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Invasion, establishment, and range expansion of two parasitic nematodes in the Canadian Arctic

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Abstract

Climate warming is occurring at an unprecedented rate in the Arctic and is having profound effects on host-parasite interactions, including range expansion. Recently, two species of protostrongylid nematodes have emerged for the first time in muskoxen and caribou on Victoria Island in the western Canadian Arctic Archipelago. *Umingmakstrongylus pallikuukensis,* the muskox lungworm, was detected for the first time in 2008 in muskoxen at a community hunt on the southwest corner of the island and by 2012, it was found several hundred kilometers east in commercially harvested muskoxen near the town of Ikaluktutiak. In 2010, *Varestrongylus* sp., a recently discovered lungworm of caribou and muskoxen was found in muskoxen near Ikaluktutiak and has been found annually in this area since then. Whereas invasion of the island by *U. pallikuukensis* appears to have been mediated by stochastic movement of muskoxen from the mainland to the southwest corner of the island, *Varestrongylus* has likely been introduced at several times and locations by the seasonal migration of caribou between the island and the mainland. A newly permissive climate, now suitable for completion of the parasite life cycles in a single summer, likely facilitated the initial establishment and now drives range expansion for both parasites.

Keywords: Arctic, climate change, emerging disease, *Ovibos moschatus*, parasite invasions, Protostrongylidae, *Rangifer tarandus*, *Umingmakstrongylus pallikuukensis*, *Varestrongylus*

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Introduction

The Arctic, warming at least twice as fast as the global average (IPCC, 2007), is a key model for understanding the impacts of climate change in the biosphere (e.g., Callaghan *et al*., 2004; Lovejoy & Hannah, 2005; Parmesan, 2006; Lawler *et al*., 2009; Burrows *et al*., 2011). Arctic and high-latitude ecosystems exhibit a strong signal of climate warming, low biodiversity, and minimal confounding anthropological factors relative to temperate and tropical communities, thus making them ideal systems for exploring the intricate interactions among assemblages of hosts, parasites, and the environment (e.g., Bradley & Altizer, 2005; Burek *et al*., 2008; Marcogliese, 2008; Kutz *et al*., 2009a, b; Hueffer *et al*., 2011; Hoberg *et al*., 2013). Altered transmission dynamics, parasite invasions, and emergence of parasite-associated disease, coincident with contemporary trends in climate warming and unusually warm and wet periods, have all been predicted, but less often documented, for Arctic parasites (Kutz *et al*., 2005, 2009a, b; Laaksonen *et al*., 2010). Climate change is also having substantial impacts on the physiology, ecology, and phenology of many arctic vertebrate species (Parmesan, 2006; Lawler *et al*., 2009; Post *et al*., 2009); and to date, most of the responses have been phenotypic (Gilg *et al*., 2012) with evolutionary changes among fishes, birds, and mammals likely occurring much more slowly than those of their parasites. Concurrently, climate change is leading to range expansion from the south in aquatic, terrestrial, and marine ecosystems, with invasion by new arrays of hosts and their associated pathogens (Burek *et al*., 2008; Kutz *et al*., 2009b; Hoberg *et al*., 2013; Kashivakura, 2013).

Collectively, these climate-related phenomena are predicted to dramatically alter Arctic host-parasite dynamics resulting in a 'biodiversity paradox.' For example, northward range expansion of new hosts and their parasites may initially lead to a net increase in biodiversity; however, this may also coincide with extinctions of endemic arctic fauna when environmental changes exceed the thermal tolerances and resilience of some species and species assemblages (Kutz *et al*.,

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2009b; Gilg *et al*., 2012; Molnár *et al*., 2013b). In addition, invasive parasite species may compete directly, or indirectly [e.g., through parasite-mediated competition (Tompkins *et al*., 2000)] with the endemic parasite fauna, thereby leading to ecological perturbations and further reduction in faunal diversity. Historically, environments and species interactions in the Arctic have been strongly determined by episodic variation in climate and processes for breakdown of ecological isolation, invasion, host/geographic colonization and faunal mixing have been prominent (e.g., Hoberg *et al*., 2012).

Rapid and increasing environmental perturbation driven by climate in the central Canadian Arctic (IPCC, 2007) provides a critical opportunity to explore dynamics among populations of caribou, muskoxen and their parasites, and further expands our understanding of faunal assembly and structure. We move from the realm of prediction and modeling of climate-induced changes in host-parasite interactions in the Arctic to novel empirical field observations reported herein. Significantly, such field-based studies have, for the first time, substantiated a range of predictions in ecological time for ongoing mechanisms and responses of host-parasite assemblages to accelerating climate warming and environmental change.

Muskoxen (*Ovibos moschatus*), and caribou (*Rangifer tarandus),* keystone species and important sources of food and income for aboriginal communities across much of the Arctic (Meakin & Kurvits, 2009), are host to several parasites that are sensitive to climate (Kutz *et al*., 2009b, 2012; Meakin & Kurvits, 2009). Protostrongylid nematodes, in particular, are influenced by climatic conditions. Members of the Protostrongylidae can be pathogenic and, depending on species, can cause pneumonia, myositis, and neurological disease in their hosts. On the west-central Canadian Arctic mainland, muskoxen are infected with the protostrongylid lungworm, *Umingmakstrongylus pallikuukensis*, caribou with the muscleworm, *Parelaphostrongylus andersoni*, and both muskoxen and caribou are hosts for a recently discovered lungworm, *Varestrongylus* sp. (Kutz *et al*., 2007, 2012). The adult nematodes produce dorsal-spined first-stage larvae (DSL) that migrate through the lungs, up the trachea and are shed in the host's feces. These then invade the foot tissue of gastropods and develop to the infective third stage in these intermediate hosts. Larval development in gastropods is temperature-dependent, and transmission, abundance, and geographic range of these parasites, as well as disease outbreaks, are positively associated with environmental temperatures (Handeland & Slettbakk, 1994; Kutz *et al*., 2002, 2005; Jenkins *et al*., 2006).

Protostrongylids are common in caribou and muskoxen across the arctic mainland, but until recently, despite extensive postmortem and fecal examinations on over a thousand muskoxen and caribou on Banks and Victoria Islands since the early 1990s (Kutz *et al*., 2012; Hughes, 2006; Adamczewski *et al*., 1995; Gunn *et al*., 1991; M. Dumond, unpublished data, M. Branigan personal communication), they had never been detected in the Arctic Archipelago. Previous research on *U. pallikuukensis* suggested that the geographic range of this parasite was historically constrained by climatic conditions and host population bottlenecks (Hoberg *et al*., 1995; Kutz *et al*., 2005). Empirically based degree-day models for the development for *U. pallikuukensis* in gastropods demonstrated that (i) in the core of its mainland range in the central Canadian Arctic, climate warming during the 1990s resulted in a tipping point shifting the development of the parasite from a 2-year to a 1-year lifecycle (Kutz *et al*., 2005); and (ii) in the Arctic Archipelago, climatic conditions from 2000 to 2006 were, for the first time in recent history, theoretically sufficiently warm to support annual transmission of the parasite (Fig. 1) (Peacock, 2007). Herein, we describe recent surveys demonstrating the emergence of *U. pallikuukensis*, as well as *Varestrongylus* sp., in muskoxen on Victoria Island, Nunavut and discuss mechanisms for invasion, establishment, and range expansion for both parasite species.

Materials and methods

Victoria Island, shared by Nunavut and the Northwest Territories in the western Arctic archipelago of Canada is 217 291 km^2, and is home to 20–30% of the global muskox population and to the Dolphin and Union caribou herd (*R. t. groenlandicus)* (Gunn & Forchhammer, 2008; Poole *et al*., 2010). Both species are important to the Inuvialuit and Kitlinermiut peoples for food, income, and culture. Muskoxen on the island have been commercially harvested since the mid 1990s with 100–300 animals typically taken annually and subjected to thorough postmortem inspection to ensure food safety.

In 2008, in response to concerns of community members and the local abattoir about muskox health and sustainability, we initiated a study to establish baseline data for infectious disease, including zoonoses, in muskoxen on south Victoria Island. Health assessments occurred from 2008 to 2012 and included: examination of lungs and feces from muskoxen killed during subsistence community hunts on southwestern Victoria Island; intensive sampling of muskoxen taken during the commercial harvests near the community of Ikaluktutiak 200–300 km further east on Victoria Island; and through targeted fecal surveys and opportunistic postmortem examination of dead muskoxen in the region between the commercial and community harvests in August 2011 (Table 1; Fig. 1). Fresh fecal samples from individual caribou (n = 8) of the Dolphin and Union herd were also opportunistically collected during the targeted muskox fecal surveys. Examination for protostrongylid nematodes included Baermann extraction

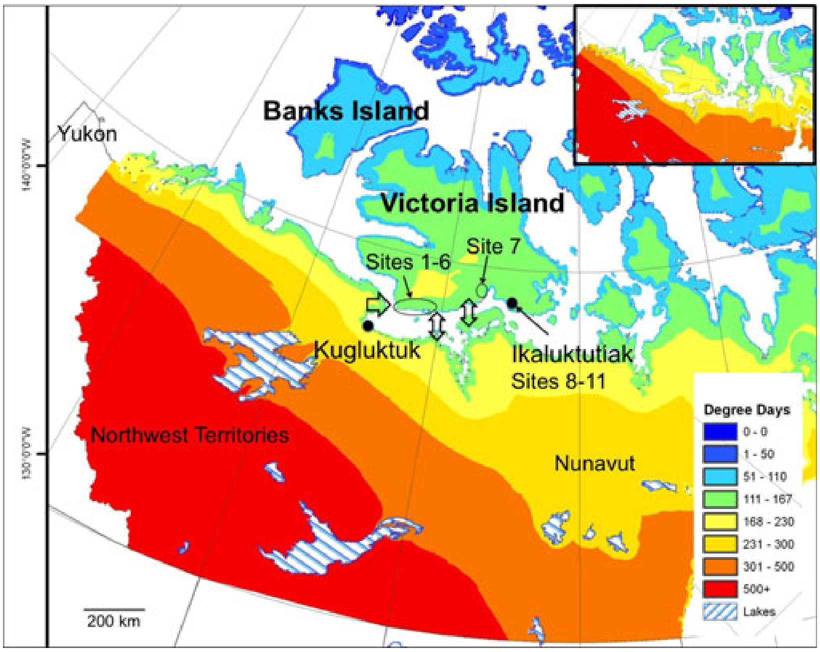

Fig. 1 Study sites and continuous degree-day surface map showing accumulation of degree-days for the development of *U. pallikuukensis* from first (L1) to infective third (L3) stage. From 2000 to 2006, development of *U. pallikuukensis* from L1 to L3 (167 degree-days accumulated) could occur in a single summer on southwestern Victoria Island whereas previously it couldn't (data not provided, see Peacock, 2007). Inset shows accumulation of degree-days based on a 2 °C increase in temperature over the 2000–2006 temperatures. Degree-day maps are adapted from those in Peacock R., 2007 and were generated using residual kriging based on data from 72 weather stations with hourly temperature data May through October. The degree-day calculations for *U. pallikuukensis* development were based on that by Kutz *et al.*, 2005. Unidirectional arrow indicates hypothesized site of muskox movement between the mainland and island, bidirectional arrows indicate main regions for caribou migration although this movement occurs across almost all of the southern edge of the island.

of the feces from muskoxen and caribou for DSL (Forrester & Lankester, 1997) and detailed dissection of the lungs (muskoxen only) for cysts containing adult parasites (Kutz *et al.*, 1999). Adult nematodes were identified based on morphology using microscopy (Hoberg *et al.*, 1995). The DSL cannot be distinguished to species based on morphology and thus were identified by sequencing the internal transcribed spacer-2 region of the nuclear ribosomal DNA (ITS-2) (Kutz *et al.*, 2007). Representative parasite specimens and DNA sequences were deposited at the US National Parasite collection at the US Department of Agriculture and GenBank, respectively. A representative subset of lungworm cysts was fixed in 10% formalin, stained with hematoxylin-eosin, and examined histologically.

Results

Community hunts and field studies on southwestern Victoria Island

In 2008, we detected DSL in 100% of 28 fecal samples tested from hunter-harvested muskoxen on southwest Victoria Island (Table 1). The ITS-2 region was sequenced for 33 DSL and these were identified as *U. pallikuukensis* (Table 1). Adult *U. pallikuukensis* were subsequently isolated from lung cysts of most of these muskoxen – cysts were not found in lungs from a few animals where only partial lungs were submitted. Parasite cysts were small, there was no gross and minimal histological evidence of cyst mineralization, and there were few degenerate cysts (Fig. 2a, b and c). We classified these lesions as recent because *U. pallikuukensis* infections accumulate with age and, when parasites have been established for an extended period of time, the cyst size is highly variable and degenerate and mineralized cysts are common (Gunn & Wobeser, 1993; Hoberg *et al.*, 1995). *Umingmakstrongylus pallikuukensis* was subsequently detected in all sampled muskoxen from southwest Victoria Island including the community hunts from 2009 to 2011 and at a low intensity in fecal surveys in 2011 (Table 1).

One of eight caribou sampled (12.5%) in 2011 was positive for DSL (0.47 larvae per gram, 12.8 g of feces tested in two Baermanns) (Fig. 3). The caribou was an adult male sampled on August 16th at 68°41.068′N 111°22.066′W. Three of the six larvae were successfully sequenced at the ITS-2 region and identified as the putative new species of *Varestrongylus* (Kutz *et al.*,

Table 1 Prevalence and median intensity of cysts of *U. pallikuukensis* and dorsal-spined larvae (DSL) of *U. pallikuukensis* or *Varestrongylus* sp. in muskox lungs and/or feces, and results from sequencing of the ITS-2 region for a subset of DSL. Samples were collected from 2008 to 2012 at different locations along the south coast of Victoria Island, Nunavut

Site	Sampling date	n[*]	Cyst[†]prev. (%) median (range)	n[‡]	DSL[§]prev. (%) median (range)	Sequenced[¶] DSL/hosts	DSL ID[‖] U/V	Accession numbers[**] and additional comments
Southwest Victoria Island, Community hunts, 68°30′N 112°43′W to 68°35′N 111° 41′W								
1	25-Feb-08	31	93.57 (1–20)	28	10017 (0.4–62)	31/5	31/0	GB JX312090-JX312099
2	11-Apr-09	15	93.3 12.5 (1–56)	14	10070 (19–327)	-	-	
3	20-Dec-09	0	na	19	10071 (24–255)	-	-	
4	14-Apr-10	26	100 20 (9–50)	25	10073 (15–190)	-	-	
5	14-Dec-10	5	100 41 (12–85)	-	-	-	-	
South central Victoria Island, Fecal survey and mortality event, 68°30.5′N 112°33.0′W to 68°37.0′N 110°52.3′W								
6	23-Aug-11	3	100	44	958.9 (1.5–434)	-	-	Field necropsies on three animals found dead during fecal surveys. One animal had >25cysts, the other two had ‘many’
South central Victoria Island, Mortality event, 69°22.5′N 106°58′W								
7	26 Aug-10	4	0	na	na	na	na	Field necropsies on 4 animals.
Southeast Victoria Island, Commercial Harvests, within 40 km radius of Ikaluktutiak, 69°6.6′, 105°8.4′W								
8	Mar 2009	24	0	182	0	na	na	
9	Mar 2010	62	0	162	3.7 0.5 (0.2–0.8)	9/6	0/9	GB JX312170-75
10	Feb 2011	94	0	94	5.3 1.0 (0.2–1.8)	22/5	0/22	GB JX312176-80
11	Mar 2012	45	4(1–4)	42	31.0 1.4 (0.2–7.5)	45/10	1/44	USNPC 105705-07 GB JX312181-90, JX312192

[*] Number of sets of lungs examined.

[†] Cysts of *U. pallikuukensis*. Lungs dissected down all major airways to bronchioles as described by Kutz *et al*., 1999.

[‡] Number of fecal samples examined. If lungs examined, these were from the same animals.

[§] Feces examined using Baermann test and three aliquots of 100 μl each were examined. If all three aliquots were negative, the entire sediment was examined. Intensity reported as larvae per gram of feces examined.

[¶] Number of DSL sequenced from number of hosts. Range of 1–7 DSL/host sequenced. Methods as per Kutz *et al*., 2007. All DSL isolated in 2010 & 2011 commercial harvests were sequenced whereas only up to 6 from each positive animal in 2012 was sequenced. DSL from sites 2–6 were not sequenced as these were *U. pallikuukensis* endemic regions and sensitivity for detection of *Varestrongylus* would be extremely low because of differences in nematode species fecundity.

[‖] Number of DSL of each species identified (*U. pallikuukensis/Varestrongylus*).

[**] USNPC Adult nematodes physical specimens accessioned at US National Parasite Collection. GB accessioned in Genbank.

2007) and the sequence of one deposited in GenBank (accession number JX312191).

Commercial harvests, Ikaluktutiak 2008–2012

In 2010, DSL were found for the first time in feces from 6 of 162 (3.7%) commercially harvested muskoxen near Ikaluktutiak (Table 1). These were identified based on ITS-2 as the putative new species of *Varestrongylus* and were found in individual muskoxen from all subsequent commercial harvests. In 2012, DSL and adults of *U. pallikuukensis* were detected for the first time at the commercial harvest and at least one muskox was infected with both lungworm species (Table 1).

Discussion

Our results indicate that *U. pallikuukensis* has recently invaded the southwest corner of Victoria Island and is expanding its range eastwards on the island. Despite extensive fecal and postmortem examinations by scientists, and ongoing subsistence harvesting by local hunters, this parasite had not previously been detected on

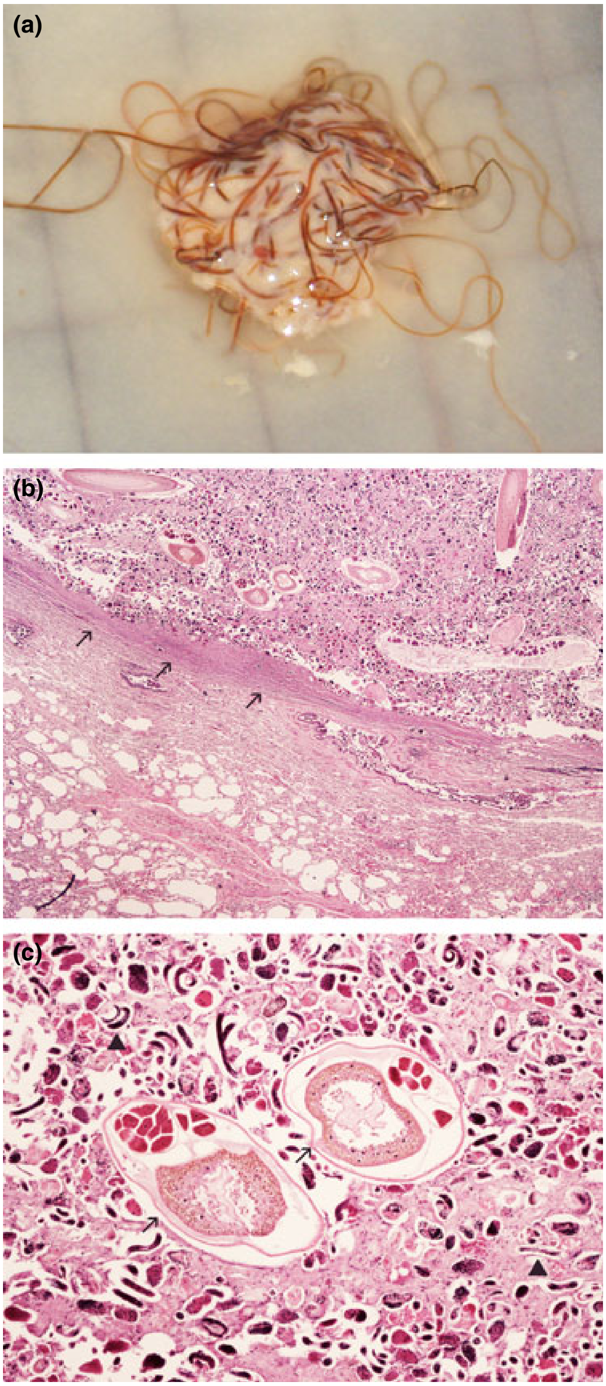

Fig. 2 Cysts containing *U. pallikuukensis.* (a) Contents of a cyst demonstrating fine, long adult nematodes. Finer debris includes eggs and larvae. No gross mineralization is apparent. (b) Histological section (HE, 2×) demonstrating a parasitic cyst that compresses the adjacent bronchi and alveoli. A thin fibrous cyst wall (arrows) surrounds cross-sections of adult parasites, eggs, and larvae in the lumen of the cyst (c) Histological section (HE, 10) of cyst containing adult nematodes (arrow) and densely packed matrix of eggs, larvae (arrowheads) and cellular debris.

Fig. 3 A dorsal-spined larva (DSL) of *Varestrongylus* isolated from the feces of a muskox collected near Ikaluktutiak, Nunavut, in March 2012. Note the typical morphology of the tail with a dorsal spine and 'kinked' tail sheath.

the island (Kutz *et al.*, 2012; Hughes, 2006; Adamczewski *et al.*, 1995; Gunn *et al.*, 1991; M. Dumond, unpublished data, M. Branigan personal communication). Further supporting the hypothesis of this recent invasion and establishment on the island are the lower prevalence and intensity of infection and the characteristics of the lungworm cysts themselves. That is, where *U. pallikuukensis* is well-established, prevalence approaches 100% and the pulmonary cysts vary greatly in size and stage of development with some soft cysts and others that have thick cyst walls and contain considerable debris and mineralized material (Gunn & Wobeser, 1993; Hoberg *et al.*, 1995). In contrast, cysts from animals examined on Victoria Island were relatively small (1–2 cm) and soft with little to no debris or mineralization.

Introduction of the parasite to the island was most likely mediated through muskox movements. Genetic data and hunter observations suggest that infrequent dispersal of muskoxen between the mainland and Victoria Island has occurred historically (M. Dumond, unpublished data). Other mechanisms for introduction are possible, but less plausible. DSL are very resistant to environmental extremes and, although not previously demonstrated, conceivably could be transported on migratory birds in the summer, or on the equipment of hunters (e.g., sleds, hunting tools, boots, etc.) moving between the mainland and island in the winter. DSL may also survive transport through the digestive tract of carnivores (Bryan *et al.*, 2010) and thus could be dispersed by bears, wolves, foxes, wolverines, or perhaps even birds, feeding on infected muskoxen. Introduction of infected gastropods to the island is another possible source of invasion; however, harsh climatic conditions (desiccation, freezing temperatures, and salinity) would limit survival of gastropods during long distance transport on birds or equipment over an open ocean or sea ice.

Whereas introduction of *U. pallikuukensis* to Victoria Island through the mechanisms mentioned above may have occurred sporadically over many decades, its successful establishment on the island is most likely a result of a recently permissive climate. Until recently, development rate of larval stages in gastropods would have been restricted by cool climatic conditions (Kutz *et al.*, 2005; IPCC, 2007) (Fig. 1), and this, combined with only sporadic introduction involving few larvae/host animals, would have prevented parasite establishment.

In the past decade, however, parasite invasion from the mainland and establishment on the island may have been facilitated through two interacting mechanisms emerging from short-term extreme events and longer term gradual changes. First, an increase in ephemeral but severe icing events, such as that reported in 2004 in the western Arctic, may increase dispersal of muskoxen across the sea ice in search of food (e.g., Nagy & Gunn, 2009). This heightened mobility of hosts directly enhances the potential for range expansion of pathogens. Concurrently, incremental change in the arctic climate over decades have led to longer and warmer summers (IPCC, 2007) and thus increasingly permissive environments for larval development, establishment of parasite populations, and perpetuation of an endemic cycle of transmission within a single summer season on southern Victoria Island (Fig. 1). The impact of this warming on gastropod intermediate hosts has not been studied, but is expected to also enhance gastropod populations at the northern extent of their range. Our observations of lungworm establishment and expansion on Victoria Island provide direct empirical evidence, predicted and consistent with the developmental-temperature model for lungworms outlined by Kutz *et al.* (2005), for ongoing geographic expansion under current climate warming scenarios. In contrast to assertions that responses for host-pathogen assemblages to climate warming will involve shifts in distribution we suggest, based on an unequivocal and ongoing expansion event onto Victoria Island, that the range of interactions among hosts, pathogens and climate will be more nuanced, involving multiple mechanisms, including broadened ranges overall for some assemblages (also see Molnar et al. 2013 Brooks & Hoberg, 2007; Burek *et al.*, 2008; Molnár *et al.* 2013a). This may be particularly true for parasites like the protostrongylids that have life history strategies (i.e., sheltered in gastropods) that allow them to cope with extremes in temperatures (Molnár *et al.*, 2013a).

Establishment of *Varestrongylus* sp., parasitic in both muskoxen and caribou, was also likely previously prohibited because of unsuitable climatic conditions on Victoria Island. In contrast to *U. pallikuukensis,* however, its introduction to the island could have been mediated by either host species. The Dolphin and Union caribou herd, estimated at 27 787 ± 7537 (95% CI) animals in 2007 (Dumond & Lee, 2013), migrates annually between the mainland (winter) and Victoria Island (summer) (Poole *et al.*, 2010). *Varestrongylus* sp. commonly occurs in barrenground and woodland caribou on the mainland (Kutz *et al.*, 2007, 2012) and caribou from the Dolphin and Union herd, infected on their core winter range on the mainland, have likely transported the parasite to the island on an ongoing basis through repeated migratory events across multiple locations. Although these caribou have undergone this migration since the 1970s, the potential for establishment of *Varestrongylus* sp. has changed over time in response to a shifting climate regime (Fig. 1) (IPCC, 2007).

We confirmed *Varestrongylus* larvae in the feces from a caribou sampled on Victoria Island in August 2011, but do not know if this was a result of exposure while on the mainland or on the island. In contrast, detection of *Varestrongylus* in muskoxen near Ikaluktutiak over consecutive years demonstrates that the lifecycle is now being completed on the island. That is, with the exception of rare dispersal events mentioned previously, muskoxen are non/minimally migratory and infection in this species indicates an endemic cycle with exposure to infective stages on the island. The low, but apparently increasing prevalence of *Varestrongylus* in muskoxen from 2010 to 2012, supports a hypothesis of recent establishment of this parasite on the island; in mainland regions where it is well-established, prevalence in muskoxen approaches 100% (Kutz *et al.*, 2007, 2012). Detection of *Varestrongylus* in muskoxen near Ikaluktutiak, before the appearance of *U. pallikuukensis* at this location, further supports a hypothesis of caribou-mediated introduction of the parasite. As with *U. pallikuukensis,* parasite invasion of the island as a result of human, predator/scavenger, or gastropod-mediated introductions are possible, however, the annual migration of caribou remains the most plausible hypothesis.

It is probable that, historically, multiple and independent events of parasite introduction to Victoria Island have occurred for *Varestrongylus,* and to a lesser extent *U. pallikuukensis,* without parasite establishment. Our data demonstrate that these parasites are now well-established on the southwest and southcentral region of the island and their range and abundance appear to be expanding and increasing. Degree-day models for *U. pallikuukensis* suggest that climate warming may be playing a key role, where temperatures are now permissive for a one-year developmental cycle, thus facilitating establishment and subsequent geographic expansion of this parasite on the island (Fig. 1). Similar mechanisms are likely at play for *Varestrongylus,* although thermal tolerances and specific characteristics for parasite development and survival are unknown for this species.

Two gastropods, *Deroceras laeve* and *Vertigo* sp., proven and suspected intermediate hosts, respectively, are present on Victoria Island at low densities (Kutz *et al.*, 2001, 2007; S. Kutz, A. Dumond, G. Verocai unpublished data). Their distribution and ecology at this high latitude, particularly with respect to climatic conditions and protostrongylid transmission, remain unknown, although both will play an important role in parasite abundance and range expansion. Importantly, if suitable gastropod intermediate hosts are present on northern Victoria Island and adjacent islands, under increasingly permissive climatic conditions *Varestrongylus* sp. may colonize yet a new host at these latitudes, the endangered Peary caribou (*R. t. pearyi).*

Emergence of *U. pallikuukensis* and *Varestrongylus* provides a unique opportunity to investigate, in a relatively simple ecosystem undergoing accelerating climatic change, the mechanisms and patterns of geographic colonization by parasites, establishment, and subsequent range expansion in real time. Lungworm emergence on Victoria Island is a powerful model system for understanding processes of parasite invasions, faunal assembly and structuring of host-parasite communities in ecological and evolutionary time, and can provide direct insights into large scale historical events (e.g., Hoberg & Brooks, 2013; Galbreath & Hoberg, 2012; Hoberg *et al.*, 2012). Further, the events unfolding on Victoria Island constitute an important analog for understanding historical processes of episodic expansion, geographic colonization, host switching and the assembly of mosaic faunas of nematodes among ungulates through the late Pliocene and Quaternary (e.g., Hoberg, 2005; Hoberg *et al.*, 2012).

As the current processes of invasion and expansion of the two protostrongylids on Victoria Island are mediated by two distinctly different mechanisms involving different host species, it further affords direct tests of predictions and consequences in population genetics for parasites undergoing range expansion (Hoberg, 2010). For example, Hewitt (1996) defined the expectations resulting from biotic expansion and colonization on broad fronts involving a large number of animals (phalanx or leading edge dispersal) in contrast to isolated trajectories with few animals (pioneer dispersal); this represents, respectively, a potential contrast for *Varestrongylus* in caribou and *U. pallikuukensis* in muskoxen. Phalanx events should thus result in relatively homogeneous population genetic structure with expansion and establishment, whereas the importance of fine scale founder events, fragmentation and heterogeneous structure are emphasized under a scenario for pioneer dispersal. These processes are also played out in a spatial/temporal continuum involving what may be extensive geographic ranges or corridors and recurrent, continuous or episodic events (e.g., Hoberg, 2005; Hoberg & Brooks, 2008; Wilson, 2009).

Exploring patterns of expansion for these two parasites (one host generalist, one host specialist; one migratory and one nonmigratory host) will provide broader insights into ecological and evolutionary barriers and facilitators for pathogen invasion and emergence (Wilson, 2009; Hoberg *et al.*, 2012; Kutz *et al.*, 2012). Interestingly, to date *P. andersoni* has not been found on the island. Although this absence may reflect inadequate sampling of caribou, it may also reflect historical constraints related to host associations and biogeography (Hoberg *et al.*, 2012; Kutz *et al.*, 2012).

Emergence of *U. pallikuukensis* and *Varestrongylus* on Victoria Island has significance for sustainability of muskox and caribou populations, and, therefore, the local economy, socio-cultural well-being, food-web structure and function, and ecosystem health. These parasites may also serve as indicators for invasions of other less obvious pathogens (e.g., viruses and bacteria) from the mainland. Recent widespread mortality events of muskoxen on Victoria and Banks Islands (ProMEDmail, 2012) suggest that there has been a shift in ecological conditions and host-pathogen interactions in the western Arctic Archipelago. Understanding the processes involved in geographic colonization is important as emergence of new pathogens among naive populations frequently has severe short-term, and sometimes long-term, population level effects. For caribou, establishment of *Varestrongylus* in muskoxen on the island is likely to substantially increase the infection pressure for these cervid hosts. Muskoxen greatly outnumber caribou, and are highly suitable hosts for *Varestrongylus*. This will amplify the parasite on the caribou summer range, with potential detrimental consequences for the Dolphin and Union caribou, and eventually also for Peary caribou. Determining the dynamics of these host-parasite interactions in a regime of rapid climate warming, and their role in different host species and populations, is critical for understanding the future sustainability of these highly valued, keystone, wildlife species, and to provide insights into broader processes and generalities of emerging diseases globally.

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