



BIRTH RATES AND NEONATE SURVIVAL IN A PARASITE RICH MOOSE POPULATION IN VERMONT, USA

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ABSTRACT: Moose (*Alces alces*) populations are declining across much of their southern geographic range in North America. In Vermont and other northeastern states, measurable declines are attributed to low calf survival and reduced productivity associated with persistent winter tick (*Dermacentor albipictus*) parasitism. In 2017–2020, we studied 75 radio-collared female moose (38 calves and 37 adults) in Vermont to examine physiological, spatial, and temporal parameters relative to calf survival and adult productivity. Physiological measures included concentration of fecal glucocorticoid metabolites (fGCM) which reflects stress, and urea nitrogen:creatinine ratios in urine (UN:C) which proxy nutritional state. The pregnancy rate at capture across years was 0.67 (95% CI = 0.50 – 0.80), and was negatively related to presence of lungworm (*Dictyocaulus* spp.). The birth rate calculated as the average number of offspring delivered per adult female was <1.0 overall (2017–2020, LCI = 0.22, UCI = 0.86), similar across years, but increased with age. Logistic exposure models indicated that daily calf survival to 60 d increased as Julian birth date and days since birth increased (log odds = 0.0819, SE = 0.0215). The per capita independence rate, or rate that adult females add independent calves to the population, was negatively related to UN:C ratios and positively with fGCM. Further, this rate was related to autumnal habitat use of adult females; it was greater in home ranges characterized by large amounts of mature (canopy) evergreen forests and wetland habitats, and small amounts of mixed forests and elevation than in ranges with abundant levels of mixed forest at high elevation. We conclude that winter ticks can negatively affect moose fecundity, and efforts to reduce host (moose) density through harvest or parasite (host) abundance through habitat manipulation may improve productivity and recruitment in local moose populations.

ALCES VOL. 58: 51–73 (2022)

Key words: *Alces alces*, birth rate, calf survival, moose, parasitism, population decline, winter tick

The moose (*Alces alces*) is an iconic species ecologically, economically, and culturally important in many regions including the northeastern United States where a major population expansion began in the 1970s in Maine, New Hampshire, and Vermont (Wattles and DeStefano 2011). However, populations in these states have declined

measurably in the last 10–15 years, except in much of central and northern Maine (Timmermann and Rodgers 2005, 2017, Franzmann and Schwartz 2007, Jensen et al. 2018). More specifically, moose at their southern range boundary in northern Vermont and New Hampshire have undergone purposeful harvest reductions (VFWD 2009,

Musante et al. 2010, Jones et al. 2017, Timmermann and Rodgers 2017, Ellingwood et al. 2019, Jones et al. 2019). The Vermont population peaked at ~4,800 individuals in 2005, with highest abundance and density in the northeast corner of the state (VFWD 2009). In response, increased hunting permits were allocated to maintain densities at ecological and cultural carrying capacity (VFWD 2009). However, over the past decade this population has continued to decline (45% since 2010) below the management goal despite reducing hunting permits. By 2017, the statewide population was only ~1,665 moose based on hunter sighting reports (VFWD 2018). Survival analyses of radio-collared moose from 2017 to 2019 indicated that calf survival from January to May was low (<0.50 ; DeBow et al. 2021), and associated with winter tick (*Dermacentor albipictus*) parasitism and other internal parasites like meningeal worm (*Parelaphostrongylus tenuis*) and lungworm (*Dictyocaulus* spp.) (DeBow et al. 2021, Rosenblatt et al. 2021).

Winter tick epizootics, documented in Vermont as part of a larger study, refer to years in which severe parasitism results in calf mortality rates ≥ 0.5 within a given population (Musante et al. 2007). During their questing season in autumn, winter tick larvae attach to moose and take their last and largest blood meal in March–April when calves typically succumb to malnutrition and acute anemia (Musante et al. 2007). The adult females detach after this last meal, lay eggs in the leaf litter, and their subsequent larvae quest in autumn at these sites (Samuel 2004). Blouin et al. (2021a) found that habitat selection by maternal cows during the autumnal questing period (September–November) influenced winter survival of its calf.

Birth rate, defined as the number of calves produced per adult female per year, is a function of age, body size, and individual

health during the autumn breeding season (Saether and Haagenrud 1983, Testa and Adams 1998) with larger females producing calves earlier and more frequently (Adams and Pekins 1995, Testa and Adams 1998). Moose have a relatively low reproductive rate producing single calves most often, with twinning and triplets possible in ideal habitat conditions and population expansion (Boer 1992). For example, historic twinning rates in Vermont from 1993 to 2015 were ~21% (VFWD 2018) but twinning is rare currently. Yearlings (2-year-olds when birthing) are capable of reproduction but have a threshold of 200kg (field-dressed body weight), below which they rarely ovulate (Saether and Heim 1993, Adams and Pekins 1995, Sand 1996). Adult twinning and yearling pregnancy rates are useful indicators of the overall health of a population as they potentially indicate habitat status and/or resource limitation (Franzmann and Schwartz 1985, Boer 1992, Adams and Pekins 1995, Eberhardt 2002, Boertje et al. 2019). However, in adjacent New Hampshire where epizootics occurred in 3 successive years (2014–2016), yearling pregnancy and twinning rates were 0% and the adult birth rate was only 51% in optimal habitat (Jones et al. 2017).

The survival rate of newborns influences population dynamics of large herbivores (Gaillard et al. 2000), with moose calves (<1 year of age) undergoing three distinct stages of development (Franzmann and Schwartz 2007). “Prenatal” is defined as pre-birth or gestational when growth is dependent on the nutritional condition of the dam. The “neonate” stage occurs in the initial 1.5–2 months of life when growth and survival are largely dependent upon the mother’s milk and direct care (Schwartz 1992b, 1992c). “Independence” is when the calf is no longer solely reliant on the direct care of its mother and weaning is mostly complete. Identifying and understanding factors that promote

survival of neonates to independence is especially important when annual recruitment is low as in the Vermont moose population.

The rate at which independent calves enter a population strongly influences long-term population viability (Schwartz 1992b, 1992c). This rate, hereafter the per capita independence rate, encompasses pregnancy, birth, and neonate survival rates in aggregate, and may be measured at the population level as an annual rate or at the individual level. Highly stressed and/or nutritionally deprived adult females are less likely to bring a calf to independence (DelGiudice 1995). Further, pregnant cows that carry a high winter tick load are compromised physiologically, and are likely more susceptible to other diseases, parasites, and predation (Murray et al. 2006, Musante et al. 2007, Pekins 2020). Given that these effects may be cumulative and carry through time (Wingfield et al. 1998, Keech et al. 2000, Parker 2003, Evans et al. 2006), sustained winter tick parasitism is potentially a long-term, disruptive impact to population recovery in Vermont and New Hampshire. In response, we monitored female moose to evaluate factors influencing reproduction and productivity in a population with heavy winter tick parasitism in northeastern Vermont. Our primary objectives were to estimate: 1) pregnancy rate, 2) per capita birth rate, 3) neonate survival to independence (60-days post-partum), and 4) the per capita independence rate. To better interpret these rates, we also evaluated physiological condition of moose in winter and their habitat use patterns during the autumnal questing period of winter ticks.

STUDY AREA

We conducted the study in northeastern Vermont, USA, from 2017 to 2020 within Wildlife Management Units (WMU) E1 and E2 (Fig. 1) due to the relatively high density of moose (~0.39 moose/km²; VFWD 2009).

The study area occurred primarily within Essex County, encompassed 21 townships, and covered 1,738 km². The outer boundaries were U.S. Rt. 2 north to the Canadian border and Rt. 114 east to the Connecticut River; WMU E1 and E2 are separated by VT Rt. 105 with E1 to the north and E2 to the south (Fig. 1).

Forest composition of the study area was largely northern hardwoods. Yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*) were at mid and higher elevations, with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) on most elevated peaks. Lowlands and wet areas were primarily comprised of black spruce (*Picea mariana*), balsam fir, eastern white cedar (*Thuja occidentalis*), and speckled alder (*Alnus incana*). The study area included both federal and state managed forests, and privately owned, actively managed commercial forest. These large ownerships created a mosaic of forest age classes with a constant presence of regenerating forest due to commercial forest harvests (Blouin et al. 2021b). Smaller parcels of private lands were concentrated along the edge of the study area.

Predation pressure on moose is generally low given the extirpation of cougars (*Puma concolor*) and wolves (*Canis lupus*) (DeGraaf and Yamasaki 2001), and few records exist of predation by other large carnivores, including black bear (*Ursus americanus*) and coyotes (*Canis latrans*) despite their common occurrence throughout the study area (DeGraaf and Yamasaki 2001, Musante et al. 2010, DeBow et al. 2021). Vermont's moose harvest is a lottery-based permit system, with total permits set by the Vermont Fish and Wildlife Department (VWFD) to meet population objectives. During the study (2017–2019), a moose hunt was held only in 2017 and 2018 with 40 and 10 moose harvested, respectively (VFWD 2020). Competition from white-tailed

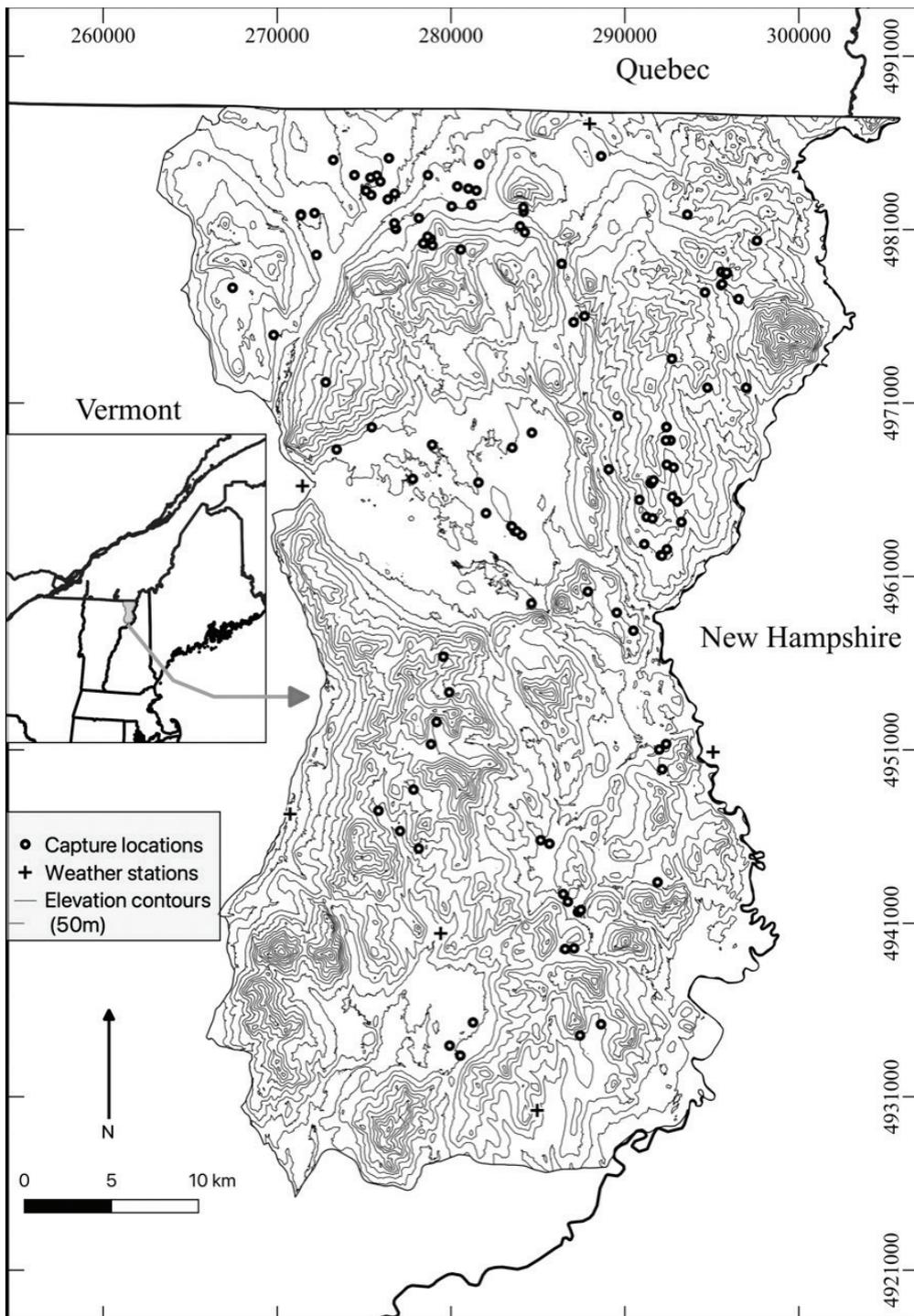


Fig. 1. Study area (1,738 km²) for assessing moose reproductive performance (2017–2019) in northeastern Vermont, USA. The northern boundary adjoins Quebec, Canada and the eastern boundary adjoins New Hampshire, USA. White circles represent locations of radio-collared animals (n = 126). Crosses (n = 4) represent locations of weather stations.

deer (*Odocoileus virginianus*), the only other ungulate, was presumably minimal given the abundance of forage and low deer density ($\sim 7/\text{mile}^2$; VFWD 2020).

We defined annual seasons as summer (June–August), fall (September–November), winter (December–February), and spring (March–May). Ambient temperature can reach 32 °C (~ 17 °C average) in summer and -40 °C (~ -8 °C average) in winter; average daily temperature was ~ 11 °C (National Climate Data Center [NCDC] 2019). Annual precipitation ranged from 100 to 110 cm per year (NCDC 2019) with average snow fall ranging 220–250 cm annually (NCDC 2019); depth varies with elevation.

METHODS

Capture and Health Assessment

We measured pregnancy rates, birth rates, and neonate survival rates by capturing and radio-collaring female moose. We radio-collared adult cows (age ≥ 2) and calves (age ~ 6.5 months) and monitored them from 2017 to 2019 (Fig. 1). Less intensive monitoring occurred in 2020 when neonate survival to 60 d was recorded once in August (see beyond – **Per Capita Independence Rate**). Animals were captured by aerial net-gunning by helicopter and physical restraint during 3–6 day periods in January, 2017–2019 (Native Range Capture Services, Elko, Nevada). Aerial darting (3 mg Carfentanil, reversed by 300 mg Naltrexone; ZooPharm, Windsor Colorado, USA) was used only 3 times in the rare circumstance where netting posed a threat to the health of a target individual.

We fit each moose with a Survey Globalstar V7.1 GPS collar (VECTRONIC Aerospace GmbH, Berlin, Germany) equipped with a very high frequency (VHF) beacon that transmitted from 0600 to 1800 hr and a global positioning system (GPS) sensor that transmitted a GPS location every 13 h. The GPS fix interval

was chosen to ensure fixes would be staggered through time. Collars weighed ~ 0.85 kg; adult collars were sized to the individual, whereas calf collars were sized to 96 cm and retrofitted to individual size with duct tape and medical latex cord to allow for expansion at ~ 1 year as described in Musante et al. (2010). Collars were not designed to detach. Animal capture and handling followed guidelines of the American Society of Mammologists (Sikes et al. 2016) and all protocols were approved by the University of Vermont Institutional Animal Care and Use Committee (protocol #17-035).

Biological samples and physical measurements were collected on all captured animals to gauge individual condition. A body condition score was assigned from palpation of the spine, ribs, and rump: 1-very thin, 2-thin, 3-normal, 4-fat (Hundertmark and Schwartz 1998). Tick abundance was indexed from counts at the shoulder and rump where ticks were counted on four, 10 cm transects in each area (Bergeron and Pekins 2014). Blood (30 mL) was collected from the jugular vein in two, 10 mL clot activator vacutainers and a 10 mL EDTA vacutainer; clot activator vacutainers were spun in a centrifuge for serum and EDTA vacutainers were inverted immediately to ensure mixing. A fecal sample was collected from the rectum for screening to identify and estimate internal parasites at the University of Maine Animal Health Laboratory, Orono, Maine, USA. The McMasters flotation technique was used to determine the number of eggs/g fecal matter for tapeworms (*Moniezia* sp.) and roundworms (*Nematodirus* sp., *Coccidia* spp., and *Strongylidea* sp.), and the Baermann method was used to identify and quantify the number of lungworm larvae (*Dictyocaulus* sp.).

Pregnancy Rate

The pregnancy-specific protein-B test was used with serum samples to measure pregnancy status at BioPRYN WILD, Moscow,

Idaho, USA; accuracy is 99% in non-pregnant cows and 93–95% in pregnant cows. Due to small sample sizes, we evaluated 6 univariate logistic regression models to estimate the probability of pregnancy at capture as a function of individual covariates (Table 1). Individual covariates included body condition score at

capture, year of capture, fecal lungworm, roundworm (*Nematodirus* sp.), eggs per gram (EPG), and tapeworm counts. An intercept model was used to estimate the average rate of pregnancy across cows. Logistic regression analyses were conducted with the `glm()` function in R (R Core Team 2017), and compared

Table 1. Covariates used to assess birth rate, daily survival of neonates, and recruitment of calves to day 60 for moose in northeastern Vermont, USA (2017–2020). Objective number refers to the specifically numbered objectives in the introduction section. Predicted effects are predicted negative (-) or positive (+) effects of a given variable.

Covariate Name	Description	Objective	Predicted Effect	References
Individual Adults				
Year +	Year of capture	1	+/-	Adams and Pekins 1995
Condition	Body condition score of each adult cow at capture (1 = very thin, 2 = thin, 3 = normal, 4 = fat).	1	+	Bergeron et al. 2013; Hundertmark and Schwartz 1998
EPG	Total parasite eggs per gram of fecal matter observed using the modified McMaster flotation technique.	1	-	Murray et al. 2006
Lungworm	Total number of lungworm (<i>Dictyocaulus</i> sp.) eggs observed in feces using the modified McMaster flotation technique.	1	-	Murray et al. 2006
Roundworm	Total number of roundworm (<i>Nematodirus</i> sp., <i>Coccidia</i> spp., and <i>Strongylidea</i> sp.) eggs observed in feces using the modified McMaster flotation technique.	1	-	Murray et al. 2006
Ticks at Capture	Individual tick counts from capture. This is the total number of ticks counted on four 10 cm transects on the shoulder and rump	1	-	Samuel 2004
Age +	Age of adult cow during a given year (2+, 3+, 4+).	2	+	Adams and Pekins 1995
UNC	Urea nitrogen (UN) and creatinine (C; mg/dl) ratio obtained from urine collected in snow during winter months.	4	-	Rosenblatt et al. 2021
fGCM	Glucocorticoid metabolite concentrations (fGCM) collected from fecal pellets obtained during winter months.	4	+	Rosenblatt et al. 2021
QPC1	First principal component describing female core home range habitat during the peak winter tick fall questing period. See Table 2.	4	0	Blouin et al. 2021a

Table 1 (continued)

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Covariate Name	Description	Objective	Predicted Effect	References
QPC2	Second principal component describing female core home range habitat during the peak winter tick fall questing period. See Table 2.	4	-	Blouin et al. 2021a
QPC3	Third principal component describing female core home range habitat during the peak winter tick fall questing period. See Table 2.	4	+	Blouin et al. 2021a
QPC4	Fourth principal component describing female core home range habitat during the peak winter tick fall questing period. See Table 2.	4	-	Blouin et al. 2021a
Interval Neonates				
Birth date	Date of birth for neonate moose as recorded by direct observation.	3	+	Jones et al. 2017
Days Since Birth	Number of days since neonate was born.	3	+	Jones et al. 2017
Collar temperature	Average temperature (Celsius) as recorded by the radio-collar affixed to an adult female.	3	-	Schwartz 2007; McCann et al. 2013
Precipitation	Average daily precipitation during the breeding season (15 Sep–15 Oct) of the breeding season prior to obtaining pregnancy test.	3	+/-	National Climate Data Center
Distance traveled	Average daily linear distance traveled between GPS points during exposure period	3	-	Blouin et al. 2021b
Mean Temp	Average temperature (Celsius) of observation interval as estimated from the National Climate Data Center.	3	-	Schwartz 2007; McCann et al. 2013
Min Temp	Minimum temperature (Celsius) of observation interval as estimated from the National Climate Data Center.	3	-	Schwartz 2007; McCann et al. 2013
Max Temp	Maximum temperature (Celsius) of observation interval as estimated from the National Climate Data Center.	3	+	Schwartz 2007; McCann et al. 2013

with AIC model selection methods (Burnham and Anderson 2002).

Per Capita Birth Rate

We measured birth rates in 2017–2019 from field observations (hereafter “walk-ins”)

conducted on all radio-collared adult cows, including calves that survived to reproductive age (≥ 2 years old). Neonates were tracked on foot with handheld telemetry equipment from 01 May to 31 July. Each animal was tracked to within sighting distance (typically ~20–50 m)

to verify presence of a calf; care was taken to minimize disturbance. Previous fieldwork in New Hampshire and Maine (Jones et al. 2017) and our observations indicate that walk-ins have no apparent effect on calf survival or abandonment.

Visual observation of each cow was attempted 2–3 times weekly each summer season. Presence of a calf was determined by actual sighting or obvious sign (i.e., tracks, beds, vocalizations). The frequency of walk-ins allowed for confident determination of presence or absence of unique events such as twinning. Parturition date was assigned by backdating the estimated age of a calf when first observed. Initial calf age (days) was based on coordination, mobility, wet or dry appearance, and presence of an umbilical cord (Larsen et al. 1989). Adults observed without a calf through 31 July were categorized as non-productive, producing 0 calves.

We used generalized estimating equations (Harden and Hilbe 2003) to estimate population level birth rates (presence or absence of offspring) as a function of year and age, as both are known to influence per capita birth rates. Because teeth were not collected at capture, we assigned each adult cow to one of four age categories: 2, ≥ 3 , ≥ 4 , and unknown. Individuals were classified initially as adult or calf (8–9 months old) at capture. All adults were of “unknown” age the first year but assumed to be ≥ 2 years old. In subsequent years, each adult advanced one year in age, and was classified as ≥ 3 or ≥ 4 depending on the year of study. Surviving female calves were assigned to their appropriate age class in successive years. Further, the age of 16 cows was assigned post-mortem after aging their central incisors. Analyses were conducted with R package, geepack (Højsgaard et al. 2006).

Neonate Daily Survival to Independence

Daily neonate survival was estimated from direct observations (2017–2019) during the

walk-ins. A cow with calf was monitored 2–3 times weekly to document survival of the neonate(s). Loss of a neonate was confirmed from observation of a carcass or by its continual absence in three subsequent walk-ins. In the latter case, the date of death was assigned as the mid-point between its last observation and date first missing (Musante et al. 2010, Jones et al. 2017). When mortality was suspected, we increased observations and field searches for calf sign (beds, tracks, scat). Deceased calves were assessed informally on site to possibly identify cause of death (e.g., predation, broken bones, environmental hazards, malnourishment).

Daily survival rate of unmarked neonates was estimated using the Shaffer logistic exposure model, a generalized linear model that allows for varying visitation intervals (Shaffer 2004). Each period between walk-ins constituted a binomial trial where t = the number of days in the interval, and $\theta = s^t$ was the probability that the calf survives the interval, where s is the daily survival rate that depends on the value of explanatory variables such as individual or temporal covariates (Shaffer 2004). Exposure intervals were created for each neonate from the date of birth to date of death or 60 d (independence from mother), whichever came first. The interval length was computed as the number of days between walk-ins, with calf fate (survive or die) assigned each interval.

The Shaffer logistic exposure model easily incorporates both interval-specific and individual covariates to assess their effects on daily survival. For each neonate, we measured interval-specific variables (averages) including calf age and local weather conditions from NOAA stations (precipitation, minimum, mean, and maximum temperature; Table 1). We used the R package adehabitatLT (Calenge 2006) to compute the average distance moved by

each cow in each interval. Individual neonate covariates included Julian birth date and age (d) (Table 1).

We constructed 13 univariate and additive models that combined temporal and individual covariates (informed by studies cited previously) to estimate daily survival probability (Table 1); models were ranked using AICc (Burnham and Anderson 2002). Assumptions described by Shaffer (2004) included: 1) neonates were accurately aged at first sighting, 2) fate was accurately determined, 3) field observations did not influence survival, and 4) neonates survived or failed independently of one another. We implemented the Shaffer logistic exposure model in R with the glm function that used the Shaffer logistic exposure link function provided by Bolker (2019).

Per Capita Independence Rate

We assessed the adult per capita independence rate (the probability an adult cow produces an independent calf) in two ways. First, for a subset of adult cows ($n = 44$), we collected urine and fecal samples from 20 January to April 7 (2017–2019) to measure fecal glucocorticoid metabolites (fGCM) concentrations and urea nitrogen:creatinine ratios (UN:C) as proxies for chronic stress and nutritional restriction, hypothesizing that neonate survival is related to the cow's physiological condition. We used GPS locations, VHF radio-telemetry, and tracking to collect random “fresh” samples of 5–7 fecal pellets and 10 mL of snow urine from each defecation or urination site located. Cow and calf samples were distinguished by the size of tracks, pellets, or back tracking for positive identification. Samples were collected with a rubber glove to minimize contamination. Samples were stored in a Whirl-Pak (Nasco, Madison, Wisconsin, USA) and frozen at -20°C . Fecal samples were shipped overnight for subsequent

steroid and protein extraction; steroid metabolites were extracted by boiling approximately 0.2 g of dried material in 10 mL of 95% ethanol, after which the supernatant was dried and reconstituted in 1 mL of 95% methanol. Enzyme-linked immunosorbent assays were used to quantify fGCM concentrations (ELISA; Enzo Life Sciences ADI-900-071). We melted snow urine samples and subsampled 1 mL of urine to measure urea nitrogen (UN) and creatinine (C) concentration (mg/dL) (Biovet, Inc., Barneveld, Wisconsin, USA). These data were expressed as a ratio (UN:C) and ratios were then \log_e -transformed to normalize variance (see Rosenblatt et al. 2021 for additional details).

We used generalized estimating equations (Harden and Hilbe 2003) to estimate per capita independence rate (at the population level) as a function of the annual median fGCM and UNC concentrations of the adult cow. Random effects were included because certain individuals were represented multiple years. Second, we summarized the per capita independence rates per breeding cow as the total number of offspring reared to day 60 out of total number of years observed. We included 2020 observations in this analysis, although cows were observed only once (in August ~60–90 days post-partum) to determine presence of a calf. We related these rates to the habitat conditions in each cow's average core home range during the autumnal questing period of winter ticks. To describe habitat in the core range, we used 4 recently developed Principal Component Analysis rasters that included 30 m² land cover composition (deciduous forest, coniferous forest, mixed forest, and wetland from the National Land Cover Data, NLCD 2019), 30 m² layers describing terrain characteristics (elevation and slope) (VCGI 2002), and 10 m² lidar (light detection and ranging) variables

Table 2. A Principal Component Analysis of landcover and lidar variables that described moose habitat in northeastern Vermont, USA. Evergreen, deciduous, mixed, and wetland describe habitat composition as measured by the National Landcover Database (30 m² pixel resolution; 2016). Canopy (vegetation > 6 m), Cover (vegetation between 3 – 6 m), Forage (vegetation < 3 m), and Shrub (vegetation between 0.2 and 2 m) describe habitat structure as measured through 10 m² lidar imagery (USGS 2016) rescaled to 30 m². The elevation raster from VCGI (Vermont Center for Geographic Information 2002) provided elevation in meters. The cumulative proportion indicates that the first four components explain 78% of the total variance of the data.

Variable	QPC1	QPC2	QPC3	QPC4	QPC5	QPC6	QPC7	QPC8	QPC9
Cumulative Proportion	0.33	0.55	0.67	0.78	0.87	0.94	0.99	1.00	1.00
Evergreen	0.15	0.42	0.54	0.19	0.53	0.03	0.11	0.44	0.00
Deciduous	-0.35	-0.46	-0.03	0.27	-0.02	0.22	-0.45	0.59	0.00
Mixed	0.05	0.47	-0.57	-0.40	-0.07	0.21	0.02	0.49	0.02
Wetland	0.35	-0.07	0.32	0.08	-0.74	0.07	0.32	0.33	-0.01
Canopy	-0.33	0.36	0.25	0.06	-0.21	0.73	-0.14	-0.32	0.00
Cover	0.25	0.42	-0.07	0.37	-0.25	-0.33	-0.64	-0.07	-0.17
Forage	0.53	-0.12	-0.14	0.17	0.13	0.30	-0.15	-0.10	0.72
Shrub	0.49	-0.22	-0.16	0.10	0.21	0.41	0.02	-0.07	-0.67
Elevation	-0.21	0.14	-0.40	0.74	0.00	0.00	0.48	-0.01	0.02

(USGS 2016) that characterized forest age structure (Table 2; see Blouin et al. 2021a, 2021b). Each raster was rescaled to a 200 m² resolution where pixel values provided the average of the underlying cells (Fig. 2). The home range cores were 50% fixed kernels (Worton 1989) using radio-collar locations between 19 September and 15 November, the peak questing period of winter ticks in the region (Healy et al. 2018); analyses were performed in R package ade-habitatHR (Calenge 2006). Home ranges were overlaid on the 4 QPC (fall questing principal component) rasters, and average home range QPC scores were calculated by individual across years. We used binomial regression to analyze the successful rate to independence (fractions that represent the number of successes in n trials), where successes were the number of years in which an adult female successfully reared a calf to independence, and trials was the number of years the adult was alive in May to give

birth. We used the glm() function in R to fit the model (successes, trials) ~ QPC1 + QPC2 + QPC3 + QPC4.

RESULTS

We captured and radio-marked 37 cows and 38 female calves (~8 months old); none were recaptured. Survivors remained in the study, increasing in age class through time. Tick counts ranged from 4–98 (median = 19.0) on cows and 0–84 on calves (median = 29.7). Mean body condition at capture was 2.83 and 2.57 (3 = normal) for cows and calves, respectively (see DeBow et al. 2021).

Pregnancy Rate

The average, 2-year rate (2017 and 2018) was 67% (24 of 36); 19 of 30 (63%) in 2017 and 5 of 6 (83%) in 2018. The intercept model predicted a similar pregnancy rate (0.67, 95% CI = 0.50 – 0.80, Table 3). Only lungworm level was negatively related to pregnancy rate ($z = -2.31$; Table 3).

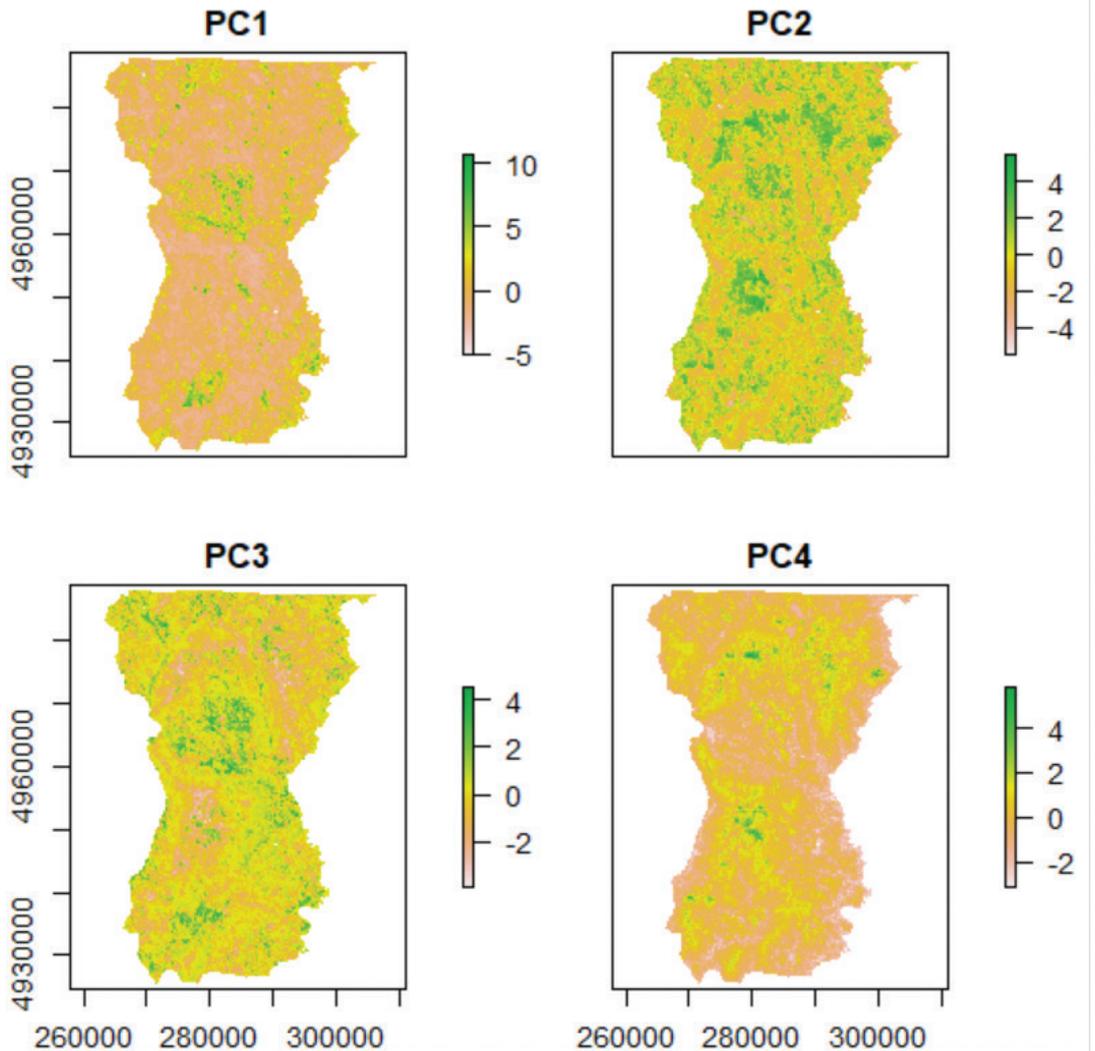


Fig. 2. Mapped distribution of four principal components describing habitat variables for moose in northeastern Vermont, USA. Each component is a combination of structural components (represented by lidar data; USGS 2016) and composition variables (represented by NLCD data; NLCD 2019), meters for elevation, and degrees for slope. See Table 2 for loadings. Cell size is 200 m² and axes include UTM (Universal Transverse Mercator) Easting and Northing coordinates.

Per Capita Birth Rate

The overall birth rate was 0.57 (63 of 110) ranging from 0.62 (26 of 42) in 2018 to 0.53 (21 of 40) in 2019. Yearling (age = 1–2) and adult (age \geq 3) birth rates were 0.08 (1 of 13) and 0.64 (62 of 97), respectively. Twinning was documented once only (2017; rate = 0.01). The mean and median birth date were both 18 May, with 87% of births (55 of 63)

within one week of this date. The annual mean birth date was 18, 17, and 21 May in 2017, 2018, and 2019, respectively. The earliest and latest births were 07 May 2019 and 06 June 2019.

The annual birth rate estimated with generalized estimating equations was similar among years (2017 CI = 0.25 – 0.85; 2018 CI = 0.34 – 0.89; 2019 CI = 0.12

Table 3. Logistic regression model selection results examining probability of pregnancy of adult female moose at capture ($n = 36$) in northeastern Vermont, USA (2017–2018) as a function of individual covariates. EPG = Total parasite eggs per gram of fecal matter using the modified McMaster flotation technique. Please see Table 1 for covariate terms.

Model	K	LL	AICc	Delta AICc	AICc Wt	Parameter	Estimate	Std. Error	z value	Pr(> z)
Lungworm	2	-17.24	38.84	0.00	0.96	Intercept	1.38	0.46	2.98	0.0048
						Lungworm	-1.72	0.75	-2.31	0.0280
Condition	2	-21.64	47.64	8.80	0.01	Intercept	-2.93	2.35	-1.25	0.1834
						Condition	1.29	0.83	1.55	0.1200
Intercept	1	-22.91	47.95	9.10	0.01	Intercept	0.69	0.35	1.96	0.0584
Year	2	-22.42	49.20	10.36	0.01	Year 2017	0.55	0.38	1.44	0.1409
						Year 2018	1.06	1.16	0.92	0.2620
EPG	2	-22.79	49.94	11.10	0.00	Intercept	0.77	0.39	1.98	0.0560
						EPG	-0.01	0.03	-0.51	0.3509
Roundworm	2	-22.88	50.12	11.27	0.00	Intercept	0.73	0.37	1.94	0.0608
						Nematodirus	-0.01	0.03	-0.28	0.3836
Ticks	2	-22.91	50.18	11.34	0.00	Intercept	0.74	0.56	1.33	0.1651
						Ticks	0.00	0.02	-0.11	0.3967

Table 4. Generalized estimating equation for birth rate of adult female moose in northeastern Vermont, USA (2017–2019). Coefficients are on the log-odds scale. LCI = lower 95% confidence interval; UCI = upper 95% confidence interval.

Parameter	Estimate	Std Error	Wald	Pr(> W)	Birth rate LCI	Birth rate UCI
Intercept (Age 3, 2017)	0.316	0.712	0.197	0.657	0.25	0.85
Year 2018	0.741	0.710	1.091	0.296	0.34	0.89
Year 2019	-0.620	0.688	0.814	0.367	0.12	0.67
Age > 4	0.960	0.640	2.246	0.134	0.43	0.90
Age 2	-3.266	1.105	8.731	0.003	0.00	0.25
Unknown	-0.223	0.718	0.096	0.757	0.16	0.77

- 0.67), but increased with age (Table 4). As with pregnancy rate, birth rate by yearlings was significantly lower (CI = 0 - 0.25) compared with older age groups (e.g., age > 4, CI = 0.43 - 0.9). The degree of uncertainty in classifying age groups combined with small sample size led to imprecise estimates of birth rates (Table 4); however, rates were <0.9 across years and ages.

Neonate Daily Survival to Independence

Neonate survival to 60 d post-parturition was 0.67 (42 of 63 calves) overall; annual survival was 0.63 (10 of 16), 0.69 (18 of 26), and 0.67 (14 of 21) in 2017, 2018, and 2019, respectively. Only one yearling produced a single calf during the study; that calf survived to 60 d. The average date of death ($n = 21$) was 9.6 d post-partum (range = 1–57 days),

with the majority (80%) occurring within 2 weeks; cause(s) of death was unknown.

Relative to daily probability of calf survival (Shaffer 2004), the “days since birth model” was the top-ranked carrying 55% of weight in the model set (Table 5); probability of daily survival increased with calf age (Fig. 3). The second-best model included days since birth (+ effect) and Julian day of birth (- effect) and accounted for 30% of the weight in the model set; however, because confidence intervals for Julian day of birth crossed 0 and the model’s likelihood was negligibly better than the top model, it was dropped from consideration (Table 5). Neonate daily survival from the top model was estimated as 0.97 (0.94 to 0.98, 95% CI) on day zero (day of birth) and increased steadily over time. Daily survival was nearly 1.0 (0.997) by 30 d post-partum, and 0.999 at 60 d (Fig. 3). Cumulative survival from age 0 to 60 d was at 0.65 (95% CI = 0.44 to 0.79). We detected no signal related to year, daily movement, or temporal conditions.

Per Capita Independence Rate

The independence rate per breeding adult (success rate; calf survived to 60 d) was measured in 116 events with 43 cows. As expected, the yearly sample and rate (binomial trials) varied individually because annual captures of adult cows differed, certain calves survived to reproductive age, and annual mortality of cows: 12 cows were observed 1 year, 8 in 2 years, 3 in 3 years, and 19 in all 4 years of the study. The individual success rate (binomial range = 0–1) ranged from 0 to 1, with just one female rearing a calf to independence all 4 years; only 7 cows had a success rate > 0.75. The rate increased with the median fGCM concentration and decreased with the median UN:C ratio (2017: $n = 3$; 2018: $n = 20$; 2019: $n = 21$) (Fig. 4; Table 6).

The success rate was positively related to questing home range as defined by QPC3 (Fig. 5, Table 6). Cows with core ranges characterized by large amounts of mature (canopy) evergreen forests and wetland habitats, and small amounts of mixed forests and elevation, had a higher average success rate than those with core ranges at high elevation with abundant mixed forest. None of the other PC variables (QPC1, QPC2, QPC4) were significant ($\alpha = 0.1$; Table 6).

The four uncorrelated components described 78% of the total variance of the habitat variables (Table 2). QPC1 was positively related to younger (shrub/forage) wetland habitat, and negatively related to the proportion of mature deciduous forest. QPC2 was positively related to mixed and evergreen forests that were more mature in structure and negatively related to early succession (shrub/forage) deciduous forests. QPC3 was positively related to mature (canopy) evergreen forests and wetland habitats and negatively related to mixed forests and elevation. QPC4 was positively related to higher elevation deciduous and evergreen forests of all age classes and negatively related to mixed forest composition (Table 2, Fig. 2).

DISCUSSION

Recent declines of moose populations in several regions along their southern range boundary in North America present unique management challenges in maintaining sustainable, viable populations (Timmermann and Rodgers 2017). These declines are compounded by a low-moderate fecundity and reflect the demographic vulnerability of peripheral populations to changing environmental conditions (Ruprecht et al. 2016). Not surprisingly, we found that birth rate and productivity increased with age, yet significant annual variation existed. The overall adult pregnancy rate was 0.67, a 48% reduction relative to the average corpora lutea count of 1.3

Table 5. AICc and parameter estimates of 13 univariate and multivariate logistic exposure models (Shaffer 2004) used to estimate moose calf survival to 60 days in northeastern Vermont, USA (2017–2019). Both univariate and additive models that combined temporal and individual covariates were considered. Coefficients are on the log-odds scale. UCI and LCI represent 95% upper and lower confidence intervals, respectively.

Model	LL	AICc	Delta_AICc	AICcWt	Parameter	Estimate	Std. Error	UCI	LCI
Days Since Birth	-75.90	155.80	0.00	0.55	Intercept	3.37	0.36	4.08	2.66
					Days Since Birth	0.08	0.02	0.12	0.04
Days Since Birth + Birth date	-75.55	157.10	1.24	0.30	Intercept	8.58	5.76	19.87	-2.70
					Birth date	-0.04	0.04	0.04	-0.12
					Days Since Birth	0.08	0.02	0.12	0.04
Year + Days Since Birth	-75.50	159.00	3.21	0.11	Intercept	3.04	0.50	4.01	2.07
					2018	0.43	0.56	1.53	-0.67
					2019	0.51	0.61	1.71	-0.69
					Days Since Birth	0.08	0.02	0.12	0.04
Day Of Year	-78.50	161.00	5.17	0.04	Intercept	-5.23	2.59	-0.15	-10.31
					Julian	0.06	0.02	0.10	0.03
Max Temp	-82.90	169.80	14.03	0.00	Intercept	0.87	1.08	2.98	-1.24
					Max Temp	0.20	0.05	0.30	0.10
Min Temp	-85.35	174.70	18.84	0.00	Intercept	3.70	0.50	4.68	2.73
					Min Temp	0.18	0.07	0.31	0.06
Birthday + Temp + Precipitation	-83.65	175.30	19.48	0.00	Intercept	13.26	5.75	24.53	2.00
					Precipitation	-0.07	0.07	0.06	-0.20
					Min Temp	0.23	0.07	0.37	0.08
					Birth Julian	-0.07	0.04	0.01	-0.15
Min Temp + Precipitation	-84.85	175.70	19.92	0.00	Intercept	3.77	0.50	4.75	2.79
					Precipitation	-0.07	0.07	0.06	-0.21
					Min Temp	0.21	0.07	0.34	0.07
Intercept	-89.60	181.20	25.42	0.00	Intercept	5.18	0.24	5.64	4.71
Birthdate	-89.00	182.00	26.17	0.00	Intercept	11.91	5.77	23.21	0.60
					Birth Julian	-0.05	0.04	0.03	-0.13
Distance traveled	-89.30	182.60	26.80	0.00	Intercept	4.97	0.35	5.65	4.29
					Distance traveled	0.00	0.00	0.00	0.00
Precipitation	-89.60	183.20	27.42	0.00	Intercept	5.15	0.34	5.82	4.48
					Precipitation	0.01	0.08	0.16	-0.14
Year	-89.10	184.20	28.41	0.00	Intercept (2017)	4.80	0.41	5.60	3.99
					2018	0.53	0.56	1.63	-0.57
					2019	0.52	0.61	1.72	-0.67

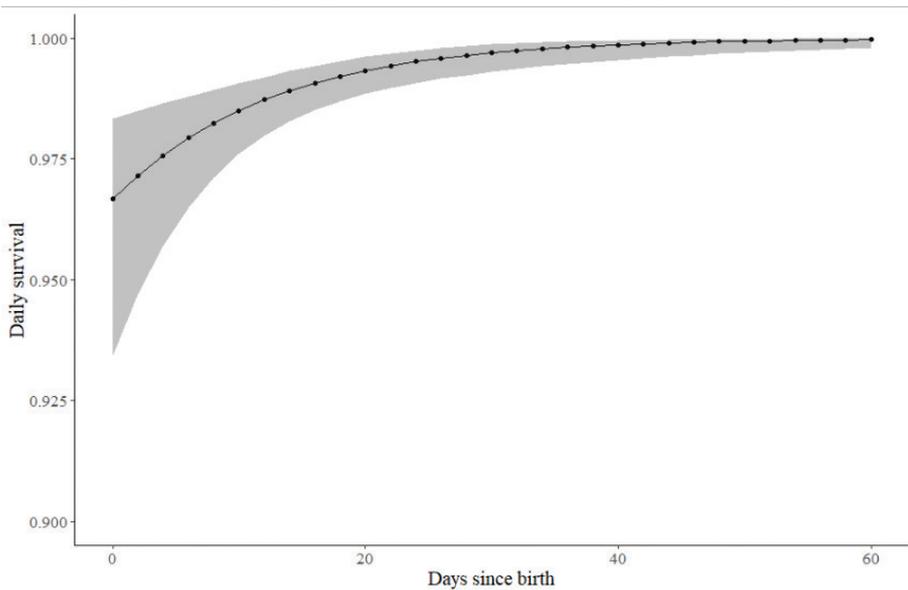


Fig. 3. Daily survival estimates of neonate moose in northeastern Vermont, USA based on days since birth as estimated from the Shaffer logistic exposure survival model (2004). Shaded areas indicate the 95% confidence intervals.

in >3 year-old cows in 2003 when the population was >2 × larger and less impacted by winter ticks (VFWD 2009). The negative relationship between lungworm infestation and pregnancy may signify an additive and compounding effect to winter tick parasitism that reduces fitness and ovulation rate (Ballweber 2021). Likewise, the low birth rate of adult cows (0.57) and the single case of twinning suggests that nutritional condition (fitness) of cows was possibly compromised early in the reproductive cycle.

Calf age was the strongest predictor of daily survival, similar to observations in New Hampshire (Jones et al. 2017) and Minnesota (Severud et al. 2019), and as in white-tailed deer (Gaillard et al. 2000) and red deer (*Cervus elaphus*) (Smith and Anderson 1996). However, the overall survival rate to 60 d was ~0.67, measurably lower than elsewhere in North America (Boer 1992, Schwartz 1992c, VFWD 2009, Boertje et al. 2019) and expected at the study area latitude (Ruprecht et al. 2016). It was less than in New Hampshire

(0.77) and Maine (0.94) in related studies conducted with alike methods (Jones et al. 2017), as well as in New Hampshire (0.71) in 2002 to 2005 (Musante et al. 2010). Although documenting births and calf survival can be challenging and uncertain at times, as in earlier research (Jones et al. 2017), we used highly trained field staff to maintain continuous and intensive monitoring each summer (~1700 observations) to ensure continuity with regional datasets.

The low birth, calf survival, and independence rates we found suggest a declining population occupying sub-optimal habitat with limited resources (Franzmann and Schwartz 1985, Boer 1992, Malmsten et al. 2014, Blouin et al. 2021b). Moose in adjacent northern New Hampshire and central Maine have similar characteristics, yet regional habitat there and in our study area is considered near optimal for moose as commercial timber harvests provide constant availability of regenerating forest (Dunfey-Ball 2017, Jones et al. 2017, 2019, Blouin et al. 2021b).

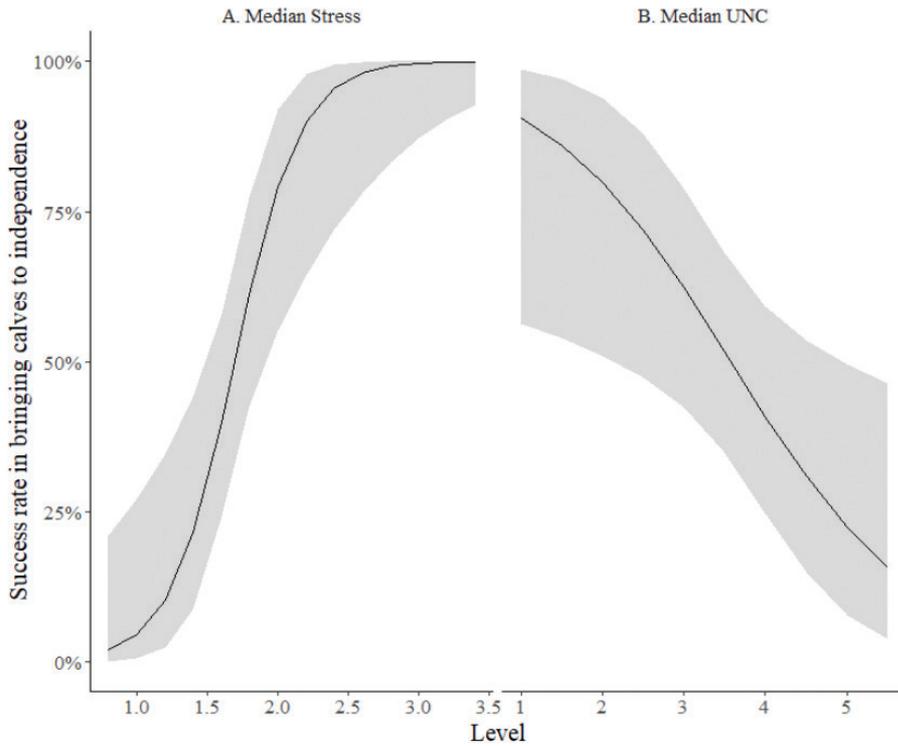


Fig. 4. Relationships between binomial independence probability (the proportion of successful rearing of offspring to day 60 out of total years observed per female) and median fecal glucocorticoid metabolites (fGCM) concentrations, which is a proxy for stress, (left) and median UN:C ratios (right). Analyses were based on 25 individual adult female moose in northeastern Vermont, USA (2017–2019).

Table 6. Generalized estimating equations relating the binomial probability of successfully rearing moose offspring to day 60 (independence rate) in northeastern Vermont, USA (2017–2020) as a function of fall questing habitat (Questing HR) and average physiological metrics from fecal and urine samples collected from January to April. ¹fGCM = concentration of fecal glucocorticoid metabolites. ²UNC = urea nitrogen:creatinine ratio.

Analysis	Parameter	Estimate	Std. Error	z	Pr(> z)
Questing HR	Intercept	-0.135	0.247	-0.550	0.584
	QPC1	0.031	0.199	0.150	0.878
	QPC2	-0.190	0.315	-0.600	0.546
	QPC3	0.633	0.380	1.660	0.096
	QPC4	0.669	0.502	1.330	0.183
Physiology	Intercept	-4.437	1.936	5.250	0.022
	fGCM ¹	4.343	1.427	9.270	0.002
	Median UNC ²	-0.875	0.369	5.620	0.018

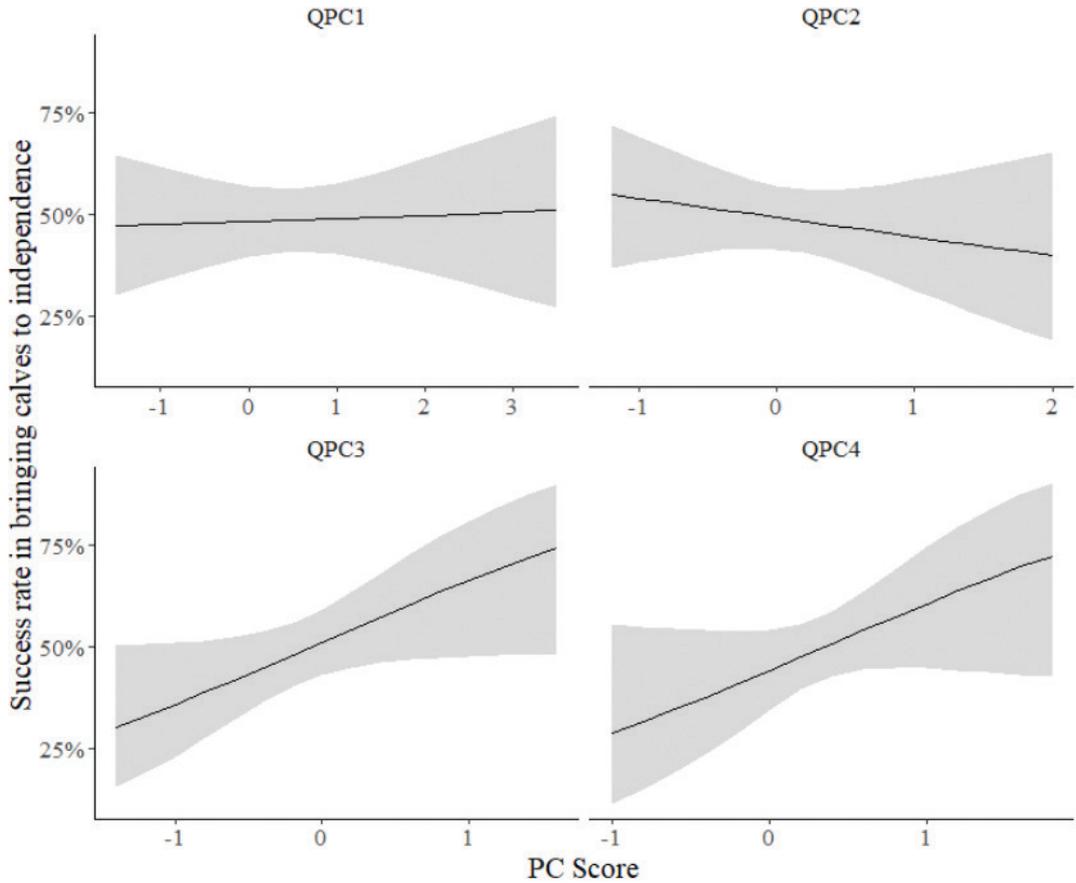


Fig. 5. Binomial independence probability (the proportion of successful rearing of offspring to day 60 out of total years observed per adult female moose) in relation to their average home range habitat condition during the winter tick fall questing period. The binomial success rates in adding a calf to independence was positively related to questing home range as defined by QPC3, which was positively influenced by mature (canopy) evergreen forests and wetland habitats and negatively influenced by mixed forests and elevation. Analysis was based on 25 individual adult female moose in northeastern Vermont, USA (2017–2019).

Although habitat quality and forage resources influence reproductive performance, our study area consisted of ~35% optimal moose habitat based on availability of regenerating forest, including adequate winter range (Dunfey-Ball 2017). A more recent analysis of habitat using fine-scale (10 m²) lidar derived variables documented that 34% of the study area consisted of vegetation <3 m tall (Blouin et al. 2021b), providing an optimal source of moose forage and important

component of a reproductive cow's home range. Although we did not evaluate the nutritional landscape in terms of forage quality, moose forage on a wide variety of plants, with forage quantity (consumption) most important to nutritional condition (Shipley 2010).

The regional frequency of winter tick epizootics – 5 in 6 years (2014 to 2019; Jones et al. 2019, Powers 2019, DeBow et al. 2021) – is historically unique (Samuel 2004)

and arguably, strongly influenced dynamics of the study population. The bioenergetic impacts associated with this sustained level of parasitism directly affects ovulation rate, gestation, birth rate, lactation, maturation, and recruitment in moose (Musante et al. 2007, Jones et al. 2017, 2019, Pekins 2020). Although we did not collect specific health-related metrics post-capture, the average condition score of cows and calves at capture was below “normal,” indirect evidence that moose were compromised by winter tick parasitism in good habitat. Although we could not definitively parse out the relative influences of predation, habitat condition, or parasitism, the latter two factors are presumably most important because predation is limited to nominal loss of neonates to black bears (Jones et al. 2017). Further, regional research indicates that climate change and macro- and microhabitat use influence winter tick abundance and infestation of moose (Dunfey-Ball 2017, Jones et al. 2019, Pekins 2020, Powers and Pekins 2020, Blouin et al. 2021a, 2021b, Rosenblatt et al. 2021).

Blouin et al. (2021a) found a relationship between habitat use by maternal cows during the questing period of winter ticks (autumn) and winter survival of its calf. Cows with surviving calves used areas with greater proportions of young (shrub/forage) deciduous forests, and with higher proportions of mature (canopy) evergreen or mixed forests and wetlands at lower elevations (Blouin et al. 2021a, +QPC3 effect). Likewise, we found that these same habitat features were related to the independence rate (+QPC3; Tables 2 and 6). Healy et al. (2018) found overlapping habitat use by cows in autumn and spring, and more specifically, Blouin et al. (2021a) found a relationship between that specific overlap and cows that lost their calf. Both studies suggest a self-sustaining cycle of winter tick

parasitism associated with regenerating forest, specifically, optimal foraging habitat that harbors highest abundance of winter ticks (Powers and Pekins 2020) due to seasonal foraging preferences of moose.

Further, signals in fecal stress metabolite concentrations and UN:C ratios reflected the low independence rate presumably related to declining nutritional condition from winter tick infestation (Pekins 2020). Specifically, UN:C ratios in calves (Ellingwood et al. 2019, Rosenblatt et al. 2021) are positively related to the adult engorgement period of winter ticks that coincides with highest calf mortality. However, these metrics can be influenced by multiple variables including weather, habitat, and nutritional condition that often change through time. We found a negative relationship between UN:C ratios and overall probability of recruiting calves to independence, but surprisingly, a positive relationship with fGCM. Elevated fGCM concentrations in cows that successfully recruit a calf may indicate maternal programming to better cope with adverse conditions (Sheriff et al. 2017), or may simply reflect the influence of pregnancy on fGCM concentrations (Dantzer et al. 2014). The negative correlation between UN:C ratios and recruitment aligns with our understanding of the physiological toll of winter ticks on calves and cows during the final trimester of pregnancy (Keech et al. 2000, Pekins 2020).

A plausible hypothesis explaining low birth and calf survival rates of moose is the nutritional demand of increased and compounding parasitism from winter ticks (Jones et al. 2019, Pekins 2020). Further, adult reproduction is likely impacted through the nutritional costs of repeated winter tick parasitism (Samuel 2004, Pekins 2020), reducing a cow's ability to recuperate with each event. To compensate, cows may give birth to

compromised calves with low survival and predetermined mortality (Schwartz 1992a, 1992c) or fail to reproduce in successive years (Jones et al. 2019); either scenario aids subsequent recruitment through increased compensatory growth and fitness of that individual cow (Pekins 2020). Further monitoring of these temporal effects of winter tick parasitism may provide comprehensive understanding of the complex relationships among parasitism, reproduction, and population dynamics in moose.

MANAGEMENT IMPLICATIONS

Given that our study was conducted during a period of sustained winter tick epizootics, the low birth and calf survival rates were most likely a direct result of high and incessant parasitism. Winter tick abundance on the landscape would need to decline to counteract this effect by disrupting the host-parasite relationship. Moose (host) population reduction would theoretically decrease the distribution, abundance, and density of winter ticks on the landscape, effectively reducing infestation of individual moose and increasing productivity. Although moose harvests in Vermont were purposefully reduced and terminated temporarily, harvest will restart in 2022 as a possible proactive management strategy to address winter tick parasitism (Ellingwood et al. 2020). Forest management that provides quality browse and optimal cover distributed widely across the landscape may improve condition of cows, increase recruitment, and minimize local abundance of winter ticks that help perpetuate epizootics. Because much of the regional moose population is contiguous, sharing similar habitat, resources, and constraints, coordinated management strategies may best address the impact of winter tick parasitism.

ACKNOWLEDGMENTS

We thank W. Cottrell for veterinarian consultation which was funded by the Vermont Fish and Wildlife Department. We are also grateful for the support of the U.S. Fish and Wildlife Service National Wildlife Refuge System – Nulhegan Division, and land access from Weyerhaeuser Company, LandVest Inc., and many private landowners. Support from P. J. Pekins and L. E. Kantar was instrumental in the design and follow through of this study as well as the hard work of a dedicated field staff including T. R. Smith, C. Lampart, L. A. Rossier, and D. P. Hotchkiss. At the time of publication, data were not publicly available from the Vermont Fish and Wildlife Department. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The Vermont Cooperative Fish and Wildlife Research Unit is jointly supported by the U.S. 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 U.S. Fish and Wildlife Service Division of Wildlife and Sportfish Restoration – Wildlife Restoration Program, the U.S. Geological Survey (Grant/Cooperative Agreement No. G19AC00241), Safari Club International Foundation, and Vermont Electric Company.

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