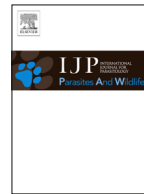




Contents lists available at SciVerse ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Divergent parasite faunas in adjacent populations of west Greenland caribou: Natural and anthropogenic influences on diversity[☆]



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ARTICLE INFO

Article history:

Received 15 April 2013

Revised 18 May 2013

Accepted 21 May 2013

Keywords:

Arctic

Invasions

Marshallagia marshalli

Nematoda

Teladorsagia boreoarcticus

Rangifer tarandus

ABSTRACT

Gastrointestinal parasite diversity was characterised for two adjacent populations of west Greenland caribou (*Rangifer tarandus groenlandicus*) through examinations of abomasa and small intestines collected from adult and subadult females during late winter. Three trichostrongyline (Trichostrongylina: Nematoda) species were identified from the abomasa, although none were recovered from the small intestines, with faunal composition differing between the caribou populations. In caribou from Kangerlussuaq-Sisimiut, *Marshallagia marshalli* and *Teladorsagia boreoarcticus* were highly prevalent at 100% and 94.1%, respectively. In contrast, *Ostertagia gruehneri* was found at 100% prevalence in Akia-Maniitsoq caribou, and was the only abomasal parasite species present in that population. We hypothesise that parasite faunal differences between the populations are a consequence of parasite loss during caribou colonisation of the region approximately 4000–7000 years ago, followed by a more recent spill-over of parasites from muskoxen (*Ovibos moschatus wardi*) and semi-domesticated Norwegian reindeer (*Rangifer tarandus tarandus*) introduced to Kangerlussuaq-Sisimiut and Akia-Maniitsoq regions, respectively, in the 20th century.

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1. Introduction

Trichostrongyline (Trichostrongylina: Nematoda) nematodes are ubiquitous gastrointestinal parasites of the abomasa and small intestines of ruminants (Anderson, 2000), have been linked to disease in wild and domestic animals (Conti and Howerth, 1987; Myers and Taylor, 1989; Gulland, 1992), and may negatively affect body condition and survival of wild ungulates (Hudson et al., 1992; Stien et al., 2002; Newey et al., 2004). In *Rangifer* sp. (i.e. caribou and reindeer) trichostrongyline nematodes are not known to cause acute disease, but several studies have documented negative associations between nematode intensity and the body condition, weight gain and fecundity of female caribou (Arneberg et al., 1996; Albon et al., 2002; Stien et al., 2002; Hughes et al., 2009). It has also been suggested that these nematodes may be regulating reindeer populations in the absence of predators (Albon et al., 2000, 2002), indicating that knowledge of these parasites may be

key to understanding the patterns of cyclic abundance which characterise many *Rangifer* populations, such as those in west Greenland (Melgaard, 1986).

Barrenground caribou (*Rangifer tarandus groenlandicus*) are native to Greenland's west coast and occur in several populations isolated by fjords, mountains and the Sukkertoppen ice cap (Melgaard, 1986; Cuyler et al., 2011). Genetic studies confirm that these populations are closely related (Jepsen et al., 2002) and originate from North American barren-ground caribou (*R. t. groenlandicus*) (Roed, 2005). Colonising caribou likely began arriving some 4000–7000 years ago, possibly following glacial ice bridges, and colonised the coast of this predator-free region from North to South (Melgaard, 1986). Until the 20th century, caribou were the only large terrestrial mammal native to west Greenland (Melgaard, 1986; Cuyler et al., 2002, 2005, 2011; Cuyler, 2007). This is no longer the case and two of the largest populations, Kangerlussuaq-Sisimiut (67°03'N, 50°59'W) and Akia-Maniitsoq (64°34'N, 51°44'W), have had recent contact with imported non-native ungulates. Caribou in the Kangerlussuaq-Sisimiut range are sympatric with muskoxen (*Ovibos moschatus wardi*) imported from northeast Greenland in 1962 (Boertmann et al., 1992), whereas in Akia-Maniitsoq the native caribou population has mixed with semi-domesticated Norwegian reindeer (*Rangifer tarandus tarandus*) imported in 1952 (Cuyler, 1999) and is also sympatric with

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feral Greenlandic sheep (*Ovis aires*), translocated from southern sheep farms (Rose et al., 1984; Cuyler pers. comm.).

Previous research, based on analyses of faecal samples from the Kangerlussuaq-Sisimiut and Akia-Maniitsoq populations, suggested that these populations have a divergent gastrointestinal parasite fauna (Steele et al., in press), but species-level identifications have only been done for parasites collected from Kangerlussuaq-Sisimiut (Clausen et al., 1980; Korsholm and Olesen, 1993). These studies reported the presence of nematode species common in *Rangifer* sp., specifically *Nematodirella longissimespiculata* (reported as *N. longispiculata*) (Clausen et al., 1980), *Marshallagia marshalli* and *Teladorsagia circumcincta* (Korsholm and Olesen, 1993). The putative identity of *T. circumcincta* in this population, however, is in question (Hoberg et al., 1999).

The goal of this study was to define abomasal and small intestinal nematode diversity in these caribou populations. We hypothesised that the fauna of these caribou would differ from that of their North American ancestors due to parasite loss during colonisation and may also reflect parasite spill-over from imported muskoxen from northeast Greenland sheep, and Norwegian reindeer.

2. Materials and methods

2.1. Study area and sample collection

Kangerlussuaq-Sisimiut and Akia-Maniitsoq are the largest populations of caribou in west Greenland, with respective estimates of 98,300 (71,500–132,400) and 24,000 (16,667–31,311) (Cuyler et al., 2011). Caribou in these populations are genetically closely related (Jepsen et al., 2002) and the Akia-Maniitsoq population is considered to have originated from a colonisation event by animals from Kangerlussuaq-Sisimiut, likely between 1500 BCE and 1200 CE (Melgaard, 1986). Contemporary movement of caribou between Kangerlussuaq-Sisimiut and Akia-Maniitsoq is believed restricted by the Sukkertoppen ice cap (Cuyler and Ostergaard, 2005) and this barrier is considered to have been present in its current form for more than 5000 years (Melgaard, 1986). Both populations are isolated from other caribou populations by extensive fjords (Melgaard, 1986; Cuyler et al., 2011).

Female caribou and their calves-at-heel were collected opportunistically from these populations as part of the CircumArctic Rangifer Monitoring and Assessment (CARMA) Network initiatives during International Polar Year (Kutz et al., in press). Collections occurred over several days and were clustered in each population's range, Akia-Maniitsoq from Mar. 29 to Apr. 13, 2008 ($n = 47$) and Kangerlussuaq-Sisimiut ($n = 49$) from Mar. 3 to 17, 2009. Sample collections from mature animals (≥ 1 year), including the removal and freezing of the abomasa and small intestines, occurred within four hours of caribou being shot. Animals were later aged using cementum ageing of incisors (Reimers and Nordby, 1968).

2.2. Parasitological procedures

The abomasa and the proximal 3 m of small intestines from adult and subadult animals were initially processed at the Greenland Institute of Natural Resources in February 2010, where they were thawed, opened (along the greater curvature for abomasa) and washed three times into a bucket to clean the mucosa. The volume of each organ wash was adjusted to 1 L and two 10% (100 mL) aliquots were collected. The sediment from these aliquots was later combined, due to a shortage of sampling containers, to create a single 20% aliquot per animal and 10% formalin or 70% ethanol was added to raise the volume to 100 mL. To quantify lumen larvae in the abomasa, subsamples of the 20% aliquots were examined at 40 \times magnification using gridded petri-dishes and all larvae, in

addition to adult nematodes, were counted and collected in these subsamples. For the majority of the aliquots, two 2.5 mL subsamples, each representing 5% of the aliquot (0.5% of the abomasal contents), were examined and the larval counts averaged; however, for four Akia-Maniitsoq animals and three Kangerlussuaq-Sisimiut animals two subsamples of 5 mL, each representing 10% of the aliquot, were examined and for five other Kangerlussuaq-Sisimiut animals only one 5 mL subsample was examined. Following examination for larvae, the remainder of the aliquot was rinsed through a 150 μ m sieve and material on the sieve examined under 25 \times magnification and only adult nematodes were counted and collected. Aliquots from the small intestines were not examined for larvae, but all other procedures were the same as for the abomasa.

Larvae were not identified to developmental stage or species. Adult nematodes of both sexes were identified following morphological descriptions based on published literature (Skrjabin et al., 1954; Lichtenfels et al., 1988a,b, 1990; Fruetel and Lankester, 1989; Lichtenfels and Pilitt, 1989, 1991; Hoberg et al., 1993, 1999, 2012; Lichtenfels and Hoberg, 1993). Nematodes were primarily identified under 40 \times magnification using body size and characteristics of the reproductive system, but if inconclusive, specimens were mounted in lactophenol and the oesophageal valve and synlophe were examined at 400 \times magnification. Nematodes collected from both populations are stored with the US National Parasite Collection (USNPC: Kangerlussuaq-Sisimiut: 105425–105424, 106264–106330 and Akia-Maniitsoq: 106223–106263).

2.3. Statistical analyses

Within populations, the Student's *t* test was used to compare differences in mean species proportion, the Spearman's Rank test to compare intensities, which for both larva and adult reflect the total per abomasum, and the Chi-Square test to compare prevalence. The Mann-Whitney *U* (MW) test was used to compare median intensity of nematode infection between caribou populations. All tests were performed using STATA 11 (StatCorp LP, College Station, USA) with significance at $p \leq 0.05$.

3. Results

Abomasa from 30 adult (≥ 3 years) and four subadult (1–2 years) caribou from Kangerlussuaq-Sisimiut and from 34 adults and seven subadults from Akia-Maniitsoq were examined; small intestines were available from 16 animals (13 adults and three subadults) from each population. As there were no significant differences between subadult and adult caribou within a population in regards to nematode diversity or intensity, results are presented by population.

Nematodes were found in the abomasa of all animals and median total adult nematode intensity did not differ significantly between Kangerlussuaq-Sisimiut (470; range = 60–1940) and Akia-Maniitsoq (675; range = 80–2290) (MW; d.f. 1, $p = 0.3$). Kangerlussuaq-Sisimiut animals had significantly higher median lumen larva intensities (2500; range = 200–11,800) than those from Akia-Maniitsoq (1100; range = 150–8800) (MW; d.f. 1, $p = 0.0001$). No nematodes were recovered from the small intestines of animals from either population (Table 1).

In Kangerlussuaq-Sisimiut caribou, nematodes corresponding to descriptions of *M. marshalli* and *Teladorsagia* spp. were recovered. As two species of morphologically similar *Teladorsagia* spp. have been reported in *Rangifer* populations (i.e. *T. boreoarcticus/T. circumcincta*) (Bye and Halvorsen, 1983; Bye, 1987; Fruetel and Lankester, 1989; Korsholm and Olesen, 1993; Hoberg et al., 1999) a subsample of specimens in good condition (39 males and

10 females) were further examined by collaborators at the US National Parasite Collection. Only *T. boreoarcticus* was found in this subsample and we are confident that only this species was present, as we were more than 90% certain to have detected *T. circumcincta* had it been at least 5% prevalent (WinEpiScope v2.0, The University of Edinburgh, Edinburgh, SCO).

In the samples from Kangerlussuaq-Sisimiut caribou, the prevalence of *M. marshalli* was 100% and that of *T. boreoarcticus* was not significantly different (94.1%) (Chi-squared; $p = 0.15$). *M. marshalli* had a median intensity of 420 nematodes per abomasum (range = 50–1690), whereas intensity of *T. boreoarcticus* was significantly lower (median 45; range = 5–250) (Spearman's Rank test; $p = 0.0015$), and represented a significantly smaller component of a given individual's parasite fauna; on average just $9.9\% \pm 6.4$ SD compared to *M. marshalli* at $89.8\% \pm 6.4$ SD (Student's *t* test; d.f. 62, $p < 0.0001$). Nine animals had female nematodes that were in poor condition and could not be definitively identified, but these were a small component of species diversity ($1.9\% \pm 2.0$ SD).

All male nematodes recovered from Akia-Maniitsoq caribou were morphologically identified as *Ostertagia* spp. under $40\times$ magnification. In *Rangifer* sp., *Ostertagia gruehneri*, *Ostertagia leptospicularis* and *Ostertagia ostertagi* have been reported (Fruetel and Lankester, 1989; Guðmundsdóttir, 2006; Kutz et al., 2012) and are superficially morphologically similar. To determine species identity, up to 50 male nematodes from each host were mounted and examined at $400\times$ magnification. Only *O. gruehneri* was found and it was assumed that all remaining un-mounted males, and all females, were this species. Prevalence of *O. gruehneri* was 100% (median 675; range = 80–2290) and this was the only species identified in the abomasa of caribou from Akia-Maniitsoq (Table 1).

4. Discussion

4.1. Gastrointestinal parasite diversity of west Greenland Caribou

This study provides new information on the gastrointestinal parasite fauna of two caribou populations in west Greenland. *T. boreoarcticus* and *M. marshalli* were the only species found in Kangerlussuaq-Sisimiut caribou, which is in contrast to previous reports of *M. marshalli* and *T. circumcincta* (Korsholm and Olesen, 1993) and we support the hypothesis that the previous identification of *T. circumcincta*, done prior to the description of *T. boreoarcticus*, is in error (Hoberg et al., 1999). *O. gruehneri* was the sole abomasal species present in Akia-Maniitsoq caribou. This divergence in parasite fauna was unexpected, as genetic studies (Jepsen et al., 2002; Roed, 2005) and the archeological record (Melgaard, 1986) indicate that these Greenland caribou originated from the

same source of North American barren-ground caribou (*R. t. groenlandicus*) and would have been expected to have a similar parasite fauna. Differences in year of sampling may have influenced our results and some differences in nematode and larva intensity could be related to annual variation, however such variation would not account for the differences in diversity described here. The complexity of ecosystems and species interactions means it is often difficult to identify the factors and events which have influenced parasitic fauna in wild ungulate populations; however, west Greenland is a remarkably simple, isolated system with detailed information regarding the history of its ungulate populations. This enables us to explore how natural and anthropogenic processes may structure parasite fauna in arctic environments.

4.2. Processes of parasite loss

The colonisation history of west Greenland caribou from North America (Melgaard, 1986) would suggest that their parasite diversity should be similar to that of North American barren-ground caribou herds – typically high abundance of *O. gruehneri* with lower prevalence and intensity of *M. marshalli* and *T. boreoarcticus* (Fruetel and Lankester, 1989; Hoar et al., 2009; Kutz et al., 2012). Further, a similar fauna between the two Greenland populations was expected. Instead, parasite diversity was reduced from that described in North American surveys and composition differed between the populations. Natural process (e.g. founder effects, decreases in host density, and differences in climate) may account for some, but not all of these differences, suggesting anthropogenic pressures were key influences on contemporary parasite diversity.

A key feature of this diversity is that *O. gruehneri*, which is highly abundant in North American caribou populations (Kutz et al., 2012), is common in Akia-Maniitsoq caribou, but absent from those in Kangerlussuaq-Sisimiut. This pattern would not have been caused by founder effects as caribou colonised, i.e. that parasite species, usually those that rely on faecal-oral transmission, are lost with increasing distance from the dispersal point (Torchin and Lafferty, 2009). This process would be expected to create a longitudinal gradient in parasite diversity and for *O. gruehneri* to be present in Akia-Maniitsoq caribou it would have to have been present in those in Kangerlussuaq-Sisimiut. Once present, it would be unlikely for *O. gruehneri* to not persist in caribou due to its high prevalence and extended longevity on pasture (Carlsson et al., 2012; Hoar et al., 2012a; Kutz et al., 2012). Some localised parasite loss can occur when a host population density falls below a minimal threshold for parasite transmission (Anderson and May, 1981; Lyles and Dobson, 1993), but to have removed *O. gruehneri* from Kangerlussuaq-Sisimiut, caribou densities would have needed to

Table 1

Prevalence, intensity, and species proportion (per host, total nematodes of a given species divided by total nematodes) of abomasal trichostrongylines in subadult and adult female caribou from the Kangerlussuaq-Sisimiut (KS) and Akia-Maniitsoq (AM) populations in west Greenland. (P = % positive samples), intensity (Median (Min. – Max.)) and species proportion (S/P, Mean^a (SD)).

	n	Total			<i>Ostertagia gruehneri</i>		<i>Marshallagia marshalli</i>			<i>Teladorsagia boreoarcticus</i>		
		P	Larva Intensity	Adult Intensity	P	Intensity	P	Intensity	S/P (SD)	P	Intensity	S/P (SD)
KS												
Subadult	4	100	1400 (200–3900)	373 (125–550)	–	–	100	340 (115–435)	88.3 (6.6)	100	30 (10–110)	11.2 (6.5)
Adult	30	100	3000 ^b (1100–11800)	525 (60–1940)	–	–	100	468 (50–1690)	90.0 (6.5)	93.3	45 (5–250)	9.7(6.5)
Total	34	100	2500 ^c (200–11800)	470 (60–1940)	–	–	100	420 (50–1690)	89.8 (6.4)	94.1	45 (5–250)	9.9 (6.4)
AM												
Subadult	7	100	800 (300–1700)	910 (460–1370)	100	910 (460–1370)	–	–	–	–	–	–
Adult	34	100	1300 (150–8800)	573 (80–2290)	100	573 (80–2290)	–	–	–	–	–	–
Total	41	100	1100 (150–8800)	675 (80–2290)	100	675 (80–2290)	–	–	–	–	–	–

^a Mean species proportion for the population is calculated using only those animals with multi-species infections, $n = 32$.

^b $n = 29$.

^c $n = 33$.

decrease to very few animals, which historically has not been observed (Melgaard, 1986; Cuyler et al., 2011). Further, at such low densities, we would expect that *M. marshalli* and certainly *T. boreoarcticus*, commonly present at lower prevalence and intensity, would have been removed as well. Therefore, although caribou in west Greenland undergo large scale cyclic patterns of abundance (Melgaard, 1986; Cuyler, 2007), it is unlikely that these cycles resulted in the loss of any of these parasite species.

Climate can limit parasite distribution and there are some significant differences in climate between these two regions. Inland areas of the Kangerlussuaq-Sisimiut range have a steppe climate characterised by low precipitation and pronounced yearly temperature fluctuations, whereas Akia-Maniitsoq sees high precipitation and more moderate temperature ranges (Tamstorf, 2001). *M. marshalli* is highly successful in arid steppe climates (Meradi et al., 2011), and might be expected to be more abundant in Kangerlussuaq-Sisimiut than in Akia-Maniitsoq, but the climate in Akia-Maniitsoq would not necessarily be unsuitable for *M. marshalli*. Similarly, *O. gruehneri* persists across much wider ranges of environmental conditions than the differences seen between these ranges (Hoar et al., 2012a; Kutz et al., 2012), and it is highly unlikely that climate has limited its distribution in west Greenland.

Further, as caribou are believed to have colonised Greenland between 5550 and 2300 BCE (Melgaard, 1986) it is unlikely that over this time frame, even with minimal movement of animals between populations, the nematode faunas would have remained so diametrically different. As recent intermittent observations of muskoxen in Akia-Maniitsoq (Cuyler et al., 2009; Jensen, 2010) suggest the Sukkertoppen ice cap does not currently completely isolate the two regions, at least for muskoxen, this would suggest that the differences in parasite species diversity are relatively recent.

4.3. Impacts of contemporary introductions

Based on the above discussions, it appears that historical natural processes alone cannot explain the contemporary nematode faunas in Kangerlussuaq-Sisimiut and Akia-Maniitsoq caribou. However, if during colonisation all endemic abomasal nematodes were lost, as could happen during a rapid and unidirectional colonisation event, the current nematode faunas may then be a consequence of recent parasite spill-over from sympatric ungulates. A possible example of such a phenomenon may be found in Iceland's introduced reindeer as the current population originates from a small group of animals introduced from Norway in 1787 (Thórisson, 1984). These reindeer lack all abomasal nematodes typical of *Rangifer* spp. hosting only those species associated with the domestic ungulates with which they are sympatric (Guðmundsdóttir, 2006). Within the last 60 years, a similar situation may have occurred in west Greenland following the importation of muskoxen and Norwegian reindeer to this region and their respective sympatry with caribou from Kangerlussuaq-Sisimiut and Akia-Maniitsoq.

M. marshalli and *T. boreoarcticus* could have been introduced to Kangerlussuaq-Sisimiut caribou in 1962 with the importation of 27 juvenile muskoxen from northeast Greenland following a year-long stopover at the Copenhagen Zoo in Denmark (Boertmann et al., 1992). Faecal samples from animals descended from the same source population contained *Marshallagia* spp. and "Strongyle"-type eggs (Steele, 2013), likely *M. marshalli* and *T. boreoarcticus* as these species dominate the abomasal fauna of muskoxen (Samuel and Gray, 1974; Alendal and Helle, 1983; Hoberg et al., 1999; Kutz et al., 2012).

O. gruehneri is often found at 100% prevalence in Norwegian reindeer (Bye, 1987) and could have been introduced to Akia-Maniitsoq caribou with the efforts to establish reindeer herding from 1952 to 1998 in this region. Movement of animals between the im-

ported and native populations was common towards the end of the operation (Cuyler, 1999) and this sympatry would have facilitated parasite spill-over to the caribou. No parasites previously reported in Greenlandic sheep (Rose, 1990) were found in these caribou.

Based on the known biogeography of this region, the introduction of different abomasal nematode species through anthropogenic processes provides a simple and elegant explanation for the divergent fauna seen in Kangerlussuaq-Sisimiut and Akia-Maniitsoq. Definitive conclusions await studies using molecular techniques to determine the relatedness of these parasite populations to their putative sources.

4.4. Additional comments on parasite faunas and ecology

Median larva intensity was significantly different between Kangerlussuaq-Sisimiut and Akia-Maniitsoq caribou, likely reflecting differences in the life histories of the dominant nematode species present. *Ostertagia gruehneri* is well known for inhibited development during the winter (Hoar et al., 2012b) suggesting larvae would be expected as arrested fourth stage larvae in the abomasal mucosa and few would be recovered from the lumen; whereas *M. marshalli* is transmitted and develops throughout winter (Carlsson et al., 2012) and these larvae would have been collected using our methodology.

In both populations, median adult nematode intensity was unexpectedly low when compared to that of similar studies (Halvorsen and Bye, 1999; Irvine et al., 2000; Hrabok et al., 2007; Hughes et al., 2009). This may reflect differences between *Rangifer* subspecies, environmental conditions, or sampling methodologies. Nematode intensity was also significantly higher in a previous survey from the Kangerlussuaq-Sisimiut region occurring in the summer (Korsholm and Olesen, 1993), but this was most likely due to season of sampling as intensities of both *O. gruehneri* and *T. boreoarcticus* would be expected to be significantly higher in the summer than compared to late winter (Irvine et al., 2000; Kutz et al., 2012).

Prevalence of *T. boreoarcticus* approached 100% in Kangerlussuaq-Sisimiut caribou (Table 1), which was surprising as it is typically much less common, particularly in European reindeer populations, where prevalence ranges between 3% and 60% (Bye and Halvorsen, 1983; Bye, 1987; Bye et al., 1987; Irvine et al., 2000; and see also Kutz et al., 2012). *Ostertagia gruehneri* was missing from this population, and the higher prevalence of *T. boreoarcticus* may have been a consequence of enemy or competitive release (Shea and Chesson, 2002). Alternatively, *T. boreoarcticus* appears to be more abundant in caribou which are sympatric with muskoxen (Bye et al., 1987; Hughes et al., 2009). Therefore, although *T. boreoarcticus* is not typically considered an important pathogen in *Rangifer* sp. (Kutz et al., 2012), it may play a greater role than previously thought in populations that are sympatric with muskoxen or lacking *O. gruehneri*.

No adult nematodirines were recovered from the small intestines of caribou from either population. This was unexpected as faecal samples from nine of the animals examined from Kangerlussuaq-Sisimiut had previously tested positive for nematodirine eggs (Steele et al., in press). As only the first 3 m of the small intestine were processed and a 20% aliquot examined, it is possible that species present at low intensities were not detected or that the adults were located more distally in the intestine and were not captured during sampling.

5. Conclusion

This study highlights key differences in parasite fauna between the two largest populations of west Greenland caribou and sug-

gests that introductions of non-native ungulates have played a major role in structuring parasite fauna in these two adjacent populations. These differences in parasite fauna may, and perhaps should, raise concerns regarding management strategies which look to supplement declining caribou populations (e.g. Hummel and Ray, 2008). Importantly, this case highlights that even populations that are closely related geographically and/or genetically may maintain vastly divergent pathogen faunas and comprehensive health assessments are warranted in order to avoid unintentional animal health and conservation consequences of human-mediated translocations.

Acknowledgements

Funding for this research was provided by: Arctic Institute of North America Grant-in-Aid; Environment Canada International Polar Year funding for the CARMA Network; NSERC Discovery, NSERC Northern Supplement, NSERC Special Opportunities grants; Northern Supplement Training Program funding; with stipend support from the University of Calgary and the University of Calgary, Faculty of Veterinary Medical Sciences.

Thank you to Uumasut Nakorsaat veterinarian: Dr. Marner Nolsøe; Greenland regional hunting officers: Hans Mølgaard and Vittus Nielsen; Greenland Institute of Natural Resources staff: Josephine Nyman, Sofie Jeremiassen, Tuperna Larsen and Lars Maltha Rasmussen; CARMA members: Wendy Nixon, Rán Þórarinsdóttir and Bob White; Staff of the US National Parasite Collection: Arthur Abrams and Patricia Piliitt; Zackenberg Research Station BioBasis Assistant: Lars H. Hansen; and members (and guests) of the University of Calgary's Veterinary Parasitology/Bacteriology lab, with special thanks to Renée Been, Dean Brown, Chantal van Es, Jennifer Halasz, Jesse Invik, Lynn Klassen, Rheanne Ritchie, Guilherme Verocai and Jayninn Yue.

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