

Research Article

Effects of Winter Ticks and Internal Parasites on Moose Survival in Vermont, USA

JACOB DEBOW,^{1,2} Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, 302 Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA

JOSHUA BLOUIN, Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, 302 Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA

ELIAS ROSENBLATT, Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, 302 Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA

CEDRIC ALEXANDER, Vermont Fish and Wildlife Department, 374 Emerson Falls Road, St Johnsbury, VT 05819, USA

KATHERINA GIEDER, Vermont Fish and Wildlife Department, 271 North Main Street, Suite 215, Rutland, VT 05701, USA

WALTER COTTRELL, Vermont Fish and Wildlife Department, 374 Emerson Falls Road, St Johnsbury, VT 05819, USA

JAMES MURDOCH, Wildlife and Fisheries Biology Program, Rubenstein School of Environment and Natural Resources, University of Vermont, 302 Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA

THERESE DONOVAN , U.S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, 302 Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA

ABSTRACT Moose (*Alces alces*) have experienced considerable declines along the periphery of their range in the northeastern United States. In Vermont, the population declined 45% from 2010 to 2017 despite minimal hunter harvest and adequate habitat. Similarly, nearby populations recently experienced epizootics characterized by >50% mortality. Declines have largely been associated with the effects of winter ticks (*Dermacentor albipictus*), but uncertainty exists about the effects of environmental and other parasite-related conditions on moose survival. We examined patterns of moose survival among a radio-collared population ($n = 127$) in Vermont from 2017 to 2019. Our objectives were to estimate causes of mortality and model survival probability as a function of individual and landscape variables for calves (<1 yr) and adults (≥ 1 yr). Observed adult survival was 90% in 2017, 84% in 2018, and 86% in 2019, and winter calf survival was 60% in 2017, 50% in 2018, and 37% in 2019. Winter tick infestation was the primary cause of mortality (91% of calves, 25% of adults), and 32% of all mortalities had evidence of meningeal worm (*Parelaphostrongylus tenuis*). Other sources of mortality such as vehicles, harvest, predation, deep snow, and other parasitic infections were negligible. The best supported calf model included sex differences and negative effects of tick engorgement (%/week) and parasite level (roundworm and lungworm). The best supported adult model included the effect of cumulative tick engorgement (cumulative %/week), which negatively affected survival. Our results indicate that winter tick engorgement strongly affects survival, and is probably compounded by the presence of meningeal worm and other parasites. Reduced tick effects may be achieved by decreasing moose density through harvest and managing late winter habitat to minimize tick density. Management of white-tailed deer (*Odocoileus virginianus*) density may also affect the transmission of meningeal worm. © 2021 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS *Alces alces*, meningeal worm, moose, parasitism, population decline, winter tick.

Moose (*Alces alces*) are an important component of forest ecosystems and occur widely throughout northern North America, Europe, and Asia (Timmermann and Rodgers 2005,

Franzmann and Schwartz 2007). Populations in North America span the majority of Canada and Alaska, and across the northern border of the contiguous United States and into the Rocky Mountains (Franzmann and Schwartz 2007). Populations of moose can also be found throughout the northern New England region of the United States (Maine, New Hampshire, Vermont, and Massachusetts), which represents the southeastern periphery of their North American distribution. Local densities are often positively associated with spruce-fir land cover and land with active timber harvest (DeGraaf and Yamasaki 2001, Lenarz et al. 2009).

Moose play important cultural and ecological roles in New England. Viewing and hunting moose are valuable

Received: 28 September 2020; Accepted: 20 April 2021

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

¹E-mail: Jacob.R.DeBow@wildlife.nh.gov

²Current Address: New Hampshire Fish and Game Department, 629B Main Street, Lancaster, NH 03584, USA

intrinsic and economic activities for local communities (Timmermann and Rodgers 2005). Moose also exert major ecological influences because of their large size and metabolic requirements (Franzmann and Schwartz 2007). They affect ecosystem dynamics directly as an important prey species for top predators and scavengers, and indirectly through their browsing (Wallgren et al. 2013). For example, at high moose densities, over-browsing and excessive bark stripping can affect forest regeneration success enough to influence forest management plans and how commercial forest prescriptions are applied (Timmermann and Rodgers 2005, Wallgren et al. 2013).

The moose population in Vermont is managed as a game species and has experienced large fluctuations in past decades (Vermont Fish and Wildlife Department 2009). Rebounding from extirpation in the early 1900s, moose responded favorably to young forests created through commercial forestry and the absence of large predators during the 1980s and 1990s (Alexander 1993). By 2005, the population had grown to approximately 4,800, higher than ever previously recorded in the state (Vermont Fish and Wildlife Department 2009). Vermont's Fish and Wildlife Department responded to this growth and accompanying conflict by increasing the number of moose hunting permits to slow growth and maintain densities at a level that reflected a balance between their ecological and cultural carrying capacities (C. E. Alexander, personal observation). After reaching an estimated 3,000 moose in 2010, the state reduced the number of permits to maintain its population goal. Despite decreased hunting pressure, the population continued to decline to an estimated 1,665 in 2017, 45% below the target population. Population density at that time in the northeastern part of the state, where the largest number of moose occur, was estimated at 0.39/km² (C. E. Alexander, personal observation). This trend is not unique to Vermont; moose populations decreased throughout New England and in other regions along their southern distribution in North America (Murray et al. 2006; Lankester 2010; Jones et al. 2017, 2019; Timmermann and Rodgers 2017).

Hypotheses explaining this decline vary regionally, but many implicate climate factors (McCann et al. 2013, Jones et al. 2017). Moose are adapted to cold climates, with large body size and thick dark hair evolved for maximum heat retention (Lenarz et al. 2009). High ambient temperature negatively affects moose by decreasing movement and feeding while increasing physiological stress (Lenarz et al. 2009, McCann et al. 2013). These effects are most significant with unusually warm spring temperatures when moose have yet to shed their winter coats (Lenarz et al. 2009, Dou et al. 2013).

Changes in climate, combined with biotic community structure, may also promote increased encounter rates with parasites. Land use change after European colonization and a warming climate permitted expansion of white-tailed deer (*Odocoileus virginianus*) northward (Dawe and Boutin 2016, Weiskopf et al. 2019). Elevated moose densities in New England in the late 1900s increased the encounter rate between moose and deer-associated parasites and pathogens

(Timmermann and Rodgers 2017). Unlike deer, however, moose have yet to develop effective behavioral strategies (e.g., programmed grooming) to limit risks from these parasites (Samuel 2004, 2007; Murray et al. 2006), although post-infection stimulus grooming may reduce winter tick levels on hosts (Addison et al. 2019).

Of the parasites that coexist with deer, meningeal worms (*Parelaphostrongylus tenuis*) and winter ticks (*Dermacentor albipictus*) have the greatest effect on moose (Samuel 2004, Musante et al. 2007, 2010; Lankester 2010; Jones et al. 2017). White-tailed deer are the definitive host of meningeal worm and typically do not succumb to the associated lesions they cause. As a dead-end host, the meningeal worm is thought to be almost always fatal in moose, and can have population-level effects in areas with high deer density (Lankester 2010). A larger concern lies in the winter tick, with recent studies in New Hampshire and Maine concluding winter ticks are the primary cause of mortality for moose in New England (Musante et al. 2007, 2010; Bergeron et al. 2013; Dunfey-Ball 2017; Jones et al. 2017, 2019; Ellingwood et al. 2019), with some moose hosting >50,000/individual (Jones et al. 2019).

Other parasites that affect moose in New England include lungworm, roundworm, nasal bot fly (*Cephenemyia* spp.), large American liver fluke (*Ciolooides magna*), and a variety of tapeworms (primarily *Moniezia* spp.) and *Taenia ovis krabbei* (Franzmann and Schwartz 2007, Jones et al. 2019). These and a variety of other parasites can be found during necropsies or in hunter-harvested animals but are often considered secondary factors to mortality (Musante et al. 2010, Jones et al. 2019).

Even though moose are adapted for long, cold, snowy winters, they can be negatively affected by severe winter weather (Dussault et al. 2005, Lundmark and Ball 2008). Moose are adapted to survive winter in a negative nutritional balance, metabolizing stored fat to compensate for a low-protein diet (Franzmann and Schwartz 2007, Ellingwood et al. 2019). As that fat store begins to diminish in late winter, moose rely heavily on the nutritious forage that emerges with the onset of spring (Schwartz 1992). In the case of a long and high snowfall winter, spring vegetation growth can be delayed and energetic expenditures exceed forage inputs (Franzmann and Schwartz 2007). This can cause direct mortality to moose, especially in younger age classes and smaller individuals (Ellingwood et al. 2019). When paired with the energy expense associated with winter tick infestations, individuals can become weak and succumb more quickly (Ellingwood et al. 2019).

Finally, anthropogenic sources of mortality may also be a factor contributing to moose mortality in Vermont and the northeastern United States. Moose avoid highly humanized areas because of decreases in moose habitat associated with landscape development (Wattles and DeStefano 2011). The most notable form of direct mortality is vehicle collisions as moose often congregate in the spring at salt licks, which are roadside pools of water that concentrate sodium chloride used on roadways during winter to melt snow and ice (Leblond et al. 2009,

Danks and Porter 2010). Moose, like other cervids, require salt in the spring and are attracted to these concentrated pools (Leblond et al. 2009). Congregations of moose on roadways during low-light hours, paired with their dark silhouette, makes them especially susceptible to vehicle collisions (Leblond et al. 2009).

The recent and continuing decline of moose in Vermont presents a significant management challenge for agencies charged with maintaining viable populations. Populations in nearby regions have experienced periodic epizootics (>50% parasite-induced mortality) in the 9–12-month age group, which lends urgency to understanding factors associated with these declines (Musante et al. 2010, Bergeron et al. 2013, Jones 2016). As an animal with a relatively low reproductive rate, moose may be more susceptible to cumulative effects from consecutive epizootics that cause large-scale mortality of the juvenile age class (Musante et al. 2007). Occurrence of large-scale mortality, paired with the life-history characteristics of moose, could lead to extirpation of moose from Vermont if current trends continue.

We examined survival patterns of radio-collared moose in Vermont to better understand declines and provide information to resource managers. Survival characteristics are well studied in New Hampshire and Maine, but little demographic information exists on the population in Vermont, which is characterized by different habitat conditions and is important for regional connectivity, especially with Canada (Krester and Glennon 2011). The objectives of our study were to assess the health of radio-collared moose at time of capture, determine causes of mortality by monitoring and following the fates of the marked population, and estimate survival probability for calf and adult age classes while accounting for the effects of temporal and individual covariates.

STUDY AREA

We conducted the study in northeastern Vermont from 2017–2019 (Fig. 1). The study area was composed of 2 state wildlife management units (WMU), E1 and E2, where moose density was consistently higher ($\sim 0.39/\text{km}^2$) than other regions in the state (Fig. 1; Vermont Fish and Wildlife Department 2009). The study area was 1,738 km^2 , ranged from roughly 240 m to 1,015 m in elevation, occurred mostly within Essex County, and encompassed 21 towns. Boundaries of the study area were United States Route 2 north to the Canadian border and Vermont Route 114 east to the Connecticut River. Vermont Route 105 separated WMU E1 and E2 with E1 to the north and E2 to the south (Fig. 1).

The study area largely consisted of northern hardwoods, including yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and beech (*Fagus grandifolia*) in mid and higher elevations, and red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) on elevated peaks. Lowlands and wet areas were primarily composed of black spruce (*Picea mariana*) and speckled alder (*Alnus incana*). A mosaic of forest age classes were present throughout the study area as a result of differing forest management approaches on public and

private ownership. During this study approximately 30% was conserved in federal- or state-managed forests and saw little timber harvest, and approximately 45% was owned by private companies that actively harvested timber. Potential predators included coyote (*Canis latrans*) and black bear (*Ursus americanus*). White-tailed deer are the only co-existing ungulate, and their densities fluctuate throughout the study area but were estimated at 1.93–3.86 deer/ km^2 in 2020 (Vermont Fish and Wildlife Department 2021).

The study area had 4 distinct seasons: summer (Jun–Aug), fall (Sep–Nov), winter (Dec–Feb), and spring (Mar–May). Summer temperatures can reach 32°C in the study area, with annual temperature averaging 11°C (National Climate Data Center 2019). Annual precipitation typically ranges from 100–110 cm/year (National Climate Data Center 2019). Average snowfall totals range between 220 cm and 250 cm annually (National Climate Data Center 2019) and can vary considerably with elevation.

METHODS

Capture and Health Assessment

Over a period of 3–6 days in January of 2017, 2018, and 2019, we affixed radio-collars to a sample population of adult females (≥ 1 yr old), and female and male calves (<1 yr old). Capture was mainly by aerial net-gunning via helicopter and physical restraint, and by aerial darting in rare circumstances where netting was unsafe and posed a considerable risk to the target individual (Musante et al. 2010, Jones et al. 2017).

Native Range Capture Services (NRCS, Elko, NV, USA) conducted all moose captures. They attached ear tags with a unique identifying number (Global Large Female, Allflex USA, TX, USA) to each moose. Additionally, they fitted each moose with a Survey Globalstar V7.1 GPS collar (VECTRONIC Aerospace GmbH, Berlin, Germany) equipped with a very high frequency beacon that operated from 0600 to 1800, and a global positioning system (GPS) sensor that transmitted a GPS location every 13 hours. Locations were sent daily to a server and accessed remotely through the program GPS Plus X (VECTRONIC Aerospace GmbH). Collars on females weighed approximately 0.85 kg and those on males weighed approximately 0.90 kg. Each radio-collar was equipped with a mortality switch that triggered when collars were immobile for 5 consecutive hours. Calf collars had expandable collar webbing to accommodate growth. Animal capture and handling followed guidelines of the American Society of Mammalogists (Sikes et al. 2016) and all protocols were reviewed and approved by the University of Vermont Institutional Animal Care and Use Committee (protocol 17-035).

Capture crews collected biological samples and physical measurements to gauge individual condition. These included feces, hair, winter ticks, and 30 ml of blood from each captured moose. We also counted all ticks that intersected 4 10-cm transects on the shoulder and rump ($n = 8$ total transects) and used the sum of counts as an index of

total ticks on each animal. Capture crews collected a sample of feces from the rectum of each individual to screen for internal parasites. Laboratory technicians used the McMaster flotation technique to determine the presence of the egg stage of tapeworms (*Moniezia* spp.), roundworms (*Nematodirus* spp.), protozoans (Family Coccidia), and strongyles (Family Strongylidae) and abundance of lungworms (*Dictyocaulus* spp.; University of Maine Animal Health Laboratory, Orono, Maine, USA). Capture crews weighed calves using a net and crane scale system suspended from the cargo hook of the capture helicopter. We used the Welch 2-sample *t* statistic to compare average weight and tick load between age and sex groups.

Cause of Mortality

For collared animals that died, we conducted field necropsies generally within 24 hours of death to determine the cause of mortality. We grouped deceased animals into 2 age classes: calf and adult. Age classes were separated by birthday, with calves collared in January of each year moving into the adult age class on 18 May (observed mean calving date) of that same year. Thus, we measured calf mortality in the winter of their first year (1 Jan–18 May) and adult mortality annually (1 Jan–31 Dec). We classified yearlings as adults.

Necropsy protocols followed standard procedures and an approach used in New Hampshire and Maine (Jones 2016).

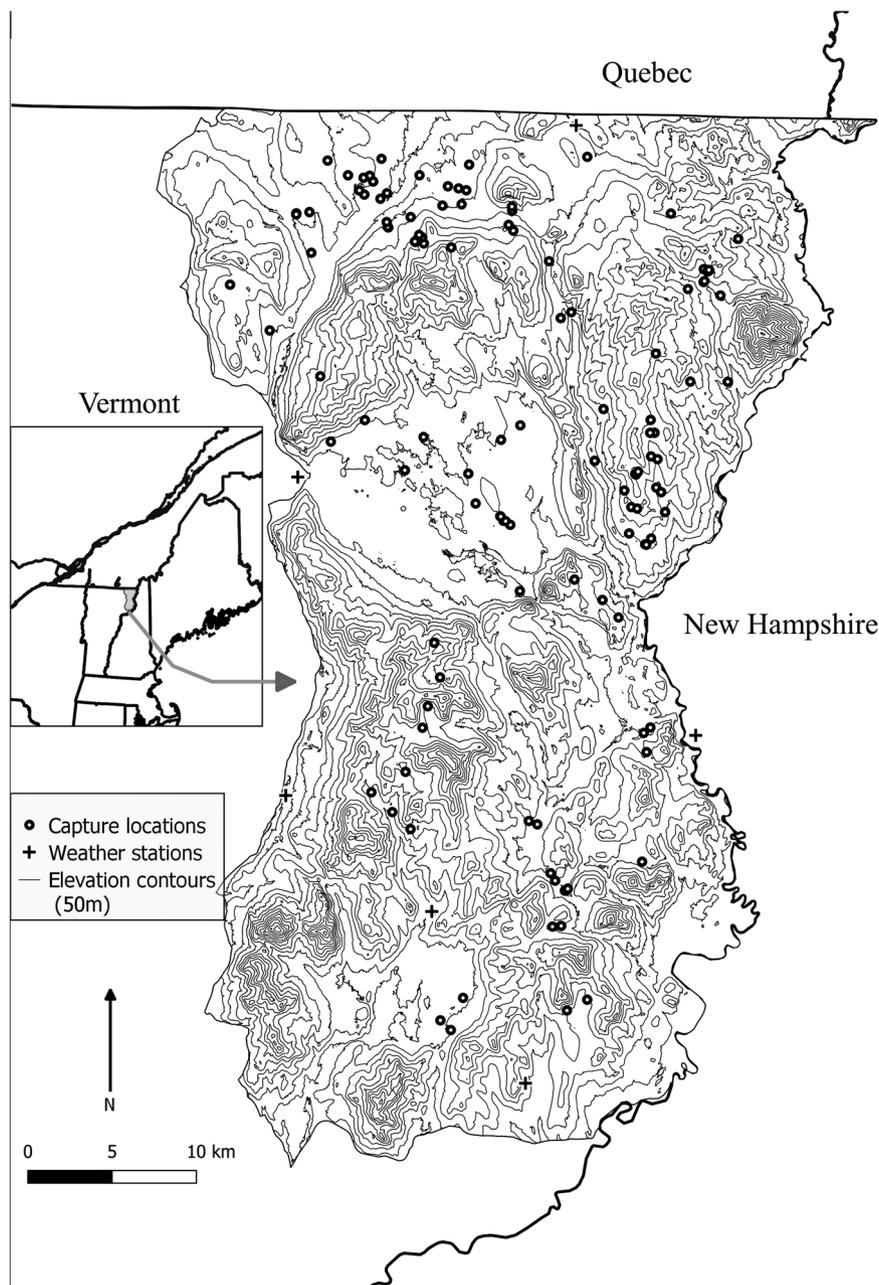


Figure 1. Study area (1,738 km²) for assessing moose survival (2017–2019) in northeastern Vermont, USA. The northern boundary adjoins Quebec, Canada and the eastern boundary adjoins New Hampshire, USA. Black circles represent the capture locations of radio-collared animals. Crosses represent locations of weather stations.

Table 1. Covariates used to explain survival probability in moose in northeastern Vermont, USA, 2017–2019, based on data from 127 radio-collared animals. Covariates included those that were hypothesized to affect individuals and the broader population.

Type	Covariate name	Description	Measure	Predicted effect on survival	Data source	Reference	
Temporal	Snow depth	Average resting snow depth per specified time period (week, month, season, year)	depth in cm	–	NCDC ^a	Dunfy-Ball (2017)	
	Maximum temperature	Average maximum temperature per specified time period (week, month, season, year)	°C	–	NCDC	McCann et al. (2013)	
Individual	Days with snow >70 cm	Number of days resting snow was >70 cm per specified time period (week, month, season, year)	depth in cm	–	NLCD ^b	Franzmann and Schwartz (2007)	
	Engorgement period	% of ticks on a moose in female engorged adult stage throughout time	%	–	Drew and Samuel (1989)	Musante et al. (2007)	
	Cumulative engorgement period	Compounding effect of engorgement period. Adds the % of engorged females on an animal to the week prior through time.	%	–	Drew and Samuel (1989)	Musante et al. (2007)	
	Week	Week of the year	week	–	field data	Jones (2016)	
	Month	Month of the year	month	–	field data	Jones (2016)	
	Age	Age class of individual: calf (<1 yr), and adult (>1 yr)	calf, adult	+	field data	Franzmann and Schwartz (2007)	
	Sex	Sex of individual	female, male	–	field data	Franzmann and Schwartz (2007)	
	Year captured	Year animal was captured	year	+	field data	Jones (2016)	
	Tick count at capture	Number of ticks per tick count at capture (4 × 10-cm transects on rump and shoulder)	year ticks	–	field data	Jones (2016)	
	Weight of calf at capture	Weight of individual calves at capture	kg	+	field data	Jones (2016)	
Rasters	Lungworm	McMaster flotation technique used for fecal parasitology. Covariate represents exact number of lungworm eggs found per 5 g of dried weight feces	eggs/5 g	–	field data	Franzmann and Schwartz (2007)	
	Tapeworm	McMaster flotation technique used for fecal parasitology. Covariate represents presence or absence of tapeworm eggs in fecal float	present, absent	–	field data	Franzmann and Schwartz (2007)	
	Roundworm	McMaster flotation technique used for fecal parasitology. Covariate represents presence or absence of roundworm eggs in fecal float	present, absent	–	field data	Franzmann and Schwartz (2007)	
	Evergreen	Areas where >75% of tree species >5 m maintain their leaves year-round	%	+	NLCD	Franzmann and Schwartz (2007)	
	Mixed	Areas where neither deciduous nor evergreen species are >75% of total tree cover	%	+	NLCD	Franzmann and Schwartz (2007)	
	Developed - all	All developed layers combined. Included open, low, medium, and high development. Encompasses all paved roads and buildings	%	–	NLCD	Franzmann and Schwartz (2007)	
	Deer probability of occurrence	Mean probability of deer occurrence within an individual's home range	probability	–	Pearman-Gillman et al. (2020)	Alexander (1993)	
	Snowmobile trails	% of an individual's home range occupied by snowmobile trails	%	–	VCGI ^c	Lankester (2010)	
							Colescott and Gillingham (1998)

^a 2019 National Climate Data Center.

^b 2019 National Land Cover Data.

^c Vermont Center for Geographic Information.

We began with an external exam that included documenting body condition, presence or absence of external lesions, color of all mucous membranes (nostrils, conjunctiva, oral, and vaginal), hair loss, and number of winter ticks (following the same protocol from capture). We then collected tissue samples from the auxiliary lymph node, diaphragm, heart, lung, liver, kidney, spleen, pancreas, rumen, abomasum, spinal cord (dorsal, thoracic, lumbar), femur bone marrow, and brain. We also collected a central incisor from individuals >1 year of age for cementum annuli analysis to determine exact age (Sergeant and Pimlott 1959). We fixed tissue samples in 10% buffered formalin (10:1 formalin to tissue ratio) for pathological analysis at the New Hampshire Veterinary Diagnostic Laboratory (Durham, NH, USA).

We determined the primary cause or causes of mortality for each animal that died based on field observation and pathological results. Pathologists often assigned multiple variables to the final cause of death. Therefore, we grouped cause of death into the 3 most common mortality types: winter tick, meningeal worm, and other. Many animals fit into multiple categories (e.g., tick-induced mortality with meningeal worm lesions present) and thus had >1 cause of death. We diagnosed tick-induced mortality using field observations such as high tick counts, severe weight loss, hair loss, and emaciation. Histopathologic findings of serous atrophy of fat consistent with emaciation confirmed the contribution to the diagnosis (Musante et al. 2007, New Hampshire Veterinary Diagnostic Laboratory 2019). Pathologists diagnosed mortality due to meningeal worm based on observations of the parasite or cellular evidence of infection within the brain or spinal cord tissue (New Hampshire Veterinary Diagnostic Laboratory 2019). Pathologists recorded presence of adult nematodes (lungworm) during gross or histopathologic examination of lung tissue, and associated inflammation consistent with parasitic pneumonia when it occurred.

The other mortality class included uncommon forms of mortality such as motor vehicle collisions, natural mortality, and unknown causes. We identified road kill moose by firsthand accounts (driver, observer, or police records), deceased moose on the side of the road that displayed physical trauma, or presence of an accident scene (i.e., blood and broken pieces of vehicle; Del Frate and Spraker 1991). Natural mortality included, but was not limited to, deep snow, predation, legal hunter harvest, and rare or uncommon pathological diseases. Mortalities classified as unknown were often a product of compromised tissue samples. This occurred when scavengers found a carcass before we performed the necropsy, or a mortality beacon did not alert investigators at the time of death, extending the post-mortem interval and allowing natural decomposition to begin before we could sample an individual.

Survival by Age Class

We estimated weekly survival rates of calves and monthly survival rates of adults using a known fates modeling approach (Kaplan and Meier 1958, Pollock et al. 1989), following methods similar to those applied in studies of moose

in New Hampshire and Maine (Musante et al. 2010, Jones 2016). The known fates analysis allowed for staggered entry of individuals into the analysis as subsequent captures occurred and the censoring of individuals due to collar malfunctions and missing animals (Pollock et al. 1989). Assumptions of this model include 1) radio-collared individuals are representative of the population, 2) survival rates among individuals are independent, 3) correct fates are known, 4) fate is independent of censoring, and 5) radio-collars do not affect survival (Pollock et al. 1989).

We created encounter histories from radio-collar signals to estimate survival rates. For example, a weekly history of 1111110 in a given year indicated that a calf was alive (1) during the first week of capture, transmitted a signal for 5 additional weeks, and then died or experienced collar failure (0). We converted histories to live-dead format for the known fates analysis (White and Burnham 1999).

We evaluated the influence of temporal and individual covariates on moose survival (Table 1). Temporal covariates affected the moose population as a whole through time and included measures of weather severity. We compiled maximum summer temperature and snow depth at weekly and monthly time periods from the National Oceanic Atmospheric Administration (NOAA; National Climate Data Center 2019). We also examined number of days snow was >70 cm because this depth impedes moose movement (Franzmann and Schwartz 2007). We compiled data for each measurement and averaged data from 6 weather stations across the study area (Fig. 1; National Climate Data Center 2019). Weather stations represented relative changes to climactic variables throughout the study area and did not depict various microclimates associated with elevation and sun exposure.

We also quantified the effect of the winter tick life cycle on moose as a temporal variable. Drew and Samuel (1989) intentionally infected moose with winter ticks to document the proportion of adult males, non-engorged females, and engorged females on a moose in any given week (Fig. 2). Compared to adult females, the nymph stage and adult

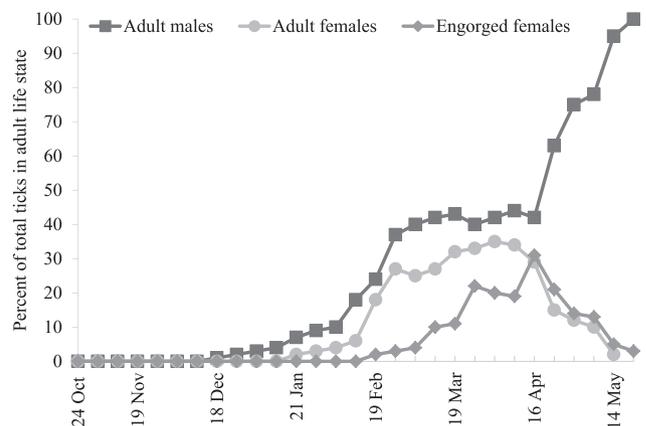


Figure 2. Percentage of winter ticks in varying adult life stages by week (24 Oct–15 May) as counted on intentionally infected moose in Alberta, Canada (Drew and Samuel 1989). In any given week, the percent of the total number of ticks/moose was calculated for adult male, non-engorged adult females, and engorged adult females.

males consume a negligible blood meal (Musante et al. 2007). An adult female winter tick consumes 1.70–2.55 g (Addison et al. 1998) of blood during its last life stage, and becomes engorged. This feeding varies over time and concentrates during an 8-week period from early March until all females (engorged or not) have disengaged from the animal (Drew and Samuel 1989, Musante et al. 2007). We used the weekly percentage of the total tick load composed of engorged adult females (i.e., engorgement period), as measured by Drew and Samuel (1989), to quantify the temporal effect of ticks on moose (Drew and Samuel 1989, Addison et al. 1998, Musante et al. 2007). Furthermore, we quantified the cumulative proportion of feeding adult female ticks for each week to capture the cumulative effect of sustained, large blood meals by this age class (Table 1). Both engorgement period and cumulative engorgement period

were variables that we assumed affected the moose population as a whole. To incorporate these effects by individual, we multiplied each individual's ticks at capture by engorgement period (designated as tick : engorgement period). Similarly, we created the tick : cumulative engorgement period covariate by multiplying tick counts at capture by the cumulative engorgement period. These variables thus expressed an index of tick effects over time for each individual moose. We assumed the temporal patterns of winter tick engorgement and detachment expressed in Drew and Samuel (1989) held for adults and calves in our region.

Individual covariates that may affect an animal's probability of survival included sex, year of capture, tick count at capture, weight at capture, and home range characteristics. Home range land cover covariates included percentage of evergreen, mixed, and development (primarily roads) within

Table 2. Age-specific models used to describe weekly moose survival probability (S) of calves (<1 yr) and monthly survival probability of adults (≥1 yr) for 127 radio-collared moose in northeastern Vermont, USA, 2017–2019. For each age class, we interpreted univariate models first to create a final model set. * indicates a model included in the final model set.

Age class	Hypothesis	Model structure	Variables
Both	*Null	S(~1)	Intercept
Calf	*Sex	S(~sex)	Sex
Both	Year	S(~year)	Year captured
Calf	Weight	S(~weight)	Weight of calf at capture
Both	Tick count at capture	S(~tick)	Individual tick counts from capture
Both	*Lungworm in fecal	S(~lungworm)	Lungworm eggs in fecal matter
Both	Tapeworm in fecal	S(~tapeworm)	Tapeworm presence in fecal matter
Both	*Roundworm in fecal	S(~roundworm)	Roundworm presence in fecal matter
Both	Evergreen winter cover (winter home range)	S(~evergreen)	% home range composed of evergreen
Both	Mixed winter cover (winter home range)	S(~mixed)	% home range composed of mixed
Both	Developed within home range (anthropogenic threats)	S(~developed)	% home range developed. Includes developed land and paved roadways
Both	Snowmobile trails	S(~snowmobile)	% home range occupied by snowmobile trails
Both	Meningeal worm potential	S(~deer)	Probability of occurrence of white-tailed deer
Both	Winter snow depth	S(~snow depth)	Average weekly or monthly snow depth throughout winter
Both	Days with snow >70 cm	S(~over 70 cm)	Average days/week or month snow depths were >70 cm
Both	*Female winter tick engorgement period (engorged female)	S(~engorgement period)	Weekly % of tick load composed of adult females throughout feeding cycle
Both	*Cumulative engorgement	S(~cumulative engorgement)	Compounding effect of engorgement period.
Calf	*Week through winter	S(~week)	Week of winter 1 Jan–18 May
Adult	Month throughout the year	S(~month)	Month of the year (1–12)
Adult	Heat stress	S(~heat)	Average monthly max. temperature
Both	*Tick load effect on engorgement	S(~tick × engorgement period)	Weighted effect of % adult winter ticks on the number of ticks at capture
Calf	*Tick load effect on cumulative engorgement	S(~tick × cumulative engorgement)	Weighted effect of cumulative % adult winter ticks on the number of ticks at capture
Calf	*Winter tick and individual sex	S(~engorgement period + sex)	Female winter tick engorgement period + individual sex
Calf	*Winter tick and internal parasites	S(~engorgement period + roundworm + lungworm)	Female winter tick engorgement period + internal parasites
Calf	*Winter tick, internal parasites, and sex	S(~engorgement period + roundworm + sex + lungworm)	Female winter tick engorgement period + internal parasites + individual sex
Calf	*Cumulative winter tick effect and individual sex	S(~cumulative engorgement + sex)	Cumulative female winter tick engorgement period + individual sex
Calf	*Cumulative winter tick effect and internal parasites	S(~cumulative engorgement + roundworm + lungworm)	Cumulative female winter tick engorgement period + internal parasites
Calf	*Cumulative winter tick effect, internal parasites, and sex	S(~cumulative engorgement + roundworm + sex + lungworm)	Cumulative female winter tick engorgement period + internal parasites + individual sex

Table 3. Summary of moose captured in northeastern Vermont, USA, during January of 2017, 2018, and 2019. We captured females exclusively for the adult age class (≥ 1 yr old), whereas we captured calves (< 1 yr old) indiscriminate of sex.

Year	Adult	Calf		Total
		Female	Male	
2017	31	14	16	61
2018	6	9	21	36
2019	0	15	15	30
Total	37	38	52	127

home range boundaries (Table 1). We estimated individual home ranges from radio-collar locations as 95% fixed kernels (Worton 1989) with the R package *adehabitatHR* (Calenge 2006). For each home range, we compiled spatial information from the 2016 National Land Cover Dataset (NLCD; Dewitz, 2019) by clipping the nationwide base map to the extent of our study area and extracting all relevant rasters (Table 1). Extracted rasters contained a binary representation of a single land cover class at the 30×30 -m scale to be used in home range statistics. We also estimated the proportion of each home range consisting of snowmobile trails (Colescott and Gillingham 1998) and the potential overlap with deer as the average deer probability of occurrence based on a model developed by Pearman-Gillman et al. (2020).

We developed an *a priori* set of candidate models that explored a variety of hypotheses related to the effects of temporal and individual covariates on survival (Table 2). We split candidate models into 2 distinct model sets: calf age class and adult age class (Musante et al. 2010, Jones 2016). For each age class, we first evaluated univariate models as a

preliminary analysis. We then developed a final model set for each age class that included any variables from the preliminary analysis that significantly affected survival (i.e., coefficients with 95% CIs that did not cross zero) and whose effects were ecologically meaningful (i.e., coefficients in the hypothesized direction for moose survival). We included univariate and additive models in the final model set for each age class.

Calves.—We estimated weekly calf survivorship from the time of capture (early Jan) until 18 May. We considered multiple univariate hypotheses for survival, including the null model where survivorship was constant for all calves, a sex model in which survivorship was estimated separately for male and female calves, and a year model in which survivorship was estimated uniquely for each year of the study (Table 2). We assessed several univariate hypotheses based on information at capture, including the weight of an individual calf and relative tick load based on tick counts. We derived univariate hypotheses related to internal parasite load (Table 2) from results of fecal floatation counts of samples taken at capture and variables included both quantitative measurements and presence-absence counts of ova of lungworms, tapeworms, and roundworms (Franzmann and Schwartz 2007, Musante et al. 2007).

Other hypotheses related to the home range characteristics of each calf (1 Jan–18 May). The winter home range hypotheses (Table 2) considered the amount of mixed and evergreen forest within the individual's home range; these land cover types provide important cover and forage for calves during winter months (Rempel et al. 1997). The anthropogenic threats hypotheses (Table 2) evaluated the proportion of an individual's home range composed of developed areas

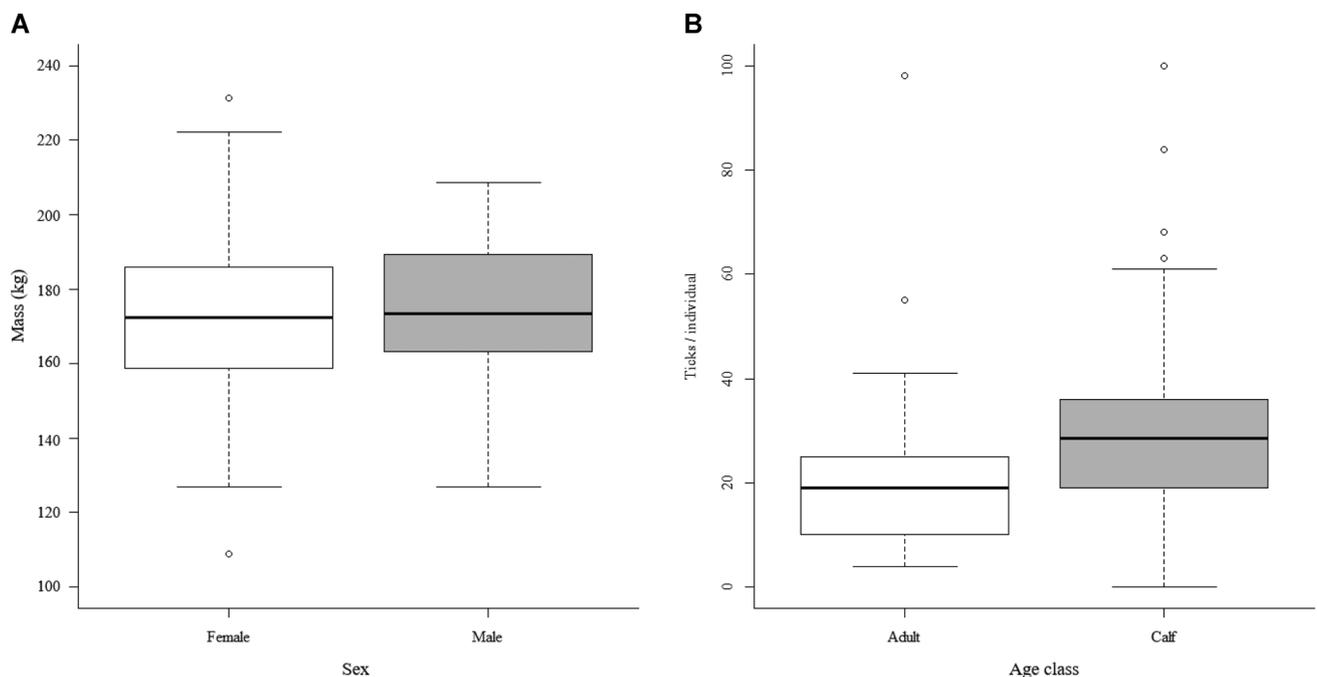


Figure 3. Box plots of the health summary of moose monitored in northeastern Vermont, USA, January 2017, 2018, and 2019. A) Average mass of calves by sex at capture. B) Distribution of average winter tick count at capture (number of ticks counted/cumulative 80 cm of transects on the moose) by age class. The adult age class (≥ 1 yr old) is represented solely by females. Sex of captured calves (< 1 yr old) was unbiased.

Table 4. Percent of moose monitored in northeastern Vermont, USA, with tapeworm, lungworm, roundworm, coccidia, and strongyles by age class and year. We used a modified McMaster flotation technique on feces collected at time of capture to identify the presence of each parasite. All captures occurred in January of 2017, 2018, and 2019. We did not capture or sample adult females in 2019.

Age	Year	Tapeworm		Lungworm		Parasitic roundworm		Coccidia		Strongyles	
		%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Adult	2017	0	0	23	7	10	3	0	0	7	2
	2018	0	0	17	1	17	1	0	0	0	0
Calf	2017	23	7	73	22	27	8	0	0	0	0
	2018	50	15	73	22	40	12	0	0	0	0
	2019	13	4	63	19	27	8	0	0	0	0
Total	Adult	0	0	22	8	11	4	0	0	6	2
	Calf	29	26	70	63	31	28	0	0	0	0
	Both	21	26	56	71	25	32	0	0	2	2

(including all paved roads) and snowmobile trails (Colescott and Gillingham 1998, DeGraaf and Yamasaki 2001). The meningeal worm potential hypothesis estimated the risk of infection and disease of meningeal worm transmitted from deer within each individual's home range.

The remaining univariate hypotheses considered temporal variables that affected the calf population as a whole (Table 2). We evaluated 2 hypotheses related to snow conditions including average weekly snow depths and number of days snow was >70 cm throughout the winter (McRoberts et al. 1995, Franzmann and Schwartz 2007, National Climate Data Center 2019). The engorgement period hypothesis used data from Drew and Samuel (1989; Fig. 2) to model weekly survival rate as the expected percentage of an individual's winter tick load that was composed of engorged females (Drew and Samuel 1989, Musante et al. 2007). The cumulative engorgement period hypothesis added prior weeks' percent engorged female winter ticks to the current week's value (Samuel 2004) to evaluate the effect of previous and current feeding on moose by adult female ticks. We further evaluated if these engorgement effects were magnified by the individual covariate, ticks at capture (tick : engorgement period and tick : cumulative engorgement period). Lastly, the week hypothesis considered the week number of the winter as a linear relationship (Jones 2016), with 1 January being the start of week 1.

Adults.—We estimated monthly adult survival probability from the time they entered adulthood (age ≥ 1) until death. We applied all capture, home range, and temporal covariates used for the univariate calf models to adults with the exception that the temporal interval was 1 month in duration. Additionally, we measured the effect of temperature using the average maximum monthly temperature because temperatures above 20°C are known to have negative effects on moose (Renecker and Hudson 1986, 1990; McCann et al. 2013).

We assessed each model using the known fates modeling approach with the R package RMark (Laake et al. 2013). For each age class, we used model selection techniques to evaluate the relative support of each model and determine the best model in the set. We ranked models using Akaike's Information Criterion adjusted for small sample size (AIC_c), and considered models with $\Delta AIC_c < 2$ to have strong empirical support (Burnham and Anderson 2002). We performed all analyses in R (R Core Team 2017).

RESULTS

We captured 37 adults and 90 calves (each ~8 months old at time of capture; Table 3). The sex ratio of calves was equal (50%) in 2017 and 2019, but strongly skewed towards males in 2018 by chance (70% male; Table 3).

Table 5. Observed moose survivorship and cause of mortality by year and age class of radio-collared moose in northeastern Vermont, USA, 2017–2019. Histopathology assigned >1 primary cause of mortality in some cases; therefore, an animal may be represented more than once in the cause of death column (e.g., a calf moose could succumb to winter ticks but also have lesions associated with meningeal worm present at time of death). We did not remove dropped collars from the total number of individuals when calculating observed survivorship because collars dropped after the respective survivorship monitoring period.

Year	Age	Number	Dropped collars	Deaths	Observed survivorship (%)	Cause of death							
						Winter tick		Meningeal worm		Other		Lungworm present	
						<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
2017	Adult	31	1	3	90	2		1		0		1	
	Calf	30	0	12	60	10		4		0		9	
2018	Adult	51	3	7	86	0		1		6		1	
	Calf	30	6	15	50	13		6		4		9	
2019	Adult	50	3	6	88	2		3		3		3	
	Calf	30	2	19	37	19		5		2		16	
Total	Adult	73	7	16	78	4	25	5	31	9	56	5	31
	Calf	90	8	46	49	42	9	15	33	6	13	34	74
	All	127	15	62	51	46	74	20	32	15	24	39	63

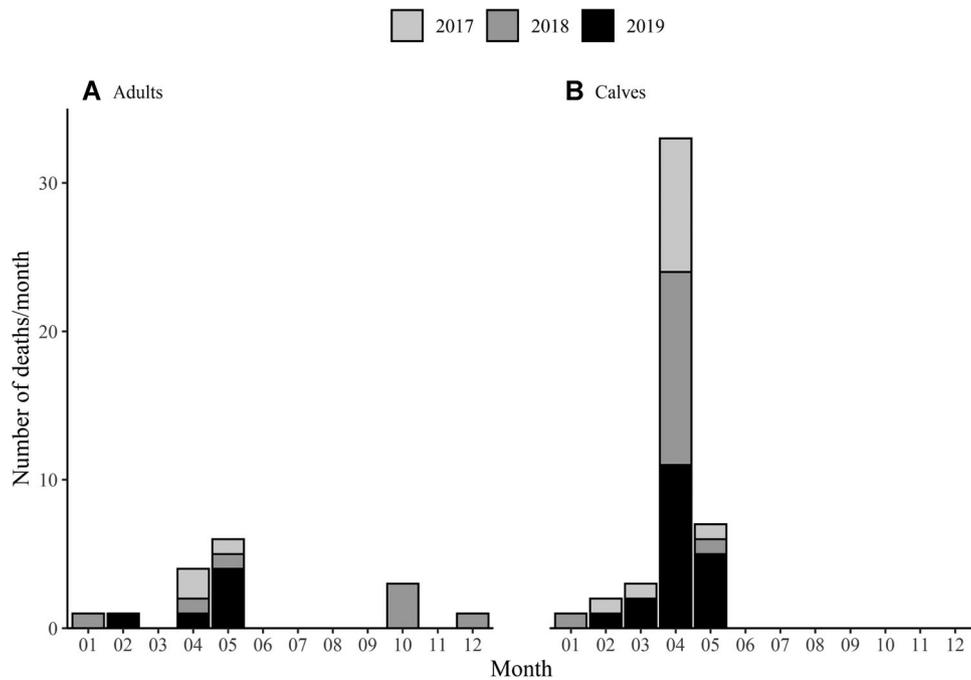


Figure 4. Number of mortalities by month (2017–2019) in adult (≥ 1 yr old; A) and calf (< 1 yr old; B) radio-collared moose in northeastern Vermont, USA. January is represented by month 01, and December is represented by month 12.

Table 6. Univariate known fates model selection results for weekly calf (< 1 yr old) survival (S; mid-Jan to 18 May) for radio-collared moose in northeastern Vermont, USA, 2017–2019. Covariates consisted of individual, home range, and temporal variables; AIC_c is Akaike's Information Criterion, corrected for small sample size. An asterisk indicates a model with low variability among individuals and highly uncertain parameter estimates.

Model	AIC_c	ΔAIC_c	Weight	Parameter	Beta estimate	SE	Lower 95% CI	Upper 95% CI
S(~engagement period)	348.45	0.00	0.996	Intercept	5.0463	0.3480	4.3642	5.7283
				Covariate	-0.1142	0.0162	-0.1459	-0.0825
S(~cumulative engagement)	360.45	12.00	0.002	Intercept	4.6299	0.3021	4.0377	5.2220
				Covariate	-0.0151	0.0024	-0.0198	-0.0105
S(~week)	363.40	14.95	0.001	Intercept	5.9877	0.5324	4.9441	7.0313
				Covariate	-0.2034	0.0347	-0.2713	-0.1355
S(~snow depth)	363.66	15.21	0.000	Intercept	2.3317	0.1963	1.9469	2.7165
				Covariate	0.0056	0.0010	0.0036	0.0076
S(~tick : engagement period)	374.17	25.72	0.000	Intercept	4.1206	0.2188	3.6917	4.5496
				Covariate	-0.0018	0.0003	-0.0023	-0.0012
S(~tick : cumulative engagement)	377.60	29.15	0.000	Intercept	4.0082	0.2073	3.6019	4.4144
				Covariate	-0.0003	0.0000	-0.0004	-0.0002
S(~snow over 70 cm)	397.92	49.47	0.000	Intercept	3.2077	0.1655	2.8832	3.5321
				Covariate	0.5234	0.2247	0.0831	0.9637
S(~roundworm)	399.23	50.78	0.000	Intercept	3.7223	0.2024	3.3256	4.1190
				Covariate	-0.7858	0.3060	-1.3855	-0.1861
S(~developed)*	399.89	51.44	0.000	Intercept				
S(~sex)	400.74	52.29	0.000	Intercept	3.8887	0.2802	3.3395	4.4378
				Covariate	-0.7003	0.3332	-1.3534	-0.0471
S(~lungworm)	402.30	53.85	0.000	Intercept	3.5803	0.1729	3.2414	3.9193
				Covariate	-0.0105	0.0052	-0.0208	-0.0003
S(~1)	403.51	55.06	0.000	Intercept	3.4454	0.1514	3.1486	3.7422
S(~year)	403.65	55.20	0.000	Intercept	3.7159	0.2626	3.2011	4.2307
				Covariate	-0.2526	0.1865	-0.6181	0.1129
S(~weight)	403.82	55.37	0.000	Intercept	1.8204	1.2358	-0.6017	4.2426
				Covariate	0.0043	0.0033	-0.0021	0.0107
S(~tick)	404.94	56.49	0.000	Intercept	3.6448	0.3054	3.0462	4.2435
				Covariate	-0.0066	0.0085	-0.0234	0.0101
S(~tapeworm)	405.34	56.89	0.000	Intercept	3.4062	0.1769	3.0594	3.7530
				Covariate	0.1395	0.3421	-0.5310	0.8101
S(~evergreen)	405.36	56.91	0.000	Intercept	3.5551	0.3218	2.9243	4.1858
				Covariate	-0.9110	2.3242	-5.4664	3.6444
S(~deer)	405.48	57.03	0.000	Intercept	5.1502	9.8590	-14.1734	24.4738
				Covariate	-1.9111	11.0484	-23.5658	19.7437
S(~snowmobile)	405.49	57.04	0.000	Intercept	3.4045	0.3034	2.8097	3.9992
				Covariate	3.0175	19.5087	-35.2196	41.2546

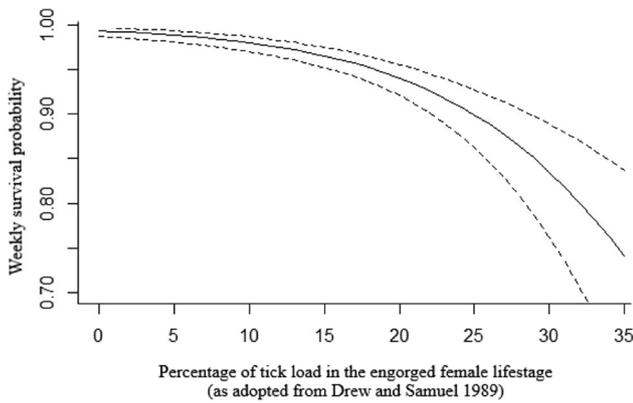


Figure 5. Weekly moose calf survival (<1 yr old \pm 95% CIs) as a function of the percentage of female winter tick load in the engorgement life stage in northeastern Vermont, USA, 2017–2019.

Health Assessment at Capture

We weighed 84 of the 90 calves captured (93%). We did not weigh some calves because of conditions that prevented the helicopter from safely hovering directly over the animal. Body weights ranged from 109–231 kg; median weight of all calves was 172.8 kg (Fig. 3A). Weight did not vary between sexes (Welch 2-sample t statistic = -0.62 , $df = 63$, $P = 0.5405$). Males ($n = 52$) ranged from 127–209 kg, with a median weight of 173.3 kg. Females ($n = 38$) ranged from 109–231 kg, with a median weight of 172.4 kg (Fig. 3A).

Tick count indices on all moose captured ranged from 0 to 100, with a median index of 25 ticks (Fig. 3B). Tick indices on adult moose ranged from 4–98 ticks, with a median index of 19.0. Calves had higher tick counts than adults (Welch 2-sample t statistic = -2.67 , $df = 68$, $P = 0.0093$), ranging from 0–100, with a median index of 28.5 (Fig. 3B). Within the calf age class, average ticks per animal did not vary by sex (Welch 2-sample t statistic = 0.08 , $df = 82$, $P = 0.9389$).

One or more of the 5 parasites measured with the modified McMaster flotation technique were present in 68% (86 of 126) of all moose tested. Coccidia and strongyles showed little to no presence in either age class (adult or calf) over the 3-year period (Table 4). Tapeworms appeared only in calves and were present in 29% (26 of 90) of calves. Parasitic roundworms were in low concentrations of both age classes across all capture years. Lungworm was the most prevalent

parasite and detected in 22% of adults and 70% of calves (Table 4).

Cause of Mortality

Observed annual winter calf survival was 60% (18 of 30) in 2017, 50% (15 of 30) in 2018, and 37% (11 of 30) in 2019. Overall observed calf survival across all 3 years was 49% (44 of 90); 8 calves and 7 adults dropped their collars and were censored in subsequent years (Table 5). Observed annual adult survival was 90% (27 of 30) in 2017, 86% (44 of 51) in 2018, and 88% (44 of 50) in 2019 (Table 5). Over the duration of the study, we recorded only 3 yearling mortalities (included in adult survival rates).

Mortalities were concentrated in the early spring each year of the study (Fig. 4). The average mortality date was 18 April for calves (mode = 20 Apr) and 9 May (mode = 07 May) for adults (Fig. 4). Over the 3-year study, winter ticks were associated with 74% of all mortalities (91% of calves and 25% of adults; Table 5). Lesions associated with meningeal worm were found in 33% of calves, 31% of adults, and 32% of all mortalities. Lastly, causes of death described by the other category comprised 24% of all mortalities and included lungworm infection ($n = 3$), septicemia ($n = 3$), unknown ($n = 3$), vehicular mortality ($n = 1$), legal hunter harvest ($n = 1$), linear necrosis ($n = 1$), deep snow ($n = 1$), and a rare protozoal parasitic encephalomyelitis ($n = 1$). Histopathologic evidence of lungworm was noted in 63% of all mortalities, although lungworms were only directly responsible for 3 recorded deaths. Lungworm presence was skewed towards calves: 74% of calves and 31% of adults had lungworm.

Survival by Age Class

Calves.—We evaluated 19 univariate known-fates models to estimate weekly calf survival (Table 2). The top ranked model, engorgement period, carried virtually all of the support of the univariate model set (Table 6). This model had a negative, non-linear effect on survival (Fig. 5). With 0% of the tick load in the engorged female life stage, weekly calf survival rate predicted from the model remained above 0.98. Weekly survival remained >0.90 until 25% of an animal's tick load was in the engorged female stage. With 35% engorgement levels, weekly survival decreased rapidly, falling to 0.75 (Fig. 5).

Table 7. Known fates model selection results for weekly calf (<1 yr) survival (S; mid-Jan to 18 May) for radio-collared moose in northeastern Vermont, USA, 2017–2019. The final model set included univariate and multivariate models; AIC_c is Akaike's Information Criterion, corrected for small sample size.

Model	Number of parameters	AIC _c	Δ AIC _c	Weight
S(~engorgement period + roundworm + sex + lungworm)	5	341.25	0.00	0.48
S(~engorgement period + roundworm + lungworm)	4	341.42	0.18	0.44
S(~engorgement period + sex)	3	345.26	4.01	0.06
S(~engorgement period)	2	348.45	7.20	0.01
S(~cumulative tick engorgement)	2	360.45	19.21	0.00
S(~week)	2	363.40	22.15	0.00
S(~tick : engorgement period)	2	374.17	32.92	0.00
S(~tick : cumulative engorgement)	2	377.60	36.36	0.00
S(~roundworm)	2	399.23	57.98	0.00
S(~sex)	2	400.74	59.49	0.00
S(~lungworm)	2	402.30	61.06	0.00
S(~1)	1	403.51	62.26	0.00

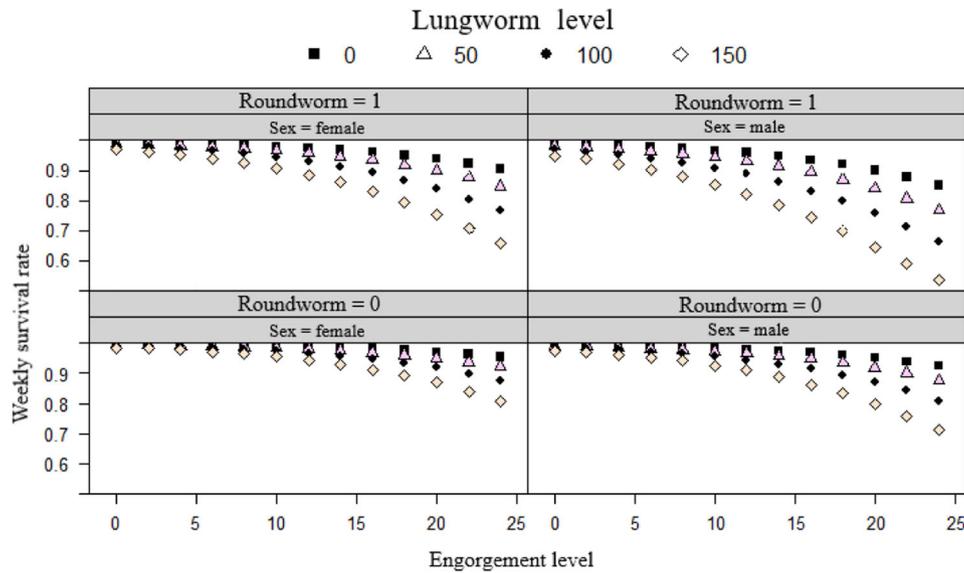


Figure 6. Predicted weekly survival rates of female (A) and male (B) calf (<1 yr old) moose in northeastern Vermont, USA (2017–2019), based on the female winter tick engagement period (% of an individual's tick load that is in the adult female life stage), lungworm ova per 5 g of fecal matter at capture, and presence (1) or absence (0) of roundworm at capture, and sex.

Variables with coefficients that were significantly different than 0 included engagement period, cumulative engagement period, week, snow depth, tick : engagement period, tick : cumulative engagement period, days with snow >70 cm, roundworm, sex, and lungworm (Table 6). For

multivariate models, we ensured that all variables within a given model were uncorrelated. For example, cumulative engagement period and week were the second and third top models, respectfully, but were both highly correlated with engagement period; therefore, we considered only

Table 8. Univariate known fates model selection results for monthly adult (≥ 1 yr) survival (S; 1 Jan–31 Dec) for radio-collared moose in northeastern Vermont, USA, 2017–2019. Covariates consisted of individual, home range, and temporal variables; AIC_c is Akaike's Information Criterion, corrected for small sample size. An asterisk indicates a model that did not converge.

Model	AIC_c	ΔAIC_c	Weight	Parameter	Beta estimate	SE	Lower 95% CI	Upper 95% CI
S(~tick : cumulative engagement)	125.35	0.00	0.53	Intercept	4.7429	0.3501	4.0567	5.4290
				Covariate	-0.0015	0.0004	-0.0022	-0.0008
S(~cumulative engagement)	125.65	0.29	0.45	Intercept	5.2920	0.5269	4.2594	6.3247
				Covariate	-0.0626	0.0173	-0.0965	-0.0287
S(~tick)	133.11	7.76	0.01	Intercept	5.0652	0.4350	4.2126	5.9179
				Covariate	-0.0372	0.0116	-0.0598	-0.0146
S(~tick : engagement period)	136.77	11.42	0.00	Intercept	4.4382	0.3138	3.8232	5.0531
				Covariate	-0.0018	0.0008	-0.0034	-0.0002
S(~engagement period)	137.49	12.14	0.00	Intercept	4.5378	0.3667	3.8190	5.2565
				Covariate	-0.0561	0.0325	-0.1199	0.0077
S(~year captured)	137.57	12.22	0.00	Intercept	4.4505	0.3353	3.7933	5.1076
				Covariate	-1.0493	0.6089	-2.2427	0.1441
S(~1)	138.11	12.75	0.00	Intercept	4.2274	0.2794	3.6798	4.7750
				Covariate	3.6475	0.5536	2.5624	4.7326
S(~evergreen)	138.76	13.41	0.00	Intercept	3.6475	0.5536	2.5624	4.7326
				Covariate	5.1811	4.6848	-4.0010	14.3633
S(~developed)*	139.58	14.23	0.00	Intercept				
S(~month)	139.60	14.25	0.00	Intercept	3.8973	0.5215	2.8752	4.9194
				Covariate	0.0602	0.0853	-0.1070	0.2273
S(~snowmobile)	139.65	14.30	0.00	Intercept	3.9262	0.5134	2.9199	4.9326
				Covariate	28.7201	43.6177	-56.7706	114.2109
S(~snow >70 cm)	139.70	14.35	0.00	Intercept	4.1551	0.2960	3.5749	4.7353
				Covariate	0.0824	0.1428	-0.1975	0.3623
S(~roundworm)	139.96	14.61	0.00	Intercept	4.2703	0.3036	3.6753	4.8654
				Covariate	-0.3191	0.7758	-1.8396	1.2014
S(~lungworm)	139.98	14.63	0.00	Intercept	4.2739	0.3102	3.6659	4.8820
				Covariate	-0.0962	0.2514	-0.5889	0.3964
S(~deer)	140.08	14.73	0.00	Intercept	7.3788	16.6047	-25.1663	39.9239
				Covariate	-3.5354	18.6173	-40.0252	32.9544
S(~tapeworm)*	140.11	14.76	0.00	Intercept				
				Covariate				

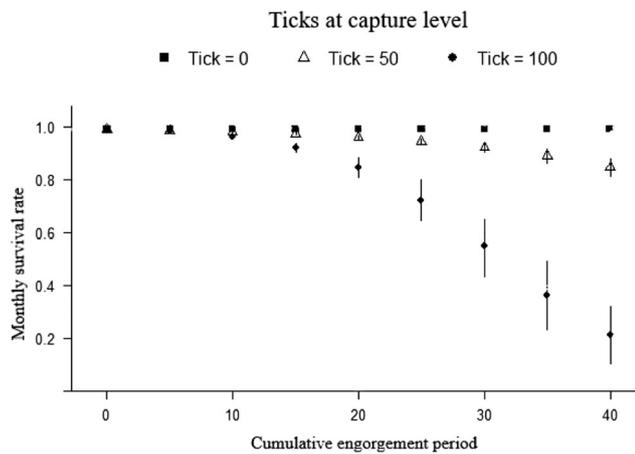


Figure 7. Monthly adult (≥ 1 yr old) moose survival rate for radio-collared moose in northeastern Vermont, USA, 2017–2019, as a function of the cumulative effect of the female winter tick engorgement period (cumulative % of an individual's tick load that is in the engorged adult female life stage) scaled to an individual's tick index at capture (number of ticks counted/cumulative 80 cm of transects on moose) based on the top-ranking univariate survival model. Error bars are standard errors.

engorgement period for additive models (Table 6). Snow depth and days with snow >70 cm showed positive effects on calf survival; however, most moose mortalities occurred as snowpack was declining. We considered the positive relationship between snow depth variables and survival as spurious correlations because this period coincided with peak cumulative tick engorgement (Fig. 4). We removed development (primarily roads) from consideration because the model produced unrealistic parameter estimates. Roundworm, sex, and lungworm showed significant betas and ecologically accurate directionality. Therefore, we used combinations of engorgement period, cumulative engorgement, roundworm, sex, and lungworm to create the final known-fates model set for calves (Table 7).

Of the 12 models in the final model set for calves, 2 top models carried $>90\%$ of the total model set weight and had strong empirical support (Table 7). The top model considered the effects of engorgement period, roundworm, sex,

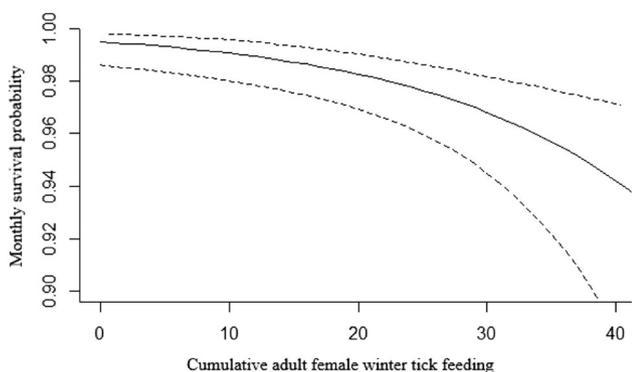


Figure 8. Monthly adult (≥ 1 yr old) moose survival rate for radio-collared moose in northeastern Vermont, USA, 2017–2019 ($\pm 95\%$ CI) as a function of the cumulative effect of the female winter tick engorgement period through time (cumulative % of an individual's tick load that is in the engorged adult female life stage) based on the second-ranking univariate survival model.

and lungworm (Fig. 6). Generally speaking, survival decreased as the percent of tick load in the engorged female life stage increased (Fig. 6). Presence of roundworm (top panels; Fig. 6) contributed to overall decreased weekly survival. Male calf survival (Fig. 6B) was lower than females (Fig. 6A), but there was uncertainty in this estimate because the confidence slightly overlapped 0 (Fig. 6). Lastly, weekly survival decreased rapidly as lungworm loads at capture increased (symbols; Fig. 6). The second-ranked model considered only engorgement period, roundworm, and lungworm, but the effects were similar and consistent with the top model.

Adults.—Among the monthly adult survival models, the only covariates that showed significance were related to ticks. These included tick : cumulative engorgement period, cumulative engorgement period, tick, and tick : engorgement period (Table 8).

From the univariate model set tick : cumulative engorgement period and cumulative engorgement period were the 2 top models carrying 53% and 45% of the total model set weight, respectively (Table 8). Both of these models showed negative effects on monthly adult survival. The greater number of ticks an individual had at capture, the greater the effect of cumulative engorgement period on survival (Fig. 7). The cumulative engorgement period model showed decreasing monthly survivorship with increased cumulative winter tick feeding. Survivorship remained above 0.96 until the effect of cumulative winter tick feeding reached 30 (i.e., 30% of entire tick load has been in the engorged adult age class up to this point), at which time survivorship began to decrease rapidly, falling below 0.9 once cumulative feeding reached 50 (Fig. 8).

DISCUSSION

The decline of moose populations along the southern periphery of their range has created management challenges, especially in the northeastern United States, where populations experience extremely high winter tick loads and periodic epizootics (Timmermann and Rodgers 2017). The population in Vermont has been largely unstudied, yet the area represents an important landscape for connecting the broader moose population between the northeastern United States and Canada (Krester and Glennon 2011). Winter ticks represented the primary cause and driver of mortality in Vermont, with similarly high moose mortality rates to those reported in New Hampshire and Maine (Jones et al. 2019). Our study had 2 results that add to a more comprehensive understanding of moose in the region. The first is that moose survival was associated with a measure of the female winter tick engorgement stage. Studies elsewhere have pointed to the effects of winter ticks on moose without directly incorporating the effects of individual tick loads and the tick life cycle on survival. The second is that our study indicated a relatively high frequency of internal parasites, especially compared to other New England states (Jones et al. 2019). Survival was influenced by the presence of these parasites in calves, suggesting that they compound the effects of winter ticks and contribute to

lower rates of recruitment into the adult age class, which could have population-level effects.

Calf Survival

Calf survival in our study was low for a population that experiences little to no natural predation as a result of the extirpation of wolves (*Canis lupus*), which represent a primary source of calf mortality in other regions such as Minnesota, USA (Severud et al. 2019), and relatively low densities of coyote and black bear. Our results indicate that calf survival was largely associated with increased parasitism, namely substantial depletion of fat caused by ectoparasitism of winter ticks along with the presence of internal parasites and, to an uncertain degree, sex. For comparison, our calf model predicted that survival estimates of female calves that experienced no parasitism remained above 93% from 1 January to 18 May (first birthday), whereas survival estimates of male calves that experienced winter tick infestations, presence of roundworm, and moderate lungworm infections during that same period were below 24% (Fig. 6). Peak mortality dates and overall mortality trends over the 3-year period of our study closely followed winter tick feeding patterns (Drew and Samuel 1989, Samuel 2004). Further, gross field necropsy and histopathologic observations associated 91% of all calf mortalities with high winter tick infestations. In a companion study, Blouin et al. (2021b) showed that survival of calves to 1 year may be linked to habitat use during their first fall, when winter ticks are questing.

Calf mortality has also been driven by winter tick infestations in nearby states. For example, ticks accounted for 91% of mortalities in New Hampshire and 85% of mortalities in Maine in comparable radio-telemetry studies between 2014 and 2016 (Jones et al. 2019). The observed survival rate (49%) of calves from January to May across our Vermont study was higher than rates reported in those studies: New Hampshire = 39% and Maine = 38% (Fig. 9B; Jones et al. 2019). The differences may be explained by 3 consecutive years of tick epizootics experienced in the region during the New Hampshire and Maine study in which >50% of 9–12-month-old calves died (Jones et al. 2019). During our study, radio-marked moose experienced epizootics in 2018 and 2019 but not 2017 when survival was 60%.

Vermont calves had one of the highest rates of lungworm occurrence (70%) reported among moose and >2 times the incidence of lungworm ova in feces collected at capture than in New Hampshire and Maine (32%, and 28% of monitored individuals, respectively; Jones et al. 2019). Historically considered an incidental parasite in moose (Franzmann and Schwartz 2007), recent increases in occurrence of >50% in calves in New England states suggest that coinfection by this nematode could exacerbate the effects of other parasitic diseases (e.g., associated with winter tick and meningeal worm; Marcogliese and Pietrock 2011).

Occurrence and abundance of tapeworm, roundworm, and coccidia parasites by comparison were relatively similar to data from the New Hampshire and Maine studies

(Jones et al. 2019). These parasites are common in wild cervid populations and considered incidental (non-pathogenic in the case of tapeworms) in moose (Franzmann and Schwartz 2007). Roundworm infection was present in our top model, but there was no recorded cause of death from roundworm.

Although moose home ranges overlapped with areas of high deer occurrence, the deer model had little empirical support. But we believe there may be an association with deer on the landscape because a third of calf mortalities showed clinical signs of meningeal worm, which rely on deer for their life cycle (Lankester 2010). In aberrant hosts, clinical signs usually manifest themselves in 30–60 days but can vary depending on infection level (Gandolf and Beest 2020). All calves exposed to meningeal worm must contract it within the first summer or fall of their life, suggesting that the occurrence of this parasite was relatively high within our study area. Lack of support for the deer model may reflect the limitations of our deer covariate, which was based on occupancy probability during the breeding season (Pearman-Gillman et al. 2020) and not patterns of density (e.g., wintering areas that concentrate deer during deep-snow months) that probably better describes meningeal worm distribution.

Signs of winter tick-related mortality (serous atrophy of fat and emaciation) closely resemble those associated with limited forage and poor habitat quality; however, we found no evidence that calf survival rate was linked to habitat quality. All calves at necropsy died with a full rumen of assumed high quality winter forage, reflecting the large percentage of optimal habitat (5–35%) available to moose in northern Vermont and the New England region given the mosaic of large-scale timber operations and state and federally managed lands within the study area (Dunfey-Ball 2017, Blouin et al. 2021a; C. E. Alexander, personal observation).

Adult Survival

Annual adult survival over the 3-year period (88%) was higher than that reported in declining populations, including those in New Hampshire (83%; Powers 2019; Fig. 9A) and Minnesota (79%; Murray et al. 2006, Lenarz et al. 2009), but similar to rates in stable or increasing populations such as in Ontario, Canada (90%; Murray et al. 2012). Under ideal conditions (i.e., no parasitism), our estimated survival rates were >0.90, consistent with that of a stable or increasing population. But when confronted with moderate winter tick infestations, annual adult survival estimates drop to 0.68. Winter ticks are often not associated with adult mortality because adults have larger body mass and fat stores to compensate for increased blood loss and decreased nutritional status (Samuel 2004, Jones 2016). But at the beginning of our study, winter ticks were responsible for a larger subset of adult mortality than expected (Table 5). It is possible that Vermont moose experienced epizootic years that were reported in the neighboring state of New Hampshire before our study began (Jones 2016). If so, adult moose have been subject to high winter tick infestations 5 out of the last 6 years (2014–2019). Multiple years of heavy parasitism may have weakened the overall health of adults in the Vermont

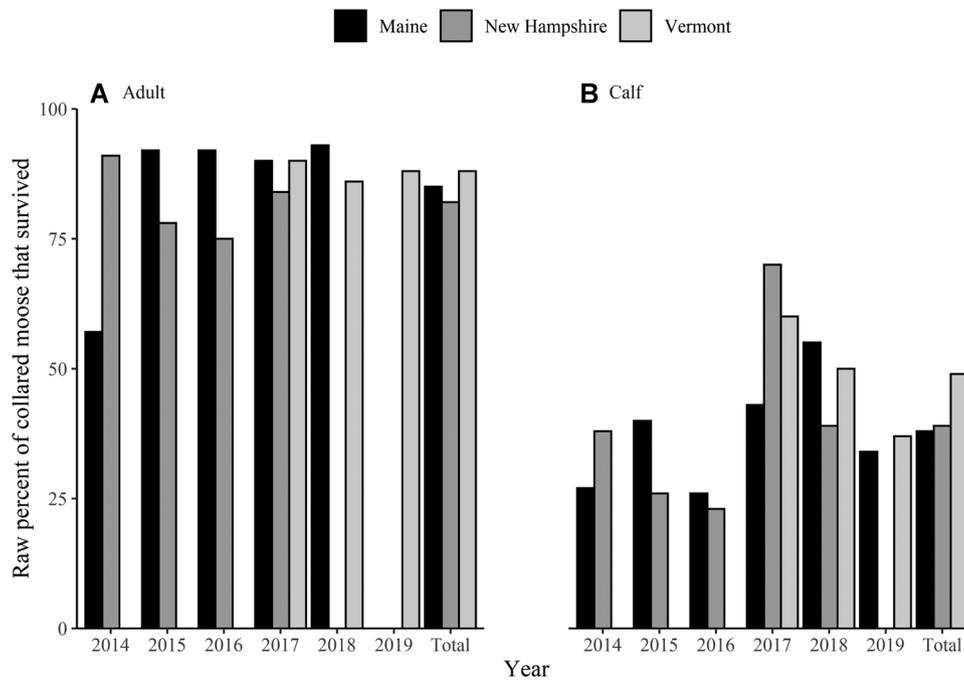


Figure 9. Observed annual survival of radio-marked adult (≥ 1 yr old; A) and calf (< 1 yr old; B) moose during 6 years (2014–2019) of moose research in Vermont, New Hampshire, and Maine, USA. We obtained New Hampshire and Maine survival rates from Ellingwood (2019), Jones (2019), and Powers (2019).

population and made them more susceptible to anemia, serous atrophy of fat, and the effects of parasitism as observed in other parasite-host systems such as lungworm (*Umingmakstrongylus pallikuukensis*) in muskox (*Ovibos moschatus*; Kutz et al. 2001, Marcogliese and Pietrock 2011).

Meningeal worm comprised $< 10\%$ of overall mortality in populations in New Hampshire, Minnesota, and Michigan (Dodge et al. 2004, Murray et al. 2006, Jones 2016) yet was associated with 31% (5/16) of adult moose mortalities in our data. Moose population decline associated with meningeal worm has occurred when white-tailed deer densities exceed 5 deer/km² on the landscape (Whitlaw and Lankester 1994). Deer densities were relatively low throughout the study area, estimated at 1.93–3.86 deer/km² (Vermont Fish and Wildlife Department 2021). Localized deer densities can increase during periods of deep snow when they congregate in winter yards, or stands of high cover trees like balsam fir (*Abies balsamea*) and northern white cedar (*Thuja occidentalis*) that provide thermal cover and shelter from wind during the winter (Ozoga and Gysel 1972). Lankester and Peterson (1996) found that the concentration of gastropods infected with meningeal worm larvae in known deer wintering areas was 4 times higher than throughout their summer range in Minnesota. Several large deer yards existed within the study area and, if the Minnesota findings apply to Vermont, may have increased the infection rate of Vermont moose. Like with calves, our top model for adults did not include deer, which may reflect limitations of the covariate used.

Internal parasites, snow conditions, and habitat were not significant predictors of adult survival rate. The immune system of an adult moose is known to be more robust and effective at minimizing the effects of parasite loads after

their first year, which may explain the lack of support for the effect of internal parasites (Franzmann and Schwartz 2007). Similarly, snow conditions in Vermont rarely exceed 90 cm, which is considered the height at which adult locomotion is restricted (Franzmann and Schwartz 2007). Moreover, 5–35% of the study area is considered to be optimal habitat (i.e., characterized by ample regeneration and softwood cover; Dunfey-Ball 2017).

MANAGEMENT IMPLICATIONS

Our results indicated that both external and internal parasites increased mortality of moose calves in Vermont, with winter ticks being the most important factor affecting mortality in calves and adults. Winter ticks, meningeal worm, and lungworm are density-dependent parasites whose presence on the landscape is determined by host availability. Reduction of primary host density could disrupt the parasite-prey relationship that has formed in moose herds and potentially increase calf survival. If harvest is chosen as a method of reduction, consideration of the age and sex of targeted animals will be important to ensure the persistence of individuals with high reproductive value. In healthy moose populations, proactive measures could be taken to reduce the spread of parasites by preventing population increases of host species.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank B. A. Mosher, S. D. McKay, 2 anonymous reviewers and J. McDonald for their reviews and constructive comments. We are grateful for the

support of the United States Fish and Wildlife Service National Wildlife Refuge System—Nulhegan Division, and land access from Weyerhaeuser Company, LandVest, and many private landowners. Support from P. J. Pekins and L. E. Kantar was instrumental in the design and follow through of this study. We thank the hard work of a dedicated field staff including T. R. Smith, C. Lampart, L. A. Rossier, and D. P. Hotchkiss. Veterinary consultation was provided by the Vermont Department of Fish and Wildlife. The Vermont Cooperative Fish and Wildlife Research Unit is jointly supported by the United States Geological Survey, University of Vermont, Vermont Fish and Wildlife Department, and Wildlife Management Institute. Funding was provided by the Vermont Fish and Wildlife Department in cooperation with the United States Fish and Wildlife Service Division of Wildlife and Sportfish Restoration—Wildlife Restoration Program, the University of Vermont, Vermont Fish and Wildlife Cooperative Research Unit, Safari Club International Foundation, and Vermont Electric Company.

LITERATURE CITED

- Addison, E. M., D. J. H. Fraser, and R. McLaughlin. 2019. Grooming and rubbing behavior by moose experimentally infested with winter ticks (*Dermaacentor albipictus*). *Alces* 55:23–35.
- Addison, E. M., R. McLaughlin, and J. Broadfoot. 1998. Effects of winter tick (*Dermaacentor albipictus*) on blood characteristics of captive moose (*Alces alces*). *Alces* 34:189–199.
- Alexander, C. E. 1993. The status and management of moose in Vermont. *Alces* 29:187–195.
- Bergeron, D. H., P. J. Pekins, and K. Rines. 2013. Temporal assessment of physical characteristics and reproductive status of moose in New Hampshire. *Alces* 49:39–48.
- Blouin, J., J. DeBow, E. Rosenblatt, C. Alexander, K. Gieder, N. Fortin, J. Murdoch, and T. Donovan. 2021a. Modeling moose habitat use by age, sex, and season in Vermont, USA using high-resolution Lidar and National Land Cover Data. *Alces* 57:in press.
- Blouin, J., J. DeBow, E. Rosenblatt, J. Hines, C. Alexander, K. Gieder, N. Fortin, J. Murdoch, and T. Donovan. 2021b. Moose habitat selection and fitness consequences during two critical winter tick life stages in Vermont, USA. *Frontiers in Ecology and Evolution* 9:642276.
- Burnham, K., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer, New York, New York, USA.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modeling* 197:516–519.
- Colescott, J. H., and M. P. Gillingham. 1998. Reaction of moose (*Alces alces*) to snowmobile traffic in the Greys River Valley, Wyoming. *Alces* 34:329–338.
- Danks, Z. D., and W. F. Porter. 2010. Temporal, spatial, and landscape habitat characteristics of moose—vehicle collisions in western Maine. *Journal of Wildlife Management* 74:1229–1241.
- Dawe, K. L., and S. Boutin. 2016. Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution* 6:6435–6451.
- DeGraaf, R. M., and M. Yamasaki. 2001. New England wildlife: habitat, natural history, and distribution. University Press of New England, Lebanon, New Hampshire, USA.
- Del Frate, G. G., and T. H. Spraker. 1991. Moose vehicle interactions and an associated public awareness program on the Kenai Peninsula, Alaska. *Alces* 27:1–7.
- Dewitz, J. 2019. National Land Cover Database (NLCD) 2016 products (version 2.0). U.S. Geological Survey data release. <https://doi.org/10.5066/P96HHBIE>. Accessed Jul 2020.
- Dodge, W. B., S. R. Winterstein, D. E. Beyer, and H. Campa III. 2004. Survival, reproduction, and movements of moose in the western Upper Peninsula of Michigan. *Alces* 40:71–85.
- Dou, H., G. Jiang, P. Stott, and R. Piao. 2013. Climate change impacts population dynamics and distribution shift of moose (*Alces alces*) in Heilongjiang Province of China. *Ecological Research* 28:625–632.
- Drew, M. L., and W. M. Samuel. 1989. Instar development and disengagement rate of engorged female winter ticks, *Dermaacentor albipictus* (Acari:Ixodidae), following single- and trickle- exposure of moose (*Alces alces*). *Experimental and Applied Acarology* 6:189–196.
- Dunfey-Ball, K. R. 2017. Moose density, habitat, and winter tick epizootics in a changing climate. Thesis, University of New Hampshire, Durham, USA.
- Dussault, C., J.-P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicœur. 2005. Linking moose habitat selection to limiting factors. *Ecography* 28:619–628.
- Ellingwood, D., P. J. Pekins, and H. Jones. 2019. Using snow urine samples to assess the impact of winter ticks on moose calf condition and survival. *Alces* 55:13–21.
- Franzmann, A. W., and C. C. Schwartz. 2007. Ecology and management of the North American moose. University Press of Colorado Boulder, Boulder, USA.
- Gandolf, R., and J. Ter Beest. 2020. Meningeal worm (*Parelaphostrongylus tenuis*). Fact sheet in P. Brock, G. Cole, and R. Sim, editors. Infectious disease manual: infectious diseases of concern to captive and free ranging wildlife in North America. American Association of Zoo Veterinarians Animal Health and Welfare Committee, Yulee, Florida, USA.
- Jones, H. 2016. Assessment of health, mortality, and population dynamics of moose in Northern New Hampshire during successive years of winter tick epizootics. Thesis, University of New Hampshire, Durham, USA.
- Jones, H., P. J. Pekins, L. E. Kantar, M. O'Neil, and D. Ellingwood. 2017. Fecundity and summer calf survival of moose during 3 successive years of winter tick epizootics. *Alces* 53:85–98.
- Jones, H., P. Pekins, L. Kantar, I. Sidor, D. Ellingwood, A. Lichtenwalner, and M. O'Neal. 2019. Mortality assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermaacentor albipictus*) epizootics in New Hampshire and Maine (USA). *Canadian Journal of Zoology* 97:22–30.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457–481.
- Krester, H., and M. Glennon. 2011. Evaluating genetic connectivity and re-colonization dynamics of moose in the Northeast. <<https://nsrcforest.org/sites/default/files/uploads/krester09full.pdf>>. Accessed 17 Mar 2019.
- Kutz, S. J., E. P. Hoberg, and L. Polley. 2001. A new lungworm in muskoxen: an exploration in Arctic parasitology. *Trends in Parasitology* 17:276–280.
- Laake, J. L., D. S. Johnson, and P. B. Conn. 2013. marked: an R package for maximum likelihood and Markov chain Monte Carlo analysis of capture–recapture data. *Methods in Ecology and Evolution* 4:885–890.
- Lankester, M. W. 2010. Understanding the impact of meningeal worm, *Parelaphostrongylus tenuis*, on moose populations. *Alces* 46:53–70.
- Lankester, M. W., and W. J. Peterson. 1996. The possible importance of wintering yards in the transmission of *Parelaphostrongylus tenuis* to white-tailed deer and moose. *Journal of Wildlife Diseases* 32:31–38.
- Leblond, M., C. Dussault, J. P. Ouellet, M. Poulin, R. Courtois, and J. Fortin. 2009. Management of roadside salt pools to reduce moose–vehicle collisions. *Journal of Wildlife Management* 75:2304–2310.
- Lenarz, M. S., M. E. Nelson, M. W. Schrage, and A. J. Edwards. 2009. Temperature mediated moose survival in Northeastern Minnesota. *Journal of Wildlife Management* 73:503–510.
- Lundmark, C., and J. P. Ball. 2008. Living in snowy environments: quantifying the influence of snow on moose behavior. *Arctic, Antarctic, and Alpine Research* 40:111–118.
- Marcogliese, D. J., and M. Pietrock. 2011. Combined effects of parasites and contaminants on animal health: parasites do matter. *Trends in Parasitology* 27:123–130.
- McCann, N. P., R. A. Moen, and T. R. Harris. 2013. Warm-season heat stress in moose (*Alces alces*). *Canadian Journal of Zoology* 91:893–898.

- McRoberts, R. E., L. D. Mech, and R. O. Peterson. 1995. The cumulative effect of consecutive winters' snow depth on moose and deer populations: a defence. *Journal of Animal Ecology* 64:131–135.
- 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.
- Murray, D. L., K. F. Hussey, L. A. Finnegan, S. J. Lowe, G. N. Price, J. Benson, K. M. Loveless, K. R. Middel, K. Mills, and D. Potter. 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.
- Musante, A. R., P. J. Pekins, and D. L. Scarpitti. 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. 2019. Climate data online: dataset directory. <<https://www.ncdc.noaa.gov/cdo-web/>>. Accessed 25 Mar 2019.
- New Hampshire Veterinary Diagnostic Laboratory. 2019. Pathology report. New Hampshire Veterinary Diagnostic Laboratory, Durham, USA
- Ozoga, J. J., and L. W. Gysel. 1972. Response of white-tailed deer to winter weather. *Journal of Wildlife Management* 36:892–896.
- Pearman-Gillman, S., J. Katz, R. Micky, J. Murdoch, and T. Donovan. 2020. Predicting wildlife distribution patterns in New England USA with expert elicitation techniques. *Global Ecology and Conservation* 21:e00853.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Powers, B. 2019. Assessing the relationships of winter ticks, weather, and a declining moose population in Northern New Hampshire. Thesis, University of New Hampshire, Durham, USA.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rempel, R. S., P. C. Elkie, A. R. Rodgers, and M. J. Gluck. 1997. Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. *Journal of Wildlife Management* 61:517–524.
- Renecker, L. A., and R. J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. *Canadian Journal of Zoology* 64:322–327.
- Renecker, L. A., and R. J. Hudson. 1990. Behavioral and thermoregulatory responses of moose to high ambient temperatures and insect harassment in aspen-dominated forests. *Alces* 26:66–72
- Samuel, B. 2004. White as a ghost: winter ticks & moose. Federation of Alberta Naturalists, Manitoba, Canada.
- Samuel, W. M. 2007. Factors affecting epizootics of winter ticks and mortality of moose. *Alces* 43:39–48.
- Schwartz, C. C. 1992. Physiological and nutritional adaptations of moose to northern environments. *Alces Supplement* 1:139–155.
- Sergeant, D. E., and D. H. Pimlott. 1959. Age determination in moose from sectioned incisor teeth. *Journal of Wildlife Management* 23:315–321.
- Severud, W., T. R. Obermoller, G. D. DelGiudice, and J. R. Fieberg. 2019. Survival and cause-specific mortality of moose calves in northeastern Minnesota. *Journal of Wildlife Management* 83: 1131–1142.
- Sikes, R. S., J. A. Bryan II, B. J. Danielson, J. Eggleston, M. R. Gannon, W. L. Gannon, D. W. Hale, B. R. Jesmer, D. K. Odell, L. E. Olson, et al. 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Timmermann, H. R., and A. R. Rodgers. 2005. Moose: competing and complementary values. *Alces* 41:85–120.
- Timmermann, H. R., and A. R. Rodgers. 2017. The status and management of moose in North America—circa 2015. *Alces* 53:1–22.
- Vermont Fish and Wildlife Department. 2009. Big game management plan 2010–2020, creating a road map for the future. Vermont Fish and Wildlife Department, Agency of Natural Resources, Montpelier, USA.
- Vermont Fish and Wildlife Department. 2021. Big game management plan 2020–2030, maintaining abundant and healthy big game populations within their ecological and social carrying capacities for Vermonters. Vermont Fish and Wildlife Department, Agency of Natural Resources, Montpelier, USA.
- Wallgren, M., R. Bergström, G. Bergqvist, and M. Olsson. 2013. Spatial distribution of browsing and tree damage by moose in young pine forests, with implications for the forest industry. *Forest Ecology and Management* 305:229–238.
- Wattles, D. W., and S. DeStefano. 2011. Status and management of moose in the northeastern United States. *Alces* 47:53–68.
- Weiskopf, S. R., O. E. Ledee, and L. M. Thompson. 2019. Climate change effects on deer and moose in the Midwest. *Journal of Wildlife Management* 83:769–781.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: S120–S139.
- Whitlaw, H. A., and M. W. Lankester. 1994. A retrospective evaluation of the effects of parelaphostromylosis on moose populations. *Canadian Journal of Zoology* 72:1–7.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

Associate Editor: John McDonald.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.