81% (n = 69). Parturition occurred from 10–31 May (n = 83) in both study areas and the median parturition date was 19 May (n = 45, New Hampshire only). Birthing was highly synchronous all years with 90% occurring from 14–25 May. The mean age at first observation (n = 29) was 1.8 d (SD = 1.4) and only 2 calves were first detected at ≥ 5 days old in New Hampshire; calf age at first observation was less specific in Maine due to differing methodology (~90% of calves were observed during their first week of life).

Calving rates were similar in New Hampshire (56%, n = 86) and Maine (58%, n = 62) ($P = 0.87$), and among years in both states (New Hampshire: $\chi^2 = 2.60, P = 0.27$; Maine: $\chi^2 = 0.43, P = 0.80$) (Table 1). No births by yearling cows (n = 17) or twinning by adults (n = 148) was documented in either state;

Table 1. Annual and total observed fecundity rates of radio-collared adult cow moose in northern New Hampshire and western Maine, during 2014–2016. Sample sizes are given in parentheses. Rates did not differ by year or study area ($P > 0.05$).

	Adult Cow Productivity %		
	Pregnancy Rate	Calving Rate	Successive Calving Rate
New Hampshire			
2014	76 (21)	67 (21)	NA
2015	75 (16)	45 (33)	29 (17)
2016	88 (8)	59 (32)	18 (28)
All Years	78 (45)	56 (86)	22 (45)
Maine			
2014	90 (20)	55 (20)	NA
2015	75 (4)	55 (20)	55 (11)
2016	NA	64 (22)	25 (12)
All Years	88 (24)	58 (62)	39 (33)
Combined	81 (69)	57 (148)	24 (78)

thus, the fecundity rate was equivalent to the calving rate. The successive calving rate was 22% ($n = 45$, range = 18–29%) in New Hampshire and 39% ($n = 33$, range = 25–55%) in Maine; the successive calving rate did not differ between years (New Hampshire: $\chi^2 = 0.29$, $P = 0.59$; Maine: $\chi^2 = 1.04$, $P = 0.31$) or study area ($P = 0.60$), and overall was 24% ($n = 78$) (Table 1).

Unmarked calf survival

Calf survival to 60 days averaged 77% ($n = 47$) in New Hampshire and 94% ($n = 36$) in Maine (Fig. 2). There was no difference in annual survival at either site, ranging from 64–87% in New Hampshire ($\chi^2 = 2.04$, $P = 0.36$) and 91–100% in Maine ($\chi^2 = 1.35$, $P = 0.51$). Although survival was not different ($P = 0.06$) between study sites and the combined rate was 86%, survival in Maine was 17% higher. Nearly all mortality in New Hampshire (82%) and Maine (100%) occurred within 7 d post-birth when it was higher than in the remainder of the 60-d period (NH: $\chi^2 = 9.0$, $P = 0.01$; ME: analysis precluded).

DISCUSSION

Calf survival, pregnancy, and successive calving rates were higher in Maine and could be considered biologically different resulting in a population trajectory ~5% higher than that in New Hampshire. However, we do not believe that the populations are measurably different because 1) the method for detecting calves in Maine probably resulted in Maine calves being a few days older (with higher summer survival) at first detection than in New Hampshire, 2) the predominance of pregnancy data originated from only a single year in Maine, and 3) substantial variation in the 2 years of successive calving data reduces the potential accuracy of these parameters to indicate any difference between the study sites. Importantly, the New Hampshire and Maine study sites demonstrated similar trends of low adult fecundity and high summer calf survival, suggesting that a combined dataset is representative of the larger study area, and that the moderate variation in specific parameters was due to inherent variance associated with methodology and sample size.

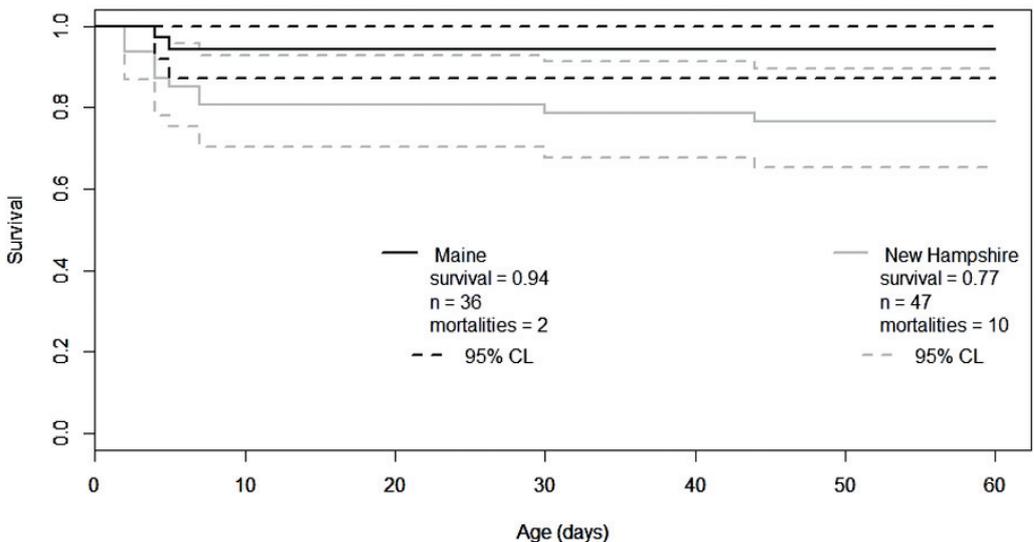


Fig. 2. Kaplan-Meier survival curve for unmarked calf moose from birth to 60 days old collected at study sites in northern New Hampshire and western Maine, 2014–2016.

Most calf mortality in New Hampshire (82%) and all in Maine occurred in the first few days of life (≤ 7 days post-partum) when calves are most susceptible to predation by black bears (Franzmann and Schwartz 1985). Black bear density within the study areas was high enough to incur predation (Ballard 1992), but calf survival was much higher than in populations held at low density by predation (76% loss in weeks 0–8; Gasaway et al. 1992). Calf survival in Maine (94%) was higher than in populations in Scandinavia with minimal predation (87%; Ericsson et al. 2001), further suggesting that early calf survival estimates in Maine were probably artificially high. Calf survival in New Hampshire was similar to that measured previously (71%; Musante et al. 2010) and the combined New Hampshire and Maine calf survival rate (88%) was similar to that in Scandinavia (Ericsson et al. 2001). Again, this survival estimate is probably biased high due to the later detection date of certain Maine calves; albeit, if so, the Maine calving rate was underestimated.

The median parturition date (19 May) and predominant calving season (14–25 May) were similar to those identified previously in New Hampshire (Musante et al. 2010) and central Ontario (Addison and McLaughlin 1993), but earlier than in Alaska (Testa et al. 2000b, Bertram and Vivion 2002). The timing and synchronous birthing pulse (90% in 10 d) occurs across North America (Keech et al. 2000, Testa et al. 2000b) and has been hypothesized as a response to maximize use of high quality forage in summer (Bowyer et al. 1998) and to minimize the influence of predation (Testa et al. 2000b). Forage availability is probably not as important in the northeastern United States given the longer growing season relative to Alaska.

Our productivity measures were similar to those associated with a declining population, but these parameters often vary

regionally because they reflect unique and multiple conditions in moose populations (Table 2). The average pregnancy rate was similar to the North American average (84%; Boer 1992), but the yearling pregnancy and adult twinning rates were low compared to other declining populations (Boer 1992, Murray et al. 2006, Lenarz et al. 2010). Yearling pregnancy and adult twinning rate are directly related and considered indicators of the relative nutritional status in moose populations (Franzmann and Schwartz 1985, Boer 1992), and reflect habitat quality and body weight (Adams and Pekins 1995). The decline in yearling pregnancy from 20% in 2002–2005 (Musante et al. 2010) to 0% in 2014–2016 corresponds with declines in ovulation rate (proximate measure for yearling pregnancy) and dressed body weight measured from 1998 to 2009 in New Hampshire (Adams and Pekins 1995, Bergeron et al. 2013). The lack of twinning in 2014–2016 also corresponds with a decline in the corpora lutea count since 2002–2005 in New Hampshire, suggesting a similar, but more subtle decline in physical condition of adult cows (Bergeron et al. 2013).

It is hypothesized that the lack of reproduction by yearling cows is caused by high annual infestations of winter ticks on calf moose, and consequently, reduced fitness and fecundity of surviving yearlings (Musante et al. 2010, Bergeron et al. 2013). Calf moose that survive an epizootic event ($>50\%$ mortality) are likely in poor condition (McLaughlin and Addison 1986) which will be reflected in lower body weight, ovulation rate, and productivity as yearlings (Peterson 1977, Saether and Heim 1993, Keech et al. 1999). Adult cows with high winter tick infestations are also presumed to be in poorer condition due to the compounding energetic costs associated with winter ticks, gestation, and lactation while consuming a protein-deficient diet until spring green-up

Table 2. Productivity measures from moose populations across the southern range of moose in North America. Pregnancy rates were from serum progesterone levels, calving rates and twinning rates from direct observation, except for North American averages where pregnancy rates were from intrauterine counts, and twinning rates from direct observation and intrauterine counts. Twinning rates are for yearling and adult cows.

Location	Population Change	Adult Pregnancy Rate	Yearling Pregnancy	Calving Rate	Twinning Rate	Source
New Hampshire and Maine	Decreasing	82	0	57	0	This study
Northwestern Minnesota	Decreasing	48	<20	45	19	Murray et al. 2006
North America	Average Decreasing	84	18	–	5	Boer 1992
Northeastern Minnesota	Decreasing	–	–	78	–	Lenarz et al. 2010
Norway	n/a	–	–	77	–	Stubsjøen et al. 2000
New Hampshire 2002-2005	Stable	85	20	75	11	Musante et al. 2010
Upper Peninsula Michigan	Stable/Increasing	74	–	65	19	Dodge et al. 2004
Southern Ontario	Increasing	87	2	–	17	Murray et al. 2012
North America	Average	84	49	–	33	Boer 1992

occurs 2–3 weeks post-birth (Musante et al. 2007, Schwartz and Renecker 2007). Reduced productivity in adult cows is consistent with the low rates of calving and successive calving measured in 2014–2016.

Decline in physical condition during late winter and early spring that stems from parasites is analogous to decline in physical condition that influences productivity following years of deep snow (Mech et al. 1987) or harsh winter conditions (colder temperatures, greater maximum depth and duration of snow pack and shorter growing season; Sand 1996). Reduced productivity from a decline in physical condition of adult cows is expressed by low twinning rates (Mech et al. 1987, Sand 1996), lower calf:cow ratios in autumn (Rolley and Keith 1980), and reduced weight and viability of 9-month old moose calves (Peterson et al. 1982). Because prenatal mortality is low in

deer and moose (Verme and Ulrey 1984), these parameters likely reflect still births or undersized and behaviorally abnormal calves predisposed to mortality (Keech et al. 2000).

The potential effect of winter on productivity during the subsequent year is attributed to the inability of cows to fully recover or compensate in one year (Mech et al. 1987). The energetic costs of prior gestation and lactation are evident in maternal adult cows that have less fat, lower pregnancy rates, and smaller embryos in autumn, and body condition in autumn is positively correlated with pregnancy and calving rate, and negatively with reproductive losses and neonatal mortality the following spring (Testa and Adams 1998). These relationships illustrate that adult cows must compensate for the demands of pregnancy and lactation, and may require a year to recover which reduces productivity in the population (Mech et al. 1987). Poor

body condition in late winter-early spring may affect productivity 3 years later because calves born to cows in poor condition are smaller and remain so (Peterson 1977, Keech et al. 2000), reducing their survival and increasing age to sexual maturity (Mech et al. 1987, Saether and Heim 1993, Keech et al. 1999).

The large difference between our measured pregnancy rate (82%) and calving rate (57%) can be attributed to a variety of outcomes including resorption, still birth, or undersized and behaviorally abnormal calves predisposed to mortality; however, the specific outcome for any individual could not be determined. Adult cows in poor condition produce smaller neonates that experience higher mortality and slower development (Peterson 1977, Keech et al. 2000). Certainly a portion of neonatal mortality could be attributed to the compromised condition of calves as a consequence of marginalized adult cows, given the clear association of frequent, high winter tick infestations and the declining condition and productivity in this population. Similarly, the low successive calving rate (24%) suggests that maternal costs and inadequate compensatory growth prevented subsequent reproduction. The successive calving rate was 3x higher (75%) a decade earlier when a single epizootic occurred in a 4-year period in New Hampshire (Musante et al. 2010).

The effect of high winter tick infestations on body condition and productivity is analogous to malnutrition associated with poor habitat (Albon et al. 1983, Albright and Keith 1987). But an important distinction is that such malnutrition affects physical nutrition in all age classes (Peterson 1977, Skogland 1983, Messier and Crête 1984), induces starvation before old age (Bergerud et al. 1983), and high browsing rates are evident (Albright and Keith 1987). Field-dressed body weight, antler dimensions, and the onset of sexual maturity are correlated with the

physical condition of moose (Schwartz and Hundertmark 1993, Schmidt et al. 2007). Since 1988 these measurements have declined measurably in yearling moose throughout the region, yet only slight downward trends have occurred in adult age classes (Bergeron et al. 2013, Andreozzi et al. 2015). Yearling condition reflects, in part, condition as a calf. The marked decline in body weight and productivity of yearling cows, yet subtle decline in other age classes, reflects the negative effects of frequent epizootics on productivity (Bergeron et al. 2013). Neither this or the previous study (Musante et al. 2010) in the same area attributed any mortality to starvation (>350 radio-collared animals), and browsing intensity on the landscape is considered low-moderate overall (Bergeron et al. 2011). Further, the rate of annual forest harvest in the region has been relatively stable at 1–3% of the landscape since 1990, providing continuous availability of optimal foraging habitat (15–20% of the landscape in 4–16 year-old regenerating forest) through both growth and decline of the moose population (Ball 2017).

Moose are at the southern edge of their continental range in this region and snow depth of 70 cm that impedes moose mobility and >90 cm that confines movement and increases mortality (Coady 1974) occur infrequently. The winter of 2016 had nearly snowless conditions and temperatures slightly above normal (0.3°C, NCDC weather data), yet an epizootic occurred and the trend of low productivity continued. Given the low adult productivity measured here, and the lack of productivity and deterred growth of yearlings, yet the lack of starvation and the constant production of optimal foraging habitat, it is evident that the winter tick, not habitat, is the predominant influence on this regional moose population. Continued slow decline in this population is predicted if the frequency of epizootics remains high.

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REFERENCES

- ADAMS, K. P., and P. J. PEKINS. 1995. Growth patterns of New England moose: yearlings as indicators of population status. *Alces* 31: 53–59.
- ADDISON, E. M., and R. F. McLAUGHLIN. 1993. Seasonal variation and effects of winter ticks (*Dermacentor albipictus*) on consumption of food by captive moose (*Alces alces*) calves. *Alces* 29: 219–224.
- ALBRIGHT, C. A., and L. B. KEITH. 1987. Population dynamics of moose, *Alces alces*, on the south-coast barrens of Newfoundland. *Canadian Field Naturalist* 101: 373–387.
- ALBON, S. D., B. MITCHELL, and B. W. STAINES. 1983. Fertility and body weight in female red deer: A density-dependent relationship. *Journal of Animal Ecology* 52: 969–980.
- ANDREOZZI, H. A., P. J. PEKINS, and L. E. KANTAR. 2015. Analysis of age, body weight and antler spread of bull moose harvested in Maine, 1980–2009. *Alces* 51: 45–55.
- BALL, K. R. 2017. Moose and winter tick epizootics in northern New England's changing climate. M.S. Thesis, University of New Hampshire, Durham, New Hampshire, USA.
- BALLARD, W. B. 1992. Bear predation on moose: a review of recent American studies and their management implications. *Alces Supplement 1*: 162–276.
- BERGERON, D. H., P. J. PEKINS, H. F. JONES, and W. B. LEAK. 2011. Moose browsing and forest regeneration: a case study. *Alces* 47: 39–51.
- , ———, and K. RINES. 2013. Temporal assessment of physical characteristics and reproductive status of moose in New Hampshire. *Alces* 49: 39–48.
- BERGERUD, A. T., W. WYETT, and B. SNIDER. 1983. The role of wolf predation in limiting a moose population. *The Journal of Wildlife Management* 47: 977–988.
- BERTRAM, M. R., and M. T. VIVION. 2002. Moose mortality in eastern interior Alaska. *The 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.
- BOWYER, R. T., V. VAN BALLEMBERGHE, and J. G. KIE. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. *Journal of Mammalogy* 79: 1332–1344.
- BRODERS, H. G., A. B. COOMBS, and J. R. McCARRON. 2012. Ectothermic responses of moose (*Alces alces*) to thermoregulatory stress on mainland Nova Scotia. *Alces* 48: 53–61.
- COADY, J. W. 1974. Influence of snow on behavior of moose. *Le Naturaliste Canadian* 101: 417–436.
- CROSSLEY, A. 1987. Summer pond use by moose in northern Maine. M. S. Thesis, University of Maine, Orono, Maine, USA.

- DEGRAAF, R. M., M. YAMASAKI, W. B. LEAK, and J. W. LANIER. 1992. New England wildlife: management of forested habitats. General technical report NE-144. Radnor, PA: United States Department of Agriculture, U. S. Forest Service, Northeast Forest Experiment Station, Radnor, Pennsylvania, USA.
- DODGE, W. B. JR., S. R. WINTERSTEIN, D. E. BEYER, JR., and H. CAMPA III. 2004. Survival, reproduction and movements of moose in the western Upper Peninsula of Michigan. *Alces* 40: 71–85.
- 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.
- FRANZMANN, A. W., and C. C. SCHWARTZ. 1985. Moose twinning rates : a possible population condition assessment. *Journal of Wildlife Management* 49: 394–396.
- . 2000. Moose. Pages 578–600 in S. Desmarais and P. R. Krausman, editors. *Ecology and Management of Large Mammals of North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- GASAWAY, W. C., R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLEYHOUSE, R. O. STEPHENSON, and D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120.
- JONES, H. F. 2016. Assessment of health, mortality, and population dynamics of moose in northern New Hampshire during successive years of winter tick epizootics. M. S. Thesis, University of New Hampshire, Durham, New Hampshire, USA.
- KEECH, M. A., R. D. BOERTJE, R. T. BOWYER, and B. W. DALE. 1999. Effects of birth weight on growth of young moose: do low-weight neonates compensate? *Alces* 35: 51–57.
- , T. R. 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. *The Journal of Wildlife Management* 64: 450–462.
- LANKESTER, M. W. 2010. Understanding the impact of meningeal worm, *Parelaphostrongylus tenuis*, on moose populations. *Alces* 46: 53–70.
- LARSEN, D. G., D. A. GAUTHIER, and R. L. MARKEL. 1989. Causes and rates of moose mortality in southwest Yukon. *Journal of Wildlife Management* 53: 548–557.
- LENARZ, M. S., J. FIEBERG, M. W. SCHRAGE, and A. J. EDWARDS. 2010. Living on the edge: viability of moose in northeastern Minnesota. *Journal of Wildlife Management* 74: 1013–1023.
- MCGRAW, A. M., J. TERRY, and R. MOEN. 2014. Pre-parturition movement patterns and birth-site characteristics of moose in northeast Minnesota. *Alces* 50: 93–103.
- MCLAUGHLIN, R. F., and E. M. ADDISON. 1986. Tick (*Dermacentor albipictus*)-induced winter hair-loss in captive moose (*Alces alces*). *Journal of Wildlife Diseases* 22: 502–510.
- MECH, D. L. 1983. *Handbook of Animal Radio Tracking*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- , R. E. MCROBERTS, R. O. PETERSON, and R. E. PAGE. 1987. Relationship of deer and moose populations to previous winter's snow. *Journal of Animal Ecology* 56: 615–627.
- MESSIER, F., and M. CRÊTE. 1984. Body condition and population regulation by food resources in moose. *Oecologia* 65: 44–50.
- MURRAY, D. L., E. W. COX, W. B. BALLARD, H.A. WHITLAW, M.S. LENARZ, T.W. CUSTER, T. BARNETT, and T.K. FULLER. 2006. Pathogens, nutritional deficiency, and climate influences on a declining

- moose population. *Wildlife Monographs* 166: 1–30.
- , K. F. HUSSEY, L. A. FINNEGAN, S. J. LOWE, G. N. PRICE, J. BENSON, K. M. LOVELESS, K. R. MIDDEL, K. MILLS, D. POTTER, A. SILVER, M-J. FORTIN, B. R. PATTERSON, and P. J. WILSON. 2012. Assessment of the status and viability of a population of moose (*Alces alces*) at its southern range limit in Ontario. *Canadian Journal of Zoology* 90: 422–434.
- MUSANTE, A. R., P. J. PEKINS, and D. L. SCARPITTI. 2007. Metabolic impacts of winter tick infestations on calf moose. *Alces* 43: 101–110.
- , ———, ———. 2010. Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. *Wildlife Biology* 16: 185–204.
- NATIONAL CLIMATE DATA CENTER (NCDC). 2016. Climate Data Online Daily Summaries January-December, 2014–2016. <<https://www.ncdc.noaa.gov/cdo-web/datasets#GHCNDMS>> (accessed January 2017).
- PETERSON, R. O. 1977. Wolf Ecology and Prey Relationships on Isle Royale. National Park Service Scientific Monograph Series No. 11. U. S. Government Printing Office, Washington, D. C., USA.
- , J. M. SCHELDER, and P. W. STEPHEN. 1982. Selected skeletal morphology and pathology of moose from the Kenai Peninsula, Alaska and Isle Royale, Michigan. *Canadian Journal of Zoology* 60: 2812–2817.
- ROLLEY, R. E., and L. B. KEITH. 1980. Moose population dynamics and winter habitat use at Rochester, Alberta, 1965–1979. *Canadian Field-Naturalist* 94: 1–9.
- SAETHER, B-E., and M. HEIM. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *Journal of Animal Ecology* 62: 482–489.
- SAMUEL, W. M. 2004. White as a Ghost: Winter Ticks and Moose. Natural History Series, Volume 1. Federation of Alberta Naturalists, Edmonton, Alberta, Canada.
- SAND, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia* 106: 212–220.
- SCHMIDT, J. I., J. M. VER HOEF, and R. T. BOWYER. 2007. Antler size of Alaskan moose *Alces alces gigas*: Effects of population density, hunter harvest and use of guides. *Wildlife Biology* 13: 53–65.
- SCHWARTZ, C. C. 2007. Reproduction, Natality, and Growth. Pages 141–145 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, D. C., USA.
- , and K. J. HUNDERTMARK. 1993. Reproductive characteristics of Alaskan moose. *The Journal of Wildlife Management* 57: 454–468.
- , and L. A. RENECKER. 2007. Nutrition and energetics. Pages 441–478 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, D.C., USA.
- SKOGLAND, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. *Oecologia* 60: 156–168.
- STUBSJØEN, T., B. E. SAETHER, E. J. SOLBERG, M. HEIM, and C. M. ROLANDSEN. 2000. Moose (*Alces alces*) survival in three populations in northern Norway. *Canadian Journal of Zoology* 78: 1822–1830.
- TESTA, J. W., and G. P. ADAMS. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). *Journal of Mammalogy* 79: 1345–1354.
- , E. F. BECKER, and G. R. LEE. 2000a. Movements of female moose in relation to birth and death of calves. *Alces* 36: 155–162.

- , ———, ———. 2000b. Temporal patterns in the survival of twin and single moose (*Alces alces*) calves in southcentral Alaska. *Journal of Mammalogy* 81: 162–168.
- VAN BALLEMBERGHE, V., and W. B. BALLARD. 2007. Population Dynamics. Pages 223–246 *in* A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, D. C., USA.
- 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, Harrisburg, Pennsylvania, USA.