



Contents lists available at SciVerse ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

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

Brief Report

A Nearctic parasite in a Palearctic host: *Parelaphostrongylus andersoni* (Nematoda; Protostrongylidae) infecting semi-domesticated reindeer in Alaska



Guilherme G. Verocai^{a,*}, Manigandan Lejeune^b, Greg L. Finstad^c, Susan J. Kutz^{a,b}

^a Department of Ecosystem and Public Health, Faculty of Veterinary Medicine, University of Calgary, 3330 Hospital Drive NW, Calgary, Alberta, Canada T2N 4N1

^b Canadian Cooperative Wildlife Health Centre – Alberta Node, Faculty of Veterinary Medicine, University of Calgary, 3330 Hospital Drive NW, Calgary, Alberta, Canada T2N 4N1

^c Reindeer Research Program, School of Natural Resources and Agricultural Sciences, University of Alaska – Fairbanks, AK, USA

ARTICLE INFO

Article history:

Received 17 January 2013

Revised 12 March 2013

Accepted 14 March 2013

Keywords:

Animal translocation

Alaska

Caribou

Muscleworm

Protostrongylidae

Rangifer tarandus

Reindeer industry

ABSTRACT

Parelaphostrongylus andersoni is a muscle-dwelling protostrongylid nematode that infects caribou and white-tailed deer across North America, and can cause significant muscular and pulmonary pathology in these species. We collected 44 fecal samples from semi-domesticated reindeer (*Rangifer tarandus tarandus*) from the Kakarak herd of western Seward Peninsula, Alaska, USA. This herd has no record of historical contact and extremely limited possibility of contemporary contact with native Grant's caribou (*Rangifer tarandus granti*) of the Western Arctic herd. Fecal samples were processed using the Baermann technique, and 22.7% ($n = 10$) were positive for protostrongylid dorsal-spined larvae (DSL). Genomic DNA extracted from individual DSL from each of the ten positive reindeer (total of 48 DSL) was amplified by PCR targeting the ITS-2 region of ribosomal RNA. Forty of 48 DSL were successfully sequenced and confirmed as *P. andersoni* and one representative sequence for each of the ten positive samples was deposited in GenBank. No other protostrongylids, including *Varestrongylus* sp., presumed to be widespread across caribou range, and *Elaphostrongylus rangiferi*, which could have been introduced with reindeer from Eurasia, were detected in these samples. *P. andersoni* is likely widespread among introduced reindeer in Alaska, potentially causing subtle but deleterious effects with negative economic impacts on commercial herding activities.

© 2013 Australian Society for Parasitology Published by Elsevier Ltd. All rights reserved.

Introduction

Parelaphostrongylus andersoni Prestwood, 1972 is a muscle-dwelling nematode of the family Protostrongylidae Leiper, 1926 that infects caribou (*Rangifer tarandus* spp.) and white-tailed deer (*Odocoileus virginianus* spp.) across North America (Lankester, 2001; Asmundsson et al., 2008). White-tailed deer are considered the primary host, and caribou were likely colonized in zones of contact during the Pleistocene (Carreno and Lankester, 1994). The life cycle of *P. andersoni* is complex and, as typical for all protostrongylids, requires gastropod intermediate hosts for development of larvae from first to the infective third stage (Anderson, 2000). Adult parasites reside in skeletal muscles and can cause significant muscular pathology that compromises the mobility of animals, whereas eggs and larvae can cause significant pulmonary disease. Disease linked to muscular or pulmonary pathology may lead to increased predation (Nettles and Prestwood, 1976; Pybus and Samuel, 1981; Lankester and Hauta, 1989).

P. andersoni has been confirmed in three caribou subspecies: Grant's (*Rangifer tarandus granti*), barren-ground (*Rangifer tarandus groenlandicus*), and woodland (*Rangifer tarandus caribou*), from Alaska to eastern Canada, including Newfoundland (Lankester and Hauta, 1989; Lankester and Fong, 1998; Ball et al., 2001; Kutz et al., 2007). It is generally accepted that *P. andersoni* has a virtually continuous distribution across caribou range in mainland North America and Newfoundland (Lankester and Hauta, 1989; Hoberg et al., 2008). Despite fairly extensive investigation based on combined fecal analyses and molecular diagnostics, this species has never been detected in sympatric ungulates such as muskoxen (*Ovibos moschatus*), moose (*Alces americanus*), or Dall's sheep (*Ovis dalli*) (Jenkins et al., 2005a; Kutz et al., 2007), suggesting host fidelity to *Rangifer* at high latitudes of the Nearctic. In fact, unequivocal species level identification of protostrongylids relies on morphologic and/or molecular identification of adult specimens, or molecular identification of larvae of morphologically indistinguishable species (e.g., protostrongylids within the genera of *Parelaphostrongylus*, *Elaphostrongylus*, *Varestrongylus*, *Umingmakstrongylus*, and *Muellerius*, that produce larvae provided with a dorsal spine) recovered from feces (Jenkins et al., 2005a; Kutz et al., 2007).

* Corresponding author. Tel.: +1 403 210 7869; fax: +1 403 210 7882.

E-mail addresses: gui.verocai@ucalgary.ca (G.G. Verocai), mlejeune@ucalgary.ca (M. Lejeune), gfinstad@alaska.edu (G.L. Finstad), skutz@ucalgary.ca (S.J. Kutz).

The history of introductions of Eurasian reindeer, *Rangifer tarandus tarandus*, to North America begins in 1892, when animals from Chukotka, eastern Russia, were translocated to Seward Peninsula, western Alaska, to establish semi-domestic herds. Additional reindeer from the Tunguska region, Eastern Siberia, were introduced in 1901 (Finstad et al., 2006). The intent was to provide the local aboriginal people, the Inupiat, with a reliable source of meat that would complement caribou hunting and, yet more significant, the reduced harvest of marine mammals (primary source of protein) negatively impacted by the whaling industry. Cyclical fluctuations in caribou populations and varying migratory paths for these ungulates meant they could not be depended on as a constant source of food, and in fact, caribou virtually disappeared from most of the Seward Peninsula during the mid-1800s (Finstad et al., 2006). Today on the Seward Peninsula, reindeer are maintained as commercial livestock using modern management practices (Oleson, 2005; Finstad et al., 2006).

The knowledge of biodiversity, distribution and impacts, of protostrongylid faunas in native North American ungulates has increased substantially throughout the last decades (see Hoberg et al., 2008; Kutz et al., 2012); however, no attention has been given to free-ranging introduced ungulates such as the Eurasian reindeer. In the few parasitological studies that have been done on semi-domesticated reindeer in North America, protostrongylids were not reported (Hadwen, 1922; Dikmans, 1939; Choquette et al., 1957). In this paper we provide the first report of a native North American protostrongylid, the muscle-worm *P. andersoni*, in a herd of introduced semi-domesticated reindeer from Seward Peninsula, Alaska, USA, and discuss the broader significance of host movements and colonization for structuring the protostrongylid fauna of ungulates in North America.

Material and methods

Study population

The Kakarak reindeer herd was established in Alaska from the original reindeer introductions when 1280 animals were brought from Russia between 1882 and 1901 (Finstad et al., 2006). This herd ranges on the western portion of the Seward Peninsula, approximately between 65° 16'N and 64° 35'N, and 165° 56'W and 164° 37'W (Fig. 1), near Teller, Alaska, and has recently been the most productive herd on the peninsula. Unofficial counts in 2012 by the Reindeer Herders Association estimated the herd size at 5000 reindeer. Animals are free-ranging and brought into corral systems once or twice a year for handling (marking of calves and castration of adult males, vaccinations and other veterinary services), as well as for harvest of antler velvet, but anti-parasitic treatment has not been administered in the last 15 years.

The Kakarak reindeer herd has had no known historical contact with native caribou. In the 1990s the Western Arctic caribou herd (WAH), which historically migrated on the far eastern part of the peninsula began expanding its range westwards (Fig. 1). This resulted in significant loss for many reindeer herders as their animals would join the migration of the WAH (Finstad et al., 2006; Rattenbury et al., 2009) (Fig. 1). To prevent contact with caribou and subsequent loss of reindeer to the caribou herds, for the last decade the Kakarak reindeer have been intensively herded and held in a restricted area on the western portion of their historical range near the town of Teller (Finstad, unpublished data).

Fecal sampling and analyses

Fresh fecal samples ($n = 44$) from reindeer of the Kakarak herd were collected from the ground in October, 2010. The sampled

group of reindeer consisted mainly of adult females and a few adult males and calves of 5–6 months, but feces could not be identified to individual. Approximately 5 g of feces from each sample were evaluated for the presence of protostrongylid dorsal-spined larvae (DSL) using a modification of the beaker Baermann technique (Forrester and Lankester, 1997). Larvae from each positive host were collected individually in a 0.2 mL tubes containing 5 μ L of deionized H₂O and stored frozen at -20°C .

Molecular identification

Genomic DNA (gDNA) lysate was prepared from 48 larvae from all ten DSL-positive reindeer (3–5 DSL per positive animal). Briefly, to each tube containing a DSL, 25 μ L of lysis buffer (0.5 mg/mL of proteinase K, 10 \times PCR buffer) was added and incubated at 65 $^{\circ}\text{C}$ for 60 min followed by 95 $^{\circ}\text{C}$ for 15 min. DNA lysate was diluted 1:5 in DNase, RNase free deionized H₂O and stored at -20°C until further use. For PCR, a protocol modified from Kutz et al. (2007) was performed using primers NC1 (5'-ACGTCTGGTT-CAGGGTTGTT-3') and NC2 (5'-TTAGTTTCTTTTCTCCGCT-3') targeting the ITS-2 region of rRNA gene. For a 20 μ L PCR reaction: 10.2 μ L of sterile ddH₂O, 4 μ L of 5 \times PCR buffer + MgCl₂, 0.4 μ L of 10 mmol dNTPs, 2 μ L (10 μ M) of each primer, 0.2 μ L of Taq Phusion HF DNA polymerase, 0.2 μ L of bovine serum albumin (20 mg/mL), and 1 μ L of diluted DNA lysate was added. The amplification conditions used were an initial 2 min denaturation at 98 $^{\circ}\text{C}$, followed by 35 cycles of 98 $^{\circ}\text{C}$ for 10 s, 52.5 $^{\circ}\text{C}$ for 30 s, and 72 $^{\circ}\text{C}$ for 30 s. A final extension of 72 $^{\circ}\text{C}$ for 5 min was followed by cooling to 4 $^{\circ}\text{C}$. Reagent-only reactions were used as negative controls. Amplicons of 40 DSL were cleaned using ExoSAP-it[®] and sequenced directly using NC2 primer to obtain partial ITS-2 sequence. To obtain complete ITS-2 sequence, PCR was repeated with DNA template of ten DSL (one from each DSL-positive animal) out of the 40 whose ITS-2 amplification was initially successful. Amplicons thus obtained were sequenced from both ends using primers NC1 and NC2 with BigDye Terminator Cycle Sequencing (Applied Biosystems).

Sequences (3–5 per each DSL-positive animal) were edited using FinchTV 1.4.0 and MEGA version 5 (Tamura et al., 2011). BLAST searches were used to compare the resulting sequences to ITS-2 rRNA sequences available in GenBank, and aligned by Clustal W with MEGA version 5 (Tamura et al., 2011).

Results and discussion

Ten reindeer fecal samples (22.7%; $n = 44$) were positive for DSL, with counts ranging from approximately 0.2–50 larvae per gram of fresh feces. Partial and complete sequences for the ITS-2 of all 40 DSL were confirmed as *P. andersoni* based on 99–100% similarity on BLAST analysis with sequences available in GenBank. Complete ITS-2 sequences (460 bp) of ten DSL were deposited in GenBank under the accession numbers: JQ 946524 to JQ 946533.

We document for the first time, the occurrence of *P. andersoni* in semi-domesticated reindeer, demonstrating infections with a Nearctic protostrongylid in an introduced Palearctic host. The Kakarak reindeer herd has no historical or contemporary contact or shared range use with the WAH, thus direct transmission from caribou to these reindeer is unlikely (Fig. 1). Rather, the presence of *P. andersoni* in the Kakarak herd may be explained by: (I) invasion from the WAH through sequential events of host colonization; (II) through anthropogenic or natural introduction of reindeer from other herds to the Kakarak herd; or, less likely, (III) its presence in the original reindeer introduced from Russia.

Invasion through sequential host colonization may have occurred in an east to west direction from the WAH. Temporal overlap (seasonal sympatry) between caribou and reindeer, or between

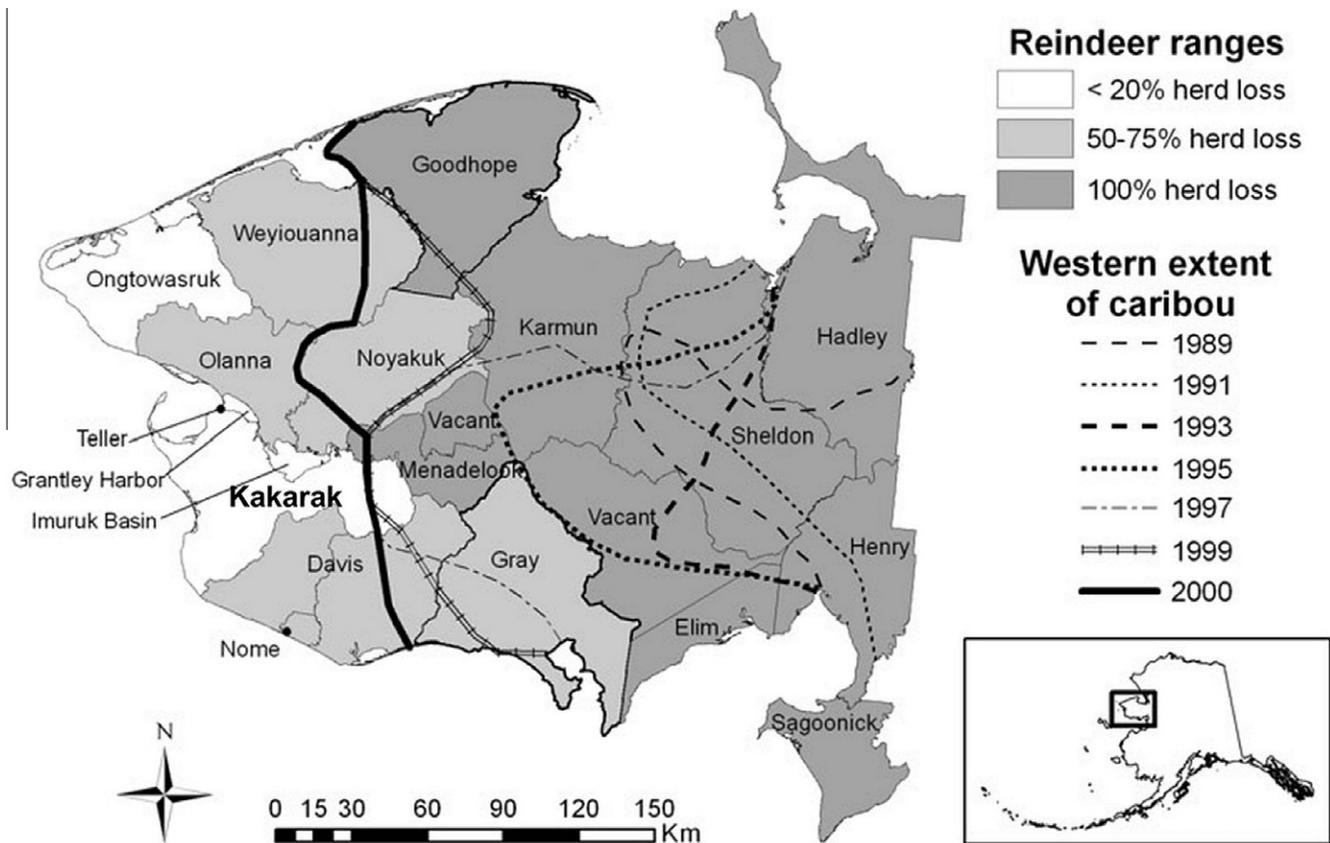


Figure 1. Map of the Seward Peninsula, Alaska, showing semi-domesticated reindeer herd ranges including the Kakarak herd (bold), and reindeer herd loss to Western Arctic caribou herd; and the western limits of caribou migration from 1989 to 2000 (modified from Finstad et al. (2006) and Rattenbury et al. (2009)).

different reindeer herds, could have occurred (and there is genetic evidence of such (Mager, 2012)), but would not be necessary for parasite establishment and transmission between herds. Host-switching could occur through ingestion of gastropods infected with L3 of *P. andersoni* if grazing occurs in an area where an infected herd was present months, or even the year before, as suggested by Hoberg et al. (2002) for other protostrongylid-ungulates system. Thus, in the course of over a hundred years of reindeer residence on Seward Peninsula, Alaska, *P. andersoni* may have been transferred from the WAH to other sympatric reindeer herds, and secondarily expanded through those herds to adjacent herds with overlapping ranges, until reaching the westernmost areas of the Seward Peninsula. Animal exchange between herds or herd admixture via natural animal movement may also be responsible for the invasion of *P. andersoni* into the Kakarak herd. This exchange of reindeer has occurred through a program by the Bureau of Indian Affairs to loan animals for new herders to start or build up herds and these 'loans' were paid back by loaning the same number of animals to the next herder in line when their herd increased (Finstad et al., 2006). Additionally, based on satellite telemetry data of radio-collared animals and observations, reindeer from the adjacent Davis herd left their home range and commingled with the Kakarak herd in 2002–2004, and the Noyakuk reindeer herd, which commingles extensively with WAH, has mixed with Kakarak animals on several occasions between 2000 and 2009 (Finstad, unpublished data). Thus infected reindeer originating from herds with direct contact with WAH may have entered the Kakarak herd on multiple occasions. The last, but perhaps less likely, hypothesis is that a lineage of *P. andersoni* was brought with reindeer from Eurasia. There have been no comprehensive studies on protostrongylid fauna of reindeer of the Russian Far East, which together with Alaska and the Yukon Territory, once formed Beringia, one of

the glacial refugia for *Rangifer* during the Pleistocene (Hoberg et al., 2012). A deeper molecular study comparing the genetics of *P. andersoni* larvae from the Kakarak reindeer and others from its wide geographic range could further support the hypothesis of its Nearctic origin.

The fact that the Kakarak herd has not been treated with anti-parasitic drugs for over a decade may have enabled the establishment of *P. andersoni*, especially if this is a recent parasite introduction event. Additionally, during the last decade the Kakarak reindeer herd has been maintained at very high density in a restricted area to avoid animal loss to the WAH. This intensive herd management has resulted in overgrazing of many lichen ranges and may also have facilitated the establishment and spread of parasites within the herd.

The reindeer industry in Alaska is an important economic activity, and has been severely impacted due to animal loss to the WAH, estimated at over \$16 million in 1990–2000s (Carlson, 2005; Finstad et al., 2006; Rattenbury et al., 2009). In addition to this direct impact, native caribou may have indirect impacts on the reindeer industry through the spillover of pathogens, as potentially has happened with *P. andersoni*. Protostrongylid nematodes may also have subtle, but substantial impacts on individual animals, negatively affecting growth and survival (Jenkins et al., 2005b; Kutz et al., 2012). Thus, muscular and pulmonary disease caused by *P. andersoni* on individual animals may influence herd productivity and lead to economic losses. In addition, the additive effect of coinfections with other pulmonary nematodes potentially present in this herd, such as *Varestrongylus* and *Dictyocaulus*, might result in more severe cases of verminous pneumonia, as suggested by Kutz et al. (2012). Generally, under current climate warming scenarios, protostrongylid parasites in northern ungulate hosts are predicted to increase (Handeland and Slettbakk, 1994; Ball et al.,

2001; Kutz et al., 2009). Understanding these impacts, and implementing adaptive management strategies, such as range management and use of anthelmintic drugs, may be helpful. Notably though, a handful of studies on anthelmintic efficacy against protostrongylids species in wild North American ungulates suggests that deworming may be met with variable success (Samuel and Gray, 1988; Jenkins et al., 2005b).

Three other protostrongylid species are reported from *Rangifer* in North America. Two are native to the Nearctic, *Varestrongylus* sp. and *Parelaphostrongylus odocoilei* (Hobmaier & Hobmaier, 1934), and the third, *Elaphostrongylus rangiferi* (Mitskevich, 1960), is an introduced Palearctic species (Anderson, 2000; Lankester, 2001; Kutz et al., 2012). *Varestrongylus* sp., an as yet undescribed species that appears to be widespread across caribou range in North America and occurs in sympatry with *P. andersoni* (Kutz et al., 2007; Verocai et al., 2011), was not found in our study. We are uncertain if this apparent absence reflects insufficient sample size or true absence.

In contrast, the occurrence of *P. odocoilei* is rather unlikely in the region. This species has only been reported twice in *Rangifer*, and in both cases in woodland caribou, from Alberta (Gray and Samuel, 1986) and the Northwest Territories (Jenkins et al., 2005a). In Alaska, its distribution is restricted to the interior and southeastern regions in Dall's sheep and mountain goats (*Oreamnus americanus*) (Jenkins et al., 2005a; Hoberg et al., 2008) and sympatric Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) (Huby-Chilton et al., 2006). Note that these authors erroneously referred to *Odocoileus hemionus* from southeastern Alaska simply as black-tailed deer, *Odocoileus hemionus columbianus*.

The third species, *E. rangiferi*, was a major concern of the introduction of Eurasian reindeer to North America (Lankester and Fong, 1989). This parasite was introduced to North America in 1908 with the translocation of Norwegian reindeer to the island of Newfoundland. It is now established across many native caribou herds in Newfoundland, and causes significant outbreaks of neurological disease (Lankester and Fong, 1989, 1998; Ball et al., 2001). Despite several other reindeer introductions to North America (Scotter, 1972; Godkin, 1986; Lankester and Fong, 1989), *E. rangiferi* has not been reported outside of Newfoundland (Kutz et al., 2012).

Although *E. rangiferi* has not been reported in reindeer from Chukotka, the main source of introduced animals, it is reported from the Buryatia region near Lake Baikal (Kontrimavichus et al., 1976), which is not far from the Tunguska region, the source of at least one of the reindeer introductions to Alaska (Finstad et al., 2006). If *E. rangiferi* was present in the introduced reindeer, it may have been lost at the time of their introductions to Alaska in the late 1890s and early 1900s. Such parasite loss would be consistent with that documented for other introduced populations of reindeer on Iceland (Gundmundsdóttir, 2006) and South Georgia Island in the South Atlantic Ocean (Leader-Williams, 1980), and consistent with the general processes of parasite loss across a taxonomically wide range of introduced host populations (Torchin et al., 2003). Nevertheless, the apparent absence of *E. rangiferi* in Alaskan reindeer or caribou cannot be assured. Logistical and financial constraints make it challenging to document the occurrence (or absence) of parasites in remote areas of the Arctic (Kutz et al., 2007; Hoberg et al., 2008).

Although reindeer and the caribou share many parasite species, such as gastrointestinal nematodes (e.g., *Ostertagia gruehneri* Skrjabin, 1929 and *Marshallagia marshalli* (Ransom, 1907)) (Bye and Halvorsen, 1983; Halvorsen, 1986; Stien et al., 2002; Kutz et al., 2012), it is interesting that these two conspecific hosts, appear to have a divergent native Protostrongylid fauna (Lankester, 2001; Kutz et al., 2012). This parasite group is thus a useful system to investigate parasite exchange among wild ungulates when ecological barriers are removed. In fact, host switching is a rather

common phenomena in protostrongylid-ungulate systems in North America (Hoberg, 2010, 2012). In an evolutionary time scale, we have as an example *P. andersoni* passing from deer (*Odocoileus* sp.) to caribou (Carreno and Lankester, 1994). In more recent times *Protostrongylus stilesi* Dikmans (1939), has colonized muskoxen sympatric with Dall's sheep (Hoberg et al., 2002). In both of these cases, as in our study, the introduced population acquired a novel pathogen from the native host. In contrast, native bighorn sheep (*Ovis canadensis*) acquired *Muellerius capillaris* (Mueller, 1889), from domestic caprine primary hosts (Ezenwa et al., 2010). In all of these scenarios, breakdown in barriers for ecological isolation resulted in successful parasite invasion and subsequent establishment of new hosts-parasite associations (Hoberg et al., 2012; Kutz et al., 2012). For *P. andersoni*, the conspecificity of the native (caribou) and the introduced (reindeer) hosts, not surprisingly, did not pose a barrier for parasite transfer. Similarly, ecological conditions on the Seward Peninsula, including gastropod intermediate host availability, climate, and habitat use (herd management), were suitable for maintenance of this protostrongylid.

P. andersoni, a Nearctic protostrongylid nematode, occurs in semi-domesticated reindeer; a Palearctic host introduced to western Alaska, and might also infect other reindeer herds in Alaska and Canada. The occurrence of this parasite in reindeer may lead to diminished productivity for infected animals and thus may have detrimental impacts for individual animals and commercial herds. Molecular tools permitting high throughput analyses of larvae of morphologically indistinguishable species will greatly facilitate broader biodiversity assessment and contribute to management of both semi-domesticated reindeer and wild caribou.

Financial support

This work was supported by the Faculty of Veterinary Medicine, University of Calgary, Alberta Innovates Health Solutions, and the CircumArctic Rangifer Monitoring and Assessment Network (CARMA, <http://www.carmanetwork.com>), NSERC Canada International Polar Year Funding, and the Reindeer Research Program, University of Alaska, Fairbanks.

Acknowledgments

We acknowledge Leslie Davis, Graduate Student with the Reindeer Research Program, University of Alaska – Fairbanks, who assisted with reindeer fecal sample collection. Also, we would like to thank Jayninn Yue, Dean Brown and Jesse Invik for lab assistance, Dr. John S. Gilleard for kindly permitting the use of his lab facilities and equipment for molecular analyses. We thank Dr. Eric P. Hoberg (United States National Parasite Collection, US Department of Agriculture), Dr. Murray Lankester, and an anonymous reviewer for their valuable contributions to this manuscript.

References

- Anderson, R.C., 2000. Nematode Parasites of Vertebrates. Their Development and Transmission. CAB Publishing, Oxford.
- Asmundsson, I.M., Mortenson, J.A., Hoberg, E.P., 2008. Muscieworms, *Parelaphostrongylus andersoni* (Nematoda: Protostrongylidae), discovered in Columbia white-tailed deer from Oregon and Washington: implications for biogeography and host associations. *J. Wildl. Dis.* 44, 16–27.
- Ball, M.C., Lankester, M.W., Mahoney, S.P., 2001. Factors affecting the distribution and transmission of *Elaphostrongylus rangiferi* (Protostrongylidae) in caribou (*Rangifer tarandus caribou*) of Newfoundland, Canada. *Can. J. Zool.* 79, 1265–1277.
- Bye, K., Halvorsen, O., 1983. Abomasal nematodes of the Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik). *J. Wildl. Dis.* 19, 101–105.
- Carlson, S.M., 2005. Economic impact of reindeer–caribou interactions on the Seward Peninsula. University of Alaska, Fairbanks, p. 101.

- Carreno, R.A., Lankester, M.W., 1994. A reevaluation of the phylogeny of *Parelaphostrongylus* Boev and Schulz, 1950 (Nematoda, Protostrongylidae). *Syst. Parasitol.* 28, 145–151.
- Choquette, L.P.E., Whitten, L.K., Rankin, G., Seal, C.M., 1957. Note on parasites found in reindeer (*Rangifer tarandus*) in Canada. *Can. J. Comp. Med.* 21, 199–203.
- Dikmans, G., 1939. Helminth parasites North American semidomesticated and wild ruminants. *Proc. Helm. Soc. Wash.* 6, 97–101.
- Ezenwa, V.O., Hines, A.M., Archie, E.A., Hoberg, E.P., Asmundsson, I.M., Hogg, J.T., 2010. *Muellerius capillaris* dominates the lungworm community of Bighorn sheep at the National Bison Range, Montana. *Journal of Wildlife Diseases* 46, 988–993.
- Finstad, G.L., Kielland, K.K., Schneider, W.S., 2006. Reindeer herding in transition: historical and modern day challenges for Alaskan reindeer herders. *Nomadic Peoples* 10, 31–49.
- Forrester, S.G., Lankester, M.W., 1997. Extracting protostrongylid nematode larvae from ungulate feces. *J. Wildl. Dis.* 33, 511–516.
- Godkin, G.F., 1986. The reindeer industry in Canada. *Can. Vet. J.* 27, 488–490.
- Gray, J.B., Samuel, W.M., 1986. *Parelaphostrongylus odocoilei* (Nematoda, Protostrongylidae) and a protostrongylid nematode in woodland caribou (*Rangifer tarandus caribou*) of Alberta, Canada. *J. Wildl. Dis.* 22, 48–50.
- Gundmundsdóttir, B., 2006. Snikjudýr í hreindýrum á Íslandi. University of Iceland, Reykjavík, p. 100.
- Hadwen, S., 1922. Society proceedings: the helminthological society of Washington. *J. Parasitol.* 9, 38–39.
- Halvorsen, O., 1986. Epidemiology of reindeer parasites. *Parasitol. Today* 2, 334–339.
- Handeland, K., Slettback, T., 1994. Outbreaks of clinical cerebrospinal elaphostrongylosis in reindeer (*Rangifer tarandus tarandus*) in Finnmark, Norway, and their relation to climatic conditions. *J. Vet. Med. B – Infect. Dis. Vet. Public Health* 41, 407–410.
- Hoberg, E.P., 2010. Invasive processes, mosaics and the structure of helminth parasite faunas. *Rev. Sci. Tech. OIE* 29, 255–272.
- Hoberg, E.P., Kutz, S., Nagy, J., Jenkins, E.J., Elkin, B., Branigan, M., Cooley, D., 2002. *Protostrongylus stilesi* (Nematoda: Protostrongylidae): ecological isolation and putative host-switching between Dall's sheep and muskoxen in a contact zone. *Comp. Parasitol.* 69, 1–9.
- Hoberg, E.P., Polley, L., Jenkins, E.J., Kutz, S., Veitch, A., Elkin, B., 2008. Integrated approaches and empirical models for investigation of parasitic diseases in northern wildlife. *Emerg. Infect. Dis.* 14, 10–17.
- Hoberg, E.P., Galbreath, K.E., Cook, J.A., Kutz, S.J., Polley, L., 2012. Northern host-parasite assemblages: history and biogeography on the borderlands of episodic climate and environmental transition. *Adv. Parasitol.* 79, 1–97.
- Huby-Chilton, F., Chilton, N.B., Lankester, M.W., Gajadhar, A.A., 2006. Single-strand conformation polymorphism (SSCP) analysis as a new diagnostic tool to distinguish dorsal-spined larvae of the Elaphostrongylinae (Nematoda: Protostrongylidae) from cervids. *Vet. Parasitol.* 135, 153–162.
- Jenkins, E.J., Appleyard, G.D., Hoberg, E.P., Rosenthal, B.M., Kutz, S.J., Veitch, A.M., Schwantje, H.M., Elkin, B.T., Polley, L., 2005a. Geographic distribution of the muscle-dwelling nematode *Parelaphostrongylus odocoilei* in North America, using molecular identification of first-stage larvae. *J. Parasitol.* 91, 574–584.
- Jenkins, E.J., Hoberg, E.P., Polley, L., 2005b. Development and pathogenesis of *Parelaphostrongylus odocoilei* (Nematoda: Protostrongylidae) in experimentally infected thinhorn sheep (*Ovis dalli*). *J. Wildl. Dis.* 41, 669–682.
- Kontrimavichus, V.L., Delyamure, S.L., Boev, S.N., 1976. Metastrongyloidea of domestic and wild animals. In: Ryzhikov, K.M. (Ed.). *Principles in Nematology*, Moscow, p. 240.
- Kutz, S.J., Asmundsson, I., Hoberg, E.P., Appleyard, G.D., Jenkins, E.J., Beckmen, K., Branigan, M., Butler, L., Chilton, N.B., Cooley, D., Elkin, B., Huby-Chilton, F., Johnson, D., Kuchboev, A., Nagy, J., Oakley, M., Polley, L., Popko, R., Scheer, A., Simard, M., Veitch, A., 2007. Serendipitous discovery of a novel protostrongylid (Nematoda: Metastrongyloidea) in caribou, muskoxen, and moose from high latitudes of North America based on DNA sequence comparisons. *Can. J. Zool.* 85, 1143–1156.
- Kutz, S.J., Jenkins, E.J., Veitch, A.M., Ducrocq, J., Polley, L., Elkin, B., Lair, S., 2009. The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host–parasite interactions. *Vet. Parasitol.* 163, 217–228.
- 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 Arctic ungulates of North America and Greenland: a view of contemporary diversity, ecology and impact in a world under changes. *Adv. Parasitol.* 79, 99–252.
- Lankester, M.W., 2001. Extrapulmonary lungworms of cervids. In: Samuel, W.M., Pybus, M.J., Kocan, A.A. (Eds.), *Parasitic Diseases of Wild Mammals*, second ed. Iowa State University Press, Ames, p. 576.
- Lankester, M.W., Fong, D., 1989. Distribution of elaphostrongylid nematodes (Metastrongyloidea, Protostrongylidae) in Cervidae and possible effects of moving *Rangifer* spp. into and within North America. *Alces* 25, 133–145.
- 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., Fong, D., 1998. Protostrongylid nematodes from caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) in Newfoundland. *Rangifer*, 73–83.
- Leader-Williams, N., 1980. Observations on the internal parasites of reindeer introduced into South Georgia. *Vet. Rec.* 107, 393–395.
- Mager, K.H., 2012. Population structure and hybridization of Alaskan caribou and reindeer: integrating genetics and local knowledge. Department of Biology and Wildlife, University of Alaska, Fairbanks, p. 230.
- Nettles, V.F., Prestwood, A.K., 1976. Experimental *Parelaphostrongylus andersoni* infections in white-tailed deer. *Vet. Pathol.* 13, 381–393.
- Oleson, H.J., 2005. Changing strategies in Seward Peninsula reindeer (*Rangifer tarandus caribou*) management. University of Alaska, Fairbanks, Alaska.
- Pybus, M.J., Samuel, W.M., 1981. Nematode muscleworm from white-tailed deer of Southeastern British Columbia. *J. Wildl. Manage.* 45, 537–542.
- Rattenbury, K., Kielland, K., Finstad, G., Schneider, W., 2009. A reindeer herder's perspective on caribou, weather and socio-economic change on the Seward Peninsula, Alaska. *Polar Res.* 28, 71–88.
- Samuel, W.M., Gray, J.B., 1988. Efficacy of ivermectin against *Parelaphostrongylus andersoni* (Nematoda, Metastrongyloidea) in white-tailed deer (*Odocoileus virginianus*). *J. Wildl. Dis.* 24, 491–495.
- Scotter, G.W., 1972. Reindeer ranching in Canada. *J. Range Manage.* 25, 167–174.
- 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.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.* 28, 2731–2739.
- Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., Kuris, A.M., 2003. Introduced species and their missing parasites. *Nature* 421, 628–630.
- Verocai, G.G., Kutz, S.J., Simard, M., Hoberg, E.P., 2011. A newly discovered *Varestrongylus* species (Nematoda: Protostrongylidae) in ungulates at high latitudes of North America: taxonomy and phylogeny. Proceedings of the 23rd International Conference of the World Association for the Advancement of Veterinary Parasitology. Buenos Aires, Argentina.