

WILDLIFE BIOLOGY

Research article

Variation in prevalence and intensity of macroparasites in moose and their interactions with winter tick load in eastern Canada

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Wildlife Biology

2024: e01205

doi: [10.1002/wlb3.01205](https://doi.org/10.1002/wlb3.01205)

Subject Editor:

Christophe Bonenfant

Editor-in-Chief: Ilse Storch

Accepted 15 March 2024



Wild animals are infected with a large diversity and abundance of parasites that can affect their behavior, growth, body condition, and ultimately their survival. Although the adverse effects of parasites and the mechanisms involved in the interactions between a host and its parasites are generally well studied, much less is known about the additive or synergistic effects of multiple parasite species on a host. Moose populations in eastern Canada are infected by several species of endoparasites. In the last decades, the intensity of infestations by winter ticks, an ectoparasite, on moose have increased as a result of increased moose densities and favorable weather conditions that benefit winter tick survival. We aimed to document the diversity, intensity, prevalence, and distribution of different parasite species of moose in southern Quebec, Canada. We then evaluated the potential interaction between winter tick and endoparasites of moose, and we evaluated the effect of the simultaneous presence of ticks and endoparasites on moose body condition. To do so, we collected organs to identify and count endoparasite species, estimate winter tick abundance, and measure subcutaneous fat thickness from 174 hunted moose in fall 2019 in 8 regions of Quebec. Our results showed that the prevalence and intensity of winter tick and gastrointestinal parasites differed among regions, as well as the prevalence of the heart parasite *Taenia krabbei* and the intensity of lung parasite *Echinococcus granulosus*. Moose body condition, however, was not influenced by the simultaneous presence of winter tick and endoparasites. The documentation of the interactive effects of multiple parasite species on a host is fundamental given that future environmental conditions in temperate climate will favor the reproduction, development, and survival of several parasite species, which could affect parasite diversity and abundance in the environment and modify host–parasite dynamics.

Keywords: *Alces americanus*, body condition, climatic conditions, *Dermacentor albipictus*, endoparasites, host density, moose, parasite intensity, parasite prevalence, polyparasitism, winter tick



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Introduction

Parasitism is a well-known driver of health in wildlife populations (Thompson et al. 2010, Marcogliese and Pietrock 2011). Studies have shown that parasites can have detrimental effects on growth, reproduction, and survival of animals (Thomas et al. 1999, Agnew et al. 2000). Various factors can influence the effect of parasitism on a host, such as host behavior, physiology, and immunity, which could explain the differences in burdens among individuals of different sex and age classes (Wilson et al. 2002). Many studies on long-lived mammals have shown that parasite-associated mortality is higher in youngest and oldest hosts, and that parasite species richness and prevalence are higher for males than females (Lynsdale et al. 2017, Habiq et al. 2018, Świslocka et al. 2020).

Many parasite species can interact within a common host, which exacerbate the negative effect that a single parasite species could have on a host and could also make it more vulnerable to secondary parasitic infections (Musante et al. 2007). For instance, in willow ptarmigan *Lagopus lagopus*, Holmstad et al. (2008) showed a positive relationship between lice load (order Mallophaga, suborder Ischnocera) and endoparasite load. Similarly, mice *Mus musculus* that were heavily infected by *Echinococcus multilocularis* (a gut-infecting nematode) were also infected by *Mesocestoides corti* (a liver-infecting cestode), while mice more lightly infected by *E. multilocularis* were not infected by *M. corti* (Cox 2001). In addition, it has been shown that polyparasitism can further deteriorate host body condition. For instance, Lello et al. (2005) showed that wild rabbits *Oryctolagus cuniculus* infected by more than three helminth species had a worse body condition compared with rabbit infected by only one helminth.

External factors are also known to influence parasite infection, such as host population density and weather (Arneberg et al. 1998). Because parasite transmission is density dependent, the increased contacts between individuals at high density augment opportunities for transmission, thus increasing parasite load at the individual and population levels (Ryder et al. 2007). Also, warmer weather is most often favorable for parasitic development, which could not only increase the number of parasites available to infect hosts, but also allow longer periods of parasite transmission (Kovats et al. 2001, Kutz et al. 2005). With climate change, we expect increases of parasite load and introduction of new parasite species in northern environments (Hoar et al. 2012). This phenomenon could be detrimental for host populations present in those environments because they might not be adapted to the new parasites species or to live in an environment with higher parasite load (Weiskopf et al. 2019).

The complex relationships among parasites, the body condition of hosts, and the environment are currently at play in the eastern moose populations of Canada. Over the past decades, frequency and intensity of winter tick *Dermacentor albipictus* infestations on moose have increased in that region, potentially due to warmer temperatures and high moose density in comparison to historical conditions, as it is the case in the northeast United States (Jones et al. 2019). In addition,

the high moose densities in some regions of Québec over the past few decades (Jensen et al. 2018) have potentially allowed ticks to multiply and expand their range in the province. Moose are also the host of many endoparasite species, such as lung worms that could induce pulmonary problems or intestinal worms that could cause damages to the digestive tract (Franzmann and Schwartz 1998). Therefore, moose can be simultaneously infected by many endoparasites, such as nematodes or cestodes, and winter tick, which may exacerbate the effects that a single parasite would have on their health.

We first documented the intensity, prevalence, and distribution of different parasite species of moose in several regions of Québec, Canada. Secondly, we hypothesized that winter tick infestations weaken the moose immune system and that larval tick loads in the fall are an index of the previous winter's infestation level, making moose more susceptible to secondary parasitic infections by endoparasites the following year. We predicted that an increase of winter tick load would lead to an increase of endoparasite load and vice versa. Finally, we investigated the effect of the simultaneous abundance of winter tick and prevalence of endoparasite species on moose body condition. We predicted a synergistic effect of winter tick and endoparasites species resulting in poorer moose body condition. Larvae are unlikely to affect moose body condition, but our assumption is that the parasite load we measured in the fall is a good indicator of the parasite load that a moose had the previous winter, when they are more likely to be affected by adult winter ticks. We based this assumption on the space use fidelity of moose that generally use the same areas across years (McLaren and Patterson 2021) and to positive correlations in tick prevalence and load from one year to the next (unpubl.).

Material and methods

Study area

The study area encompassed > 180 000 km² in Québec, Canada, including 8 administrative regions and 12 independent hunting zones with different moose densities and weather conditions (Fig. 1). The vegetation in the southern part of the study area is dominated by sugar maple *Acer saccharum*, American basswood *Tilia americana*, and yellow birch *Betula alleghaniensis*. The northern part of the study area is populated by balsam fir *Abies balsamea*, white spruce *Picea glauca*, and white birch *Betula papyrifera* (Saucier et al. 2010). From south to north, the mean minimum daily temperature in winter varies from -10 to -20°C and the mean maximum daily temperature in summer from 30 to 20°C (MELCC 2020). Based on aerial surveys conducted by the Ministère des Forêts, de la Faune et des Parcs (MFFP) (Lefort and Massé 2015), moose density varied from 1.4 moose 10 km⁻² to 9.0 moose 10 km⁻² in the hunting zones but may have locally reached higher levels (> 30 moose 10 km⁻²) in areas where hunting pressure is lower such as in wildlife reserves. Wolf populations are only present north of the St. Lawrence River (Fig. 1).

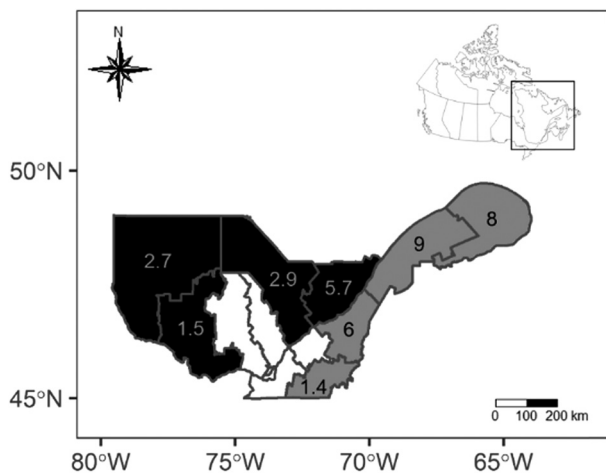


Figure 1. Study area in Québec, Canada, where we sampled winter tick on moose and obtained organs from sport hunters to evaluate endoparasites prevalence and load in fall 2019. Black areas depict administrative regions where wolves are present, while the grey areas are those where wolves are absent. No data are available in white areas. Numbers represent estimated moose population density (moose 10 km⁻²) based on the most recent aerial survey conducted by the MFFP, between 2000 and 2010 (Lefort and Massé 2015). The regions are the same used for statistical comparisons.

Data acquisition

We conducted winter tick counts on the carcasses of moose harvested during the sport hunting season between 5 September and 19 November 2019 (n=174). We estimated the number of winter tick per moose by counting tick larvae just after harvesting on three body parts (shoulder, wither, and buttock on one side of the animal) along four 10 cm vertical transects spaced 2 cm apart on each body part (total of 12 transects) (Sine et al. 2009). We used the total number of *D. albipictus* counted along the 12 transects as an indicator of moose winter tick load for statistical analyses.

We collected the heart (n=99), lungs (n=126), brain (n=95), liver (n=114), and distal intestine (n=97) of hunted moose whenever possible and kept them frozen until laboratory analyses. We cut all the organs collected into one-cm-thick slices. Each slice was observed in the laboratory to identify and count all macroparasites present in each organ. We isolated pieces of brain containing the lesions suspected to be caused by meningeal worms *Parelaphostrongylus tenuis* and preserved them in formalin to be analyzed at the Faculty of Veterinary Medicine of Université de Montréal. Because we only found one meningeal worm, we did not include this parasite in the statistical analyses. We isolated intestinal contents so that larvae and eggs of gastrointestinal parasites could be recovered, identified, and counted following a modified Wisconsin approach at the AVVLD-accredited Animal Parasitology Reference center of University of Montréal (Dryden et al. 2005). Briefly, samples were centrifuged at 1650 × g for 5 min, resuspended in saturated sucrose (Fisher Chemical, Canada), centrifuged at 650 × g for 2 min, and flotation was performed for 1 h at room temperature. The

coverslip was then removed and rinsed with 1 ml of 1 × Phosphate-Buffered Saline (PBS) to collect the eggs. Eggs were identified and counted by a certified parasitology technician.

We used subcutaneous fat thickness (mm) of moose to assess body condition (Cook et al. 2010). We measured subcutaneous fat thickness in the middle of an incision in the skin between the hip bone and the ischium (Cook et al. 2010). We noted the sex of each moose, and we collected their lower jaw incisors to determine age by counting the number of cementum annuli (Sergeant and Pimlott 1959).

Statistical analyses

To evaluate variation in parasite prevalence (percentage of infected moose in the host population) and intensity (number of parasites per infected moose) among the eight studied regions (Estrie, Chaudière-Appalaches, Mauricie, Capitale Nationale, Outaouais, Abitibi, Bas-Saint-Laurent and Gaspésie) (Supporting information), we used generalized linear models (GLM) for each parasite species (Dunn and Smyth 2018) with a binomial distribution and a logit-link function for prevalence, and a negative binomial distribution to account for over-dispersion for parasite intensity (Lindén and Mäntyniemi 2011). To allow the model to estimate the variance properly, we did not include a region when there were less than three moose collected in such regions for a given parasite species. We determined if the prevalence and parasite intensity differed among regions by comparing a model with and without region as a fixed effect using a likelihood ratio test. We used 95% confidence intervals overlap and mean comparisons to determine which regions differed in terms of prevalence and intensity for each parasite (Cumming 2009).

For the second objective, given the high variability among tested variables (Supporting information), we performed structural equation models (SEM package; Fox et al. 2021) to determine if an increase in winter tick load leads to an increase of endoparasites load and vice versa. Given missing endoparasite values for some moose (27.5% of the dataset) (Supporting information), we did data imputation using the Multivariate Imputation by Chained Equation (MICE package; Van Buuren and Groothuis-Oudshoorn 2011) and obtained 1000 datasets with imputed data through an iterative series of predictive models until convergence was met (Wilson 2021). We used all the variables for the imputation procedure and did not use any stratification procedure (blocks). We tested a model with winter tick abundance as the dependant variable, and the endoparasite load as an independent variable, as well as moose sex, age, population density, region, and sampling date as covariables. We also tested an alternative model with the total endoparasite load (all species combined) as the dependent variable and winter tick load as an independent variable with the same other covariables. We ran those models on each imputed dataset and pooled the results to obtain the final model mean estimates and 95% confidence intervals.

For the last objective, we performed mixed linear models ('LME4' package; Bates et al. 2021) between subcutaneous

fat thickness and parasite load of each species (additive effect). Given missing endoparasite values for some moose, we did the same imputation method as for our second objective. We used sex, age, moose population density, sampling date, and sex \times age and winter tick load \times endoparasites load interactions as independent variables. The later interaction allowed us to determine if the simultaneous presence of ectoparasites and endoparasites had a synergistic effect on moose body condition. We also ran a model with the interaction between winter tick load and total endoparasites load (all species confounded). We added the region as a random intercept in the model. All statistical assumptions for the three objectives were verified and fulfilled. All statistical analyses were performed in R 4.0.2 (www.r-project.org).

Results

The intensity and prevalence of *D. albipictus* and gastrointestinal worms (*Moniezia* spp., *Nematodirus* spp., *Trichuris* spp., Coccidia and Strongyles), and the prevalence of *Taenia krabbei* and the intensity of *Echinococcus viviparus* differed among regions (Table 1, Supporting information). The mean number of ticks on moose harvested in Outaouais, Abitibi, and Gaspésie was less than 10, while it was above 20 for Estrie and Chaudière-Appalaches. The number of winter ticks per moose was intermediate (between 10 and 20) in Mauricie, Capitale-Nationale, and Bas-Saint-Laurent (Fig. 2A). Prevalence of winter tick was highest in Bas-Saint-Laurent (97%, Fig. 2B). More than 85% of moose collected in Estrie, Chaudière-Appalaches, Outaouais, Abitibi, and Bas-Saint-Laurent were infested by winter ticks, while less than 40% of moose were infested in Gaspésie (Fig. 2B).

The likelihood ratio test suggested that there were differences among regions for the intensity of gastrointestinal worms (Table 1), although confidence intervals overlapped (Fig. 3A). This discrepancy might be explained by low sample size for some regions. Nevertheless, the mean number of gastrointestinal worms in moose harvested in Estrie, Chaudière-Appalaches, and Mauricie was above 10, while it was on average less than 5 in Capitale-Nationale, Outaouais,

and Bas-Saint-Laurent (Fig. 3A). Prevalence of gastrointestinal worms was 100% in Estrie and Chaudière-Appalaches, and it ranged between 60 and 75% in Capitale-Nationale, Outaouais, and Bas-Saint-Laurent. Only 36% of moose were infected by gastrointestinal worms in Mauricie (Fig. 3B).

The intensity of *E. granulosus* infection differed across regions (Table 1). Indeed, Mauricie had a mean number of 24 cysts per moose, but it was highly influenced by one individual with a very high intensity. Meanwhile moose in Capitale-Nationale, Outaouais and Bas-Saint-Laurent had an average of 10 cysts per moose (Fig. 4A). Estrie and Chaudière-Appalaches had 3 cysts of *E. granulosus* per moose on average (Fig. 4A). The prevalence of *T. krabbei* also varied among regions and moose harvested in Mauricie had the highest prevalence (66%), while there was no moose infected by this parasite in Estrie and very few in Abitibi (Fig. 4B).

For the second objective, the relationships between winter tick load and endoparasite load were not statistically significant (all p-values > 0.3). The SEM models did not reveal any effect of sex, age or moose density on winter tick load and endoparasite load (Supporting information). We did not find any correlation between moose subcutaneous fat thickness and parasite load, nor an interaction between endoparasites load and ectoparasite load (Table 2). Females, however, had a thicker subcutaneous fat layer than males, and we found a tendency for fat thickness to increase with age for females, but not for males (Table 2, Fig. 5).

Discussion

We documented regional variations in intensity and prevalence of moose macroparasites in Quebec (Canada) and tested the hypothesis that winter tick load could increase the risk of infestation by endoparasites. Further, we evaluated the interaction between winter tick and endoparasites on moose body condition. Contrary to our predictions, we did not find a positive relation between winter tick load and endoparasite load, and we did not find a relation between moose body condition and parasite load. We found, however, that parasite intensity and prevalence differed among regions for several

Table 1. Results of the likelihood ratio test on the difference in parasite intensity (number of parasites per infected host) and prevalence (percentage of infected individuals in the host population) in moose collected among eight regions in Quebec, Canada, in fall 2019. Significant variables (p-value < 0.05) are in bold. Theta value is provided for binomial negative model for parasite intensity.

Parasites	Response variable	df	X ²	p-value	Theta value
<i>Dermacentor albipictus</i>	Intensity	7	32.80	< 0.01	1.32
	Prevalence	7	22.38	< 0.01	—
Gastrointestinal worms	Intensity	5	14.24	0.01	0.84
	Prevalence	5	25.52	< 0.01	—
<i>Taenia krabbei</i>	Intensity	2	2.69	0.26	1.59
	Prevalence	7	31.62	< 0.01	—
<i>Taenia hydatigena</i>	Intensity	5	7.29	0.19	2.19
	Prevalence	7	9.49	0.22	—
<i>Dictyocaulus viviparus</i>	Intensity	—	—	—	—
	Prevalence	7	4.64	0.70	—
<i>Echinococcus granulosus</i>	Intensity	5	16.32	0.01	0.79
	Prevalence	7	10.65	0.15	—

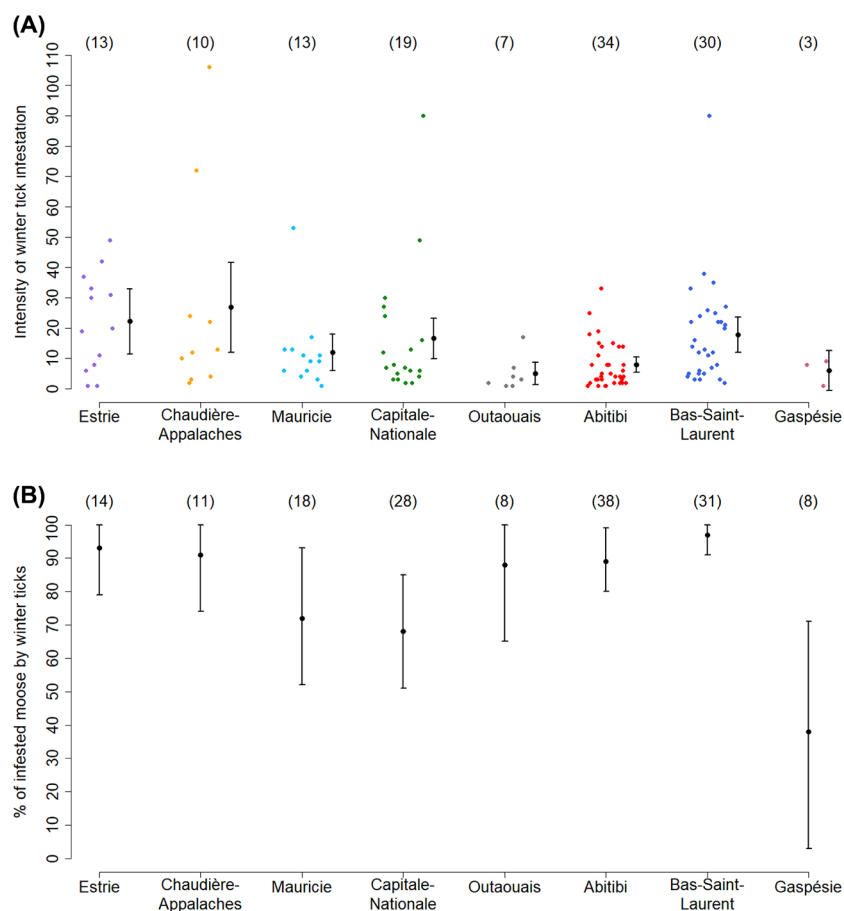


Figure 2. Intensity (A) and prevalence (B) of winter tick *Dermaacentor albipictus* larvae on moose during fall 2019 (September to November) in Quebec, Canada. Regions are presented from south (Estrie) to north (Gaspésie). Error bars represent 95% confidence intervals. Sample sizes are shown in parentheses.

of the parasites considered (*D. albipictus*, gastrointestinal worms, *T. krabbei* and *Echinococcus granulosis*).

Weather and climate are known to influence the intensity and prevalence of parasite infection (Harvell et al. 2002, Estrada-Peña et al. 2012). The two southernmost regions in our study, namely Estrie and Chaudière-Appalaches, had the highest intensity of winter tick infestation and both regions had high prevalence. *Dermaacentor albipictus* is a one-host tick with a one-year life cycle that involves four different developmental stages: 1) in fall, from September to November, larvae wait in the vegetation to climb on to a passing host; 2) in winter, from January to March, nymphs feed on the blood of their host, molt into adults and mate; 3) in spring, from March to May, engorged females drop on the ground to lay eggs; and finally 4) in summer, from June to August, eggs mostly stay on the ground and normally hatch in late summer. Thus, during almost half of the year, ticks are free in the environment and therefore directly influenced by weather conditions. Warmer temperatures are favorable for the development and survival of *Ixodidae* species (Parola et al. 2008, Eisen et al. 2016), whereas cold temperatures are negatively correlated with *D. albipictus* load on moose (Pouchet et al. unpubl.). Therefore, because Estrie and

Chaudière-Appalaches are the southernmost regions in our study area, we argue that the development and survival of winter tick is favored in those regions which may explain why more than 90% of moose were infested with ticks with an average of > 20 ticks/host along the twelve 10-cm transects (Supporting information). In addition, because winter tick expanded their range to Quebec from the United States several decades ago, southern regions have potentially a larger pool of winter tick due to their longer colonization history (Musante et al. 2010).

Like winter ticks, gastrointestinal worms have a free-living stage. The adults produce eggs inside their host that are ejected through the host feces. The larvae then develop in the grass, leaf litter and ground vegetation and moose can be infected while feeding on contaminated vegetation (Zajac 2006). Therefore, the survival and development of gastrointestinal worms are driven by climatic conditions (O'Connor et al. 2006). For example, in a study conducted in Argentina, there is a south–north gradient of *Nosema* spp. spore abundance, with the highest spore counts observed in southern areas (Pacini et al. 2016). Similarly, our results showed that all moose sampled from the two southernmost regions of the study area were infected by gastrointestinal

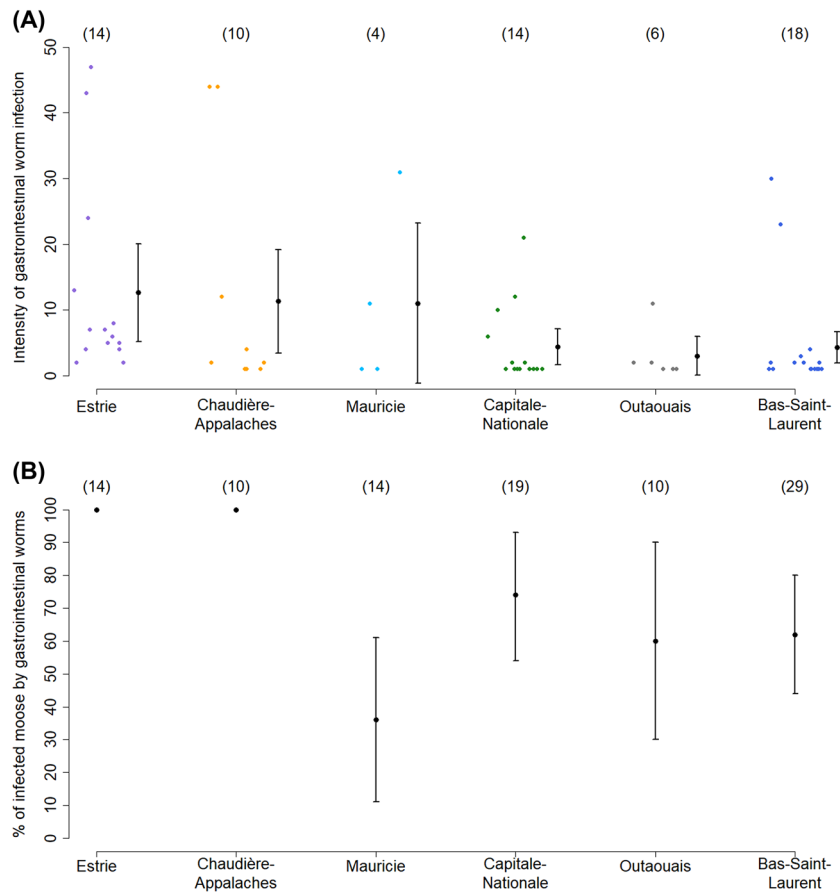


Figure 3. Intensity (A) and prevalence (B) of gastrointestinal worms in moose during fall 2019 (September–November) in Quebec, Canada. Regions are presented from south (Estrie) to north (Bas-Saint-Laurent). Error bars represent 95% confidence intervals. Sample sizes are shown in parentheses.

worms (Supporting information) and had the highest number of worms in their distal intestine.

In contrast, Estrie and Chaudi re-Appalaches were the two regions where the intensity of *E. granulosus* cysts was the lowest and less than 10% of moose were infected by *T. krabbei* cysts (Fig. 2). Unlike winter ticks and gastrointestinal worms that use moose as their final host, *E. granulosus* and *T. krabbei* use moose as their intermediate host and complete their cycle in canids, such as wolf *Canis lupus* and coyote *Canis latrans* (Samuel et al. 1976, Joly and Messier 2004). The lower prevalence and intensity of those endoparasites in those regions likely illustrate the reduced interactions between moose and canids. Wolf, the main predator of moose (Messier and Cr te 1985), is absent in those two areas while coyotes that are present in all regions do not interact with moose as much as wolves do (Georges 1976). Indeed, our results showed a relatively high intensity of *E. granulosus* in regions north of the St. Lawrence River (Mauricie, Capitale-Nationale and Outaouais) where wolf is present, compared with regions south of the river (Estrie and Chaudi re-Appalaches) where it is absent. In addition, compared with wolves, coyotes base their diet on smaller prey, such as white-tailed deer (Paquet 1992) but may occasionally feed on moose carcasses in areas

where moose population densities are high. This might explain the higher prevalence of *T. krabbei* we observed in Bas-Saint-Laurent and Gasp sie (Supporting information).

Our results showed that there was no correlation between endoparasites and winter tick loads, and their combined presence did not affect moose body condition, at least at the level of infestation we observed. We collected organs from hunted moose that were harvested during fall (5 September–19 November) when winter ticks are at the larval stage and start to climb on vegetation to attach to moose and are unlikely to affect moose body condition then. The lack of effect of parasites on moose body condition could also result from the death of moose with a heavy parasite load during the previous winter, an energy-demanding season for ungulates (Stewart et al. 2005, Toigo et al. 2006), leading to a survival bias in favor of moose in better body condition. Another potential explanation could be that moose can recover their fat reserves during summer no matter how much they were depleted during the previous winter. We surmise that measuring body condition and parasite load during winter would allow a better assessment of the relationships between the two variables, especially at the end of the winter when ticks' blood engorgement is at its maximum, which directly impact body condition.

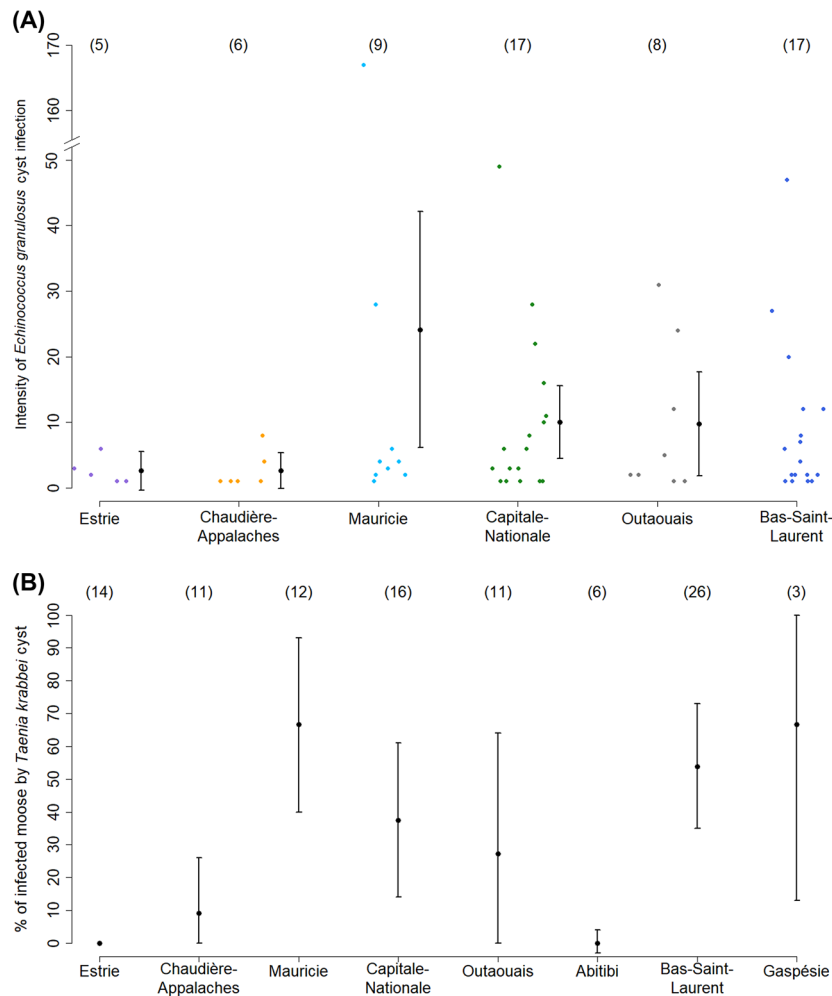


Figure 4. Intensity (A) of *Echinococcus granulosus* cysts and prevalence (B) of *Taenia krabbei* cysts in moose during fall 2019 (September–November) in Quebec, Canada. Regions are presented from south (Estrie) to north (Bas-Saint-Laurent). Error bars represent 95% confidence intervals. Sample sizes are shown in parentheses.

Considering these limitations, we had limited power to find associations between winter tick load and endoparasite load and their potential effect on body condition.

Although we did not find an effect of parasite abundance on moose body condition, we found that females had thicker subcutaneous fat than males and fat thickness increased with age for females. Our sampling occurred in fall, during and

Table 2. Results of a mixed linear model on imputed datasets explaining moose subcutaneous fat thickness in Quebec, Canada, in fall 2019.

Variables	Estimate	SE	t	p-value
Sex [Male]	−0.784	0.293	−2.677	0.007
Age	0.042	0.053	0.801	0.423
Winter tick load	−0.012	0.009	−1.359	0.174
Endoparasite load	−0.003	0.008	−0.441	0.659
Density	0.138	0.122	1.134	0.257
Sampling date	−0.013	0.016	−0.824	0.310
Sex × Age	−0.176	0.091	−1.928	0.054
Winter tick load × Endoparasite load	−0.001	0.001	−0.962	0.336

after the rutting season, a period during which male ungulates reduce their food intake and increase activity, resulting in the loss of mass and body fat, and the deterioration of body condition (Bobek et al. 1990, DelGiudice et al. 2011). Also, there is a link between fat reserves in females and fertility; and females tend to accumulate more fat reserves for future lactation needs as they age (Heard et al. 1997, Oftedal 2000). Consequently, our results of fat thickness corroborate previous studies on moose physiology and behavior.

Although we did not find any effect of polyparasitism, and the body condition of moose was not affected by their parasite load, we found a regional trend in the intensity and prevalence of some parasite species, which may be related to the abiotic conditions of these regions. Climatic conditions are expected to continue to change in the near future, such as increases in air temperature and shorter winters (Karl and Trenberth 2003, Rogelj et al. 2012), which could favor the reproduction, development and survival of several parasite species that could translate into longer transmission periods and higher intensity of infection (Kutz et al. 2005). This phenomenon

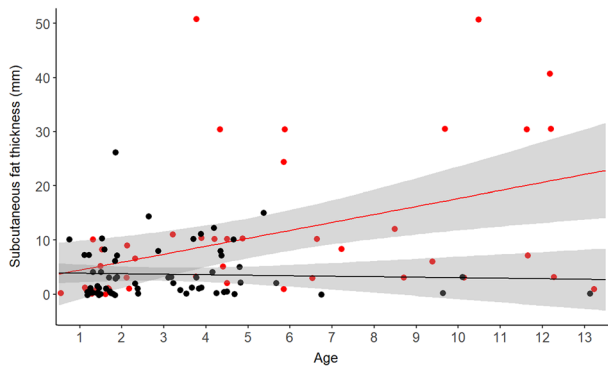


Figure 5. Predictions (solid lines) and their confidence intervals (shaded areas) of the effect of age on subcutaneous fat thickness for male (black) and female (red) moose ($n = 174$) in Quebec, Canada, in fall 2019.

could change the pattern of parasite diversity in several northern regions and lead to a modification in parasite interactions, which could have a major impact on host–parasite dynamics.

Acknowledgements – We are grateful to wildlife biologists and technicians from the Quebec Ministère des Forêts, de la Faune et des Parcs (MFFP) for their help with fieldwork and data gathering. We also thank the hunters who generously provided samples and all the employees of wildlife reserves for their help. We thank all the students of the Côté-Tremblay laboratory at Université Laval who participated in the fieldwork: B. Vuillaume, J. Fuller, E. Lemay, A. Brodeur, B. Capolla and D. De Pierre. We also thank M. Bonin, M.-C. Martin, J. Hénault-Richard, F. Doyon, C. Lacasse, and W. Lapointe for their help with lab work and M.-O. Benoit-Biancamano from the Faculty of Veterinary Medicine of Université de Montréal for her expertise in parasites identification. We thank G. Daigle for his help with statistical analyses and C. Bajzak for her invaluable help in submitting this article.

Funding – This study was funded by a Cooperative Research and development grant from the Natural Sciences and Engineering Research Council of Canada in partnership with Mitacs, Sépaq, J. D. Irving, Fondation de la Faune du Québec, Fédération québécoise des chasseurs et pêcheurs, Fédération des pourvoiries du Québec, Zecs Québec, Domtar, Nation Huronne-Wendat, Gestion Forestière Lacroix, Séminaire de Québec, Parc éoliens de la Seigneurie de Beaupré, Corporation de Gestion des Rivières Matapédia et Patapédia (CGRMP), and Parks Canada. We also thank the Héritage faune foundation for awarding the Aurèle-Blais scholarship in wildlife management to C. Pouchet.

Author contributions

Catherine Pouchet: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Christopher Fernandez-Prada:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – original

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Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1002/wlb3.01205>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.08kpr58f> (Pouchet et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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