**Variation in the intensity and prevalence of macroparasites
in migratory caribou: a quasi-circumpolar study**

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2015-0190.R2
Manuscript Type:	Article
Date Submitted by the Author:	21-Mar-2016
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Keyword:	COMPARATIVE < Discipline, parasite, caribou, Rangifer tarandus, helminth, arthropod, monitoring

Variation in the intensity and prevalence of macroparasites in migratory caribou: a quasi-circumpolar study

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Abstract

Comparative studies across time and geographical regions are useful to improve our understanding of the health of wildlife populations. Our goal was to study parasitism in migratory caribou (*Rangifer tarandus* L., 1758) of North America and Greenland. A total of 1507 caribou were sampled across twelve herds to assess seven of their main helminth and arthropod macroparasites between 1978 and 2010. We sought to determine which factors such as sex, age class, herd size, and season best explained the prevalence and intensity of those parasites. Intensity of *Hypoderma tarandi* (L., 1758) increased with age for males while the opposite was observed in females. Prevalence of *Fascioloides magna* (Bassi, 1875), *Taenia hydatigena* (Pallas, 1766), and *Cephenemyia trompe* (Modeer, 1786) was higher in adults than in calves. Prevalence of *F. magna* and *T. hydatigena* were higher at high herd size than at lower herd size. Greenland herds had the lowest prevalence of *T. hydatigena* and *Taenia krabbei* (Moniez, 1879), a higher intensity of *H. tarandi* and a higher prevalence of *C. trompe* than the other herds. Of the herds from Québec and Labrador, the Rivière-George herd had a higher prevalence of *F. magna* than the Rivière-aux-Feuilles herd. Our research provides the first comparative survey of these parasites of caribou across a broad spatial-temporal range.

Keywords: comparative, parasite, caribou, *Rangifer tarandus*, helminth, arthropod, monitoring

Résumé

Les études comparatives réalisées avec un large éventail spatio-temporel sont fort utiles pour améliorer notre compréhension de l'état de santé des populations d'animaux sauvages. Nous avons étudié le parasitisme chez le caribou migrateur (*Rangifer tarandus* L., 1758) en Amérique du Nord et au Groenland. Un total de 1507 caribous ont été échantillonnés à travers douze troupeaux pour sept de leurs principaux helminthes et arthropodes macroparasites entre 1978 et 2010. Nous avons tenté de déterminer quels facteurs tels que le sexe, la classe d'âge, la taille du troupeau et la saison expliquaient le mieux la prévalence et l'intensité de ces parasites. L'intensité de *Hypoderma tarandi* (L., 1758) augmentait avec l'âge chez les mâles alors que le contraire a été observé chez les femelles. Les prévalences de *Fascioloides magna* (Bassi, 1875), *Taenia hydatigena* (Pallas, 1766) et *Cephenemyia trompe* (Modeer, 1786) étaient plus élevées chez les adultes que chez les jeunes. Les prévalences de *F. magna* et de *T. hydatigena* étaient plus élevées à forte taille de troupeau qu'à faible taille de troupeau. Les troupeaux du Groenland avaient une plus grande intensité de *H. tarandi* et une plus grande prévalence de *C. trompe* que les autres troupeaux. Cette recherche fournit la première étude comparative de ces parasites à large échelle spatiale et géographique.

Mots-clés: comparative, parasite, caribou, *Rangifer tarandus*, helminthe, arthropode, suivi

Introduction

Determining parasite biodiversity as well as the abundance and distribution of parasites within animal populations across a species range is crucial for understanding a population's health status and detecting changes (Scott 1988; Hoberg et al. 2003; Hoberg et al. 2008). Parasitism is a major driver of health status and many studies have shown that parasites influence the fitness of organisms and populations through their effects on individual life-history components (Anderson and May 1978; May and Anderson 1978; Gulland 1992; Hudson et al. 1998; Irvine et al. 2006). Host populations often show a strong variation in the prevalence – the percent of infected individuals in the host population – and in the intensity of infection – the average number of parasites per infected host. This variability is typical for macroparasites and is a function of a number of things, including the level of exposure and the ability to mount an immune response (Hudson et al. 2002; Christe et al. 2007).

Various factors can influence parasitism. Sex of the host can impact the intensity of infection, with males often bearing higher burdens than females (Hamilton and Zuk 1982; Zuk 1990; Poulin 1996), with some exceptions (McCurdy et al. 1998; Morales-Montor et al. 2004). Physiological, morphological, and behavioral differences between females and males could operate to create a sexual bias in infection levels. For instance, steroid hormones, particularly testosterone, could depress the immune system and thus play a major role in sex differences (Zuk 1990; Folstad and Karter 1992) and generate sex-specific seasonal patterns of parasite abundance. Age of the host can also influence parasitism as the prevalence of long-lived parasites generally increase with age, starting when an animal is first susceptible to infection (Hudson and Dobson 1995). Many mechanisms could be responsible for age-dependent parasitism levels such as mortality induced by parasite infection, acquired immunity, and changes in exposure to infection with age (Hudson

and Dobson 1995; Wilson et al. 2001). Transmission rate is also thought to increase with density of the host (Arneberg et al. 1998) and host group size (Patterson and Ruckstuhl 2013) because the probability that the infectious stage of the parasite (e.g. eggs or larvae) encounters a host then increases (Côté and Poulin 1995).

Seasonality can also affect the activity and the rate of transmission of parasites. This is particularly true for vector borne pathogens and parasites that have life cycle stages that are free in the environment and whose development and/or survival are sensitive to climatic conditions (Harvell et al. 2002; Kutz et al. 2004; Kutz et al. 2009; Hoar et al. 2012). Because the rate of transmission of parasites is affected by climate, host-parasite systems could be greatly impacted by climate change (Kutz et al. 2005). In the Arctic, the effects of climate change are already evident, with mean surface temperature having increased two to three times more than for the rest of the planet in the past 150 years (Post et al. 2009; IPCC 2013). Predictions of a warmer and wetter Arctic are expected to alter host-parasite interactions by increasing transmission rates and transmission periods, by shifting temporal patterns of parasite life history and by expanding spatial range of some parasites by decreasing environmental constraints (Kutz et al. 2004; Kutz et al. 2005; Brooks and Hoberg 2007; Hoar et al. 2012). However, for some parasites the impacts of a warming arctic climate are not as clear, with extremes in heat negatively impacting transmission (Hoar et al. 2012; Molnár et al. 2013; Kutz et al. 2013b). Thus, arctic ecosystems can provide considerable insight to understand and predict the responses of host-parasite systems to warming on a global scale (Kutz et al. 2009; Davidson et al. 2011).

Caribou (*Rangifer tarandus* L., 1758) are widespread and abundant across the circumpolar Arctic (Festa-Bianchet et al. 2011). This is a keystone species supporting predator populations (Dale et al. 1994; Mowat and Heard 2006; Musiani et al. 2007), as well as affecting vegetation structure

(Olofsson et al. 2009; Champagne et al. 2012; Zamin and Grogan 2013). Caribou are also central to the culture, spirituality, and diet of northern aboriginal peoples (Hummel and Ray 2008; Festa-Bianchet et al. 2011). Many caribou herds of the Arctic are now declining (Vors and Boyce 2009) and may not recover to herd sizes prior to the declines (Festa-Bianchet et al. 2011). The causes of the declines are unknown although habitat degradation, harvesting, industrial development and climate change could be singly or cumulatively responsible (Festa-Bianchet et al. 2011). Infectious diseases and parasites may also be a contributing driver for caribou herd fluctuations but empirical data supporting this assertion remain scarce (Albon et al. 2002). Here, we report variations in prevalence and intensity of infection of the main macroparasites of migratory caribou across several Arctic regions and years that will allow comparisons among herds and serve as baseline data against which to assess caribou vulnerability to parasitism and responses to environmental change. The objectives of this study were: i) to determine which combinations of factors such as sex, age class, herd size, and season best explained the prevalence and intensity of seven of the main macroparasites of caribou and ii) to compare the prevalence and intensity of these macroparasites among twelve herds distributed across North America and Greenland.

Materials and methods

A total of 1507 caribou (Table 1) were sampled across twelve herds from Alaska to Greenland (Figure 1) between 1978 and 2010 with the greatest sampling effort in 2007-2010. Sampling was done intensively in the Rivière-George and Rivière-aux-Feuilles herds since 1978 while it was done sporadically in 1994 in the Beverly/Ahiak and Cape Bathurst herds, in 1997 and 1998 in the Bluenose East herd, and in 2000 in the Beverly/Ahiak herd. In addition, most herds were sampled intensively during the International Polar Year initiative (2007-2010), when the CircumArctic Rangifer Monitoring and Assessment Network (CARMA; www.caff.is/carma) (Russell et al.

2013) coordinated widespread sampling of migratory caribou and reindeer herds across the Arctic. Standardized sampling protocols were applied to establish baseline data on the diversity and abundance of pathogens and parasites (Kutz et al. 2013a). Animal capture and culling were done in accordance with guidelines from the Canadian Council on Animal Care. The following sampling periods were defined considering the ecology of caribou and the studied parasites: winter (December to mid-February), late winter/early spring (mid-February to April), spring migration/calving grounds (May to July), late summer (August and September), and fall migration (October and November) (Sharma et al. 2009). For *H. tarandi* and *C. trompe* (see below), we used only data collected in late winter because it is the only period of the year when larvae are clearly visible by gross examination (Nilssen and Haugerud 1994). For all other parasites, prevalence and intensity were established for all seasons when data were collected. Because different techniques to assess age were used for different herds, we used age classes as attributed in the field instead of exact age. Age criteria were as follows: calves (less than 12 months), yearlings (between 12 and 23 months) and adults (24 months and older). We used data collected from aerial surveys to divide herd sizes in five classes that could be compared across herds and accounted for both herd size and trend: low and increasing, high and increasing, around the peak, high and decreasing, and low and decreasing (Pachkowski et al. 2013).

Studied species

We studied seven of the main macroparasites of caribou: warble larvae (*Hypoderma tarandi* L., 1758), nose bot larvae (*Cephenemyia trompe* Modeer, 1786), liver cysts (*Taenia hydatigena* Pallas, 1766), giant liver flukes (*Fascioloides magna* Bassi, 1875), hydatid cysts (*Echinococcus canadensis* Batsch, 1786), lungworms (*Dictyocaulus eckerti* Skrjabin, 1931), and muscle cysts (*Taenia krabbei* Moniez, 1879) (Table 2). The lungworms reported here have not been

molecularly identified, but are likely *D. eckerti* based on the literature (Höglund et al. 2003; Kutz et al. 2012). By default, all cysts in caribou muscles have previously been described as *T. krabbei*, but Catalano et al. (2014) have recently underlined the potential for misidentification in previous studies because *T. krabbei* and *Taenia arctos* are morphologically very similar, especially in their immature form (Haukisalmi et al. 2011). *Taenia arctos* has been reported in muskoxen (*Ovibos moschatus* Zimmermann, 1780) in Greenland and in other species in North America but not in *Rangifer* (Haukisalmi et al. 2011; Lavikainen et al. 2011; Raundrup et al. 2012; Catalano et al. 2014). The muscle cysts reported here have not been molecularly identified, but are likely *T. krabbei* (S. Kutz, unpubl. data). Data were collected only by scientists and trained personnel to limit biases associated with harvest by hunting. For *E. canadensis* and *D. eckerti*, total count of cysts and worms were done on the whole surface of the lungs and in the lungs after dissecting them along the bronchi and major bronchioles. For *H. tarandi*, total count of larvae was done on the underside of the skin of the top and the sides of the back. For *C. trompe*, total count of nose bot larvae was done in the whole pharynx once the head was removed. For *F. magna* and *T. hydatigena*, total count of flukes and cysts was done in the liver after cutting it into 1 cm slices (the mesentery and omentum were not systematically examined for *T. hydatigena* thus only liver counts were used). For *T. krabbei*, total count of cysts was done in both the heart and the gastrocnemius muscle after making transverse cuts through them (Kutz et al. 2013a). *Fascioloides magna* is known to occur only in the Québec and Labrador herds (Choquette et al. 1971; Parker 1981; Huot and Beaulieu 1985) and, therefore, has not been actively sought during sampling of other herds. However, as sampling included manipulations of the liver to determine the prevalence and intensity of *T. hydatigena*, if an individual not from Quebec or Labrador was infected with *F. magna*, it would have been detected (B. Elkin, personal communication) given the size of this parasite (Pybus 2001).

Statistical analyses

We divided analyses in three parts: i) the calculation of the overall prevalence and intensity, ii) the assessment of the factors explaining the prevalence and intensity of the studied parasites, and iii) comparisons among herds. We used R software version 2.15.3 (R Development Core Team 2013) for all analyses and the level of statistical significance was set at $\alpha < 0.05$. We first calculated the overall prevalence and intensity for each parasite (means $\pm$ SE) with all the data combined. Then, we used generalized linear mixed models (GLMM) to model the effects of different factors on the prevalence and intensity of parasites. We used models with a binomial distribution and a logit link function for the prevalence, and a Poisson distribution and a log link function for intensity. We used sex, age class, herd size, and season as fixed effects, and herd and year as random effects. Except for the intensity of *H. tarandi* and the prevalence of *F. magna*, we could not include interactions in our models because there was a quasi-complete separation of data points, indicating that an independent variable predicted a dependent variable almost perfectly in certain cases. We hence included interactions between sex and age class only in the models assessing the intensity of *H. tarandi* and the prevalence of *F. magna*. The package lme4 was used to estimate the parameters with the Laplace approximation (Bates et al. 2012). The package lsmeans was used to calculate the least-squared means and to make pairwise comparisons among the different groups of factors (e.g. among the three age classes) (Lenth 2013). *P*-values obtained with these *a posteriori* pairwise comparisons were adjusted using the Tukey method (Westfall and Young 1993). Finally, we compared herds in terms of prevalence and intensity of the studied parasites. Since there were gaps in the data, we used the results from the second part of the analyses to focus on certain groups of data. After determining which factor or combination of factors had a significant effect on the prevalence and the intensity of the

studied parasites (e.g. we found an effect of sex on the prevalence), we focused the analyses on the data with sufficient sample size (e.g. we used only adults from the different studied herds to avoid a potential bias associated with age; Table 3). For all analyses, we used only groups of factors for which $n \geq 10$. Unequal sample sizes were due to different sampling effort among herds, seasons, and years. Herds that had a prevalence of 0% or 100% were excluded from herd comparisons because pairwise comparisons could not be calculated when they were included. For the giant liver flukes, we had sufficient data only from the Rivière-George herd to test for the effects of sex, age class, season, and herd size on the prevalence and intensity of flukes. However, the overall prevalence and intensity were calculated with combined data from both the Rivière-aux-Feuilles and the Rivière-George herds. We also compared the overall prevalence and intensity of giant liver flukes between these two herds. There were not enough data to conduct statistical analyses on the effects of sex, age class, season, and herd size on the intensity of nose bots, hydatid cysts, lungworms, and muscle cysts, as well as to conduct herd comparisons.

Results

Hypoderma tarandi

The overall prevalence was $97 \pm 1\%$ (95% C.I.: 96-98; see Appendix B for the overall prevalence and intensity of each parasites separated by herd, sex and age class), with no significant difference according to sex, age class, herd size (Table A1.A) and herd (Table A1.B). Akia-Maniitsoq, Cape Bathurst and Kangerlussuaq-Sisimiut herds had a prevalence of 100%. The overall intensity was 103 ± 5 warble larvae (95% C.I.: 93-112), with a minimum of 1, a median of 61 and a maximum of 1008 warble larvae. Intensity increased with age in males, but the opposite occurred in females (Figure 2; Tables A2.A, A3.A). The intensity of warble larvae in adult

females differed among herds, specifically the Greenland Akia-Maniitsoq and Kangerlussuaq-Sisimiut herds had exceptionally high counts (Figure 3A; Tables A2.B, A3.B).

Cephenemyia trompe

The overall prevalence of nose bot larvae was $22 \pm 2\%$ (95% C.I.: 18-27). Calves ($2 \pm 2\%$) had a lower prevalence than adults ($10 \pm 10\%$) ($z = -2.74$, $p = 0.02$; Tables A4.A, A5.A). The prevalence significantly differed among herds when comparing adults; Akia-Maniitsoq and Kangerlussuaq-Sisimiut herds had particularly high counts (Figure 3B; Tables A4.B, A5.B) and no larvae were detected in the Bluenose East and Cape Bathurst herds.

Taenia hydatigena

The overall prevalence of *T. hydatigena* liver cysts was $19 \pm 1\%$ (95% C.I.: 17-22). Calves ($5 \pm 4\%$) had a lower prevalence than adults ($18 \pm 9\%$) ($z = -2.90$, $p = 0.01$; Tables A6.A, A7.A). Prevalence was higher when the herd size was high and decreasing ($7 \pm 5\%$) than when it was low and decreasing ($2 \pm 2\%$) ($z = 2.74$, $p = 0.048$; Tables A6.A, A7.B). When herd size was high and decreasing, the prevalence of liver cysts differed among herds for adults. The Teshekpuk herd had a particularly high prevalence whereas no cysts were reported from the Cape Bathurst herd (Figure 3C; Tables A6.B, A7.C). Data on intensity were only available from adults. The mean overall intensity across herds was 2.3 ± 0.1 liver cysts (95% C.I.: 2.0-2.5), with a minimum of 1, a median of 2 and a maximum of 11 liver cysts. There was no significant difference according to sex, herd size, and season (Tables A8.A, A9.A). The Teshekpuk herd (1.1 ± 0.3) had fewer liver cysts than the Bathurst (2.7 ± 0.2 ; $z = 2.98$, $p = 0.02$) and Beverly/Ahiak (2.6 ± 0.3 ; $z = 2.81$, $p = 0.04$) herds (Tables A8.B, A9.B).

Fascioloides magna

Fascioloides magna was only present in the Rivière-George and Rivière-aux-Feuilles herds. The overall prevalence in these herds was $48 \pm 2\%$ (95% C.I.: 45-52, $n=777$; data from Rivière-George and Rivière-aux-Feuilles herds, see Methods). Calves had a lower prevalence ($19 \pm 9\%$) than yearlings ($70 \pm 20\%$) ($z=-3.16$, $p=0.005$) and adults ($83 \pm 7\%$) ($z=-6.56$, $p<0.001$; Tables A10.A, A11.A). Prevalence was highest during the herd peak and afterwards than at other times (Figure 4A; Tables A10.A, A11.B). Prevalence was lower during fall migration than during the rest of the year (Figure 4B; Tables A10.A, A11.C). During spring migration and when the herd size was near the peak, adults from the Rivière-George herd ($95 \pm 5\%$; $n=20$) had a higher prevalence of giant liver flukes than adults from the Rivière-aux-Feuilles herd ($40 \pm 10\%$; $n=25$) ($z=3.03$, $p=0.002$; Tables A10.B). For the intensity, there were data only available for adult females. The overall mean intensity was 12.6 ± 0.9 giant liver flukes (95% C.I.: 10.9-14.3, $n=242$), with a minimum of 1, a median of 7 and a maximum of 80 giant liver flukes. In both herds, intensity was lower when the herd size was increasing than during the peak and afterwards (Figure 4C; Tables A12.A, A13.A). Intensity was higher during spring migration than during the rest of the year (Figure 4D; Tables A12.A, A13.B). During spring migration and when the herd size was near the peak, there was no significant difference in intensity between herds (Table A12.B).

Echinococcus canadensis

The overall prevalence was $4.8 \pm 0.6\%$ (95% C.I.: 3.6-6.0) with no significant difference according to sex, age, herd size, and season (Table A14.A, A15.A). The Bathurst herd ($3 \pm 1\%$) had a lower prevalence than the Bluenose West herd ($20 \pm 10\%$) (Tables A14.B, A15.B). No cysts were reported from the Akia-Maniitsoq, Bluenose East, Cape Bathurst and Kangerlussuaq-Sisimiut herds.

Dictyocaulus eckerti

The overall prevalence for *Dictyocaulus* was $2.7 \pm 0.8\%$ (95% C.I.: 1.0-4.3). Prevalence was lower in late winter ($0.5 \pm 0.5\%$) than in late summer ($15 \pm 9\%$) ($z = -2.94$, $p = 0.009$; Tables A16.A, A17). During late winter, there was no significant difference according to herd (Table A16.B) and no *Dictyocaulus* was reported from the Beverly/Ahiak and Bathurst herds.

Taenia krabbei

The overall prevalence was $6.0 \pm 0.7\%$ (95% C.I.: 4.7-7.4) with no significant difference according to sex, age, herd size, and season (Table A18.A). The prevalence of muscle cysts was highest in the Western Arctic herd but did not differ significantly in the other herds (Figure 3D; Tables A18.B, A19). No *T. krabbei* cysts were reported from the Akia-Maniitsoq herd, but are known to occur (C. Cuyler, personal communication).

Discussion

This is the first study presenting the prevalence and intensity of infestation of seven of the main macroparasites of migratory caribou among twelve herds across North America and Greenland. This study was part of one of the most spatially and temporally intensive sampling effort for parasites of caribou across the circumpolar region. Our study is based on data that allowed us to test for individual traits (sex class and age), population characteristics (herd and herd size) and seasonal variability across a very large spatial scale. Our results revealed that sex, age, herd size, and season could partly explain the prevalence and intensity of some macroparasites of caribou and that caribou herds greatly differed in terms of parasitism.

Factors influencing prevalence and intensity

Sex

We found an effect of the sex of the host in interaction with age class on the intensity of *H. tarandi* larvae; intensity increased with age class for males while the opposite occurred in females. These results are consistent with observations from other studies showing that calves and juveniles generally had higher *H. tarandi* larvae infection intensities than adults, and males had a higher intensity than females (Helle 1980; Folstad et al. 1989; Thomas and Kiliaan 1990; Fauchald et al. 2007). Differences in the ability to mount an effective immune response to warble larvae could explain this phenomenon (Helle 1980). Indeed, in addition to the initial behavioral avoidance reactions to the presence of adult flies, caribou mount inflammatory responses to *H. tarandi* larvae when the first larval stages begin their sub-dermal migration. This migration occurs in autumn and is a vulnerable period in *H. tarandi*'s life history (Helle 1980). The higher intensity of *H. tarandi* larvae in female calves that we observed could be explained by the lower and delayed response in the production of antibodies against the migrating larvae in calves because they have not yet acquired immunity against warble infection (Åsbakk et al. 2005). In adult males, the high levels of testosterone and corticosteroids produced during the rut may impede their acquired immune response against migrating first instar of *H. tarandi* larvae, possibly explaining the higher intensity of *H. tarandi* larvae in adult males (Folstad et al. 1989). Similarly and more generally, three meta-analyses reported higher mean prevalence and intensity of infection in males than in females for arthropods, helminths, and unicellular parasites in mammals (Poulin 1996; Schalk and Forbes 1997; Moore and Wilson 2002).

Age class

We found an effect of age on the prevalence of *F. magna*, *T. hydatigena*, and *C. trompe* with adults having a higher prevalence than calves. For *F. magna*, the increase of prevalence with age may reflect a patchy spatial and temporal distribution of the parasite in the environment, a long prepatent period, and a long-lived parasite. Thus, older animals are more likely to have been exposed because they eat more than calves, and have done so over a much broader landscape and longer period of time. At the same time, because of the long prepatent period of the parasite, calves exposed late in their first summer may not have visible mature flukes in the liver until mid to late winter. Additionally, the adult parasites are long-lived, so increasing prevalence with age reflects cumulative infection over time (Pybus 2001). Indeed, mature giant liver flukes are known to live at least 5 years in white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) and may even live as long as their host (Foreyt et al. 1977; Lankester and Luttich 1988). The intensity of *F. magna* was similar in all age-classes which may reflect intraspecific competition among giant liver flukes, higher mortality of heavily infected hosts or resistance to reinfection of already infected hosts. For *T. hydatigena*, the increase in prevalence with age was consistent with the results from Thomas (1994) and may also reflect patchy exposure and cumulative infection over time. In contrast, for *C. trompe*, larvae leave the host every spring, hence there is no cumulative infection (Nilssen and Haugerud 1994) and our results of increased prevalence with age class may reflect an increased susceptibility to infection with age (Hudson and Dobson 1995). Adult female flies of *C. trompe* eject small groups of first instar larvae on the upper lip of caribou hosts and larvae migrate to the pharyngeal region where they develop (Anderson and Nilssen 1990). Flies could select adult hosts because they are larger and hence have larger pharyngeal regions, which could facilitate development of multiple larvae. Alternatively, heavily infected calves and yearlings could be more likely to die than heavily infected adults.

Herd size

The prevalence and intensity of *F. magna* and the prevalence of *T. hydatigena* was associated with herd size. Data on the prevalence and intensity of *F. magna* and *T. hydatigena* have been collected since 1978 in the Rivière-George and the Rivière-aux-Feuilles herds while data on the prevalence of *T. hydatigena* have been collected since 1994 in the Beverly/Ahiak, Cape Bathurst, and Bluenose East herds. Prevalence and intensity of *F. magna* were higher during the herd peak and immediately afterwards than at other times, and prevalence of *T. hydatigena* was highest when the herd size was high and decreasing. These two parasites are environmentally transmitted (Table 2) and may be density dependent, thus prone to increased transmission at high host density (Arneberg et al. 1998; Patterson and Ruckstuhl 2013). In large, dense groups, parasite life cycles can be accelerated because more hosts are available for colonization and reproduction (Côté and Poulin 1995). Herd size may also affect host resistance to parasites if body condition and individual performance of hosts are reduced as a consequence of the herd size (Bonenfant et al. 2009). Good body condition may increase the ability of the host to inhibit parasitism (Coop and Kyriazakis 2001). A study conducted on caribou from the Rivière-George herd found that body condition was poorer when the herd size was nearing a peak and decreasing than when the herd size was low and increasing (Pachkowski et al. 2013). Thus, the highest prevalence and intensity of *F. magna* and *T. hydatigena* we found during the herd peak may be partly explained by the poor individual body condition at this time, but poor body condition could also be the result of a high parasite infection. However, because these two parasites have indirect transmission cycles and have to go through other hosts than caribou to complete their life cycle, the effect of the caribou herd size on the development of these parasites could be mitigated if the other hosts essential for the completion of the life cycle are absent or at very low densities. Similar observations of high prevalence and intensity during the decline phase of herd size could be

explained by the retention of the parasites by these other hosts. For *F. magna*, aquatic snails of the family Lymnaeidae (Lamarck, 1799) are intermediate hosts and various stages of the parasite have been demonstrated to overwinter in snails (Pybus 2001). Hence, since the intermediate host populations are not affected by caribou abundance and *F. magna* is long-lived, high intensity of shedding may be happening in the environment even with declining caribou herd size. However, a delay in egg shedding may not take more than a year and could hence explain only partly why we found high prevalence and intensity years after the peak of the caribou population. For *T. hydatigena*, carnivores act as definitive hosts (Kutz et al. 2012) and eggs are long-lived in favourable environments, hence there could also be an ongoing shedding in the environment even when the caribou herd size is declining, especially if there is a time-lag between the caribou herd size and the population size of its predators.

Season

Season affected the prevalence and intensity of *F. magna* and the prevalence of *D. eckerti*, but not in the same manner. Prevalence of *F. magna* was lowest in the fall migration and the intensity of *F. magna* was highest in the spring migration. In white-tailed deer, mule deer (*Odocoileus hemionus* Rafinesque, 1817), and elk (*Cervus elaphus* L., 1758), *F. magna* has a prepatent period of approximately 6 months, which may explain why summer exposure to infective stages results in a peak of adult stages of the parasite in late winter and spring (Foreyt and Todd 1976; Foreyt 1996). The prevalence of *D. eckerti* was lower in late winter than in late summer, which is consistent with observed trends in muskoxen, caribou, and livestock where adult nematodes are short-lived and hypobiotic larvae (which would not be detected by our examinations) may remain in the lungs over-winter to mature the following spring (Kutz et al. 2012). The ability for *D. eckerti* to overwinter in the Arctic environment is not known, but egg and larval stages of other

species of *Dictyocaulus* do not tend to persist in the environment under subzero temperatures (Ayalew et al. 1974).

Herd comparisons

Of the twelve studied herds, Greenland herds and both Quebec/Labrador herds were different from the rest of the herds in terms of the biodiversity, prevalence and intensity of the studied parasites.

Akia-Maniitsoq and Kangerlussuaq-Sisimiut herds

In Greenland, the prevalence of *T. hydatigena* and *T. krabbei* was low, while *E. canadensis* was not detected. These three parasites require carnivore definitive hosts, and although Arctic fox (*Vulpes lagopus* L., 1758) are present, wolves (*Canis lupus* L., 1758) are absent from the range of caribou in West Greenland and domestic dogs are uncommon, most likely preventing the establishment of *E. canadensis* (Rausch 2003). Arctic fox and polar bear (*Ursus maritimus* Phipps, 1774) can be definitive hosts of *Taenia* species and could hence be responsible for maintaining these parasites in Greenland at low prevalence (Kutz et al. 2012). Caribou from Greenland had a much greater abundance of *H. tarandi* and *C. trompe*. The short migration (<200 km) of Greenland herds may be the principal factor explaining these high values (Cuyler et al. 2012), however, a relatively short host-parasite association caused by the recent introduction of these parasites to these historically isolated herds is also postulated as a reason for the high abundance. Longer migrations in North America could minimize reinfestation of *H. tarandi* and *C. trompe* by separating hosts from the areas where the larvae were dropped and adult flies eventually emerge (Thomas and Kiliaan 1990; Folstad et al. 1991).

Rivière-aux-Feuilles and Rivière-George herds

The two caribou herds from Quebec and Labrador are the only ones with *F. magna*, and the Rivière-George herd had a higher prevalence than the Rivière-aux-Feuilles herd while intensity was not significantly different. The historical biogeography of both herds may be responsible for this peculiar parasite fauna. *Fascioloides magna* tends to have a patchy distribution across North America because it is thought that it cannot persist in areas without suitable snail intermediate hosts, as well as final hosts such as deer, elk and, caribou (Wobeser et al. 1985; Pybus 2001). The limited spread of *F. magna* to caribou of northeastern Canada remains unclear but is presumed to have occurred when the southern limits of the caribou range reached the southeastern United States (Yannic et al. 2014), where white-tailed deer and the now-extinct elk also ranged (Lankester and Luttich 1988). The Rivière-George and Rivière-aux-Feuilles herds are the only migratory caribou herds originating from populations whose range overlapped that of white-tailed deer and elk during the last glaciation (Yannic et al. 2014). Interestingly, prevalence was greater in the Rivière-George herd compared to the Rivière-aux-Feuilles herd and this difference could perhaps be explained by their distinct calving grounds and summer ranges (Couturier et al. 2004; Taillon et al. 2012). For *F. magna*, development in snail intermediate hosts depends on environmental conditions. Hence, there could be a difference in the summer environmental conditions between the summer ranges of the two herds that facilitate summer transmission of *F. magna* on the summer range of the Rivière-George herd but not on the summer range of the Rivière-aux-Feuilles herd. Further investigation on the differences in habitat, percent of wetlands, temperature, humidity, and vegetation type of these two summer ranges may reveal some insights into what may be driving the transmission of *F. magna*.

The main limitation of this study was the presence of missing data due to differences in sampling effort according to herds, seasons and years. To reduce potential bias, standardized protocols were used during the sampling effort of 2007-2011, limiting the variability in data collection and allowing us to make comparisons of data from different sampling periods. However, sampling before 2007 was very similar to the standardized protocols of CARMA because they were largely inspired by the protocols used before 2007. Even if there is a potential bias due to differences in the probability of detection, this bias is reduced by the great similarity between protocols (Kutz et al. 2013a). Another limitation of this study is the small sample sizes used to assess the prevalence of some parasites in certain herds. Even if we did not include sample sizes of less than 10 culled caribou by herd, it is important to keep in mind that the results presented in this study do not represent the entire populations of migratory caribou. A strength of this study is the use of a database that spans several years and different seasons, age classes, and herd sizes across a very large spatial scale. The long-term research on the Rivière-aux-Feuilles and Rivière-George herds, combined with extensive collaboration and coordinated and standardized sampling of caribou during the International Polar year (Kutz et al. 2013a), were essential for these data to be gathered. Our study provides a substantial baseline of the macroparasites of caribou across broad geographical regions and for many herds, and establishes the foundation on which we can begin to evaluate the dynamics of parasitism in caribou over time. Further research should focus on long-term monitoring of parasites in caribou to increase our comprehension of the impacts of climate change on their life cycles and life history parameters.

Acknowledgments

We thank the Government of Canada's International Polar Year Program for the financial support awarded to the CARMA network and the following agencies for in-kind support: ArcticNet, Université Laval, Caribou Ungava, University of Calgary, Government of Nunavut, Government of Yukon, University of Saskatchewan, Nunavik Research Center, Government of the Northwest Territories, Greenland Institute of Natural Resources and the Ministère des Forêts, de la Faune et des Parcs du Québec. A.-A. Simard was supported by ArcticNet and Caribou Ungava, which is mainly funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), Hydro-Québec, Glencore Mine Raglan and the Fédération des pourvoiries du Québec and their partners. S. Kutz was supported by NSERC and Alberta Innovates. We thank J. Dau, L. Parrett, J. Invik and J. Wang for sampling and sample analyses and G. Yannic, G. Gauthier, J. Mainguy, and A. Stien for revision of an early version of the manuscript.

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Table 1: Sample sizes for sex (1=females, 2=males), age class (1=calves, 2=yearlings, 3=adults), herd size (1=low and increasing, 2=high and increasing, 3=around the peak, 4=high and decreasing, 5=low and decreasing), and season (1=winter, 2=late winter/early spring, 3=spring migration/calving grounds, 4=late summer, 5=fall migration) to assess which factors affect the prevalence – the percentage of infected individuals in the host population – and the intensity – the average number of parasites per infected host – of seven of the main macroparasites of caribou (*Rangifer tarandus* L., 1758). Data are from 2 or more herds for each parasite, except for *Fascioloides magna* (Bassi, 1875) that come only from the Rivière-George herd. The symbol « - » means that no data were collected for this category of sex, age class, herd size or season.

		Total	Sex		Age class			Herd size					Season				
			1	2	1	2	3	1	2	3	4	5	1	2	3	4	5
<i>Hypoderma</i>	Prevalence	650	528	122	63	72	515	156	176	25	225	68	-	650	-	-	-
<i>tarandi</i>	Intensity	632	516	116	63	71	498	153	173	25	218	63	-	632	-	-	-
<i>Cephenemyia</i>	Prevalence	335	281	54	24	11	300	-	77	25	166	67	-	335	-	-	-
<i>trompe</i>																	
<i>Taenia</i>	Prevalence	958	790	168	132	21	805	16	122	108	364	348	-	358	184	145	271
<i>hydatigena</i>	Intensity	171	141	30	-	-	171	-	11	22	77	61	-	80	39	34	18

<i>Fascioloides</i>	Prevalence	542	467	75	85	19	438	11	289	20	27	195	13	151	142	60	176
<i>magna</i>	Intensity	189	189	-	-	-	189	-	16	20	24	129	-	38	65	25	61
<hr/> <i>Echinococcus</i>																	
<i>canadensis</i>	Prevalence	1197	969	228	166	37	994	20	364	108	344	361	11	471	214	177	324
<hr/> <i>Dictyocaulus</i>																	
<i>eckerti</i>	Prevalence	374	288	86	29	13	332	-	104	-	145	125	-	232	-	115	27
<hr/> <i>Taenia</i>																	
<i>krabbei</i>	Prevalence	1181	927	254	163	59	959	-	294	108	425	354	11	477	198	181	314

Table 2: Description and life cycle of the seven main macroparasites of caribou (*Rangifer tarandus* L., 1758) used in our study (Davis and Anderson 1971; Fréchette 1986; Kutz et al. 2012).

Name	Classification	Length in <i>Rangifer</i> (cm)	Intermediate host(s)	Position in the intermediate host(s)	Definitive host(s)	Position in the definitive host(s)	Immature form (present in <i>Rangifer</i>)
<i>Hypoderma tarandi</i>	Order : Diptera Family: Oestridae	1–3	-	-	<i>Rangifer tarandus</i>	Sub-dermal	-
<i>Cephenemyia trompe</i>	Order : Diptera Family: Oestridae	1–3	-	-	<i>Rangifer tarandus</i>	Pharyngeal pockets and nasal sinuses	-
<i>Taenia hydatigena</i>	Phylum : Plathelminths	0.1–5	<i>Alces americanus</i> , <i>Cervus canadensis</i> , <i>Odocoileus virginianus</i> , <i>Ovis canadensis</i> , <i>Odocoileus hemionus</i> , <i>Rangifer tarandus</i> , <i>Ovibos moschatus</i>	Liver, mesentery, surface of abdominal viscera	<i>Canis latrans</i> , <i>Canis lupus</i> , <i>Lynx rufus</i> , and other carnivores	Small intestine	Cysticercus

<i>Fascioloides magna</i>	Phylum : Plathelminths	1–8	Fresh water snails	Whole body	<i>Alces americanus, Cervus canadensis, Odocoileus virginianus, Odocoileus hemionus, Rangifer tarandus</i>	Liver	-
<i>Echinococcus canadensis</i>	Phylum : Plathelminths	1–8	<i>Alces americanus, Cervus canadensis, Odocoileus virginianus, Odocoileus hemionus, Rangifer tarandus, Ovibos moschatus</i>	Lungs, liver	<i>Canis latrans, Canis lupus</i>	Small intestine	Hydatid cysts
<i>Dictyocaulus eckerti</i>	Phylum : Nematoda	1–12	-	-	<i>Alces americanus, Odocoileus virginianus, Rangifer tarandus</i>	Lungs	-
<i>Taenia krabbei</i>	Phylum : Plathelminths	0.1–1	<i>Alces americanus, Odocoileus hemionus, Rangifer tarandus</i>	Muscle, heart	<i>Canis latrans, Canis lupus, Lynx rufus, Vulpes lagopus, and other carnivores</i>	Small intestine	Cysticercus

Table 3: Sample sizes used to compare twelve caribou (*Rangifer tarandus* L., 1758) herds in terms of prevalence – the percentage of infected individuals in the host population – and intensity – the average number of parasites per infected host – for seven of their main macroparasites. The symbol « - » means that no data were collected for this herd. Herds are presented according to their spatial distribution, from West to East.

		Western Arctic	Teshekpuk	Cape Bathurst	Bluenose West	Bluenose East	Bathurst	Beverly/Ahiak	Southampton Island	Rivière-aux-Feuilles	Rivière-George	Kangerlussuaq-Sisimiut	Akia-Maniitsoq
<i>Hypoderma</i>	Prevalence	-	-	16	-	26	68	115	64	-	255	50	47
<i>tarandi</i>	Intensity	-	-	-	-	22	50	87	16	-	168	40	41
<i>Cephenemyia trompe</i>	Prevalence	-	-	15	-	26	57	113	-	-	-	40	41
<i>Taenia</i>	Prevalence	16	14	15	-	-	-	88	-	98	26	-	40
<i>hydatigena</i>	Intensity	-	11	-	-	-	50	36	-	37	21	-	-
<i>Fascioloides magna</i>	Prevalence	-	-	-	-	-	-	-	-	25	20	-	-
	Intensity	-	-	-	-	-	-	-	-	10	20	-	-
<i>Echinococcus canadensis</i>	Prevalence	20	14	16	17	53	148	97	-	220	514	50	47
<i>Dictyocaulus</i>	Prevalence	-	-	-	-	26	30	72	-	-	-	50	45

eckerti

<i>Taenia</i>														
	Prevalence	20	14	16	20	53	149	120	64	220	422	50	41	
<i>krabbei</i>														

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Figure 1. Annual range of the twelve studied caribou herds (*Rangifer tarandus* L., 1758) in North America and Greenland. Sources: 1, 2, 3, 4, 5, 6, 7 annual ranges provided by CARMA (D. Russel, personal communication); 9, 10 annual ranges based on telemetry locations (100% Minimum Convex Polygon); 8, 11, 12 annual ranges adapted from Hugo Ahlenius, UNEP/GRID-Arendal. Herds are presented according to their spatial distribution, from West to East.

Figure 2. Intensity – the average number of parasites per infected host – of warble larvae (*Hypoderma tarandi* L., 1758) according to age class in male (M) and female (F) migratory caribou (*Rangifer tarandus* L., 1758) during the late winter/early spring season (mid-February to April). Different letters denote different means within sex and age classes (Table A3.A). Error bars represent mean $\pm$ SE. Sample sizes are shown in parentheses.

Figure 3. A) Intensity – the average number of parasites per infected host – of warble larvae (*Hypoderma tarandi* L., 1758) in adult females during the late winter/early spring season (mid-February to April); B) Prevalence – the percentage of infected individuals in the host population – of nose bot larvae (*Cephenemyia trompe* Modeer, 1786) in adults during the late winter/early spring season; C) Prevalence of liver cysts (*Taenia hydatigena* Pallas, 1766) in adults when the herd size was high and decreasing; and D) Prevalence of muscle cysts (*Taenia krabbei* Moniez, 1879) in different herds of migratory caribou (*Rangifer tarandus* L., 1758). Herds are presented according to their spatial distribution, from West to East. Different letters denote different means (Tables A3.B, A5.B, A7.B, A19). Error bars represent mean $\pm$ SE. Sample sizes are shown in parentheses.

Figure 4. Prevalence – the percentage of infected individuals in the host population – of giant liver flukes (*Fascioloides magna* Bassi, 1875) according to A) herd size and B) season; mean intensity – the average number of parasites per infected host – of giant liver flukes according to C) herd size and D) season in caribou (*Rangifer tarandus* L., 1758) from the Rivière-George herd. The five seasons were defined considering the ecology of caribou and their parasites: winter (December to mid-February), late winter/early spring (mid-February to April), spring migration/calving grounds (May to July), late summer (August and September), and fall migration (October and November). Herd size was divided into five phases that accounted for both herd size and trend: low and increasing, high and increasing, around the peak, high and decreasing, and low and decreasing. For intensity, data were collected only from adult females and there was no data when the herd size was low and increasing. Different letters denote different means (Tables A11.B, A11.C, A13.A, A13.B). Error bars represent mean $\pm$ SE. Sample sizes are shown in parentheses.

Warble larvae/caribou

(F=39)
(M=24)

(F=45)
(M=26)

(F=432)
(M=66)