



Parasite prevalence, infection intensity and richness in an endangered population, the Atlantic-Gaspésie caribou

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ABSTRACT

The Atlantic-Gaspésie caribou (*Rangifer tarandus caribou*) population is a small isolated relict herd considered endangered according to the Canadian Species at Risk Act (SARA). This population has low recruitment and survival rates but the potential role of parasites on individual fitness is unknown. In this context, we explored the parasite status of this population with the aim of 1) assessing the occurrence and intensity of parasite infections and the spatial, temporal and individual variations, 2) quantifying parasite richness and investigating factors such as sex and host body condition that may be associated with this variable and 3) evaluating the effects of parasite infections on survival in the Atlantic-Gaspésie caribou population. We examined fecal samples from 32 animals captured in 2013–2014 for eggs, oocysts and larvae of parasites and detected 7 parasite species: dorsal-spined larvae protostrongylids, presumably *Parelaphostrongylus andersoni* based on PCR identification of a subset, *Nematodirus odocoilei* and other unidentified Strongyles, *Trichuris* sp., *Capillaria* sp., *Moniezia* sp. and *Eimeria* sp. For each caribou, mean parasite species richness was 1.8 ± 1.1 (SD). Sex, body condition, year and capture location did not explain parasite prevalence, intensity of infection or richness except for intensity of infection of *Capillaria* sp. that was positively influenced by body condition. Parasites did not influence survival although mortality was higher for males than for females. We suggest that the relatively low and common gastrointestinal and protostrongylid parasite infections will not be a short-term threat leading to extinction.

1. Introduction

Parasites can influence the dynamics of wildlife populations (Anderson and May, 1978; Gunn and Irvine, 2003; Hughes et al., 2009) by having negative effect on individual performance. Even when parasitism does not have direct effect on survival, infection can influence population dynamics through its effect on pregnancy rates, body mass and condition (Albon et al., 2002; Stien et al., 2002). Other studies have suggested that parasite infection can exacerbate the effects of other ecological factors on individual fitness (e.g. bad weather, Gulland, 1992) and population size leading to higher risk of stochastic events or Allee effects (Lafferty and Gerber, 2002; McCallum and Dobson, 2002; De Castro and Bolker, 2005).

The small and isolated population of Atlantic-Gaspésie caribou (*R. t.*

caribou) is of particular interest because it is the sole remnant group of caribou on the south shore of the St. Lawrence River, Canada, a relict of the herds previously inhabiting the Atlantic ecoregion (COSEWIC, 2011). This population has been in constant decline since the end of the 19th century (reviewed in St-Laurent et al., 2009) and its abundance is now evaluated at ~90 individuals (Morin, 2017). It is designate endangered since May 2000 according to the Species at Risk Act (SARA, Government of Canada, 2015) and is identified as a designatable unit (DU11), i.e. an irreplaceable component of Canada's biodiversity (COSEWIC, 2011).

Factors involved in the decline of this population are related to landscape modification. Human activity, such as forestry, promotes young stages of forest succession that provide resources for moose (*Alces americanus*) and white-tailed deer (*Odocoileus virginianus*)

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(Courtois et al., 2007; Nadeau Fortin et al., 2016). High abundance of alternative prey, paired with the presence of numerous anthropogenic linear structures (roads, trails or power lines), are known to increase the abundance and effectiveness of two incidental predators (Gaudry, 2013), coyotes (*Canis latrans*) and black bears (*Ursus americanus*). In Gaspésie, these predators were found to prey opportunistically on calves (Crête and Desrosiers, 1995), from which low survival rates were shown to be a major cause of decline (St-Laurent et al., 2009; Frenette, 2017).

Additional factors such as parasitic infections may be involved in the poor performance of this population. Landscape modification may induce higher physiological or nutritional stress levels which affect immune competence of individuals (Martin, 2009; Santicchia et al., 2015). The resulting increase of infection can lead to a decrease in adult and calf body condition and survival (Stien et al., 2002; Gunn and Irvine, 2003; Hughes et al., 2009). The presence of white-tailed deer and moose in proximity with caribou may also act as reservoir hosts for lethal parasites such as *Parelaphostrongylus tenuis* (Anderson, 1972). However, little information is available about the health of this isolated caribou population, including parasite diversity, prevalence and intensity, although Moisan (1957) opportunistically reported *Ostertagia* worms in one dead animal. In this context, the objectives of this study were 1) to assess the occurrence and intensity of parasite infections and the spatial, temporal, and individual variations, 2) to quantify parasite richness and explore if sex and host body condition are associated with this variable and 3) to evaluate the effects of parasite infections on survival in the Atlantic-Gaspésie caribou population. We expected to find higher parasite prevalence, intensity and diversity in males and in individuals exhibiting poor body condition, and predicted a negative impact of parasite infections on caribou survival.

2. Materials and methods

2.1. Study area, capture and manipulations

The Atlantic-Gaspésie caribou population is mainly constrained within the limits of the Gaspésie National Park, Québec, Canada (48°55'N, 66°16'W) and in the adjacent Matane and Chic-Chocs Wildlife Reserves. The park is located in the Chic-Chocs mountain range with many peaks exceeding 1000 m, including Mounts Logan, Albert and Jacques-Cartier. In February 2013 and 2014, 43 adult caribou were captured using a net-gun fired from a helicopter. Each individual was collared using a GPS/Argos telemetry device (model TGW-4680, Telonics Inc., Mesa, AZ) and monitored for a period of 2½ years. Sex of each animal as well as the location of capture (Mount Logan, Albert or Jacques-Cartier) were noted, while a relative index of body condition (see below for details) was recorded and fecal pellets were collected. All manipulations were approved by the Animal Welfare Committee of the Ministère des Forêts, de la Faune et des Parcs du Québec (certificate #CPA FAUNE 13-08) and of the Université du Québec à Rimouski (certificate # CPA-52-13-112). Mortalities were confirmed when collars were recovered after a mortality signal coming from the VHF beacon of the telemetry collars or when movement rates reached ~0 for several days via the Argos link. Fecal samples were collected from 32 of the 43 captured individuals which corresponds to approximately 1/3 of the entire remaining population. Fecal pellets taken directly from animals were kept cool on ice for 1–4 weeks prior to analyses for parasites. A single observer scored the body condition of 31 of the 32 individuals following a classification ranging from 1 to 4, where a value of 1 indicated an individual in bad condition showing signs of malnutrition, and 4 described an individual in good body condition with a layer of fat under skin thick enough not to have prominent bone (modified from Gerhart et al., 1996). For parsimony, we further grouped some levels of our body condition index according to the average value (3.39), ending

with a two-level factor of similar sample size (i.e. < 3.39, gathering values of 1, 2 and 3, $n = 15$; > 3.39, value of 4, $n = 16$).

2.2. Parasite analyses

Fecal samples were analyzed using 1) a modified Wisconsin double centrifuge technique (Egwan and Slocombe, 1982) for isolation and identification of nematode and cestode eggs and protozoan oocysts; 2) a modified quantitative Baermann technique, the beaker method (Forrester and Lankester, 1997), for protostrongylid larvae followed by PCR and sequencing of ITS-2 region for species determination (Verocai et al., 2013); 3) a modified fecal sedimentation (Flukefinder® Visual Difference, Moscow, Idaho, USA) for trematode eggs and; 4) a modified direct immunofluorescence technique with monoclonal antibodies (*Aqua-Glo G/C Direct Comprehensive Kit*, Waterborne, New Orleans, LA, USA) for protozoans of the genus *Giardia* and *Cryptosporidium*. However, the kit was ambiguous in detecting *Cryptosporidium* cysts so we did not include these results. The small amount of pellets by sample prevented us from replicating the analyses and drying a subsample, so we did not express the number of eggs, oocysts or larvae by gram of dried-feces. Nevertheless, the relatively similar moisture content between samples and the appropriate storing of the feces (i.e. no mold contamination) may have not affected the estimation of parasite stages (eggs, oocysts or larvae) as presented per gram of wet feces (epg, opg, lpg, respectively). The decimal numbers were rounded to the upper integer for analysis.

2.3. Parasite description

We calculated the prevalence of a parasite species as the percentage of hosts infected by that species and the intensity of the infection as the mean number of parasite eggs, oocysts or larvae per infected host (Bush et al., 1997). Co-infections may have cumulative (synergistic or antagonistic) effects on hosts (Bordes and Morand, 2009), thereby we calculated a measure of richness of parasites in each host as the number of parasite species detected in the sample.

2.4. Statistical analyses

We calculated a 95% confidence interval around the prevalence for a binomial distribution as suggested by Rózsa et al. (2000) using the “binom” package in R (R Core Team, 2015). As suggested by Rózsa et al. (2000), we calculated overall and within group means intensity because this measure is independent of sample size and prevalence. Because parasite distributions are often highly skewed, with few individuals having extremely high intensities, we also present intensity ranges and a 95% confidence interval around the mean intensity using the bias-corrected and accelerated (BC_a) bootstrap confidence interval of Efron and Tibshirani (1993; suggested by Rózsa et al., 2000) from the “bootBCa” package.

To identify which variables between years, capture locations, sex, body condition and co-infection (i.e. number of other parasite species tested positive) were associated with parasite prevalence, intensity and richness, we conducted model selection based on the Akaike information criterion corrected for small samples (AIC_c). We tested one variable in each model and calculated the unconditional confidence intervals when necessary (Burnham and Anderson, 2002). We used generalized linear models with binomial distribution for prevalence, negative binomial distribution for intensity and Poisson distribution for richness. We finally used a logistic regression to test if caribou survival (coded 0: dead; 1: alive) was affected by parasite infections. We included year and capture location to control for temporal and spatial variation, sex and body condition as well as parasite richness and the intensity of infection for each parasite independently in different models. We performed

multi-model inference when $\Delta AIC_c < 2$ (Burnham and Anderson, 2002). All statistical analyses were performed in R (R Core Team, 2015).

3. Results

We detected at least 7 parasite genera in the Atlantic-Gaspésie caribou population. Baermann examination revealed the presence of dorsal-spined protostrongylid larvae which were identified by PCR as *Parelaphostrongylus andersoni* in 5 samples tested from 2013 to 3 from 2014 (5 larvae picked at random were tested from each sample except one in 2014 where only 1 larvae was recovered). Fecal flotation tests revealed the presence of multiple nematodes (see Table 1 for details). For the Strongylida order, we identified eggs from the genus *Nematodirinae*, which were consistent morphologically (eggs ranged from 161.28–162.58 x 77.09–78.09 μm) with *Nematodirus odocoilei*; additional strongylate eggs could not be identified to genus or species based on morphology (eggs ranged from 74.52–89.03 x 34.30–52.71 μm), but may have been *Ostertagia gruehneri*, or less likely, *Teladorsagia boreoarcticus*, both common parasites of caribou across most of their range (Kutz et al., 2012). For the Trichocephalida order, we identified eggs from *Trichuris* sp. (egg measured 70.44 x 33.80 μm) and *Capillaria* sp. (eggs ranged from 48.75–52.54 x 23.47–26.26 μm). All samples tested negative for trematodes but two samples were positive for the cestode *Moniezia*, most similar to *M. benedeni* (a representative *Moniezia* sp. egg measured 79.51 x 80.54 μm). For the protozoan, oocysts from *Eimeria* sp. (oocysts ranged from 37.86–38.58 x 25.92–28.98) were identified, while all samples were negative for *Giardia* sp. cysts.

The mean richness of parasites was 1.8 ± 1.1 (SD) species with 27 caribou with at least one parasite species and 2 caribou with up to 4 parasite species in their feces. Null models were the most parsimonious to explain prevalence and intensity of infection for all but one parasite species, as the intensity of infection by *Capillaria* sp. was influenced by body condition. Individual in poor condition got, on average, 5 eggs per gram of feces less than individual in good condition ($AIC_c = 180.4$, ΔAIC_c with null model = 3.1, model weight = 0.56, unconditional confidence interval for body condition = -1.7 to -0.17). Null model was also the most parsimonious to explain individual parasite richness. The most parsimonious model explaining variations in caribou survival included sex (ΔAIC_c with null model of 8.33, model weight of 0.79,

unconditional confidence interval for sex: -6.09 to -1.11), with females having a higher survival rate (0.94) than males (0.43).

4. Discussion

Our objectives were to investigate differences in prevalence, intensity of infection and richness of parasites in an endangered, isolated caribou population, to quantify parasite richness and explore which factors, such as sex and host body condition, were associated with this variable, and to evaluate the impact of parasite infections on caribou survival. Intensity and prevalence of infection detected in the feces were generally low in this caribou population. However, infections by nematodes from *Trichuris* spp. and *Capillaria* spp. and cestodes (*Moniezia cf benedeni*) are generally uncommon in caribou in North America (Korsholm and Olesen, 1993; Kutz et al., 2012) but were found in this herd. Parasite richness was also low and not associated with any of the explanatory variables we considered, and parasite infections were not linked to caribou survival.

Dorsal-spined larvae of *Parelaphostrongylus andersoni*, strongyle-type nematodes, cestodes from the *Moniezia* genus, and protozoa from the *Eimeria* genus have a broad geographic distribution across North America (Fruetel and Lankester, 1989; Lankester and Hauta, 1989; Kutz et al., 2012). When infection intensity is high, some of these parasites may impact the health of individuals by influencing body condition, physiology and behavior (Hansen et al., 1950; Albon et al., 2002; Stien et al., 2002). Intensity of infection, based on fecal egg counts, in the Gaspésie population was relatively low and comparable to other caribou populations (Lankester and Hauta, 1989; Oksanen et al., 1990; Verocai et al., 2013). One of the two caribou infected with *Moniezia* sp. had 176 eggs per gram of feces, the highest infection from a gastrointestinal parasite recorded in this population and the highest level of infection that have been documented so far. For example, in the Chisana caribou herd in Yukon, the intensity of infection range from 3.5 to 16 eggs per gram of wet feces (Hoar et al., 2009). However, this high fecal egg count does not necessarily reflect the adult parasite burden. Tapeworms shed gravid proglottids (mature segments) which can contain hundreds of eggs. Proglottids are not even distributed among the fecal pellets, and if the pellet tested contains a proglottid there will be a high egg counts whereas the next fecal pellet may have no eggs.

Trichuris and *Capillaria* genera, from the *Trichuridae* family, are common in reindeer of Palaeartic (Hrabok et al., 2006b). While *Trichuris* spp. was detected in some caribou herds in North America (Kutz et al., 2012), *Capillaria* spp. was only reported in wild caribou in North America once by Fruetel and Lankester (1989). We may hypothesize that the infection may be a remnant of the historical diversity of the eastern caribou during the Pleistocene. Alternatively, it can be a spillover from other sympatric species such as moose that are known to be carriers of these parasites at least in captivity in Ontario (Lankester, 2002). This latter hypothesis is supported by the very high moose densities found around the Atlantic-Gaspésie caribou range, with peak densities ranging from 3.3 to 4.8 moose/km² (Lamoureux et al., 2012). Pathogenic effects of this family of nematodes on ungulates are mainly seen in young cattle; diarrhea where treatment was necessary even with low infection (Seidel and Rowell, 1996; Kutz et al., 2012), emaciation and wasting syndrome (Clauss et al., 2002) but was also associated with deaths of captive moose (Lankester and Samuel, 2007). The prevalence in our population is somewhat high, however, in a Finland reindeer population where *Capillaria* spp. were detected in more than half of the individuals, levels of infection reached 25 to over 500 eggs per gram of feces (Hrabok et al., 2006a, 2006b), an intensity ten times higher than what was observed in the Gaspésie-Atlantic caribou population.

None of the explanatory variables we considered helped to explain parasite prevalence, intensity of infection or richness, except for body condition that influenced *Capillaria* sp. intensity. Although the positive association between *Capillaria* sp. and body condition was surprising, a difference of 5 eggs per gram is unlikely to have large biological effects.

Table 1

Parasite prevalence and intensity of infection from feces of 32 Atlantic-Gaspésie caribou (designatable unit 10), Québec, Canada, in February 2013 and 2014.

Parasites	Prevalence ^a		Intensity ^b		
	Value	95% CI	Mean	95% CI	Range
Nematodes					
Strongylida					
Protostrongylidae ^c	28	14–47	11.7	6.6–18.4	1–31
Nematodirinae ^d	19	7–36	1.8	1–3.3	1–5
Unidentified strongyle	25	11–43	1.8	1.1–3.1	1–5
Trichocephalida					
<i>Trichuris</i>	6	1–21	1.0	1–1	1–1
<i>Capillaria</i>	84	67–95	7.2	5.2–11	1–34
Cestodes					
<i>Moniezia benedeni</i>	6	1–21	91.5	7–91.5	7–176
Protozoa					
<i>Eimeria</i>	9	2–25	34.3	2–64.3	2–92

^a Prevalence: % of individual tested positive for the presence of the parasite.

^b The mean intensity of the infection is the mean number of larval (LPG), egg (EPG) or oocyst (OPG) per gram of feces calculated over all samples tested positive for the parasite.

^c Polymerase chain reaction was conducted for 8 of the 9 positive cases confirming that the larvae were all *Parelaphostrongylus andersoni*. (5 larvae picked at random by positive cases, one sample did not amplify).

^d All eggs in 2013 were consistent in size and morphology with *Nematodirus odocoilei*.

Parasite intensity of infections and species richness did not have an effect on survival of collared caribou during the year following capture. Our restricted sample size, however, limits the statistical power for our analyses. It is worth noting that other unmeasured ecological factors are known to influence parasitism. For example, age and seasonal variations are related to parasite infection in many species, including caribou (Hrabok et al., 2006a; Davidson et al., 2014; Simard et al., 2016). These variables were not available because we only had one sampling period (February) and age of adult caribou was unknown. We nevertheless highlighted a male-biased mortality, a pattern generally present in other ungulates (Loison et al., 1999).

Further analyses will be of great importance to assess the global health of this endangered population. Parasite sampling should be extended throughout the year to identify seasonal patterns in infections and if possible, calves should be sampled. Many of the parasites detected in this study are known to affect young individuals in other populations or species (*Moniezia* sp. Fagbemi and Dipeolu, 1983; *Capillaria* sp. Seidel and Rowell, 1996; *Parelaphostrongylus* sp. Jenkins et al., 2005; *Nematodirus* sp. Kutz et al., 2012). In this context, although parasites may not be the direct cause of calf death in the Gaspésie population, they can influence their capacity to flee or avoid predation (Hatcher et al., 2006), the main hypothesized cause of mortality in our population.

Globally, our results suggest that infection with gastrointestinal parasites and *P. andersoni* are not a short-term threat to the Atlantic-Gaspésie caribou population. Infection intensity in this population is generally low and parasites detected are relatively common and did not affect adult survival. Our study, however, was not designed to detect other parasites, such as the blood and tissue parasites, that have been shown to be quite pathogenic in *Rangifer* elsewhere. For example, the tick transmitted parasite, *Babesia* spp., is a known cause of mortality in captive caribou (Holman et al., 1994; Kutz et al., 2012) and has recently been detected in zoo caribou in Quebec. *Toxoplasma gondii* and *Neospora caninum*, transmitted through felids and canids, respectively, are both important causes of fetal loss and weak calves in many ungulate species, including caribou (Kutz et al., 2012). The protozoa *Besnoitia tarandi* has emerged in the George and Leaf river caribou herds as a pathogen causing debilitation and possibly death (Ducrocq et al., 2012). Visual examination of the conjunctiva of 42 caribou showed no sign of infection by *B. tarandi* (unpublished data), but Ducrocq et al. (2012) documented an important underestimation of the prevalence of this infection by visual assessment compared to microscopic evaluation. *Parelaphostrongylus tenuis*, a common protostrongylid parasite of white-tailed deer in eastern North America, innocuous in this normal host, causes fatal neurological disease in caribou and is responsible for excluding caribou from other areas and failure of reintroduction efforts (Bergerud and Mercer, 1989). Finally, we recommend that future parasite surveys should consider parasites that impact calves especially *Toxoplasma gondii* and *Neospora caninum* (Kutz et al., 2012), considering that calf survival is a key demographic rate in the Atlantic-Gaspésie caribou population conservation (St-Laurent et al., 2009) and that young animals are typically more susceptible to parasitism (Hawlena et al., 2006; Souchay et al., 2013).

Conflicts of interest

None.

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References

- Anderson, R.M., May, R.M., 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. *J. Anim. Ecol.* 47, 219–247. <http://dx.doi.org/10.2307/3933>.
- Anderson, 1972. The ecological relationships of meningeal worm and native cervids in North America. *J. Wildl. Dis.* 8, 304–310.
- Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E., Halvorsen, O., 2002. The role of parasites in the dynamics of a reindeer population. *Proc. R. Soc. Lond. B Biol. Sci.* 269, 1625–1632.
- Bergerud, A.T., Mercer, W.E., 1989. Caribou introductions in Eastern North America. *Wildl. Soc. Bull.* 17, 111–120.
- Bordes, F., Morand, S., 2009. Parasite diversity: an overlooked metric of parasite pressures? *Oikos* 118, 801–806.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-model Inference: a Practical Information-theoretic Approach. Springer.
- Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83, 575–583.
- Clauss, M., Kienzle, E., Wiesner, H., 2002. Importance of the wasting syndrome complex in captive moose (*Alces alces*). *Zoo Biol.* 21, 499–506.
- COSEWIC, 2011. Designatable Units for Caribou (*Rangifer tarandus*) in Canada. Committee on the status of endangered wildlife in Canada, Ottawa.
- Courtois, R., Ouellet, J.P., Breton, L., Gingras, A., Dussault, C., 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience* 14, 491–498.
- Crête, M., Desrosiers, A., 1995. Range expansion of coyotes, *Canis latrans* threatens a remnant herd of caribou, *Rangifer tarandus*, in southeastern Quebec. *Can. Field Nat.* 109, 227–235.
- Davidson, R.K., Amundsen, H., Lie, N.O., Luyckx, K., Robertson, L.J., Verocai, G.G., Kutz, S.J., Ytrehus, B., 2014. Sentinels in a climatic outpost: endoparasites in the introduced muskox (*Ovibos moschatus wardi*) population of Dovrefjell, Norway. *Int. J. Parasitol.* Parasites Wildl 3, 154–160.
- De Castro, F., Bolker, B., 2005. Mechanisms of disease-induced extinction. *Ecol. Lett.* 8, 117–126.
- Ducrocq, J., Beauchamp, G., Kutz, S., Simard, M., Elkin, B., Croft, B., Taillon, J., Côté, S.D., Brodeur, V., Campbell, M., Cooley, D., Cuyler, C., Lair, S., 2012. Comparison of gross visual and microscopic assessment of four anatomic sites to monitor besnoitia tarandi in barren-ground caribou (*Rangifer tarandus*). *J. Wildl. Dis.* 48, 732–738.
- Efron, B., Tibshirani, R.J., 1993. An Introduction to the Bootstrap. Chapman & Hall, London, U.K.
- Egwang, T.G., Slocombe, J.O., 1982. Evaluation of the Cornell-Wisconsin centrifugal flotation technique for recovering trichostrongylid eggs from bovine feces. *Can. J. Comp. Med.* 46, 133–137.
- Fagbemi, B.O., Dipeolu, O.O., 1983. *Moniezia* infection in the dwarf breeds of small ruminants in Southern Nigeria. *Vet. Q.* 5, 75–80.
- Forrester, S.G., Lankester, M.W., 1997. Extracting protostrongylid nematode larvae from ungulate feces. *J. Wildl. Dis.* 33, 511–516.
- Frenette, J., 2017. Démographie et viabilité de la population de caribou Gaspésie-Atlantique (Mémoire de maîtrise). Université du Québec à Rimouski, Rimouski.
- Fruetel, M., Lankester, M.W., 1989. Gastrointestinal helminths of woodland and barren ground caribou (*Rangifer tarandus*) in Canada, with keys to species. *Can. J. Zool.* 67, 2253–2269.
- Gaudry, W., 2013. Impact des structures anthropiques linéaires sur la sélection d'habitat du caribou, de l'ours noir et du coyote en Gaspésie. Université du Québec à Rimouski, Rimouski.
- Gerhart, K.L., White, R.G., Cameron, R.D., Russell, D.E., 1996. Estimating fat content of caribou from body condition scores. *J. Wildl. Manag.* 60, 713–718.
- Government of Canada, 2015. Consolidated Federal Laws of Canada. Species at Risk Act. Gulland, F.M., 1992. The role of nematode parasites in Soay sheep (*Ovis aries* L.) mortality during a population crash. *Parasitology* 105 (Pt 3), 493–503.
- Gunn, A., Irvine, R.J., 2003. Subclinical parasitism and ruminant foraging strategies: a review. *Wildl. Soc. Bull.* 31, 117–126.
- Hansen, M.F., Kelley, G.W., Todd, A.C., 1950. Observations on the effects of a pure

- infection of *Moniezia expansa* on lambs. *Trans. Am. Microsc. Soc.* 69, 148–155.
- Hatcher, M.J., Dick, J.T.A., Dunn, A.M., 2006. How parasites affect interactions between competitors and predators. *Ecol. Lett.* 9, 1253–1271.
- Hawlana, H., Abramsky, Z., Krasnov, B.R., 2006. Ectoparasites and age-dependent survival in a desert rodent. *Oecologia* 148, 30–39.
- Hoar, B., Oakley, M., Farnell, R., Kutz, S., 2009. Biodiversity and springtime patterns of egg production and development for parasites of the Chisana Caribou herd, Yukon Territory, Canada. *Rangifer* 29, 25–37.
- Holman, P.J., Petrini, K., Rhyon, J., Wagner, Q.G., 1994. In vitro isolation and cultivation of a *Babesia* from an american woodland caribou (*Rangifer tarandus caribou*). *J. Wildl. Dis.* 30, 195–200.
- Hrabok, J.T., Oksanen, A., Nieminen, M., Rydzik, A., Uggla, A., Waller, P.J., 2006a. Reindeer as hosts for nematode parasites of sheep and cattle. *Vet. Parasitol.* 136, 297–306.
- Hrabok, J.T., Oksanen, A., Nieminen, M., Waller, P.J., 2006b. Population dynamics of nematode parasites of reindeer in the sub-arctic. *Vet. Parasitol.* 142, 301–311.
- Hughes, J., Albon, S.D., Irvine, R.J., Woodin, S., 2009. Is there a cost of parasites to caribou? *Parasitology* 136, 253–265.
- Jenkins, E.J., Hoberg, E.P., Polley, L., 2005. Development and pathogenesis of *Parelaphostrongylus odocoilei* (nematoda: protostrongylidae) in experimentally infected thinhorn sheep (*Ovis dalli*). *J. Wildl. Dis.* 41, 669–682.
- Korsholm, H., Olesen, C.R., 1993. Preliminary investigations on the parasite burden and distribution of endoparasite species of muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus groenlandicus*) in West Greenland. *Rangifer* 13, 185–189.
- Kutz, S.J., Ducrocq, J., Verocai, G.G., Hoar, B.M., Colwell, D.D., Beckmen, K.B., Polley, L., Elkin, B.T., Hoberg, E.P., 2012. Parasites in ungulates of Arctic North America and Greenland: a view of contemporary diversity, ecology, and impact in a world under change. *Adv. Parasitol.* 79, 99–252.
- Lafferty, K.D., Gerber, L.R., 2002. Good medicine for conservation biology: the intersection of epidemiology and conservation theory. *Conserv. Biol.* 16, 593–604.
- Lamoureux, J., Bélanger, M., Larocque, C., 2012. Inventaire aérien de l'original dans les Réserves fauniques de Matane et de Dunière, à l'hiver 2012. Ministère des Ressources naturelles et de la Faune, Rimouski, Québec.
- Lankester, M.W., 2002. Low-dose meningeal worm (*Parelaphostrongylus tenuis*) infections in moose (*Alces alces*). *J. Wildl. Dis.* 38, 789–795.
- Lankester, M.W., Hauta, P.L., 1989. *Parelaphostrongylus andersoni* (Nematoda: protostrongylidae) in caribou (*Rangifer tarandus*) of northern and central Canada. *Can. J. Zool.* 67, 1966–1975.
- Lankester, M.W., Samuel, W.M., 2007. Pests, parasites and diseases. In: *Ecology and Management of the North American Moose*. University Press of Colorado, pp. 479–517.
- Martin, L.B., 2009. Stress and immunity in wild vertebrates: Timing is everything. *Gen. Comp. Endocrinol.* 163, 70–76 9th International Symposium Avian Endocrinology.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., Jullien, J.-M., 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80, 2539–2554.
- McCallum, H., Dobson, A., 2002. Disease, habitat fragmentation and conservation. *Proc. R. Soc. Lond. B Biol. Sci.* 269, 2041–2049.
- Moisan, G., 1957. Le caribou de Gaspé III. Analyse de la population et plan d'aménagement. *Nat. Can.* 84, 5–27.
- Morin, M., 2017. Inventaire aérien de la population de caribou de la Gaspésie (*Rangifer tarandus caribou*) – Automne 2016. Ministère des Forêts, de la Faune et des Parcs, Direction de la gestion de la faune de la Gaspésie, Îles-de-la-Madeleine.
- Nadeau Fortin, M.-A., Sirois, L., St-Laurent, M.-H., 2016. Extensive forest management contributes to maintain suitable habitat characteristics for the endangered Atlantic-Gaspésie caribou. *Can. J. For. Res.* 46.
- Oksanen, A., Nieminen, M., Soveri, T., Kumpula, K., Heiskari, U., Kuloharju, V., 1990. The establishment of parasites in reindeer calves. *Rangifer* 20–21.
- R Core Team, 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rózsa, L., Reiczigel, J., Majoros, G., 2000. Quantifying parasites in samples of hosts. *J. Parasitol.* 86, 228–232.
- Santicchia, F., Romeo, C., Martinoli, A., Lanfranchi, P., Wauters, L.A., Ferrari, N., 2015. Effects of habitat quality on parasite abundance: do forest fragmentation and food availability affect helminth infection in the Eurasian red squirrel? *J. Zool.* 296, 38–44.
- Seidel, K.B., Rowell, J.E., 1996. Canadian muskoxen in Central Europe - a zoo veterinary review. *Rangifer* 16, 79–85.
- Simard, A.-A., Kutz, S., Ducrocq, J., Beckmen, K., Brodeur, V., Campbell, M., Croft, B., Cuyler, C., Davison, T., Elkin, B., Giroux, T., Kelly, A., Russell, D., Taillon, J., Veitch, A., Côté, S.D., 2016. Variation in the intensity and prevalence of macroparasites in migratory caribou: a quasi-circumpolar study. *Can. J. Zool.* 94, 607–617.
- Souchay, G., Gauthier, G., Pradel, R., 2013. Temporal variation of juvenile survival in a long-lived species: the role of parasites and body condition. *Oecologia* 173, 151–160.
- Stien, A., Irvine, R.J., Ropstad, E., Halvorsen, O., Langvatn, R., Albon, S.D., 2002. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. *J. Anim. Ecol.* 71, 937–945.
- St-Laurent, M.-H., Ouellet, J.P., Mosnier, A., Boisjoly, D., Courtois, R., 2009. Le parc national de la Gaspésie est-il un outil de conservation efficace pour maintenir une population menacée de caribou. *Nat. Can.* 133, 6–14.
- Verocai, G.G., Lejeune, M., Finstad, G.L., Kutz, S.J., 2013. A Nearctic parasite in a Palearctic host: *Parelaphostrongylus andersoni* (Nematoda; Protostrongylidae) infecting semi-domesticated reindeer in Alaska. *Int. J. Parasitol. Parasites Wildl.* 2, 119–123.