

Variation in body condition of moose calves in regions with contrasted winter conditions and tick loads

Delphine De Pierre^{a,b}, Patrick Leighton^{c,d}, Steeve D. Côté^{b,a,e}, and Jean-Pierre Tremblay^{b,a,b,e}

^aDépartement de Biologie, Université Laval, 1045, ave. de la Médecine, Québec G1V 0A6, Canada; ^bCentre d'études de la forêt, Université Laval, 2405 Rue de la Terrasse Pavillon Abitibi-Price, Local 1122, Québec, QC G1V 0A6, Canada; ^cGroupe de recherche en épidémiologie des zoonoses et santé publique (GREZOSP), Faculté de médecine vétérinaire, Université de Montréal, 3200 Rue Sicotte, Saint-Hyacinthe, QC J2S 2M2, Canada; ^dCentre de recherche en santé publique de l'Université de Montréal et du CIUSSS du Centre-Sud-de-l'Île-de-Montréal, Montréal, Québec, Canada; ^eCentre d'études nordiques, Département de Biologie, Université Laval, 1045, ave. de la Médecine, Québec G1V 0A6, Canada

Corresponding author: Jean-Pierre Tremblay (email: jean-pierre.tremblay@bio.ulaval.ca)

Abstract

For many mammals living at higher latitudes, food scarcity and snow-hindered movements associated with their first winter are synonymous of trying months. In addition, most wild animals have to cope with parasites. Many studies have been conducted on captive animals to assess consequences parasitism on health over winter, but comparable studies on wild populations are scarce for large mammals. Here, we performed winter tick (*Dermacentor albipictus* Packard, 1869) counts and collected body condition data (mass and hematological parameters) on 15 moose (*Alces alces* (Linnaeus, 1758)) calves from two distinct climatic regions in northern and southern New Brunswick (Canada) in January. The same calves were recaptured 3 months later to observe variation in body condition parameters. Higher tick loads and more drastic changes of hematological parameters, such as hematocrit and creatinine in southern individuals, suggested that this population might be suffering more from the consequences of winter tick infestation than the northernmost population. However, other parameters that were not measured in our study, such as quantity and quality of food, could influence moose calves body condition at the southeastern limit of their range.

Key words: *Alces alces* (Linnaeus, 1758), anemia, body condition, cervids, *Dermacentor albipictus* Packard, 1869, winter severity

Résumé

Pour de nombreux mammifères vivant à des latitudes élevées, le manque de nourriture et les déplacements entravés par la neige lors de leur premier hiver sont synonymes de période difficile. De plus, la plupart des jeunes mammifères sauvages doivent faire face à des charges parasitaires parfois relativement élevées. Plusieurs études ont été menées sur des animaux en captivité pour évaluer les conséquences du parasitisme sur la santé au cours de l'hiver mais les études comparables sur les populations sauvages de grands herbivores sont rares. Nous avons donc effectué des décomptes de tiques d'hiver (*Dermacentor albipictus* Packard, 1869) et recueilli des données sur la condition corporelle (masse et paramètres hématologiques) de 15 veaux d'orignaux (*Alces alces* (Linnaeus, 1758)) provenant de deux régions climatiques distinctes au nord et au sud du Nouveau-Brunswick (Canada) en janvier. Ces mêmes veaux ont été recapturés 3 mois plus tard pour observer la variation de leurs paramètres de condition corporelle. Les charges de tiques plus élevées et les changements plus radicaux des paramètres hématologiques tels que l'hématocrite et la créatinine chez les individus du sud suggèrent que cette population pourrait souffrir davantage des conséquences de l'infestation hivernale par les tiques que la population la plus au nord. Cependant, d'autres paramètres qui n'ont pas été mesurés dans notre étude, tels que la quantité et la qualité de la nourriture, pourraient influencer la condition corporelle des veaux d'orignaux à la limite sud-est de leur aire de répartition.

Introduction

Even though animals living at northern latitudes are usually well adapted to their environment, winter conditions are generally among the strongest limiting factors (Monteith et al. 2013). For northern ungulates, availability of forage as well as protein and energy contents is lower in winter

than during the rest of the year (Berteaux et al. 1998; Larter and Nagy 2001; Parker et al. 2005; Ophof et al. 2013). Thermoregulation and locomotion costs in snow also affect the energy balance of species living in cold environments (Parker et al. 1984; Jensen et al. 1999; Kautz et al. 2020). Biologging and biotelemetry of vital parameters (e.g., heart rate,

temperature, etc.) and behavior (movement, activity, etc.) offer repeated observations on the same individuals over time (Whitford and Klimley 2019), but key parameters such as body mass and hematological profiles are hard to obtain at the individual level under natural conditions. Here, we report the results of a study, based on repeated measures, of the body condition of moose (*Alces alces* (Linnaeus, 1758)) calves experiencing contrasting winter conditions and winter tick (*Dermacentor albipictus* Packard, 1869) loads.

As the largest member of the cervids, moose are adapted to cold and snowy winters of the boreal biome. Their large size limits heat loss in cold temperatures (Renecker and Hudson 1986). Moreover, moose face lower movement costs than other ungulates in deep snow due to their high brisket height (Bubenik 1998). However, as moose calves are smaller both in height and size, they experience greater relative costs of thermoregulation and movements in deep snow than adults (Schwartz et al. 1991). In addition, moose calves allocate most of their energy to growth during the first months of their life and accumulate very little fat reserves before their first winter (Cederlund et al. 1991). Moose calves are also more susceptible to predators (Sivertsen et al. 2012; Brockman et al. 2017) and parasites than adults (Ellingwood et al. 2020).

The availability of food, allowing the accumulation of energy reserves required to survive the winter, is likely the dominant factor limiting moose at the northern edge of their distribution, while direct and indirect effects of parasites on survival and recruitment may ultimately limit moose at the southern edge (Murray et al. 2006; Rempel 2011; Ruprecht et al. 2020). In North America, moose are affected by several parasites throughout the year (Lankester and Samuel 1998). One ectoparasite, the winter tick, can be found by tens of thousands on a single moose during winter (Samuel 2004a; Jones et al. 2019). Winter ticks bite into the skin of their host to feed on their blood, inducing discomfort leading to excessive grooming usually followed by hair loss and reduced time allocated to feeding or resting (Samuel 1991; Addison et al. 1998a, 2019). At the end of winter, when moose are usually the most food-deprived, female winter ticks take their biggest blood meal, consuming around 1 mL of blood per female tick (Samuel 2004b). Previous studies revealed that this blood loss, when undergone by moose experiencing heavy winter tick infestations (between 42 000 and 70 000 ticks), can lead to mass loss and deficiencies in hemoglobin (anemia) or other blood components such as albumin, which can be consumed by ticks (Glines and Samuel 1989; Addison et al. 1998a; Musante et al. 2007). To identify the cause of anemia, many blood parameters can be investigated such as reticulocytes, which are young red blood cells that increase in case of blood loss or hemolysis (regenerative anemia). The size of the red blood cells (mean corpuscular volume) can also help assess the cause of anemia as smaller red blood cells can be an indicator of problems during erythropoiesis stemming from iron deficiency, for example. Other blood parameters can be monitored to assess general health of animals like white blood cells that can indicate an inflammatory response or creatinine that informs us on the muscle mass and energy balance (Anonymous 2022). Altogether, changes in the activity budget, costs of thermoregulation, and deficiencies in blood

composition can alter body condition and eventually lead to death, as reported during epizootic winters in western Canadian provinces and northeastern United States (Musante et al. 2010; Ministère Forêts Faune et Parcs 2016; Jones et al. 2017, 2019).

Population dynamics of ticks are also affected by meteorological conditions occurring during the off-host stages of their life cycle. Spring weather is a key factor in the winter tick life cycle as this is when females drop to the ground and lay their eggs; in the absence of snow, probabilities of survival for female ticks are higher (McLaughlin and Addison 1986; Garner and Wilton 1993) while preoviposition and incubation periods shorten with increasing temperatures (Addison et al. 1998b). Egg survival, hatching, larval survival, and questing for a host are negatively affected by drought during summer and fall (Garner and Wilton 1993; Pouchet 2023). Early frosts and snowfalls reduce the activity of larvae and their success in infesting moose (Garner and Wilton 1993; Musante et al. 2007; Holmes et al. 2018). Accordingly, the prevalence and intensity of winter tick infestation on moose vary spatiotemporally according to the distribution of climate factors and meteorological conditions (Jones et al. 2019).

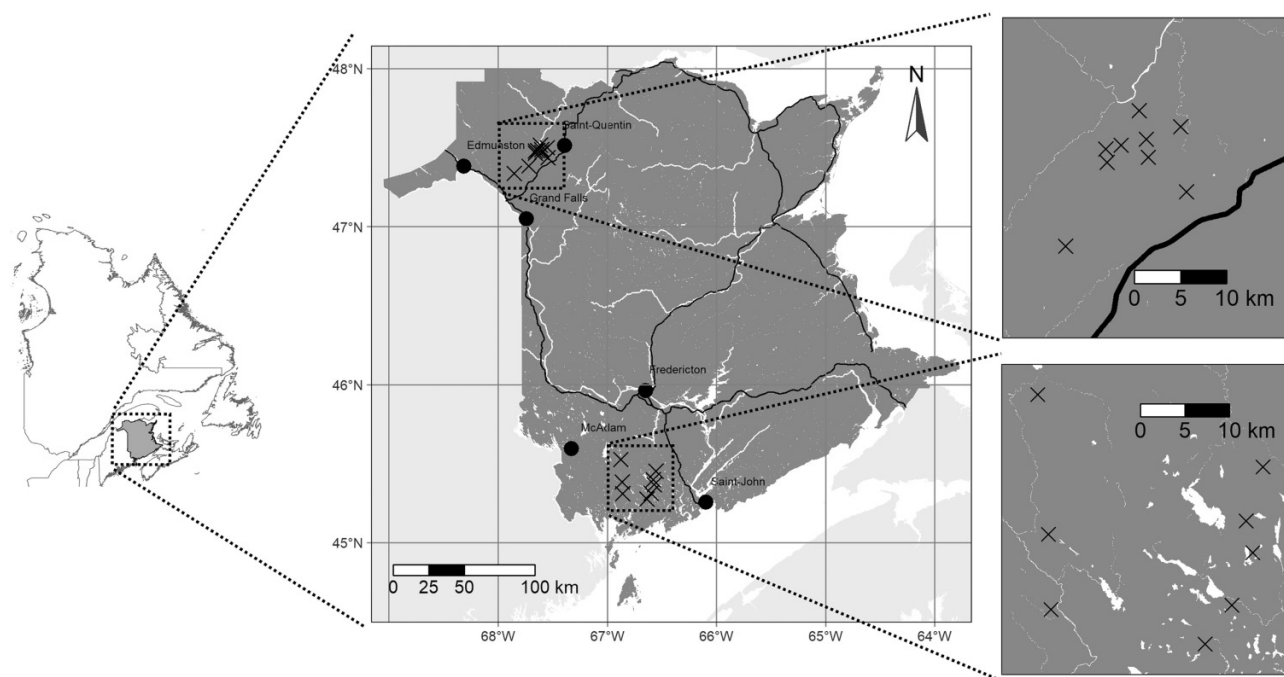
Here, we seek to shed light on the effect of winter severity and winter tick infestation on the body condition of moose calves. We studied repeated measures of body mass and hematological profiles in winter for two populations of moose at distinct latitudes in New Brunswick, Canada. The *parasite limitation hypothesis* predicts heavier winter tick loads on calves at lower than at higher latitudes due to milder meteorological conditions for ticks during their off-host life stages (Holmes et al. 2018), and accordingly a stronger decline in body mass and suboptimal hematological profiles of southern moose over the winter (Addison et al. 1994, 1998a). Alternatively, the *winter severity hypothesis* predicts a smaller overwinter decline in body mass and healthier hematological profiles for moose calves from populations at lower latitudes relative to populations at higher latitude (Renecker and Hudson 1986; Bubenik 1998).

Materials and methods

Study area

We conducted our study in two contrasting regions in terms of winter conditions: northern (N47.46°, W67.64°) and southern (N45.38°, W66.69°) New Brunswick, Canada, located 220 km apart (Fig. 1). The northern region was in the central Uplands ecoregion, more precisely in the Sisson ecodistrict, where forests are composed of balsam fir (*Abies balsamea* (L.)), white spruce (*Picea glauca* (Moench)), red spruce (*Picea rubens* Sarg.), and to a lesser extent of hardwood stands dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton). The southern area was located in the Valley lowlands ecoregion, specifically in the Mount Pleasant ecodistrict (Zelazny et al. 2007) where forests are mainly composed of red spruce associated with red maple (*Acer rubrum* Linné), white birch (*Betula papyrifera* Marshall), and balsam fir (Zelazny et al. 2007). The average temperature and precipitation from Jan-

Fig. 1. Study area showing the capture locations in January for moose (*Alces alces*) calves in northern ($n = 10$) and southern ($n = 8$) New Brunswick. Maps data GADM v4.0 (GADM 2022). Contains information licensed under the Open Government Licence—New Brunswick (Government of New Brunswick 2022). Geographic coordinate system GCS_WGS_1984.



January to April are $-6.5 \pm 2.2^\circ\text{C}$ (mean $\pm$ SD) and 78 ± 35 mm in the Sisson ecodistrict (Environment Canada 2017a) versus $-3.5 \pm 1.9^\circ\text{C}$ and 95 ± 34 mm for the Mount Pleasant ecodistrict (Environment Canada 2017b). The higher temperatures in the south influence the state of precipitation, which is more often in the form of rain than snow. Average snow accumulation in the St.-Quentin area (northern region), from the 15 January through the 25 April in 2018, was 103 ± 14 cm compared to 30 ± 17 cm in the Mount Pleasant area (southern region; P. Wiebe, pers. comm.).

Capture and handling

From 15 to 26 January 2018, we captured 18 moose calves using net-gun fired from a helicopter, and equipped calves with GPS Iridium collars (Lotek, GPS 8000 or 7000 series, Newmarket, Ontario, Canada; de Pierre 2023). Once captured, we immobilized and then tranquilized all calves with an intranasal dose of medetomidine (concentration = 10 mg/mL, dosage = 0.042 mg/kg). Medetomidine was reversed with an intramuscular dose of atipamezole (25 mg/mL, 0.24 mg/kg) (Armeno and Soli 1993; Wolkers et al. 1994b). Two calves died during winter ($n_{\text{north}} = 1$, $n_{\text{south}} = 1$) and another lost its collar ($n_{\text{south}} = 1$; Table A1). We recaptured 13 of the 15 remaining individuals between 23 April and 15 May 2018 ($n_{\text{north}} = 9$, $n_{\text{south}} = 4$; Table A1). For this capture session, because of the lack of ground snow, we immobilized calves using a dart gun from a helicopter. Eleven calves were tranquilized with a mix of medetomidine (0.029 mg/kg), ketamine (1.07 mg/kg), and telazol (0.48 mg/kg) and reversed with atipamezole (0.15 mg/kg) ($n = 11$) (Sutherland-Smith et al. 2004; Muller et al. 2007). Two calves were tranquilized with a

mix of butorphanol (0.22 mg/kg), azaperone (0.08 mg/kg), and medetomidine (0.09 mg/kg) reversed with a mix of atipamezole (0.22 mg/kg) and naltrexone (0.43 mg/kg) ($n = 2$) (Harms et al. 2018; Levine et al. 2022). All drug usage and dosages were supervised by a veterinarian (M. Oakley).

During both capture sessions, we recorded the same measures and collected the same samples for comparison purposes, except for two animals for which we could not obtain body mass in spring ($n_{\text{north}} = 1$, $n_{\text{south}} = 1$). Continuity in procedures was insured by the presence of three crew members who were present for every capture, DDP, M. Oakley, and C. Neveu. We measured body mass of calves with an electronic scale (± 0.2 kg; Salter Brecknell CS-1000, Fairmont, MN) hanging from a portable electric winch on a confined space tripod. We drew 11 mL of blood from the lateral saphenous vein or the jugular for every animal. We collected 1 mL in an EDTA tube and kept it at 4°C for a maximum of 48 h to establish a complete blood count sanguine profile via a veterinary clinic. Analyses were performed in three laboratories: Grand Falls Veterinary Clinic and Madawaska Veterinary Clinic in the north and New Brunswick Provincial Veterinary Laboratory in the south. Clinics in the north used a ProCyte Dx Hematology Analyzer calibrated every month, and the laboratory in the south used the Sysmex XT-2000iV calibrated every 6 months. We centrifuged the remaining 10 mL and froze the serum at -20°C for biochemical analysis performed at the Centre de diagnostic vétérinaire de l'Université de Montréal (CDVUM) of the Faculty of Veterinary Medicine of Université de Montréal. The same observer (DDP) counted the number of ticks on the skin along four transects of 10 cm spaced by 2 cm and repeated on four regions of the body: scapula, shoul-

Table 1. Hematological parameters used to interpret changes in the body condition of moose (*Alces alces*) calves between winter and spring in two contrasted regions of New Brunswick, Canada.

Parameter	Definition (unit)	Possible interpretation	Reference intervals		
			Equine	Bovine	Caprine
Hematocrit	Proportion of red blood cells in the total blood volume (%)	↓ indicates anemia	36–46	25–33	28–44
Reticulocytes	Count of immature red blood cells ($10^9/L$)	↑ caused by blood loss	ND	ND	ND
Mean corpuscular volume (MCV)	Mean volume of red blood cell (fL)	↓ caused by an anomaly during erythropoiesis	43–55	38–51	16–22
Eosinophils	White blood cells responding to infections that parasites cause ($10^9/L$)	↑ caused by allergic reaction or parasitic infection	0–1.2	0–1.3	0–0.08
Neutrophils	Proportion of the dominant type of white blood cells ($10^9/L$)	↑ caused by inflammation and bacterial infection	2.7–6.6	1.8–7.2	1.9–9.5
Glucose	Monosaccharide used as an energy source (mmol/L)	↓ risk of hypoglycemia	3.9–6.8	3.2–4.4	1.9–7.9
Albumin	Blood protein keeping fluid from leaking out of blood vessels (g/L)	↓ caused by malnutrition	29–36	33–43	29–40
Globulin	Blood protein involved in the immune system (g/L)	↑ caused by inflammation or infection	23–38	28–54	30–47
Iron	Constituent of hemoglobin that transports O_2 to the tissues ($\mu\text{mol/L}$)	↓ indicates anemia	17–38.8	11.5–40.1	18.3–37.7
Creatinine	Metabolic waste from creatine degradation ($\mu\text{mol/L}$)	↓ muscle mass reduction	70.8–132.7	35.4–79.7	26.6–70.8

Note: Arrows in the interpretation column indicate the direction of the change in the parameter values. Reference values were obtained from Animal Health Diagnosis Centre of the College of Veterinary Medicine of Cornell University (Anonymous 2022).

der, back, and rump (Jones et al. 2019). We further report the tick count as the mean number of ticks per transect (Table A1). The mean number of ticks per transect has been shown to be correlated with the total number of ticks on a moose (Mooring and McKenzie 1995). At recapture, some body areas could not be counted because of alopecia (complete hair loss). We then counted ticks in all areas where hair loss was not complete and adjusted the mean accordingly. All captures and handling were conducted according to the authorization to use live animals for research number 2017145-1 delivered by the Animal Care Committee of Laval University.

Body condition estimation

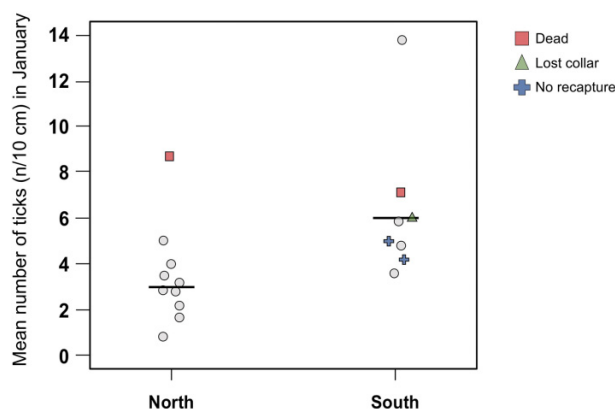
We used body mass and hematological parameters to characterize changes in body condition of moose calves over the winter. We report hematological parameters known to respond to parasitic infestations, body condition, or health issues (Table 1; Schalm 1961).

Statistical analyses

We first compared the average count of winter ticks per transect in January on moose calves captured in the north versus in the south using a general linear model procedure (SAS Institute Inc. 2016). We further wanted to explore the effect of tick load and study area on body conditions of moose. Multiple regression should include at least five observations for each independent variable to avoid overfitting, but ideally there should be 15–20 observations per independent variable (Hair et al. 1998). Given our low sample sizes ($n_{\text{capture}} = 18$,

$n_{\text{recapture}} = 13$) and the results of the previous analysis, we decided to use the region as a proxy of winter tick load and environmental conditions. We evaluated the effect of the region (north versus south) on parameters of moose body condition across winter using general linear mixed models (MIXED procedure; SAS Institute Inc. 2016). We conducted separate analyses for body mass and each hematological parameter shown in Table 1 as response variables. We included region, season (early winter and spring), and their interaction as independent fixed effects and calf identification as a random effect to account for repeated measurements on individuals. As an indicator of body condition, mass can contribute to explain part of the variation in hematological parameters. We thus ran general linear mixed models sequentially relating hematological parameters to body mass, period of capture, region, and their interaction (Type 1 sum of squares), although it involved one additional missing value in each region for calves whose body mass at recapture could not be obtained. We adjusted the p value for multiple tests using the false discovery rate, an approach less conservative than corrected Bonferroni methods but well adapted for exploratory research (MULTTEST procedure; Glickman et al. 2014; SAS Institute Inc. 2016). We visually assessed homogeneity of errors, homoscedasticity, and used Box–Cox transformations to find potentially nonlinear transformations of a dependent variable (TRANSREG procedure; SAS Institute Inc. 2016). For illustration purposes, we present means and confidence intervals (CIs) based on models run on untransformed data after assuming that the results were comparable to the models on transformed data.

Fig. 2. Comparison of winter tick (*Dermacentor albipictus*) loads in January for moose (*Alces alces*) calves ($n = 18$) from two populations in northern and southern New Brunswick. Black lines represent means.



Results

The mean winter tick load in January was almost twice as high for moose from the southern than the northern population ($t_{16} = -2.21$, $p = 0.04$, Fig. 2), even after removing one individual from the southern population with the heaviest tick load (id 18017, $t_{15} = -1.92$, $p = 0.07$).

Body mass of calves did not differ between populations ($F_{1,16} = 3.2$, adj $p = 0.2$; see Table 2 and Fig. 3 for all comparisons) unless we removed the calf with the lowest body mass from the northern population (id 18002, 141 kg in January and 138 kg in late April). Without this individual, calves were on average 20.5 kg (95% CIs: -3.6 – 44.7) heavier in the north than in the south ($F_{1,15} = 6.9$, adj $p = 0.04$, without id 18002). Body mass decreased, on average, by 9.2% (5.2%–22%) over winter ($F_{1,9} = 21$, adj $p = 0.005$), independent of the region (period $\times$ region $F_{1,9} = 0.3$, adj $p = 0.7$). Hematocrit levels also decreased throughout winter by 36% (20%–49%; $F_{1,9} = 44.8$, adj $p = 0.005$) and tended to decrease more in moose from the southern population than the northern population ($F_{1,9} = 7.2$, adj $p = 0.07$). The reticulocyte count of calves from the southern population was higher than for the northern population, especially after removing one individual with a very high reticulocyte level in spring in the northern population (id 18001: 62.2×10^9 cells/L; $F_{1,15} = 11.3$, adj $p = 0.01$). The reticulocyte count increased by 60% (-6% – 87%) from the beginning until the end of winter ($F_{1,9} = 7.4$, adj $p = 0.06$), even after removing individual 18001 ($F_{1,8} = 9.4$, adj $p = 0.04$). Mean corpuscular volume decreased throughout winter by 8.3% (1%–15%; $F_{1,9} = 23.5$, adj $p = 0.005$), and this tended to be more pronounced in calves from the southern population ($F_{1,9} = 8.4$, adj $p = 0.06$), and even more so if we removed one individual from the northern population with a faster drop in the mean corpuscular volume than other calves sampled in the same region (id 18001; 58.7 to 45.3 fL from January to its recapture in late April). Eosinophil counts did not differ among periods or regions unless we removed one calf from the northern region with a higher eosinophil count than all other moose (id 18004). Under this

condition, eosinophil count tended to decline from 0.37×10^9 cell/L (0.30, 0.44) in January to 0.27×10^9 cell/L (0.20, 0.34) in April/May ($F_{1,8} = 5.6$, adj $p = 0.09$) and to be higher in calves from the south (0.37×10^9 cell/L (0.30, 0.44) than from the north (0.28×10^9 cell/L (0.22, 0.34); $F_{1,15} = 5.1$, adj $p = 0.08$). Neutrophil counts increased over winter by 51% independent of the region (12%–76%; $F_{1,9} = 10.3$, adj $p = 0.03$). Glucose levels decreased over winter by 24% (3.5%–42%; $F_{1,11} = 12$, adj $p = 0.02$) and were lower in moose from the southern than the northern population by 19.7% (-2.0% – 37.7% ; $F_{1,16} = 9$, adj $p = 0.03$), even after removing one calf (id 18006) from the northern region who maintained a high concentration of blood glucose (10.3 mmol/L) across winter (region: $F_{1,15} = 15.8$, adj $p = 0.01$). Albumin decreased over winter by 31% (23%–38%; $F_{1,11} = 14.4$, adj $p = 0.002$) and was 15% lower in the southern population (4%–24%; $F_{1,16} = 16.5$, adj $p = 0.005$) where we also observed a statistical trend toward a more pronounced decline ($F_{1,11} = 5$, adj $p = 0.1$). Globulin levels were variable with no significant pattern (period: $F_{1,11} = 3.9$, adj $p = 0.2$, region: $F_{1,16} = 2.4$, adj $p = 0.2$, period $\times$ region: $F_{1,11} = 2.2$, adj $p = 0.3$). Iron levels decreased over winter by 47% (-3.4 , 79%; $F_{1,11} = 14.7$, adj $p = 0.01$) or by 37% after removing the calf with the sharpest decline (id 18009, 50.2 to 10.2 $\mu\text{mol/L}$; $F_{1,10} = 15.8$, adj $p = 0.01$). Creatinine remained relatively stable throughout winter in the north but declined in the south (period $\times$ region, $F_{1,11} = 26$, adj $p = 0.003$). Integrating body mass as an indicator of body condition did not significantly explain any variation in hematological parameters ($0.21 < \text{adj } p > 0.80$; Supplementary Table S1)¹. Sequential integration of the period of capture, region, or their interaction while considering body mass removed some effects previously significant (period of capture for reticulocytes ($F_{1,6} = 4.2$, adj $p = 0.23$) and glucose ($F_{1,8} = 2.9$, adj $p = 0.24$), region for glucose ($F_{1,16} = 1.7$, adj $p = 0.34$), and period $\times$ region for hematocrit ($F_{1,6} = 6.1$, adj $p = 0.18$) and mean corpuscular volume ($F_{1,6} = 5.1$, adj $p = 0.21$), but all other effects remained significant as well as the decrease in hematocrit and mean corpuscular volume overwinter ($F_{1,6} = 33.1$, adj $p = 0.02$, and $F_{1,6} = 19$, adj $p = 0.03$; Supplementary Table S1)¹.

Discussion

Our study based on repeated measures of body mass and hematological profiles of 15 moose calves in two populations at contrasting latitudes provides partial support for the parasite limitation hypothesis. In accordance with this hypothesis, we observed a heavier tick load in moose calves from a population located in central New Brunswick, Canada, compared to a second population located 220 km further north. Similarly, Pouchet (2023) reported highest intensity of winter ticks in the two southernmost regions of her study in Québec, Canada. This is likely due to climatic conditions better corresponding to the ecological niche of ticks in general and winter ticks at lower latitudes (Leighton et al. 2012; Holmes et al. 2018), especially the earlier onset of spring that frees the

¹ Supplementary Table is available with the article at <https://doi.org/10.1139/cjz-202X-XXXX>.

Table 2. Results from general linear mixed models relating body mass and hematological parameters of moose (*Alces alces*) calves to the period of capture, the region, and their interaction.

Parameter (transformation)	Variables	F	df _{num} , df _{den}	p	Adjusted p (FDR)
Body mass	Period	21.0 (22.2)	1, 9 (8)	0.001	0.005 (0.006)
	Region	3.2 (6.9)	1, 16 (15)	0.09	0.2 (0.04)
	P × R	0.3 (0.08)	1, 9 (8)	0.62	0.7 (0.86)
Hematocrit	Period	44.8	1, 9	<0.001	0.005
	Region	1.1	1, 16	0.3	0.4
	P × R	7.2	1, 9	0.03	0.07
Reticulocytes (x ⁻²)	Period	7.4 (9.4)	1, 9 (8)	0.02 (0.01)	0.06 (0.04)
	Region	4.5 (11.3)	1, 16 (15)	0.05 (0.004)	>0.1 (0.01)
	P × R	0 (0.8)	1, 9 (8)	0.98 (0.4)	0.98 (0.47)
Mean corpuscular volume (x ⁴)	Period	23.5 (31.2)	1, 9 (8)	<0.001 (0.0005)	0.005 (0.003)
	Region	0.6 (0.3)	1, 16 (15)	0.5 (0.59)	0.6 (0.68)
	P × R	8.4 (19.1)	1, 9 (8)	0.02 (0.002)	0.06 (0.01)
Eosinophils	Period	4.1 (5.6)	1, 9 (8)	0.07 (<0.05)	0.1 (0.08)
	Region	0.3 (5.1)	1, 16 (15)	0.6 (0.04)	0.7 (0.08)
	P × R	0.2 (0.04)	1, 9 (8)	0.7 (0.85)	0.8 (0.88)
Neutrophils (log)	Period	10.3	1, 9	0.01	0.03
	Region	0.7	1, 16	0.4	0.50
	P × R	0.03	1, 9	0.9	0.90
Glucose	Period	12 (13)	1, 11 (10)	0.005 (0.005)	0.02 (0.01)
	Region	9.0 (15.8)	1, 16 (15)	0.009 (0.001)	0.03 (0.01)
	P × R	2.6 (2.9)	1, 11 (10)	0.1 (0.12)	0.2 (0.17)
Albumin	Period	14.4	1, 11	<0.0001	0.002
	Region	16.5	1, 16	0.0009	0.005
	P × R	5.0	1, 11	0.05	0.1
Globulin	Period	3.9	1, 11	0.08	0.2
	Region	2.4	1, 16	0.14	0.2
	P × R	2.2	1, 11	0.17	0.3
Iron (x0.4)	Period	14.7 (15.8)	1, 11 (10)	0.003	0.01 (0.01)
	Region	1.4 (1.1)	1, 16 (15)	0.3	0.4 (0.41)
	P × R	1.4 (3.8)	1, 11 (10)	0.3	0.4 (0.13)
Creatinine (x ²)	Period	49.0	1, 11	<0.0001	0.002
	Region	0.05	1, 16	0.8	0.8
	P × R	26.0	1, 11	0.0003	0.003

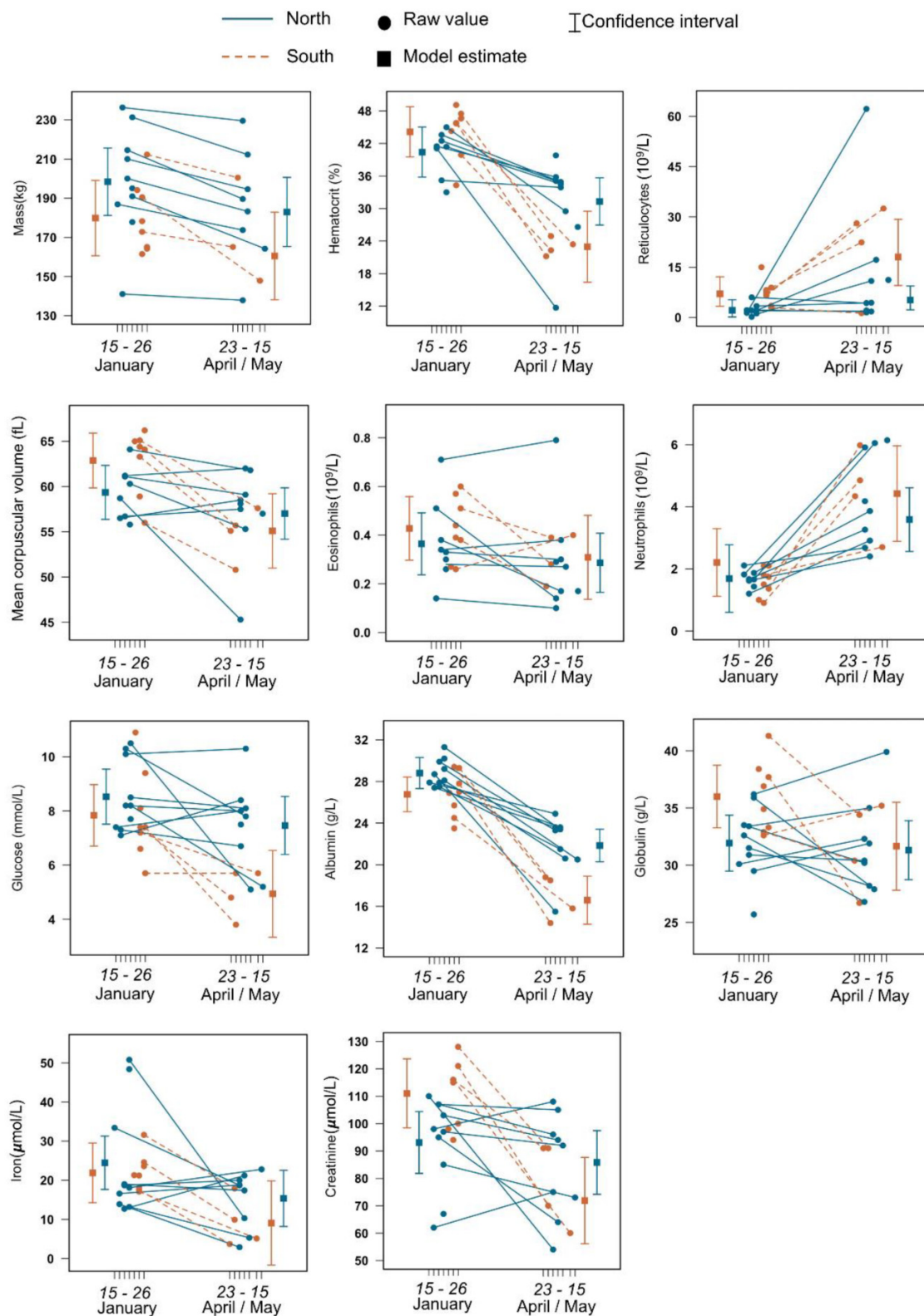
Note: Transformations for non-normally distributed variables are indicated next to the parameter name. Values in parentheses reports statistics after removing calves with unusual observations from the analyses. The last column is the adjusted *p* value for multiple tests using the false discovery rate. Bold adjusted *p* values are significant or present significant trends.

ground of snow and prevent ticks from freezing (McLaughlin and Addison 1986; Garner and Wilton 1993). The heavier tick load in the southern population did not translate into the predicted steeper decline in body mass over winter, but the differential alteration of hematological parameters, such as hematocrit volume and protein concentration, points towards a stronger negative effect of winter ticks on the health of calves at lower latitudes. Even though snow accumulation was roughly 70 cm deeper in the northern region (Wiebe, unpublished data), our results do not support the prediction of the winter severity hypothesis that calves from the southern population should have generally healthier hematological profiles than calves at higher latitudes. The amount of snow measured in the northern region of New Brunswick is known to constrain moose movement (Coady 1974), but it could be that it is not the main source of energy loss. It is

also possible that the use of moose yards and trails reduce the effect of snow depth (Lundmark and Ball 2008).

Despite a tick count on average twice as high, we could not detect a difference in the body mass of moose calves between regions. Body mass of all calves decreased at a similar rate over winter from 189 kg on average (CI 176–202 kg) in early winter to 172 kg (157–186 kg) in spring. Moose calves from the northern population tended to be heavier than their southern counterparts. This is in line with the prediction of the Bergman rule for a negative correlation between latitude and body size since a larger body reduces the surface area to volume ratio and thus thermoregulation costs (Bergman 1847). A north to south gradient in moose body mass with the larger representatives of the species in northern areas has been related to short and intense plant growing seasons, low winter temperatures, altitude, and low popula-

Fig. 3. Temporal change in body mass and hematological parameters of moose (*Alces alces*) calves from northern (solid blue line) and southern (orange dashed line) New Brunswick, Canada between early winter and spring 2018. Dots represent raw values, and values for the same individual are connected with a line. We report the parameter estimates from mixed linear models as means and 95% confidence intervals for moose calves in each region for each time period. For interpretation purposes, we present the estimates from the linear mixed models on the untransformed variables after verifying that they were comparable with the model on the normal scale. Dots occurring only in January refer to calves that either died or were not recaptured in spring. Dots occurring only in spring refer to variables that were not measured during first capture due to logistic errors.



tion densities in northern areas (Herfindal et al. 2006b). Genetic structuring along the north–south gradient could also contribute to this gradient in body mass (Herfindal et al. 2014).

The comparison of hematological profiles between regions point to a potential effect of winter ticks. We observed signs of anemia, especially in calves located in the southern region, such as a tendency for a steeper decline in hematocrit. In fact, all calves from the southern population alive in spring had hematocrit volumes under the lower limit of the reference intervals for livestock species contrarily to northern calves that had hematocrit volumes within those same intervals (Table 1). The higher reticulocyte count for all moose at the end of the winter also points towards a regenerative anemia following blood loss (Schalm 1961), likely due to blood consumption by winter ticks (Pfaffle et al. 2009). The mean corpuscular volume (MCV) of erythrocytes is used to diagnose anemia types (Schalm 1961); smaller erythrocytes are a sign of microcytic anemia that generally stems from a deficiency altering erythropoiesis (Schalm 1961). Our results showed a more pronounced decline in MCV in southern individuals (Fig. 3), which could indicate microcytic anemia. Microcytic anemia is not characteristic of regenerative anemia, which is usually caused by blood loss and generally does not directly affect erythropoiesis (Conrad 1990). However, ticks could still be a contributing factor via their effect on depleted fat reserves and blood components. Indeed, we observed a decline in glucose in all moose calves, especially in the southern study area, likely due to winter malnutrition (Niemininen 1980; Becker et al. 2010). On the other hand, the drop in albumin levels throughout winter and the lowest levels in southern individuals suggests that anemia could be the result of tick-related blood loss. In fact, ticks are mainly known to consume erythrocytes, but they can also consume albumin in great quantities (Sojka et al. 2016). When compared with livestock reference intervals, levels of albumin of calves from this study are low even in January, but especially so for southern individuals in spring (Table 2).

Results for iron showed that levels dropped during winter, but we detected no effect of the region. Some of the spring iron levels we observed were lower than the lowest reference interval from livestock (Table 1). Even if we could not detect differences in iron levels between regions, all southern calves experienced a drop in iron levels, while five of the eight northern calves did not. It is, however, not possible to determine whether ticks played a part in the decrease of iron levels for these eight calves or whether it was more likely caused by a nutritional deficiency.

One of the parameters that can be used to assess general health and detect the effect of parasites on body condition is white blood cell counts (Al-Mozan et al. 2017). In both regions, we observed an increase in neutrophil levels over winter but no effect of the region, which does not support the parasite limitation hypothesis. Values observed both in winter and spring fall within the normal range observed in livestock (Table 1). As the spring neutrophil values do not rise

above the normal range for other similar species, we can assume that if there was an immune response, it was not a severe one.

Some individuals showed a marked drop in creatinine, especially southern calves. Winter and undernutrition can provoke a decrease in blood serum creatinemia as the smaller the muscle mass is, the less creatinine is produced (Czyzowski et al. 2013). Experiments on wild boar (*Sus scrofa* Linnaeus, 1758) and red deer (*Cervus elaphus* Linnaeus, 1758) showed that undernutrition initially increased creatinine for the first 10–15 weeks, and then a decrease occurred during the following weeks (Wolkers et al. 1994a; Wolkers et al. 1994c; Czyzowski et al. 2013). Considering that food restriction started a few weeks before the first capture, it is possible that the first creatinine measure was taken during the increase phase and that the second measure in spring was during the decrease phase. Higher creatinine concentration in the blood of calves from the southern population in January might be indicative of a lower nutritional status in the south than in the north. Once again, we cannot exclude the possibility that winter ticks exacerbated the effect of winter especially for southern calves. It is, however, hard to determine whether calves were clinically experiencing low creatinine levels as reference intervals from livestock vary between taxonomic families (Table 1).

In addition to the parasite limitation hypothesis, nutritional limitation might contribute to the suboptimal hematological profiles observed in calves from the southern moose population. The fastest phenological development of plants in the south may lead to a mismatch between peaks in the availability of nitrogen and needs of females for lactation (Herfindal et al. 2006a) and decreases in maternal investment (Post and Forchhammer 2008). Nutritional limitation could explain declines in MCV and therefore hematocrit, but also glucose, albumin, iron, and creatinine. Yet, we would then expect a difference in body mass that we could not detect in our dataset. On the other hand, the most likely factor explaining the increasing trend in reticulocytes is from blood loss from hematophagous parasites.

One limit of our study is the low sample size in spring for the southern population. Out of the nine individuals captured in the south, we could only recapture four in the spring. From the 18 individuals that were captured in January, two died before recapture (one in the north and one in the south) and two died during or right after recapture (one in the north and one in the south). Both individuals that died before recapture had the second and third highest tick loads, but the calf with the highest tick load (southern population) survived its first winter. Therefore, ticks might have played a role in the first two deaths because they were quite early in the season and tick counts were high. The later deaths could be an accumulation of different factors where ticks had an impact in addition to exhaustion and starvation. We also have to consider the possibility that stress induced by the captures and consequences of drug use might have had an impact on the parameters that were monitored (Wolkers et al. 1994b; Marco et al. 1997; Topal et al. 2010).

Conclusion

The repeated measures of body condition parameters of moose overwinter provided support for the parasite limitation hypothesis through indirect inference between tick load of individual calves and their hematological profiles in contrasting regions. Disentangling the effect of tick loads versus environmental conditions through direct inference would require not only a larger sample size, but also a contrast in tick loads within regions either from natural variation or experimentation. Given a sufficient sample size, including data on the relative abundance of moose, forage availability, load of internal parasites, and meteorological conditions would improve our capacity to partition the variability in body condition, hematological profiles, and even survival in moose. A better knowledge of the factors favorable or unfavorable to winter ticks would help us to target variables likely to improve our understanding of the relationships between managed forests, the spatial distribution of ticks, and moose body condition. Widening the latitudinal gradient would also permit a better understanding of the factors affecting the health of moose calves as more extreme values could be obtained both for environmental values and tick loads.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

Patrick Leighton <https://orcid.org/0000-0001-5137-8909>

Steeve D. Côté <https://orcid.org/0000-0002-4875-1917>

Jean-Pierre Tremblay <https://orcid.org/0000-0003-0978-529X>

Author contributions

Conceptualization: DDP, PL, SDC, JT

Data curation: DDP

Formal analysis: DDP, JT

Funding acquisition: PL, SDC, JT

Investigation: DDP

Methodology: DDP, PL, SDC, JT

Project administration: JT

Resources: JT

Supervision: PL, SDC, JT

Validation: DDP

Visualization: DDP

Writing – original draft: DDP

Writing – review & editing: PL, SDC, JT

Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjz-2023-0144>.

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Appendix A

Table A1. Attributes of moose (*Alces alces*) calves captured in two regions of New Brunswick, Canada, in January 2018 and recaptured in April/May 2018.

No.	ID	Region	Sex	Capture			Recapture		Outcome	
				Date	Mass (kg)	Tick count (n/10 cm transect)	Date	Tick count (n/10 cm transect)		
1	18001	N	F	16 January 2018	236	4.0	25 April 2018	2.6		
2	18002	N	M	16 January 2018	141	2.2	25 April 2018	0.1		
3	18003	N	M	17 January 2018	210	3.5	27 April 2018	0.1		
4	18004	N	M	17 January 2018	215	2.8	25 April 2018	1.0		
5	18005	N	F	18 January 2018	195	1.7	28 April 2018	0.4		
6	18006	N	F	17 January 2018	441	2.9	27 April 2018	2.4		
7	18007	N	F	18 January 2018	200	8.7	NA	NA	Dead ^a	
8	18008	N	F	15 January 2018	187	5.0	25 April 2018	1.6		
9	18009	N	M	18 January 2018	231	0.9	27 April 2018	1.0		
10	18011	N	M	18 January 2018	191	3.2	15 May 2018	0.2		
11	18012	S	F	21 January 2018	194	4.8	NA	NA		No recapture
12	18013	S	M	22 January 2018	178	7.1	NA	NA		Dead ^a
13	18014	S	M	22 January 2018	191	5.9	13 May 2018	0.2		
14	18015	S	M	22 January 2018	173	4.9	23 April 2018	1.1		
15	18016	S	F	22 January 2018	161	6.0	NA	NA		No recapture
16	18017	S	M	26 January 2018	212	13.8	24 April 2018	0.6		Lost collar ^b
17	18018	S	M	26 January 2018	165	3.6	NA	NA		No recapture
18	18019	S	F	26 January 2018	164	4.2	24 April 2018	3.8		

^a18007 died on the 5 April 2018. 18013 died on the 25 March 2018.

^b18017 lost its collar on the 14 April.