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

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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.

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 ($\geqslant 1$ 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× 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 μm sieve and material on the sieve examined under 25× 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× 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× 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 $p \leqslant 0.05$.

3. Results

Abomasa from 30 adult ($\geqslant 3$ 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