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Many wildlife populations are experiencing a variety of environmental pressures due to the direct and indirect consequences of a changing climate. In the northeast, USA, moose *Alces alces* are declining in large part because of the increasing parasitism by winter tick *Dermacentor albipictus*, facilitated by high host density and optimal environmental conditions. To test this hypothesis, and better understand the influence of this interaction on the stability of the regional population, we constructed a population viability model using data collected through comprehensive survival and productivity studies in 2002–2005 and 2014–2018 in northern New Hampshire. Years of heavy tick infestation (epizootics) saw a marked reduction in calf survival (< 50%), adult calving (< 60%), twinning rate (< 5%) and complete loss of yearling productivity. We conducted population viability analysis using VORTEX ver. 10.2 to model this moose population for 40 years using mean demographics from both time periods, including environmental variation measured in the field during winter tick epizootic (2002, 2014, 2015, 2016) and non-epizootic (2003, 2004, 2005, 2017) years. This exercise highlights the influence of winter tick infestation on the trajectory of the population with the potential for rapid population growth or decline depending on the frequency of epizootics. We suggest a shift in moose management strategy focused on lowering moose density, assuming continued influence of climate change on the host–parasite relationship.

Keywords: *Alces alces*, *Dermacentor albipictus*, epizootic, modeling, moose, mortality, New Hampshire, population, survival, winter tick

Over the past century, moose *Alces alces* populations across the southern edge of their range in North America have repeatedly expanded and contracted (Lankester 2010). Infectious pathogens, parasites, habitat loss and nutritional deficiency are all thought to play a role in population fluctuations, and certain of these factors are influenced by a warming climate (Samuel 2004, Murray et al. 2006). The winter tick is the leading cause of the recent decline of the moose population in northern New Hampshire, USA and other parts of northern New England by causing high calf mortality and reduced fecundity in years of epizootics (Musante et al. 2010, Jones et al. 2017, 2019). The recently observed, and predicted frequency of shorter winters (Wake et al. 2014) is favorable for increased survival, longer larval questing period, and higher abundance of winter tick which together cause continuous negative impact on moose at their southern range (Jones et al. 2019).

The moose population in New Hampshire has experienced a slow but steady decline from ~7500 in the late-1990s to ~4000 in 2015 (Rines 2015). In addition, yearling and adult cows have realized a concurrent drop in body weight and ovulation rate (measured via corpora lutea counts on harvested animals; Bergeron et al. 2013, Jones et al. 2017) despite sustained availability of optimal forage habitat (4–16 year age-class forest) do to disturbance from commercial timber production (Ball 2017). This downward trend is largely the result of the interaction between a relatively high moose density in the northern region, which in combination with shorter winters, provides for an increased frequency of winter tick *Dermacentor albipictus* epizootics that translates to heightened calf mortality rates (>50%) and reduced productivity (Musante et al. 2010, Jones et al. 2017, 2019). Reexamining these population parameters will provide insight into predicting the future population dynamics of moose in northern New Hampshire and the region, and is critically important in designing and implementing local management strategies.

Comprehensive moose projects conducted in northern New Hampshire measured annual survival and productivity during both epizootic and non-epizootic years from 2002 to 2005 (Musante et al. 2010) and 2015 to 2017 (Jones et al. 2017, 2019, Ellingwood 2018). The objective of this study was to model the trajectory of northern New Hampshire's moose population to test its future viability under varying frequencies of winter tick epizootics by using the combined 8 years of population demographics measured in the field from a robust sample population of radio-marked moose.

Methods

We projected northern New Hampshire's moose population over 40 years (2018–2058) using VORTEX ver. 10.2 (Lacy and Pollak 2017), an individual-based computer simulation model for population viability analysis (PVA). PVA is a method to predict the future of wildlife populations based on mean demographic rates, and the impacts of environmental variation on these rates, including catastrophes (Brook et al. 1999, Lacy 2000). As an 'individual-based' model, each individual is represented with life events simulated and the status of each monitored in the population over time; changes in the population occur once per year as a series of discrete events (e.g. breeding, calving, mortality, ageing; Lacy 2000). Moose are categorized as calves (< 1 year old), yearlings (≥ 1 and < 2 years old) and adults (≥ 2 years old). Animals advance to their next age class on 19 May, the median date of parturition in the study area (Jones et al. 2017). Environmental variation in vital rates was incorporated into the model with random values sampled from a binomial distribution, with a specified probability and standard deviation for each life event. For each individual, should the sampled random value fall above the specified probability, the event is deemed to occur (Lacy et al. 2017). Raw sampling variance was used for this simulation, likely resulting in an overestimate of the biological variation of vital rates. The model assumed no effect of density dependence on productivity or survival.

This analysis used productivity and survival rates measured from 2002 to 2005 (Musante et al. 2010) and 2014 to 2018 (Jones et al. 2017, 2019, Ellingwood 2018), representing eight years of monitoring radio-marked moose within the same northern New Hampshire study area during epizootic and non-epizootic years (Fig. 1). Pregnancy rate reflects the proportion of cows testing positive for pregnancy at the time of capture, and was measured via blood samples (2002, 2014–2017) and ultrasound (2003). Calving rates (proportion of cows having one or more calves), twinning rates (proportion of parturient cows that have twins) and the survival of calves (0–7 months) was measured by visual monitoring (ground-telemetry homing); see Jones et al. (2017) for additional monitoring details. Successive calving was monitored across years and was defined as the proportion of individual cows that calve in consecutive years.

Survival rates used in the PVA simulation were measured on unmarked calves (0–7 months), marked-calves (8–12 months) and yearlings/adults (> 12 months) were estimated as proportions of the starting sample population and assumed equal between sexes; see Musante et al. (2010) and Jones et al. (2019) for details on survival analysis and cause-specific mortality. Annual survival rate of the 0–1 age class was calculated by combining the data from the unmarked (summer, fall) and marked (winter, spring) groups of calves; while not all marked calves were from marked adults, pooling these two groups was reasonable for an estimate as they were all monitored within the same study area. Further, there was low annual variability in calf survival through the summer and fall (Jones et al. 2017). Adults that had been monitored for < 1 year due to timing of capture were censored from survival estimates in respective years. An ANOVA test was used to examine differences in productivity, and survival between epizootic and non-epizootic years. Adults and yearlings were considered a single 'adult' age class for survival measurement due to the limited sample size of radio-marked yearlings and the difficulty in differentiating yearlings from adults at the time of capture. Adults and yearlings were considered separate cohorts for productivity measurement despite the limited sample size due to the known disparity in reproductive potential between age classes, with the potential for delayed maturation of physically compromised yearlings (Adams and Pekins 1995, Jones et al. 2017).

A starting population size (n) of 908 was used, based upon the average (2014–2017) density estimate (0.44 moose km^{-2}) developed from November observation surveys by deer hunters (Bontaites et al. 2000) in the region where radio-marked animals were monitored (~1250 km^2); this region encompasses the core of New Hampshire's moose population with the highest density estimates. The 2016–2017 estimated calf:adult age ratio was 0.18, and the adult bull:cow sex ratio was 0.41 (K. Rines, New Hampshire Fish and Game Department pers. com.). The starting adult age structure was estimated using a stable age distribution where age–sex classes were allocated according to the expected age distribution calculated from the initial N and birth and death rates (Lacy et al. 2017); age structure was assumed equal between sexes.

The impact of epizootics was simulated using the 'catastrophe' function available in VORTEX. Catastrophes are assigned a specified probability of annual occurrence, causing one-year reductions in reproduction and survival. A 24% reduction in adult calving and total loss of reproduction in the yearling age class in epizootic years was measured across eight years of radio-marked moose monitoring. Additionally, calf and adult survival were reduced by 51% and 8%, respectively (Table 1). To simulate the impact of epizootics at varying rates of occurrence, five scenarios of the model were run using catastrophe probabilities of 0.00, 0.25, 0.50, 0.75 and 1.00; 0.00 equals no future epizootics and 1.00 equals annual occurrence. To provide a thorough description of simulated population behavior, 1000 iterations of each simulation were run (Lacy et al. 2017). A stepwise approach was used to identify the frequency of epizootics that would allow the population to stabilize at its current size.

Using VORTEX's built-in ST function, we tested vital rate elasticity to determine which parameters had the largest effect on the population's mean arithmetic growth (λ) under 'epizootic' and 'non-epizootic' conditions. In separate
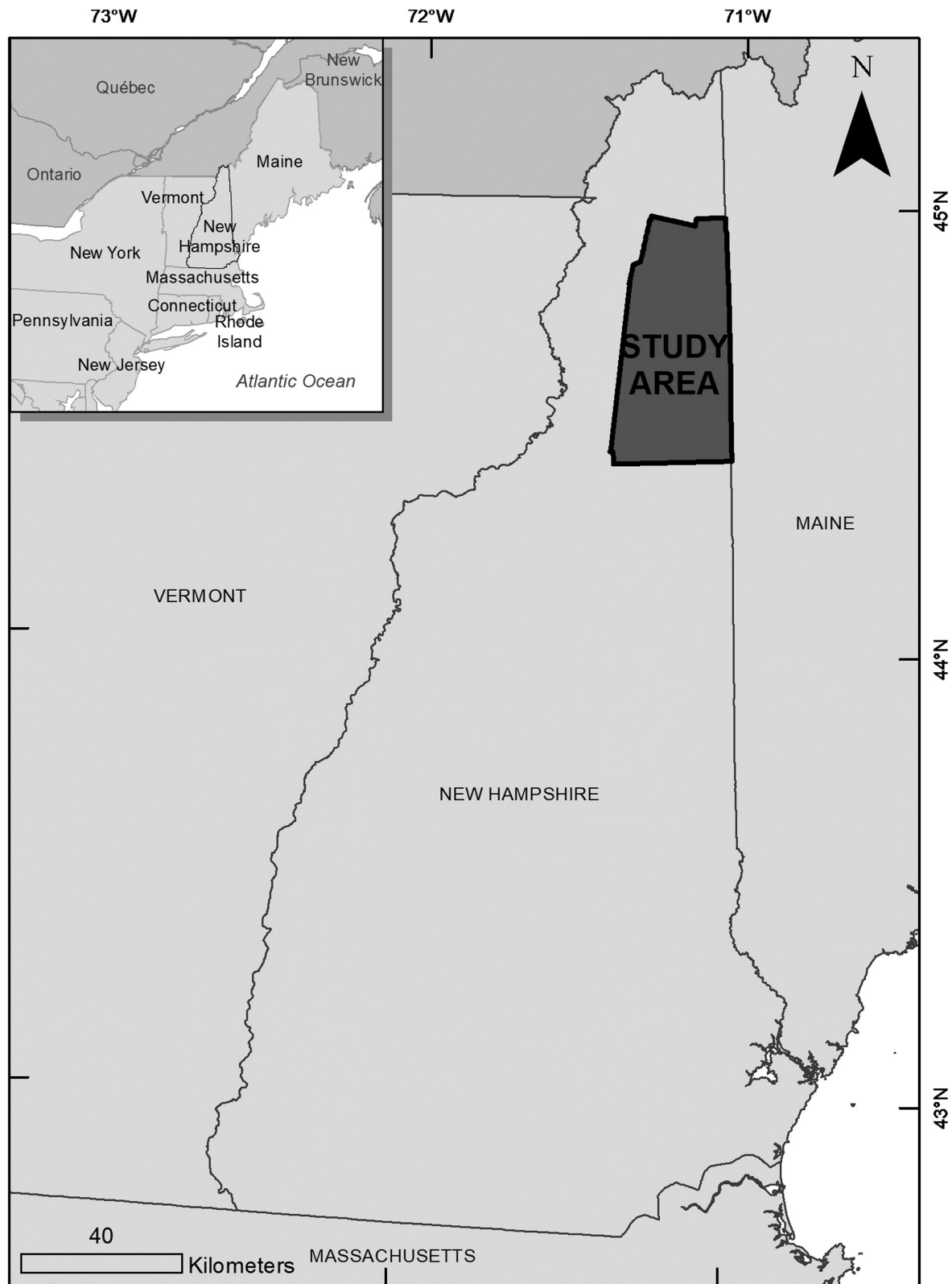
Figure 1. Study area in northern New Hampshire, USA.

simulations, we varied the following four vital rates independently within ± 10% of their baseline (mean) value: 1) calf survival, 2) yearling/adult survival, 3) yearling productivity and 4) adult productivity. We ran 1000 iterations of each condition to assure results are robust to random varia-

tion. We measured the response of the population's growth rate to changes in each parameter as $(\lambda_+ - \lambda_-)/(\lambda_0)$ where λ_+ and λ_- are the output from the adjusted parameter values and λ_0 is the mean growth rate using unadjusted parameters (Cooper et al. 2001).

Table 1. Mean calving and survival rates from radio-marked moose during epizootic and non-epizootic years in northern New Hampshire (2002–2005 and 2014–2017).

	Calving (SD)			Survival (SD)	
	Yearling	Adult	Twinning	Calf	Yearling/adult
Epizootic	0.00 (0.00)	0.64 (0.15)	0.00 (0.00)	0.34 (0.12)	0.80 (0.08)
Non-epizootic	0.16 (0.21)	0.84 (0.08)	0.08 (0.02)	0.69 (0.02)	0.87 (0.05)

Results

Productivity

The adult pregnancy rate averaged 75% annually (Table 2); 68% in 2002–2003 (n = 28) and 78% in 2014–2017 (n = 59). There was no difference in pregnancy rate by sampling method (p > 0.05); the serum assay for pregnancy is 93–95% accurate for pregnant cows (BioPRYN Wild, Moscow, ID), while the use of ultrasound eliminates the potential for false-positives (Stephenson et al. 1995). The average calving rate was 69%; 77% in 2002–2005 and 61% in 2014–2017 (Table 3). A marked decline in yearling calving rates was observed between 2002–2005 and 2014–2017 (from 40% to 0%) as well as a decline in adult twinning rates (from 12% to 1%). Further, calving rates were significantly lower in epizootic years (59%) than in non-epizootic years (79%; p < 0.05). Calves were observed with 84% of known pregnant cows across all years of the study. In 2014–2017 the successive calving rate averaged 53% and only 29, 28 and 21% of cows reared calves in successive years, respectively (Jones et al. 2017, Ellingwood 2018); 15 years earlier, this population had a successive calving rate of 75% (Musante et al. 2010).

Unmarked neonate survival

Survival of unmarked neonates to 60 days averaged 76% (n = 194) across all 8 years of monitoring; 78% of mortality occurred in the first week of life. Post-summer survival was high, and annual survival to ~8 months of age (birth through 31 Dec) averaged 75%. Cause specific mortality during this period was unidentifiable as remains were rarely located. Summer survival was not different between epizootic and non-epizootic years (p > 0.05).

Radio marked moose survival

Studies from 2002 to 2005 and 2014 to 2017 monitored 178 radio-marked calves (8–12 months old) from January to May over 8 years (14–37 calves annually). Survival rate averaged 34% in epizootic years (2002, 2014, 2015, 2016)

Table 2. Pregnancy rates of adult cows captured in northern New Hampshire, 2002, 2003, 2014–2017.

Year	No. tested	No. pregnant	Pregnancy rate
2002	24	15	0.63
2003	4	4	1.00
2014	21	16	0.76
2015	16	12	0.75
2016	9	7	0.78
2017	13	11	0.85
Total/avg.	87	65	0.75

and 69% in non-epizootic years (2003, 2004, 2017; Table 4); this difference reflected the annual difference in winter tick parasitism, the primary cause of death each year (Musante et al. 2010, Jones et al. 2019). Surviving calves entered the yearling age class on 19 May, the median parturition date measured in these studies.

Yearling and adult survival were measured with 33 radio-marked cows in 2002–2005 and 60 cows in 2014–2017. In each study, surviving calves (male and female) were included in the subsequent year's survival measurement of yearling/adult animals. Yearling/adult survival averaged 83% (range: 73–91%) and was not significantly different (p > 0.05) between studies (Table 4).

Population viability

The models representing annual epizootic probabilities (Pr) of 0.25, 0.50, 0.75 and 1.0 predicted negative mean exponential growth values of 0.01, 0.08, 0.16 and 0.28, respectively. Pr(0.25) saw a 7% reduction in population size over 40 years, while Pr(0.50), Pr(0.75) and Pr(1.0) saw more rapid declines with populating halving in less than 10 years (Fig. 2). The population maintains the potential for rapid growth at current vital rates with a positive rate of growth (r = 0.01) in the absence of future epizootics. The potential for population stability occurs at a 23% probability of annual epizootics.

Under a non-epizootic scenario, only subtle differences were identified between the relative influences of individual vital rates on population growth; population growth is most sensitive to changes in adult survival, followed by calf survival and adult productivity (Table 5). During epizootics, fluctuations in individual vital rates had minimal control on the high negative growth rate of the population. The response of population growth to yearling calving during epizootics could not be measured, as the baseline rate for this metric is zero.

Discussion

Knowledge of environmental factors influencing the shifting host–parasite balance of moose and winter ticks are important for conservation and population management. Winter tick epizootics are generally considered infrequent events, and their occurrence indicates an imbalanced host–parasite relationship resulting from the combination of high host/tick abundance with favorable environmental conditions promoting infestation (Samuel 2004). What was uncommon, however, is now common and likely to increase, with concern about winter tick parasitism spreading across North America in the mid- to southern range of moose. For example, research to specifically assess the impact of winter ticks

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Table 3. Annual reproductive rates of radio-marked cows in northern New Hampshire, 2002–2005 (Musante et al. 2010) and 2014–2017 (Jones et al. 2017, Ellingwood 2018).

Year	Calving rate (n)			Twinning rate		
	Yearling	Adult	Total	Yearling	Adult	Total
2002*	0.20 (5)	0.82 (17)	0.68	0.00	0.21	0.20
2003	1.00 (1)	0.77 (26)	0.88	0.00	0.10	0.10
2004	0.00 (5)	0.92 (24)	0.78	0.00	0.09	0.09
2005	0.44 (9)	0.89 (19)	0.74	0.25	0.06	0.10
2014*	NA	0.67 (21)	0.67	NA	0.00	0.00
2015*	0.00 (3)	0.46 (33)	0.42	0.00	0.00	0.00
2016*	0.00 (1)	0.59 (32)	0.58	0.00	0.00	0.00
2017	NA	0.76 (38)	0.76	NA	0.03	0.03

Twinning rate is defined as the proportion of parturient females having twins.
* Indicates winter tick epizootic.

on moose occurs in Quebec (J. P. Tremblay, Univ. Laval, unpubl.), Yukon (E. Chenery, Univ. of Toronto, unpubl.) and British Columbia, Canada (Kuzyk et al. 2018), and in Utah, USA (K. Hersey, Utah Division of Wildlife Resources, unpubl.).

Because most moose populations in North America south of 60° latitude experience low, annual infestation of winter ticks (Samuel 2004, 2007), it is important to understand the influence of environmental factors that shift the host–parasite balance. Further, although the frequency of epizootics is of paramount concern in population management as demonstrated here, both infestation level and population impact occur along a continuum. For example, measurable calf mortality and reduced productivity were measured in both 'non-epizootic' and 'epizootic' years in the northeast USA (Musante et al. 2010, Ellingwood 2018, Jones et al. 2019). Managers should not focus entirely on the epizootic threshold (50% survival) because the highest winter calf survival rate was only 70% from 2014 to 2017 in northern New Hampshire.

This modeling exercise emphasized the influence of winter tick epizootics on the long-term fate of the northern New Hampshire moose population. Should the recent rate of epizootics continue (75%; 2014–2017), the population is predicted to halve in as few as 10 years. This estimate is consistent with that predicted in the age-structured model RAMAS Ecolab (Setauket, NY; Akcakaya et al. 1999) used by Jones (2016) to simulate the annual effect of winter ticks. Continued, consecutive epizootics are improbable, however,

Table 4. Annual survival rates of radio-marked moose in northern New Hampshire during 2002–2005 (Musante et al. 2010, Jones et al. 2019).

Year	Survival rate		
	Unmarked calves (0–8 mo.)	Marked calves (8–12 mo.)	Marked yearling/adults (> 12 mo.)
2002*	0.73	0.50	0.73
2003	0.75	0.71	0.87
2004	0.81	0.67	0.91
2005	0.55	NA	NA
2014*	0.64	0.38	0.91
2015*	0.87	0.26	0.78
2016*	0.78	0.23	0.75
2017	0.80	0.70	0.84

* Indicates winter tick epizootic.

as both climactic conditions and host density must remain favorable for such events to occur (Samuel 2004). The effect of ticks on calf survival in 2014–2017 suggests that the current moose density is sufficient to support epizootics; therefore, fall ground conditions arguably remain the primary influence and predictor of tick abundance and epizootics.

In the absence of high winter tick infestation, the northern New Hampshire moose population maintains the potential to rebound based on the demographics in non-epizootic years, with potential for population doubling in ~10 years; likewise, an 11-year estimate was predicted by Jones (2016) when simulating low impact by winter ticks. Models simulating epizootic probabilities of 0.25–0.75 illustrate the predicted impact of epizootics at varying probability of annual occurrence. Population growth at epizootic probabilities < 0.25 is dependent on increasingly unfavorable weather conditions for ticks (drought and/or early winter) that deter either larval abundance or the length of the autumnal questing period (September–December; Aalangdong 1994, Addison et al. 2016), and the survival of adult female ticks in spring (April–May; Drew and Samuel 1986, Samuel 2007). An epizootic probability of 0.50–0.75 represents the current frequency documented in northern New Hampshire since 2014, with periodic variation in ground conditions during autumn and a slowly declining moose density that affect sustained high tick abundance. Population stability was achieved at ~23% probability of annual epizootics, consistent with the rate documented in northern New England in the early 2000s (one in four years; Musante et al. 2010). These modeled estimates are likely conservative due to a number of assumptions of the model including adult male survival rates the use of raw variance estimates, inflating the overall variation present and biasing projections low across all analyses (Staples et al. 2004).

Analysis of vital rate elasticity indicates that adult survival and productivity are the most significant demographic rates in population change. Despite the implication that juvenile survival has less influence on population growth relative to adult survival, it remains a critical component of population dynamics (Gaillard et al. 2000). As affirmed by this study, adult survival for large herbivores generally has a low coefficient of variation (< 10%) and is largely buffered from environmental variation; in contrast, juvenile survival and fecundity of young females often have high variation (CV > 30%, Gaillard et al. 2000). Considering the low variation in adult survival in epizootic and non-epizootic years,
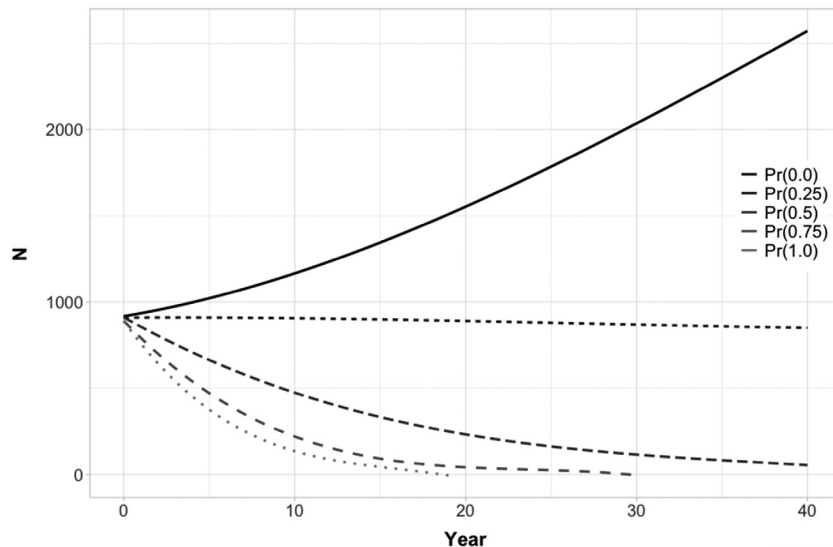
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Figure 2. Population trajectories of the northern New Hampshire moose population under varying probabilities of annual epizootics (0.0, 0.25, 0.75, 1.0).

the potential importance of juvenile survival on recruitment cannot be understated; further, the near complete lack of yearling productivity is abnormal in moose (Schwartz 2007). The grouping of yearling and adult mortality rates in the model may lead to a slight positive bias due to the reduced vulnerability to tick mortality with increasing body size/age (Musante et al. 2007).

A population's carrying capacity (K) is defined as the number of healthy animals an area can support, and is generally limited by habitat quality and quantity, with populations above K displaying poor condition due to malnutrition (Van Ballenberghe and Ballard 2007). While northern New Hampshire's moose population is symptomatic of nutritional restriction (reduced body weights, low productivity and low juvenile survival), no instances of starvation have been documented (Musante et al. 2010, Ellingwood 2018, Jones et al. 2019) and regional habitat is considered near optimal (Scarpitti et al. 2005, Bergeron et al. 2011, Ball 2017). That K is influenced by parasitism and the frequency of winter tick epizootics is evident in the data presented here and in previous studies (Samuel 2007, Musante et al. 2010, Jones et al. 2017, 2019).

Table 5. Elasticity of population growth rate (λ) to changes in moose population parameters during epizootic and non-epizootic years.

Parameter	Elasticity to λ[a]	Elasticity to λ[b]
Calf survival	−0.0028 (2)	−0.0017 (2)
Yearling survival	−0.0018 (4)	−0.0011 (3)
Adult survival	−0.0084 (1)	−0.0079 (1)
Yearling calving	0.0004 (5)	NA
Adult calving	0.0025 (3)	0.0011 (3)

Elasticity ranks on absolute values are shown parenthetically.
Relative elasticity to λ was evaluated by varying each parameter ± 10% of its baseline value; see Table 1. Negative values indicate a negative relationship between the parameter and population growth.
[a] Elasticity to changes in 'non-epizootic' conditions.
[b] Elasticity to changes in 'epizootic' conditions.

A lower moose density should eventually be realized from the continued negative impacts of high calf mortality, low productivity and delayed maturation of yearlings. A balanced host–parasite relationship was estimated to occur at a threshold density of ∼1 moose km^{-2} in Alberta, CA (Samuel 2007), a density higher than that currently estimated in the study area. Certainly moose population density is inherently difficult to measure, and estimates are subject to wide variance and repeatability issues. Further, patterns in forest harvesting (Ball 2017) and moose foraging behavior in spring and autumn (Healy et al. 2018) likely concentrate tick and moose abundance on the landscape, thereby promoting locally high infestations that add to a larger regional impact.

The interrelationships and influences of sustained quality habitat, moose foraging behavior, tick ecology and climate change point to the difficulty in identifying and predicting a threshold balance between moose density and winter tick abundance, especially at the southern range boundary of moose. And importantly, an epizootic again occurred in 2018 (60% calf mortality; P. Pekins unpubl.) marking a continuous 15-year population decline, and four epizootics in five years. This trend in successive epizootics would suggest the primary effect of climate change is an extended autumnal questing period that effectively reduces the threshold density of moose associated with high tick abundance and resultant epizootics (Jones et al. 2019). Whatever a normal balance is/was relative to moose density, tick abundance and infestation level, an extended larval questing period will allow higher infestation levels at lower tick abundance and moose density (Healy 2018).

Importantly, population decline is relatively slow because adult mortality rates are considered normal (Musante et al. 2010, Jones et al. 2019), yet individuals are not realizing optimal growth or productivity (Jones et al. 2017), traditional management goals associated with K. Accelerating decline through a more liberalized moose harvest is a possible means to reduce the impact of winter ticks, ostensibly by lowering both moose population density and relative tick abundance. Given the availability of quality habitat, a lower

moose density should yield measurably improved health and productivity metrics in the population. When above K, hunted populations are often managed through liberal harvest (Mercer and McLaren 2002); in essence, this strategy recognizes parasitism, not habitat, as a major determinant of K. Although somewhat counterintuitive when considering a declining population, a reduction in moose density through harvest management represents a possible, proactive strategy to limit the frequency and associated impacts of epizootics.

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