MORTALITY ASSESSMENT OF CALF MOOSE (*ALCES ALCES*) DURING SUCCESSIVE YEARS OF WINTER TICK (*DERMACENTOR ALBIPICTUS*) EPIZOOTICS IN NEW HAMPSHIRE AND MAINE

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ABSTRACT

Populations within ecological communities constantly fluctuate due to a multitude of interactions that can be influenced by climate change. Moose (*Alces alces* Clinton, 1822) populations in northern New Hampshire and western Maine, subunits of the largest regional moose population in the continental United States, are suspected to be declining due to increasing frequency of winter tick (*Dermacentor albipictus* Packard, 1869) epizootics that cause >50% late winter mortality of 9-12 month-old calves. To investigate this hypothesis, we collected general health measurements of calves captured at 2 study sites in January 2014-2016, and subsequently performed field necropsies and histologic examination of tissues of those radio-marked calves that died during winter/spring. At capture, calves (n = 179) were in normal (66%) and thin (32%) physical condition with high infestations of winter ticks. Most (88%) mortalities (n = 125) were associated with moderate to severe infestations of winter ticks. Gross necropsies and histologic examination found high tick infestations, emaciation, anemia, and endoparasitism; lungworm (species of the genus *Dictyocaulus* Railliet and Henry, 1907) was also found in most (87%) calves. Three consecutive years (2014-2016) of winter tick epizootics is unprecedented in the region, rare in North America, and arguably reflects a host-parasite relationship strongly influenced by climate change at the southern fringe of moose habitat.

Key Words: moose, *Alces alces*, winter tick, *Dermacentor albipictus*, epizootic, calf mortality, New Hampshire, Maine

INTRODUCTION

Populations fluctuate over time due to the interaction between the population and environmental factors that influence food and shelter, and predation, parasitism, and diseases. Insects are integral to many ecological communities as food, predator, and/or parasite and are highly sensitive to climatic conditions (Krebs 2001). Hence, insects are a primary agent that express climate change (Stange and Ayres 2010), with the potential to affect moose (*Alces alces* Clinton 1822), the largest herbivore in North America (Jones et al. 2017; Lankester 2018).

Many moose populations along the southern edge of their range in North America are in decline, including populations in Minnesota, Manitoba, Nova Scotia, and the northeastern United States (Murray et al. 2006; Lenarz et al. 2010; Wattles and DeStefano 2011; Broders 2012). Moose are subject to a diversity of natural and anthropogenic sources of mortality that vary regionally due to interactions of moose density, weather, habitat, species assemblages, and human influence (Murray et al. 2006; Van Ballenberghe and Ballard 2007). A warming climate is likely influencing moose through increased incidence of parasites and disease which are common sources of natural mortality in many populations (Samuel 2004; Murray et al. 2006; Van Ballenberghe and Ballard 2007; Lankester 2010).

In the northeastern United States, winter ticks (*Dermacentor albipictus* Packard, 1869) play a substantial role in the population dynamics of moose causing high mortality of 10-11 month-old calves and reduced productivity in yearling and adult cows (Musante et al. 2010; Bergeron et al. 2013; Jones et al. 2017). A winter tick epizootic (>50% calf mortality) was documented with radio-marked calves in northern New Hampshire in 2002 (Musante et al. 2010), and again in 2008 and 2011 based on ample field evidence in northern New Hampshire and western Maine. Reduced recruitment due to these epizootics is suspected to cause regional

population decline despite adequate optimal foraging habitat (Dunfey-Ball 2017; Jones et al. 2017). Outbreaks of epizootics are considered abrupt, periodic events in the host-parasite relationship of moose and winter ticks, typically causing local, not regional decline in moose (Samuel 2004). However, the current and predicted increasing frequency of shorter winters due to climate change (Wake et al. 2014) is favorable for increased winter tick abundance and subsequent sustained negative impact on moose at their southern range.

Since 2005, mortality assessment of moose in the northeastern United States has consisted of only cursory examination of incidental animals; however, thorough and timely necropsy of marked animals is necessary to accurately identify causes of mortality. Direct measurement of mortality factors is essential to assess the scale and impact of winter tick infestations on moose populations because heavily parasitized animals visible to the public could potentially cause biased assessment of opportunistically-collected specimens (Wünschmann et al. 2015). Other parasites and diseases that infest moose in the northeastern United States include meningeal worm (*Parelaphostrongylus tenuis* Dougherty, 1945), lungworm species of the genus *Dictyocaulus* (Railliet and Henry, 1907), *Echinococcus granulosus* (Batsch, 1786), and eastern equine encephalitis (Musante 2006; Lubelczyk et al. 2010; Lichtenwalner et al. 2014), with tick-borne bacteria of the genus *Anaplasma* (Theiler, 1910) of recent concern (Baldridge et al. 2009). Meningeal worm is a common disease causing direct mortality of moose and is prevalent when white-tailed deer density is >5/km^2 (Whitlaw and Lankester 1994; Lankester 2010).

We investigated the cause and rate of winter mortality of moose calves (9-12 months old) using radio-marked animals at a study site in northern New Hampshire and western Maine in 2014-2016. We presumed that similar ecological conditions and harvest strategies at these two study sites ~120 km apart provided an opportunity to compare and combine data sets. Physical

condition and parasite infestation were assessed at capture in January and specific cause of death was identified through field necropsies and histopathology. We hypothesized that the predominant cause of annual calf mortality would be associated with high infestations of winter ticks, but that the frequency of epizootics would be similar to that measured previously in the region (1 in 4 years; Musante et al. 2010).

STUDY AREA

The New Hampshire site (NH) was centered in the town of Milan (44 37'49"N, 71 11'11"W, Fig. 1). It encompasses ~1,250 km^2 in Wildlife Management Units C2 and portions of A2, B, and C1 and is the same area where a comprehensive population dynamics study occurred in 2002-2005 (Musante et al. 2010). The western Maine site (ME) was north and west of the town of Greenville to the Quebec border (45 33'34"N, 70 10'5"W, Fig. 1). It is ~5,620 km^2 and encompasses Wildlife Management District 8. Wildlife Management Units and Districts are geographical areas defined by the state wildlife agencies within which similar biological, geophysical, and hunting characteristics exist; they were used to guide research effort and delineate the study area boundary in ME. In 2014-2016, moose density was estimated as 0.46-0.87 moose/km^2 in NH and 0.97-1.35 moose /km^2 in ME. White-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) are sympatric with moose throughout the region and occurred at an estimated density of 2.45 deer/km^2 in New Hampshire (D. Bergeron, NHFG, pers. comm.) and 0.60 deer/km^2 in Maine (Kyle Ravanna, MDIFW, pers. comm.).

The study areas were privately-owned, managed commercial timberland and considered high quality moose habitat. The area was mountainous with elevations to 1220 m, with most as lowland valleys, rolling hills, and smaller mountains containing numerous lakes, ponds, and

rivers scattered throughout. The dominant cover type was northern hardwood forest consisting of American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), paper birch (*Betula papyrifera* Marsh.), and yellow birch (*B. alleghaniensis* Britt.). Conifer stands of mostly red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* Mill.) were common at high elevation, along with white cedar (*Thuja occidentalis* Linn.) and black spruce (*Picea mariana* Mill.) in wet lowland sites (DeGraaf et al. 1992). Year-round access was available for research personnel on logging roads, off highway recreational vehicle (OHRV) trails, and snowmobile trails.

Climate data were available from the National Climatic Data Center weather stations at York Pond, Berlin, NH (ID: GHCND:USC00279966, 44 30'1"N, 71 19'59"W) and Jackman, ME (ID: GHCN:USC00174086, 45 37'34"N, 70 14'46"W). Annual ambient temperature ranged from 32 to -32℃ in both areas. Annual precipitation ranged from 114.0 to 121.6 cm and 91.0 to 106.0 cm, and maximum snow depth ranged from 17.8 to 66.0 cm and 30.5 to 106.7 cm in NH and ME, respectively. Mean annual snowfall of 215.6 cm and maximum recorded snow depths in 2014-2016 (61.0, 66.0, and 35.6 cm) in NH were generally similar to those in ME (240.5 cm and 106.7, 53.3, and 43.2 cm). Snow depth >70 and 90 cm occurred only in ME in 2014 for 41 and 11 days, respectively. The study areas are ecologically similar based on these characteristics of wildlife abundance and composition, landscape vegetation and topography, and weather conditions.

MATERIALS AND METHODS

Capture and marking

Animal capture and handling protocols were approved by the Institutional Animal Care and Use Committee at the University of New Hampshire (IACUC #130805). Captures occurred in January 2014-2016 and were completed in ≤7 days at each study site; details are provided in Jones et al. (2017). Calves were captured via aerial net-gunning. They were quickly removed from the net, restrained with leg hobbles, and blindfolded; body temperature was monitored and the handling process typically lasted <15 min. A 30 mL blood sample was taken for subsequent blood tests from the jugular vein with a 16 ga needle and 30 mL syringe and stored in clot activator (red top tube) and EDTA (lavender top tube) vacutainers (Becton, Dickinson and Company, Franklin Lakes, NJ, USA). Blood samples were kept unfrozen and processed within 2 h of collection; red top tubes were centrifuged at 1500 rpm for 5 min to separate serum. Serum and whole blood from the EDTA tube(s) was refrigerated (3℃) or frozen (0℃) within 24 h. Refrigerated samples were analyzed within 7 days and frozen samples within 1 month. Feces were collected to screen for parasite ova and larva. Each moose was fitted with numbered ear tags color-coded by year (Allflex USA, Dallas, Texas, USA) and a VHF or GPS radio-collar. Moose in NH were fitted with either a VHF (M2610B, Advanced Telemetry Systems, Isanti, Minnesota, USA; Mod-600, Telonics, Mesa, Arizona, USA) or GPS radio-collar (GPS Plus Vertex Survey Collar, Vectronic Aerospace GmbH, Berlin, Germany); all moose in ME were fitted with the same Vectronic GPS radio-collar.

The VHF radio-collars had a motion sensor switch that indicated a 4 h period without movement that was presumed a mortality; collars were continuously monitored with a R4500S

datalogger (ATS, Isanti, MN) connected to a large omnidirectional antenna (Cushcraft CRX 150) mounted centrally in the study area. The GPS radio-collars collected 2 GPS fixes daily (0000 and 1200 hr EST) and had a VHF beacon that was active at 0700-1900 hr EST; after 6 h of non-movement, a motion sensor switch triggered a "mortality message" via e-mail and the pulse rate of the VHF signal increased. Collars were retrofitted to allow for future expansion (see Musante et al. 2010). Calves that died <4 weeks after capture were censored from survival analysis including 12 calves in NH and 4 calves in ME; 2 calves in NH that dropped collars before 12 months old were also censored.

Physical condition and parasite assessment at capture

Physical condition was subjectively assigned by palpation (thin, normal, fat) by the capture crew. Winter ticks were counted in 2, 10 x 10 cm sampling plots, one at the upper edge of the shoulder blade, and one on the rump midway between the hipbone and the base of the tail; side of moose was variable (Bergeron and Pekins 2014). Ticks were counted on 4 parallel, 10 cm transects spaced 2 cm apart in each plot. Hair was parted down to skin with a comb (Conair Styling Essentials Comb) and all visible ticks were counted along each transect by the capture crew (4-5 crew members with interannual variation; Sine et al. 2009; Bergeron and Pekins 2014); tick life stage and engorged status was not differentiated at capture. Winter ticks are the only species of tick known to occur on moose Jan-April in northern New Hampshire and Maine (Eaton 2016). Fecal samples (4-8 g) were assessed for parasite ova and larva using McMaster's and Baermann techniques (Shapiro 2010) at the University of Maine Animal Health Laboratory (UMAHL, Orono, ME); samples were refrigerated (3℃) in whirl-pak bags (Nasco Inc., Atkinson, WI, USA) for ≤7 days between collection and screening.

Cause-specific mortality

Upon alert of a mortality, the calf was located and a field assessment was completed within 24 h; in certain cases the assessment was delayed 24-72 h because of poor access/weather. The mortality site was examined for predation, scavenging, human disturbance, traumatic injury, struggle, and other moose activity. GPS coordinates and photographs were taken, and the date and time of death was assigned by back-calculating from the initial mortality signal.

Most moose were necropsied in the field, but a small subset were necropsied by trained pathologists at the New Hampshire Veterinary Diagnostic Laboratory (NHVDL) in Durham, NH and at UMAHL. Necropsy protocol was based on standard procedures (Mason and Madden 2007; Munson 2015) and generally followed the approach used in Minnesota (Wünschmann et al. 2015), but customized for field collection of samples with slight variation between study areas.

In NH, whole carcass body mass was measured with a 500 kg hanging digital scale (Roughneck, Northern Tool and Equipment, Burnsville, MN, USA) using a pulley system suspended from a brace strapped to a tree. The degree of hair-loss was rated as none, light, moderate, severe, and worst case (Samuel 2004). Whole hides were removed from certain calves and frozen (0℃) for subsequent measurement of tick abundance; the criteria were that the calf died on snow and was sampled <24 h after death from 21 March – 17 April. Frozen hides were later thawed and processed to estimate tick abundance using the doubled value of a complete half-hide count (Jones 2016).

All organs were visually assessed and the degree of emaciation was measured using a body condition score (BCS, Kistner et al. 1980) based on body musculature and fat in the

subcutaneous, cardiac, omental, and perirenal regions. Tissue and biological samples included: axillary lymph node, tongue, muscle tissue (diaphragm, backstrap, and rump), thyroid, trachea, esophagus, lung, heart, heart blood clot, kidney, adrenal gland, pancreas, urinary bladder, liver, spleen, stomach (rumen, reticulum, omasum, abomasum), small and large intestine, cecum, femur bone marrow, brain, eyeball, spinal cord (cervical, thoracic, and lumbar regions), ovaries, urine, feces, and parasites. All samples were fixed in 10% formalin (provided by NHVDL or UMAHL) or frozen (0℃). The degree of lungworm infestation was visually assessed by cutting down the airways, counting the number of lungworms, and assigning an infestation level: light (<20 adult worms), moderate (20-50), or heavy (>50). The amount of lung tissue affected by lungworm infestation was subjectively estimated; affected tissue had alternating lobules with a deep red congested appearance, a pale and firm appearance with mucoid material in the bronchioles, or a bluish pink appearance. Lungworm samples (n = 5 worms) collected in NH were sent to the USDA National Veterinary Service Laboratory (Ames, IA) for species identification using morphological assessment (Divina et al. 2000).

Marrow from the middle third of the femur was graded visually (Cheatum 1949) and percent fat content (% femur marrow fat [FMF], 14.8-44.3 g of marrow) was measured on a subset using the oven-dried weight method (Nieland 1970). Histologic examination of a subset of tissue samples (heart, lung, skeletal muscle, liver, kidney, spleen, bone marrow, tongue, esophagus, trachea, and intestine) was performed at NHVDL; the meninges and spinal cord (cervical, thoracic, and lumbar sections [2-3 cm each]) were microscopically examined for *Parelaphostrongylus tenuis* (Lankester et al. 2007) or tracts thereof (Wünschmann et al. 2015). Samples of frozen liver tissue (approximately 50 mg) were submitted to the Diagnostic Center

for Population and Animal Health at Michigan State University (East Lansing, MI) to measure iron concentration with inductively coupled mass spectroscopy.

Necropsy protocol in ME was the same except hides were not collected to estimate tick abundance, body condition was scored on a scale of 1 to 5 (very thin and emaciated to healthy and robust), and FMF was graded visually (Cheatum 1949) but not dried. The pluck (tongue, esophagus, trachea, heart, and lungs) was removed and refrigerated (3 ℃) or frozen (0 ℃) for assessment at UMAHL. The lungs were evaluated by visual scoring and comparison on a scale of 0-5 (normal to severe; 0-75% of lung parenchyma affected) where affected tissue was described the same as in NH. Absolute number of lungworms were counted unless very large numbers were present in which case they were estimated. Lung and heart tissue was visually evaluated for the presence of other parasites. Histological examination of tissue samples (heart, intestines, kidney, liver, lymph nodes, meninges, pancreas, stomach, and thyroid) was performed at UMAHL for a subset of mortalities.

Estimating total tick abundance on hides

The frozen calf hides were thawed and processed to estimate tick abundance using the method of Welch and Samuel (1989). The hide was pulled flat on a table and cut in half along the dorsal to ventral ridgeline; the lower legs were not included and the head was counted to just forward of the ears. Embedded ticks remained attached to the skin. The right or left side was selected randomly and sectioned into a grid with 10 x 10 cm quadrats; partial pieces were combined. The number of ticks were counted in each 100 cm^2 quadrat by trimming the hair with scissors to the dorsal end of the ticks (~1 cm long), slicing the quadrat into 2 x 10 cm strips, and counting the number of ticks on each strip. Ticks were recorded by life stage (nymph or adult)

and as engorged or not; ticks with >25% body inflation were classified as engorged. Tick density was calculated for each quadrat of the half-hide. Total tick abundance was calculated by doubling the half hide sum and using equations that incorporate tick density (Welch and Samuel 1989). Specifically, total abundance by density was estimated using the average density from 15% of quadrats selected randomly using the equation developed for calves:

$$\text{total abundance} = 4{,}670 + (14\,487 \times \text{number of ticks/cm}^2) \quad \text{(Equation 1).}$$

The total abundance estimate was considered conservative because adult ticks presumably detach after engorgement, others are removed prior to death of the calf, and others are lost during collection and processing of the hide.

Analysis

Annual physical condition, parasite infection, and mortality rate were compared at each study site using the Chi-square independence test and between study sites using Fisher's exact test. Mean number of winter ticks counted at capture was compared between years and study sites using analysis of variance (ANOVA). A multifactorial ANOVA was used to compare tick abundance estimates at capture with physical condition, sex, fate, year, and study site. The ANOVA results were assessed using Tukey's Honestly Significant Difference test. The proportion of ticks in each life stage on collected hides was assessed with linear regression; one outlier with 9.8% engorged nymphs on 17 April was excluded. Analyses were performed using program R (v 3.2.2, Vienna, Austria).

RESULTS

Capture-related data

A total of 179 calves were monitored, 21-37 annually at each study site: 80 (40 M:40 F) in NH and 99 in ME (41 M:58 F). Physical condition was rated for 79 calves in NH and 96 calves in ME. Most NH calves were rated as normal (52%) or thin (46%), with only 2% fat. More ME calves were rated as normal (72%, $P = 0.008$); the remainder was thin (27%) with only 1% as fat. Combined, the physical condition of most calves was normal (66%) and thin (32%), and only 2% fat. Mean tick abundance (undifferentiated by life stage) in both NH and ME was lowest in 2015 and highest in 2016 ($P > 0.05$) and combined counts were 30% higher in 2016 than in 2015 (69 vs. 53; $P = 0.014$, Fig. 2). Males had 25 and 5% fewer ticks than females in NH and ME ($P > 0.05$). Combined, tick abundance was 15% lower on males than females (56 vs. 66 ticks; $P = 0.0017$). In NH, surviving calves had 28% fewer ticks ($P < 0.005$) than those that died, and ME calves had a similar trend with 12% difference ($P > 0.05$, Fig. 3). Combined, survivors had 22% fewer ticks ($P < 0.005$, Fig. 3).

Tapeworm species of the genus *Moneizia* (Minot, 1876) and lungworm species of the genus *Dictyocaulus* were the most prevalent parasites detected in feces (n = 79 NH, 97 ME): 35 and 32% occurrence in NH, and 27 and 28% in Maine. Ova from species of the genus *Nematodirus* (Ransom, 1907) were detected in 9 and 20%, and ova from species in the superclass Coccidia in 1 and 6% of calves in NH and ME, respectively.

Cause-specific Mortality

The 3-year average, winter mortality rate of calves was 73% (range = 62-78%) in NH, 67% (range = 59-71%) in ME, and 70% combined (Fig. 4). The mortality rate of thin calves was

higher than that of normal calves in both states; the rate was significantly higher using combined data (84% vs. 65%; $P = 0.04$). The proportional mortality rate (M:F) was similar in both states (27:33 in NH, 33:34 in ME); the combined mortality rate of females averaged ~8% higher. Mortality was concentrated in March and April in both states (86% in NH and 90% in ME) and was principally associated (91% in NH, 85% in ME) with high infestations of winter ticks; no other prevalent cause of mortality was identified

Gross necropsies of NH calves ($n = 54$) indicated high infestations of winter ticks (enumerated with hide counts), emaciation (BCS < 10**,** body mass = 129 $\pm$ 29 kg), low femur marrow fat by visual inspection and oven-dried mass (15.4% average FMF, range = 6.1-32.5%), and overt signs of anemia including pale gums and organs, and effusions (fluid) within the pericardium and thoracic and abdominal cavities (Table 1). Light (28%), moderate (32%), and severe (26%) hair-loss categories were the most common; 2% had worst case and 11% had no hair-loss. Mean liver iron concentration was considered low: 91 $\pm$ 50 ppm wet weight ($n = 27$). Histologic examination ($n = 29$) in all cases revealed varying degrees of atrophy and loss of adipose tissue, inadequate marrow hematopoiesis, and/or erythropoiesis in femur bone marrow indicating poor condition and increased demand for red blood cells. One NH calf had inflammation in the meninges suggestive of infection with *P. tenuis*; however, winter ticks likely significantly contributed to its death in mid-April, given a low liver iron (23 ppm wet weight) indicative of anemia. Scavenging precluded necropsy of 4 calves and was a consequence of delayed response time (>5 days after death). Lungworm species of the genus *Dictyocaulus* were found in most NH calves (83%) at light (40%) or moderate (29%) infestation level and only 14% had heavy infestation with an estimated maximum of 150 worms; the morphology of a subset ($n = 5$ worms) were similar to *Dictyocaulus eckerti* (Skrjabin, 1931). Histologic assessment

indicated mild to moderate bronchiolitis and bronchopneumonia from intraluminal larval and adult nematodes. Even in cases of heavy infestation, only the dorsal 1/6 of each lung lobe had grossly visible affected tissue due to intraluminal nematodes; however, overall lung function was not considered impaired.

Other parasites identified in gross necropsies or on microscopic examination were *Taenia ovis krabbei* (Linnaeus, 1758) in skeletal muscle, heart, and liver, species of the genus *Sarcocystis* (Miescher, 1843) in skeletal muscle and heart of all moose, *Echinococcus granulosus* in lung tissue of a single calf, and presumed species of the genus *Trichuris* (Roederer, 1761) in the cecum of a single calf. These parasitic infections were regarded as incidental in all cases.

Gross necropsies of ME calves (n = 65) also indicated high tick infestations, emaciation (body scale < 2.5, body mass = 139 ±16 kg), low femur marrow fat by visual inspection (~25% FMF, range = 1.5-85%), and overt signs of anemia including pale gums and organs, and effusions in the pericardium and thoracic and abdominal cavities (Table 1). Most had light (45%) or moderate (39%) hair-loss; 16% had no hair-loss. Mean liver iron concentration was 68 ± 32 ppm wet weight (n = 24). The most prevalent findings from microscopic examination (n = 31) were evidence of anemia (13 calves), enteritis (6 calves), hypothyroidism (19 calves), intestinal and muscular parasitism (8 and 21 calves), and lymphoid atrophy (20 calves). Other findings included 2 calves with traumatic injuries (broken leg and broken rib piercing the thoracic cavity), 1 calf with no incisors, and 4 calves where evidence suggesting anemia was inconclusive and/or co-morbidities were suspected. These changes included renal malformation and bacterial infection (1 calf), rumenitis (1 calf), and inflammation of the meninges or brain of two calves suggestive of infection with *P. tenuis*. In all of these, combinations of emaciation, high infestation of winter ticks, and low liver iron levels suggest that winter ticks likely

significantly contributed to death, as well. Scavenging precluded necropsy of 2 calves. Lungworm species of the genus *Dictyocaulus* occurred in most ME calves (96%) at heavy (44%), moderate (33%), and light (19%) infestation levels; about half (45%) with heavy infestations had >150 adult lungworms (max = 367). The amount of grossly visible affected lung tissue was <25% of the total lung area for most calves (60%); the remainder had up to 50% affected tissue, although no assessment was done on calves with >150 worms.

Other parasites identified in ME during gross necropsies or microscopic examination were *Echinococcus granulosus*, *Taenia ovis krabbei*, and species of the genera *Moneizia*, *Sarcocystis*, and *Trichuris*. *T. o. krabbei* was common in skeletal muscle, heart, and liver of most calves; species of the genus *Moneizia* occurred in the small or large intestine of 2 calves and species of the genus *Trichuris* in the cecum of 2 calves.

Tick Abundance

The mean tick abundance on calf hides (n = 20, 11 F:9 M; all from NH) was 47,371 ticks (SD = 16 441, range = 18 664 – 95 496); mean density was 2.9 ticks/cm^2 (SD = 0.9, range = 1.0 – 4.9). The mean abundance (47 496 ± 24 042) based on the random sample of 15% of quadrats was similar ($P > 0.05$) to the half-hide estimates; individual estimates varied up to 18 - 36% between the methods. The mean coefficient of variation for tick density on 100% of quadrats was 76.9% (range = 57.5 – 126.0%). The proportions of engorged nymphs on the hides declined ($R^2 = 0.87$, $P < 0.001$) and unengorged adults increased ($R^2 = 0.66$, $P < 0.001$) from early February to early April; abundance of adult engorged ticks was low and variable throughout ($R^2 = 0.14$, $P = 0.07$; Fig. 5). Unengorged nymphs and larvae were not present.

DISCUSSION

Use of the combined dataset to describe the two populations was originally justified because of ecological and harvest management similarities and their proximity. Not surprisingly, the level and cause of mortality were similar at both sites, and no substantial differences were evident. Although the rate and degree of lungworm infestation trended higher in ME, this parasite is generally considered a secondary contributor to mortality, and lung impairment was negligible-moderate overall. Consequently, the combined data provide a robust assessment of the regional impact of winter ticks on mortality of 9-12 month-old calves. Winter tick epizootics are typically described as regional events, albeit periodic in frequency (Samuel 2004).

Capture-related data

The physical condition and level of parasitism of most calves at the January captures was normal (66%) or thin (32%) and with high infestation of winter ticks. The substantial proportion of thin calves was interpreted as a reflection of lower than expected body mass and measurement in 2017-2018 found NH calf body mass to be 17.9 kg lower than in northern Maine, a healthier and more productive population (Ellingwood 2018). However, body dimensions (Jones 2016) were similar to those measured in Ontario (Lynch et al. 1995) and Alaska (Franzmann et al. 1978) which suggests that skeletal growth was normal and that nutritional restriction was not compromising dimensional growth (Schwartz and Renecker 2007). The higher tick abundance on calves (January capture) that subsequently died in March-April is evidence of the influence of winter ticks on calf survival and that this measurement is an indicator of that mortality. Other parasites detected are typically not considered pathogenic in moose and are common across

North American moose range (Samuel et al. 1976; Hoeve et al. 1988; Pybus 1990; Lankester and Samuel 2007).

Cause-specific mortality

The predominance of calf mortality (88%) was caused by the effects of high winter tick infestations. General health and disease screening with blood samples did not identify any apparent infectious diseases or obvious nutritional restriction in NH (Jones 2016). The 10-12 month-old calves were emaciated at death with subsequent assessment finding 23% decline in body mass from capture to mortality (Ellingwood 2018) whereas 10-15% decline in body mass over the same ages occurred in Alaska (Franzmann et al. 1978). The NH and ME calves were in a similar state as nutritionally-restricted calves wintering in deep snow in Alaska (Franzmann 2000). Snow depth of 70 cm impedes moose mobility and >90 cm confines movement and increases mortality (Coady 1974); although maximum snow depth was 105 cm and snow >90 cm deep lasted 11 days in 2014, the winter of 2016 had minimal snowpack and the highest annual mortality rate (74%). Similarly, the 2002 epizootic documented in NH with radio-marked calves occurred during a nearly snowless winter (Musante et al. 2010). Although the physical condition at death is suggestive of nutritional restriction or poor habitat, the current availability of optimal foraging habitat (15-20% of the landscape in 4-16 year-old regenerating forest) is similar to that during the period of moose population expansion in the 1980-1990s (Dunfey-Ball 2017), and browsing has not measurably influenced forest regeneration regionally (Bergeron et al. 2011; Andreozzi et al. 2014; Pekins and Morano 2017).

Tick abundance measured at capture was similar in both study areas, as was the occurrence of annual tick epizootics. The necropsy results were consistent with mortality

associated with high infestations of winter ticks (Samuel 2004) and abundance estimates of 30 000-90 000 ticks on 95% of collected hides. These infestation levels cause severe protein and energy imbalance in calves during March-April (Musante et al. 2007). Adult female winter ticks take a blood meal and detach from moose over a 9-10 week period from late February to early May (Drew and Samuel 1989), peaking in weeks 4-6 (early April) when ~50% of blood loss occurs and when mortality was most prevalent. Moose, especially calves, experience an energy and protein imbalance in winter due to a naturally deficient diet (Schwartz et al. 1988), and blood loss associated with continuous nymphal and adult tick feeding since February and peaking in April exacerbates this imbalance. By April, calves have minimal fat reserves and inadequate muscle mass to compensate physiologically for the marked blood loss associated with a high tick infestation, and die from hypoproteinemia and chronic or acute anemia (DelGiudice et al. 1997; Samuel 2004; Musante et al. 2007).

Calves in our study were emaciated, with negligible fat deposits, depleted muscle mass and characteristics of anemia (pale mucous membranes) and hypoproteinemia (subcutaneous edema and cavitary effusions). Femur marrow fat content <10% in calves and <20% in adults is representative of starvation (Franzmann and Arneson 1976; Peterson et al. 1984); <30% has been related to acute malnutrition (Murray et al. 2006). Low liver iron concentrations are indicative of anemia (Carlson and Aleman 2009; Tvedton 2010; Weiss 2010) and concentrations measured here were similar to those in winter tick-infested moose in Minnesota (122 ppm) where calves and adults presumed with anemia had liver iron concentrations 50-80% lower than non-anemic animals (Wünschmann et al. 2015). Although a normal liver iron concentration is not established for moose, non-anemic adults have values of 400-500 ppm wet weight in liver tissue

(O'Hara et al. 2001; Murray et al. 2006; Wünschmann et al. 2015), a concentration that is 5x higher than reported here (83 ppm wet weight).

Tick abundance estimates on hides (95% were >30 000 ticks) indicated moderate-severe infestation levels (Musante et al. 2007), but should be considered conservative because calves died throughout the adult tick disengagement period. Although there was similarity in the abundance estimates between the two methods (doubled half-hide and 15% of quadrats), we recommend the doubled half-hide method because variation in tick density throughout the hide was higher than acceptable for subsampling (20%; Welch and Samuel 1989).

The declining proportion of engorged nymphs over time indicated that most nymphal feeding ended by mid-late March, and the low and stable proportion of engorged adults indicates that adult females detach once engorged (Samuel 2004). Therefore, tick abundance estimates should be considered conservative, and likewise, extrapolated blood loss based on these estimates. Calf mortality in March (26%) suggests that blood loss associated with nymphal feeding certainly influences and likely causes mortality prior to peak adult feeding in April; smaller calves would presumably be at highest risk. Although the quantity of blood removed per individual nymph is less than the 1-3 mL of blood removed per engorged adult female, engorged females represent ~25% of the total infestation, whereas all nymphs (100% of the infestation) take a blood meal, suggesting a large cumulative impact (Samuel 2004).

Moderate to severe infestations (30 000-70 000 ticks) induce an estimated blood loss (adult female ticks only) of 64-149% of the total blood volume in a 150 kg calf over the 8-week adult engorgement period (early March-late April), and 32-75% loss of blood volume during the 2 weeks of peak engorgement. The metabolic demand of such blood loss is 2.7-6.4% of the daily

metabolizable energy requirement over the entire period, and 9.2-12.8% during the peak period. Protein loss via blood removal would be 11.0-82.3 g daily or 33-114% of the daily protein requirement (Musante et al. 2007). This level of tick infestation would lead to chronic anemia with the potential for acute anemia during peak adult tick engorgement, assuming blood loss >40% over a short period of time causes mortality (McGuill and Rowan 1989). This daily protein loss equates to 2-4 weeks worth of the daily requirement for calves, and occurs at a time when energy and protein deficiency peaks (late winter) and calves are in their poorest condition (Musante et al. 2007). Additional blood loss from nymphal feeding in mid-winter likely compounds this deficit and accelerates mortality in compromised calves.

Other parasites observed included *Echinococcus granulosus* (Lichtenwalner et al. 2014), *Taenia ovis krabbei*, and species of the genera *Moneizia, Sarcocystis, and Trichuris*, which are common in moose, but typically have minimal clinical effect at low abundance. Lungworm (species of the genus *Dictyocaulus*) contributes to mortality in elk (*Cervus elaphus* Linnaeus, 1758) infested with winter ticks or in poor nutritional condition (Thorne et al. 2002), and in black-tailed deer (*Odocoileus hemionus columbianus* Rafinesque, 1817) with hair-loss syndrome from biting lice (*Tricholipeurus parallelus* Osborn, 1896) (Bender and Hall 2004). Lungworm is a common and relatively low pathology parasite of moose (Pybus 1990; Lankester and Samuel 2007) and likely contributes to mortality of weakened animals. In ME, where the infestation level and amount of affected lung tissue was highest, it presumably hastened mortality of certain animals. Although mortality unassociated with winter ticks was minor at both sites (~10%) and included traumatic injury/physical impairment and suspected *P. tenuis* infections, we encourage further study of the prevalence and impact of lungworms in regional moose mortality.

SUMMARY

Physical condition and parasite screening was completed on 179 calves captured and radio-marked in NH and ME during January, 2014-2016; 125 (70%) had a mortality assessment in the subsequent 4 months post-capture. High infestation of winter ticks and the resulting emaciation and severe metabolic imbalance from blood loss was found to be the primary cause of mortality in ~90% of these calves. We conclude that the 70% average calf mortality rate in 2014-2016 reflects 3 consecutive years of winter tick epizootics. This duration is similar to the most severe outbreaks recorded in North America (Samuel 2004), and occurred during mild-moderate winters. Regionally, it is suspected that epizootics have occurred in 5 of 10 years since 2007, an unprecedented frequency that reflects the influence of climate change (Dunfey-Ball 2017). Winter tick epizootics are considered abrupt events, typically lasting 1-2 years, and precipitated by the combination of high moose density and favorable conditions for abnormal tick abundance (Samuel 2004, 2007). In contrast, environmental conditions associated with climate change are continual and favorable for winter ticks, specifically later-starting winters that lengthen the autumnal questing period of larvae. We propose that such conditions facilitate frequent and sustained epizootics in the study area despite decline in moose abundance. Perpetuation of these conditions will continue to negatively impact the size, stability, and relative health of this regional population until a host-parasite balance is reached. Identifying the parameters and conditions that influence and sustain the parasitic winter tick-moose relationship in the face of climate change is essential to best manage this regional moose population.

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Tables

Table 1. Assessment of calf (*Alces alces*) mortalities associated with high winter tick (*Dermacentor albipictus*) infestations in northern New Hampshire and western Maine in 2014-2016. FMF = femur marrow fat. Hair-loss based on Samuel (2004).

	n	NH	*n*	ME	*n*	Combined
Mortality period	53	3 Feb – 1 May	57	27 Feb – 2 May	110	3 Feb – 2 May
Body Mass (kg)	35	129 ±29 kg	37	139 ±16 kg	72	136 ±17 kg
% FMF	30	12%	--	--	30	12%
FMF visual estimate	52	<20%	56	26%	108	<25%
Hair-loss Rating		(*n* = 53)		(*n* = 52)		(*n* = 105)
None		11%		16%		14%
Light		28%		46%		37%
Moderate		33%		38%		35%
Severe		26%				13%
Worst Case		2%				1%
Lungworm Infestation		(*n* = 51)		(*n* = 25)		(*n* = 76)
None		18%		4%		13%
Light (<20)		41%		20%		34%
Moderate (20-50)		27%		32%		29%
Heavy (>50)		14%		44%		24%

Figure Captions:

Figure 1. Study areas located in northern New Hampshire (NH) and western Maine (ME), 2014-2016 are shaded in dark gray. Shapefiles from MassGIS (Bureau of Geographic Information), Commonwealth of Massachusetts EOTSS.

Figure 2. Mean winter tick (*Dermacentor albipictus*) count on calf moose (*Alces alces*) captured in northern New Hampshire (NH) and western Maine (ME) in January 2014-2016. Error bars represent standard deviation. *Mean winter tick count differed for 2016 in the Combined dataset ($P < 0.05$). Sample sizes are in parentheses.

Figure 3. Winter tick (*Dermacentor albipictus*) abundance (# of ticks) measured at capture in January by fate of calf moose (*Alces alces*) in northern New Hampshire (NH) and western Maine (ME). Error bars represent standard deviation. *Mean tick abundance differed by survival ($P <0.05$). Sample sizes are in parentheses.

Figure 4. Calf moose (*Alces alces*) mortality rates (%) in northern New Hampshire (NH) and western Maine (ME) in Feb-May, 2014-2016. Mortality rates did not differ between years or study areas ($P > 0.05$). Sample sizes of all radio-marked calves are in parentheses.

Figure 5. Proportion of life stages of winter ticks (*Dermacentor albipictus*) on moose (*Alces alces*) hides collected in northern New Hampshire (NH), winter 2014-2016; $n = 19$.

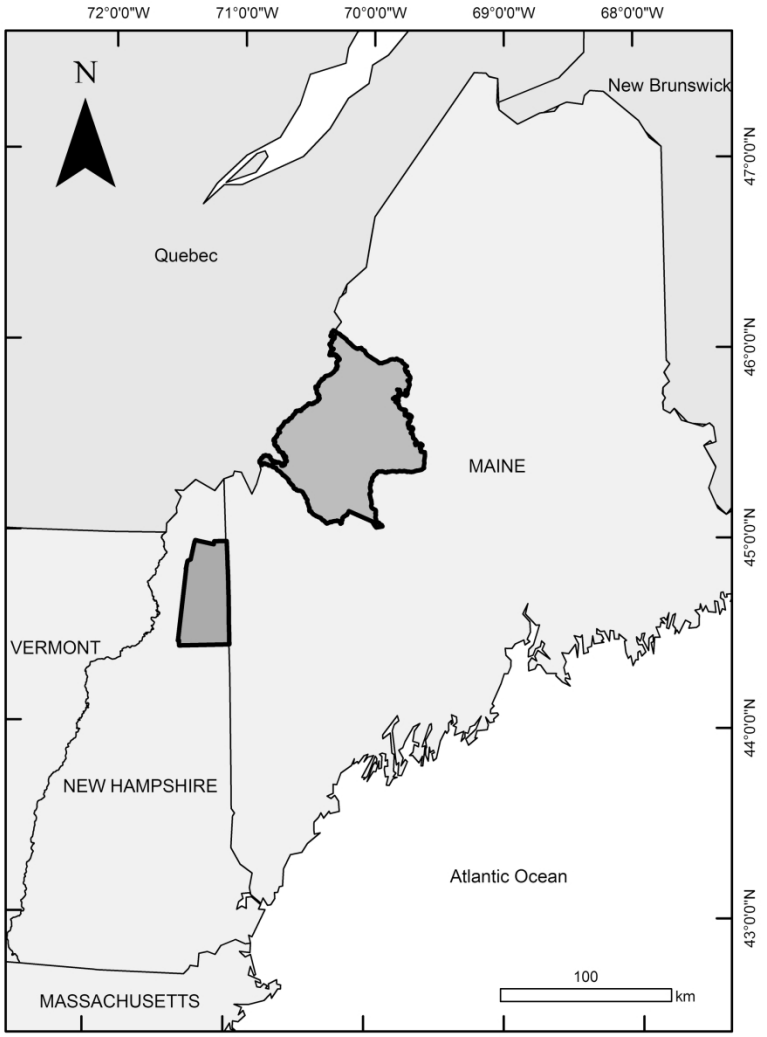

Figure 1. Study areas located in northern New Hampshire (NH) and western Maine (ME), 2014-2016 are shaded in dark gray. Shapefiles from MassGIS (Bureau of Geographic Information), Commonwealth of Massachusetts EOTSS.

215x279mm (300 x 300 DPI)

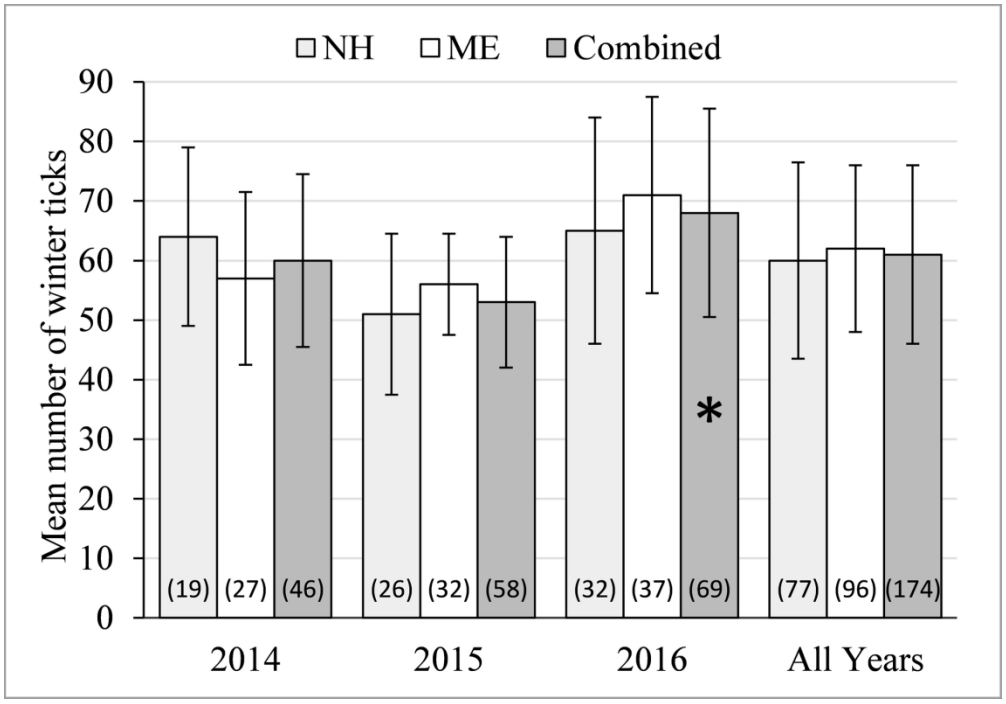

Figure 2. Mean winter tick (*Dermacentor albipictus*) count on calf moose (*Alces alces*) captured in northern New Hampshire (NH) and western Maine (ME) in January 2014-2016. Error bars represent standard deviation. *Mean winter tick count differed for 2016 in the Combined dataset ($P < 0.05$). Sample sizes are in parentheses.

86x59mm (600 x 600 DPI)

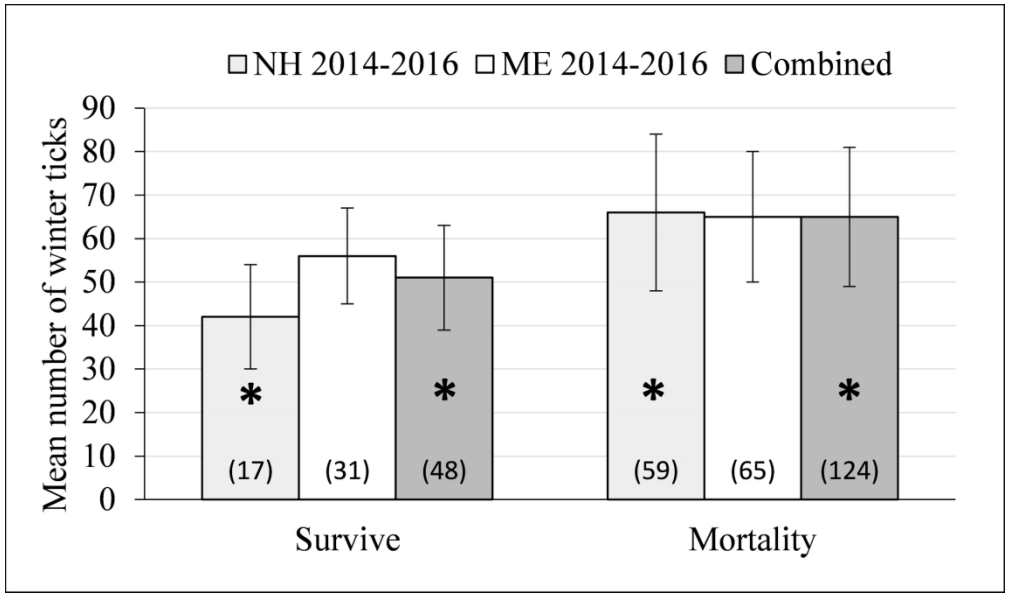

Figure 3. Winter tick (*Dermacentor albipictus*) abundance (# of ticks) measured at capture in January by fate of calf moose (*Alces alces*) in northern New Hampshire (NH) and western Maine (ME). Error bars represent standard deviation. *Mean tick abundance differed by survival (P <0.05). Sample sizes are in parentheses.

86x50mm (600 x 600 DPI)

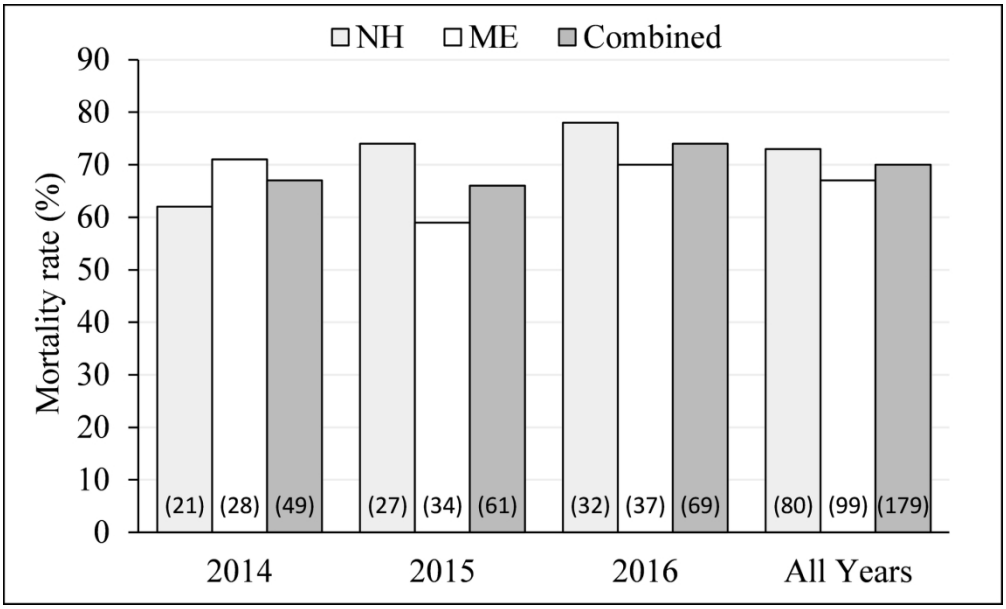

Figure 4. Calf moose (*Alces alces*) mortality rates (%) in northern New Hampshire (NH) and western Maine (ME) in Feb-May, 2014-2016. Mortality rates did not differ between years or study areas ($P > 0.05$). Sample sizes of all radio-marked calves are in parentheses.

86x51mm (600 x 600 DPI)

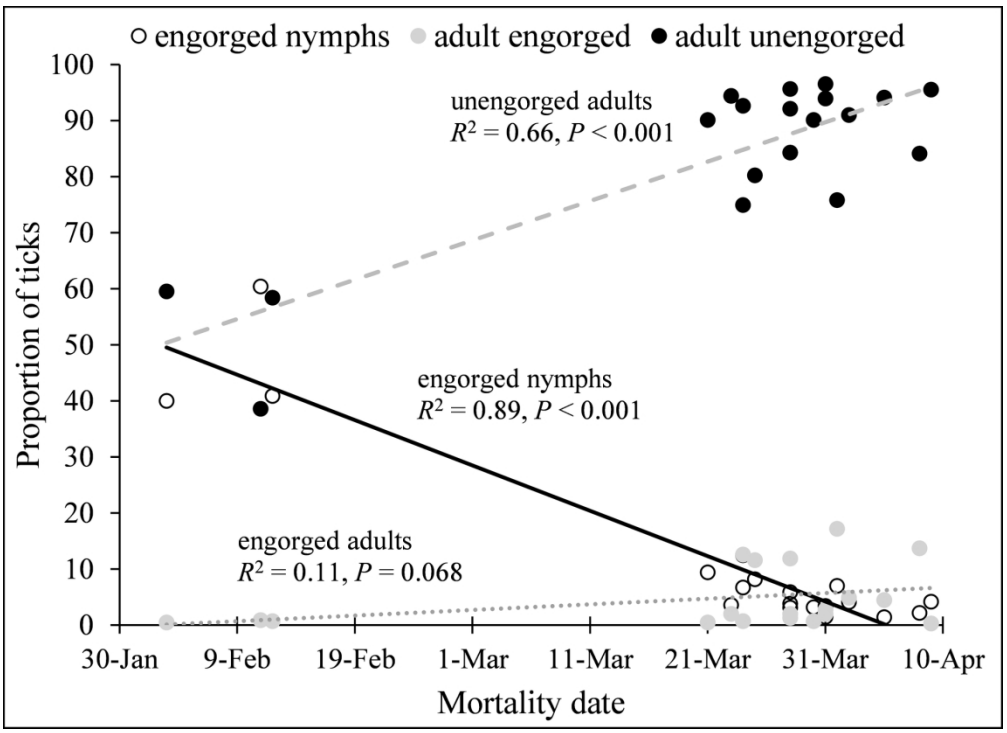

Figure 5. Proportion of life stages of winter ticks (*Dermacentor albipictus*) on moose (*Alces alces*) hides collected in northern New Hampshire (NH), winter 2014-2016; *n* = 19.

86x62mm (600 x 600 DPI)