

“Emerging” Parasitic Infections in Arctic Ungulates¹

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SYNOPSIS. Important drivers for emergence of infectious disease in wildlife include changes in the environment, shrinking habitats or concentration of wildlife, and movement of people, animals, pathogens, or vectors. In this paper we present three case-studies of emerging parasitic infections and diseases in ungulates in the Canadian north. First we discuss climate warming as an important driver for the emergence of disease associated with *Umingmakstrongylus pallikuukensis*, a nematode lungworm of muskoxen. Then we examine how *Protostrongylus stilesi*, the sheep lungworm, emerged (or re-emerged) in muskoxen after re-introduction of this host into its historical range made it sympatric with Dall’s sheep. Finally, we consider *Teladorsagia boreoarcticus*, a newly described and common abomasal nematode of muskoxen that is emerging as a disease-causing parasite and may be an important regulator for muskox populations on Banks Island, Northwest Territories. These and other arctic host-parasite systems are exquisitely tuned and constrained by a harsh and highly seasonal environment. The dynamics of these systems will be impacted by climate change and other ecological disruptions. Baseline knowledge of parasite biodiversity and parasite and host ecology, together with predictive models and long-term monitoring programs, are essential for anticipating and detecting altered patterns of host range, geographic distribution, and the emergence of parasitic infections and diseases.

INTRODUCTION

A general understanding of emerging diseases has been derived largely from studies in temperate and tropical ecosystems, and attention to such issues across arctic and subarctic environments of the northern hemisphere has been relatively limited (Rausch, 1972a, b; Handeland and Slettbakk, 1994; Lindgren *et al.*, 2000; Hoberg, 1997; Kutz *et al.*, 2001b, 2002; Hoberg *et al.*, 2003). Ironically, it is the north that is undergoing some of the most rapid rates of change, particularly climate change and, therefore, may be at the greatest risk of disease emergence (Riewe and Oakes, 1994; Cohen, 1997; Gitay *et al.*, 2002; Dobson *et al.*, 2003). For example, development of helminth parasites, and transmission of vector borne pathogens, are closely linked to climatic conditions and, therefore, very tightly constrained by length and quality of the “growing season” in the north. Seemingly small changes in temperature may have a tremendous impact on pathogen epizootiology (Kutz *et al.*, 2002; Dobson *et al.*, 2003). Other changes in the north that are altering the landscape and the interactions among people, animals, parasites, and the environment, include renewable and non-renewable resource exploration and development, movement of wildlife, and increasing encroachment of people and their domestic ani-

mals on wildlife habitat. Emergence of parasites and parasite-induced diseases as a result of one or a combination of these factors is a very real threat to the stability of wildlife populations and to human health and socio-economic well-being.

Investigating and understanding emergence of parasites and parasitic diseases in northern wildlife presents a number of challenges, the greatest of which is the absence of baseline data on parasite fauna of most northern mammals (Hoberg *et al.*, 2003). Until the last decade the literature for parasites in arctic ungulates in Canada was sparse and for the most part consisted of anecdotal reports based on the opportunistic examination of a few animals (Gibbs and Tener, 1958; Samuel and Gray, 1974; Webster and Rowell, 1980; Alendal and Helle, 1983; Wobeser, 1984; Tessaro *et al.*, 1984; Blake, 1985; Gunn *et al.*, 1991). Rarely, more comprehensive surveys were undertaken (Nielsen and Neiland, 1974; Duszinski *et al.*, 1976; Fruetel and Lankester, 1989; Lankester and Hauta, 1989; Gunn and Wobeser, 1993; Kutz, 2000, 2001). In the absence of synoptic baseline knowledge, “new discoveries” have lacked a comparative context in which to interpret the occurrence, abundance, and distribution of potential pathogens, as well as the distribution or “emergence” of disease. Without these historical baselines there remains some level of ambiguity in “new” discoveries—are the agents or disease syndromes novel (real emergence) or only newly detected in a region or host population (apparent emergence)?

Over the last 10 years the Research Group for Arctic

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Parasitology (RGAP), an informal group of zoologists, wildlife managers, and veterinarians from universities, government, and co-management organizations, has been working in the Canadian Arctic and Subarctic to advance our knowledge of the biodiversity and epidemiology of parasites in northern mammals. These studies have revealed an array of “new” parasites and associated diseases that appear to be emerging in northern ungulates (Hoberg *et al.*, 1995, 1999, 2002; Kutz *et al.*, 2000a, 2001a, b, d). Ongoing examination of these systems has provided a greater understanding of the ecology of a range of wildlife species and has raised new management issues. Perhaps most importantly is the realization that, under the current regime of rapid natural and anthropogenic change in the north, parasitic infections and diseases will continue to emerge, conceivably at an accelerated rate.

In this paper we explore three examples of helminth parasitism in muskoxen to illustrate some of the drivers for the “real” emergence of parasitic infections and diseases in northern ungulates, in particular, climate change, movement of animals, and high population density. We also discuss some of the associated management issues. Additionally, we demonstrate how the absence of baseline information and accurate diagnostic techniques can result in the ‘apparent’ emergence of some parasites.

CASE STUDIES:

UMINGMAKSTRONGYLUS PALLIKUUKENSIS—A CASE OF “APPARENT” EMERGENCE OF A PARASITIC INFECTION, AND “REAL” EMERGENCE OF A PARASITIC DISEASE DRIVEN BY CLIMATE CHANGE

A recently discovered parasite of muskoxen (*Ovibos moschatus moschatus*) serves as a case study for parasite emergence in a northern ungulate. The lung nematode *Umingmakstrongylus pallikuukensis* (Protostrongylidae) was first recognized in 1988, in radio-collared muskoxen found dead west of the Coppermine River, Nunavut (NU) (Gunn *et al.*, 1991). In 1995 it was described as a new genus and species (Hoberg *et al.*, 1995). Subsequent investigation of other possible definitive hosts (Dall’s sheep [*Ovis dalli*], domestic sheep [*O. aries*], and sympatric moose [*Alces alces*] and caribou [*Rangifer tarandus groenlandicus*]) revealed that *U. pallikuukensis* was restricted to muskoxen and its appearance was not a recent “host switch” from another northern ungulate (Hoberg *et al.*, 1995; Kutz *et al.*, 1999b, 2004).

Umingmakstrongylus pallikuukensis is a large (up to 65 cm long) nematode found in cysts in the lungs (Kutz *et al.*, 1999a, b). Adults lay eggs in the cysts, which then hatch to first-stage larvae (L1), are moved up the bronchial escalator, swallowed, and passed in the feces. First-stage larvae penetrate the foot of terrestrial gastropod intermediate hosts and develop to third-stage larvae (L3) (Kutz *et al.*, 2001c). Muskoxen become infected by ingesting gastropods containing L3 or vegetation contaminated with L3 that have

emerged from the gastropods (Kutz *et al.*, 1999b, 2000b). Larvae subsequently migrate to the lungs and mature to adult parasites in approximately three months (Kutz *et al.*, 1999b). *Umingmakstrongylus pallikuukensis* is restricted to muskoxen on the mainland of the Northwest Territories (NT) and NU in the region bordered by the Mackenzie River to the west and approximately by the Coppermine River to the east. Currently it is well established in this host population, with 76–100% of opportunistically collected fecal samples containing L1 (J.N., R. Popko, J. Nishi, unpublished data).

“Apparent” emergence of a parasitic infection

Understanding the factors leading to the discovery, or “apparent” emergence, of *U. pallikuukensis* in muskoxen in 1988 requires an examination of: (1) the historic distribution and management of muskoxen in the NT and NU, and; (2) the state of knowledge and awareness of parasitic infections in northern ungulates in this region over the past 25 years.

At the turn of the 20th century, primarily because of the fur trade and exploitation by explorers and whalers, muskox populations in the North American Arctic had dramatically declined. Muskoxen were extirpated from Alaska by the end of the 19th century, the Canadian Arctic Island populations were diminished, and only two small isolated populations had survived on the Canadian mainland, one in the east (Thelon Sanctuary, a few hundred animals) and one in the west (north of Great Bear Lake “2 or 3 animals”) (Fig. 1) (Lent, 1999). With hunting banned in 1917 the muskox populations in Canada gradually recovered. Muskoxen are now found on most of the arctic islands and across most of the arctic mainland in NU and NT (Fig. 1) (Fournier and Gunn, 1998). The remnant population near Great Bear Lake survived and descendants colonized regions east to the Coppermine River and west to the Mackenzie River. In 1997, approximately 5,500 muskoxen were reported on the mainland region bordered by the Coppermine and Mackenzie Rivers (Fig. 1) (Fournier and Gunn, 1998).

The current distribution of *U. pallikuukensis* is compatible with a relictual distribution of the parasite in the remnant muskox population north of Great Bear Lake (Hoberg *et al.*, 1995). Why then was *U. pallikuukensis* not detected previously? Low infection levels coupled with minimal contact between people and muskoxen before 1988 is the most probable explanation. Hunting of muskoxen in the NT began again in 1967, but west of the Coppermine River a strict hunting quota had been imposed and animals were taken only for subsistence purposes. Hunters typically discard lungs and it is possible that the cysts in animals with low intensities of infection would be overlooked, and cysts in those with higher intensities of infection may have been mistaken for hydatid cysts of the tapeworm *Echinococcus granulosus*. Although a limited number of studies of muskox parasites had been done in the NT and NU before 1988 (Gibbs and Tener,

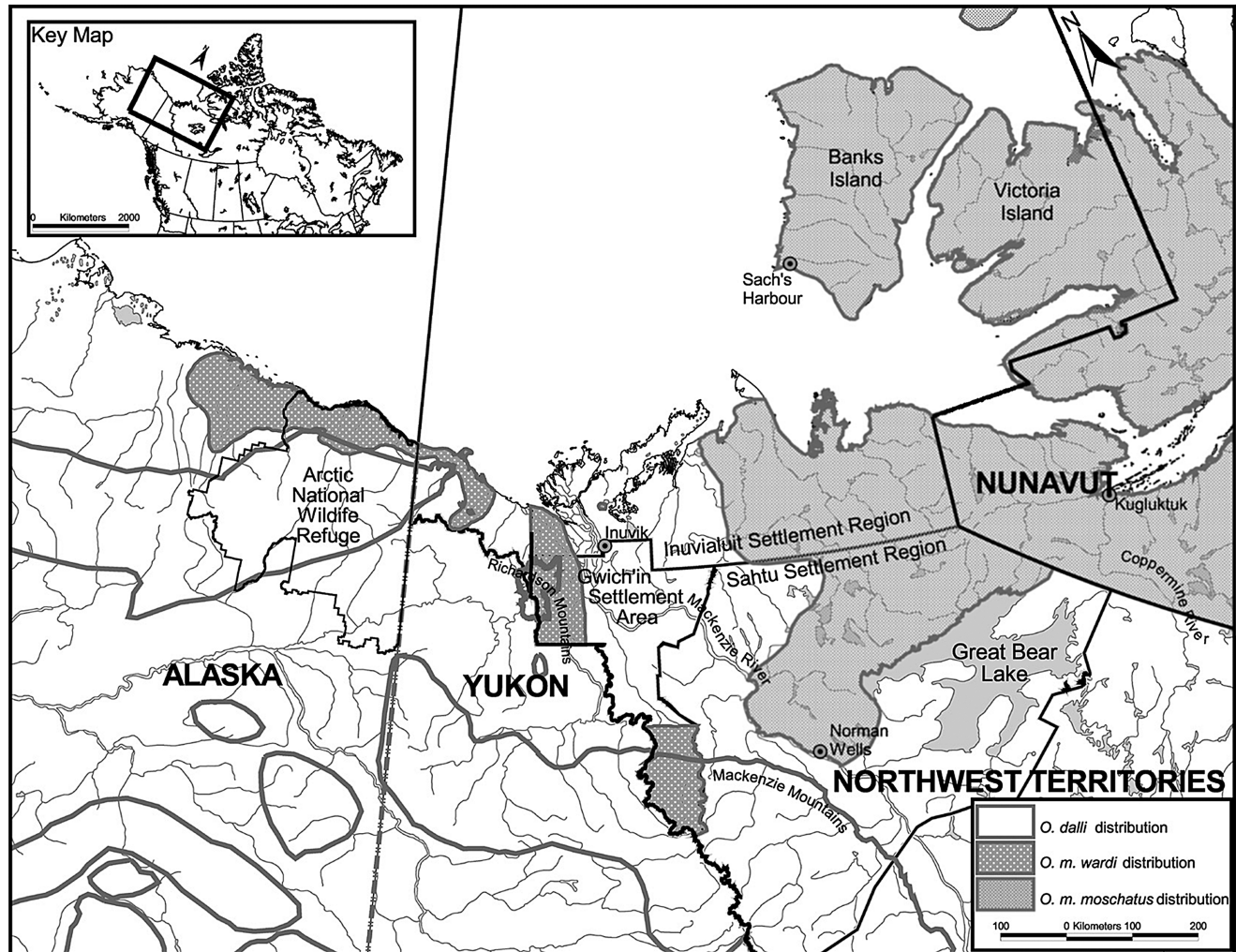


FIG. 1. Map of the muskox and Dall's sheep distribution in northern Canada and north-eastern Alaska.

1958; Samuel and Gray, 1974; Webster and Rowell, 1980; Alendal and Helle, 1983; Wobeser, 1984; Tessaro *et al.*, 1984; Blake, 1985) health investigations and commercial harvests, including detailed examination of organs and tissues, did not occur for muskoxen in this region. It is probable, therefore, that *U. pallikuukensis*, present but with a highly restricted geographic range in the first half of the 20th century, was now expanding its geographic distribution, coincidental with the recovery of the host population. We conclude that the discovery of *U. pallikuukensis* in 1988 was new only to science ("apparent" emergence), detected because of the fortuitous follow-up of mortality of radio-collared animals.

"Real" Emergence of a Parasitic Disease

Further investigations of *U. pallikuukensis*, together with population trends of the infected muskoxen, and climate warming trends, suggest that this parasite may be emerging as an important cause of clinical and sub-clinical disease in muskoxen, with a possible impact at the population level.

Umingmakstrongylus pallikuukensis currently appears to be thriving in muskoxen in the region bordered by the Coppermine and Mackenzie Rivers, NT. In the Sahtu in 2002, all of 32 fecal samples were positive for larvae of *U. pallikuukensis* and the average larval count, 1,413 larvae/gram feces, was very high (R. Popko, B. Wagner, unpublished data). Preliminary examination of lungs from adult bulls in the Inuvik region in 2003/2004 indicates 100% prevalence of infection and intensities that are frequently greater than 100 cysts/animal (J.N., unpublished data).

Climate Warming Driving Emergence

The current high levels of infection with *U. pallikuukensis* may be linked to a significant and unprecedented warming trend in the west-central Canadian Arctic and Subarctic over the last two decades. For example, annual temperatures in 18 of the last 20 years in the Mackenzie district have been above normal with an overall warming trend of 2.0°C (1948–2003) (Environment Canada, accessed 12 January 2004, http://www.msc-smc.ec.gc.ca/ccrm/bulletin/regional_e.cfm).

Temperature is a key factor influencing the epidemiology of protostrongylids, with parasite development rates increasing under warmer conditions (for example, see Kutz *et al.*, 2001c; Dobson *et al.*, 2003). Experimental work on development of *U. pallikuukensis* in the slug intermediate hosts on the tundra predicts that when summer temperatures are normal, development of L1 to L3 probably requires two years and significant overwinter mortality of slugs and larvae occurs. Conversely, in years with unusually warm summers, development occurs rapidly and a greater number of L3 become available for transmission within that same summer and over-wintering may then be unnecessary or of minimal significance (Kutz *et al.*, 2002). Similarly, earlier springs and later falls associated with climate warming also probably provide favourable conditions for larvae to develop to L3 within a single summer (Kutz *et al.*, 2001b). Retrospective studies on a related protostrongylid (*Elaphostrongylus rangiferi*) of reindeer (*Rangifer tarandus tarandus*) in Norway demonstrated that disease outbreaks associated with this parasite occur in years where summer temperatures are 1.5°C or more above normal (Handeland and Slettbakk, 1994). Together the studies on these two nematode species suggest that abnormally warm summers can result in the amplification of northern protostrongylids in both their intermediate (gastropod) and definitive (mammal) hosts, and may lead to an increase in parasite-induced disease.

The effects of *U. pallikuukensis* on survival, fecundity, and recruitment of muskoxen have not been studied. Circumstantial evidence, however, suggests that infection with this parasite, perhaps at an increasing intensity over the last 10–15 years, may be one factor driving recent declines of infected muskox populations. Since the late 1980s muskox numbers in all muskox management areas between the Coppermine and Mackenzie rivers have declined by approximately 50%. This occurred in the region immediately west of the Coppermine River from 1988 to 1994; the Inuvialuit region from 1997 to 2002; and the northern Sahtu Settlement region from 1987 to 1997 (Fournier and Gunn, 1998; J.N., unpublished data). Of five other mainland regions in the NT and NU that were surveyed during this same time period, and where muskoxen are not infected with *U. pallikuukensis*, only the Queen Maude Gulf showed a similar population decline, all others increased significantly (A. Gunn, personal communication).

Reasons for the declines of the infected muskox populations have been attributed in part to emigration and predation. Predation by grizzly bears (*Ursus arctos*) is an important cause of mortality for muskoxen on the mainland in general and recently has caused substantial declines in northeastern Alaska (Reynolds *et al.*, 2002). It is possible that muskoxen infected with *U. pallikuukensis* may be more likely to succumb to predation by grizzly bears. Observations by hunters near Kugluktuk of nasal bleeding and animals lagging behind fleeing groups indicate that *U. pallikuukensis*

may be the source of significant pulmonary compromise. Those with high infection intensities may have a reduced ability to fight or flee and, therefore, would be more susceptible to predation by grizzly bears and other predators. Other possible clinical or sub-clinical effects of infection with *U. pallikuukensis*, including effects on fecundity and recruitment, may also have important impacts on population dynamics.

Future scenarios for U. pallikuukensis

Under current climatic conditions we anticipate that infection levels with *U. pallikuukensis* will remain high in the enzootic areas. We expect that warming climatic conditions will be favorable for parasite development and will result in increased levels of infection and the occurrence of overt disease. We predict that *U. pallikuukensis* will be maintained in the muskoxen as they move south and west where climatic conditions are similar, if not warmer, and suitable gastropod intermediate hosts are available. The possible continued westward movement of muskoxen across the Mackenzie River raises a number of issues related to parasite and pathogen transmission between muskoxen and Dall's sheep in the Mackenzie and Richardson Mountains, as well as between these muskoxen (*O. m. moschatus*) and those that were introduced to Alaska from Greenland (*O. m. wardi*) and that have extended their range to the west side of the Mackenzie River (*e.g.*, see Hoberg *et al.*, 2002; Kutz *et al.*, 2004).

The spread of *U. pallikuukensis* to muskoxen east of the Coppermine River is less certain. Muskoxen from the remnant population adjacent to Great Bear Lake have colonized areas east of the Coppermine River, yet, with the exception of a few bulls, *U. pallikuukensis* has remained absent from these regions (J. Nishi, personal communication). Availability of suitable gastropod intermediate hosts may be limiting, alternatively, and perhaps more likely, current and past climatic conditions may not have been sufficiently warm or otherwise suitable for the parasite to complete its life cycle and maintain itself in this region. The 1.3°C warming trend (1948–2003) (Environment Canada, accessed 12 January 2004, http://www.msc-smc.ec.gc.ca/ccrm/bulletin/regional_e.cfm) for the arctic tundra may relax the temperature constraints, extend the seasonal windows for transmission, and result in emergence of *U. pallikuukensis* to the east of its current distribution. A model developed by Kutz *et al.* (2002) for predicting larval development rates in gastropod intermediate hosts under varying temperature regimes may prove useful for anticipating the future distribution of *U. pallikuukensis*.

PROTOSTRONGYLUS STILESI IN MUSKOXEN—A CASE OF AN EMERGING, OR RE-EMERGING, PARASITIC INFECTION RESULTING FROM THE REINTRODUCTION OF A HOST INTO HISTORICAL RANGE

A second protostrongylid parasite recently discovered in muskoxen is *Protostrongylus stilesi* (Hoberg *et al.*, 2002). This is a lung nematode common in bighorn

(*Ovis canadensis*), Stone's (*O. dalli stonei*) and Dall's (*O. d. dalli*) sheep across their ranges (Kutz *et al.*, 2001d; Nielsen and Neiland, 1974; E. Jenkins, personal communication). As with *U. pallikuukensis*, its life cycle requires a gastropod intermediate host in which development is temperature dependent. In bighorn sheep this parasite has been considered a possible predisposing factor for pneumonia outbreaks (Spraker *et al.*, 1984).

The emergence of *P. stilesi* in muskoxen in the Richardson Mountains, NT, and in the northern Yukon is the result of a series of translocations that moved muskoxen back to historical range and into contact with Dall's sheep (Hoberg *et al.*, 2002). Muskoxen were extirpated west of the Mackenzie River by the end of the 19th century. In 1935 and 1936 muskoxen were translocated from Greenland to Nunavik Island, Alaska. Descendants of these animals were moved to a variety of locations in Alaska, including the Arctic National Wildlife Refuge (ANWR) in northeast Alaska in 1969 and 1970 (Lent, 1999). This ANWR population increased rapidly and expanded its range east into the Yukon (Reynolds, 1998). Currently, these muskoxen, which maintain some degree of sympatry with Dall's sheep in a number of areas in the Yukon and NT west of the Mackenzie River, are infected with *P. stilesi*. Prior to this discovery *P. stilesi* was thought to be a parasite specific to sheep and goats; the infection of muskoxen suggested a host switch. This host switch may in fact represent the re-emergence of a parasite in muskoxen resulting from the introduction of muskoxen into historical habitat. It is probable that muskoxen and Dall's sheep were sympatric in this region prior to the 20th century and they may have shared a number of parasites and other pathogens. The sheep may or may not have maintained these pathogens in the absence of contact with muskoxen over the last 100 years. With renewed sympatry, pathogen transmission between these species is likely and may result in emerging (or re-emerging) infections and diseases in both hosts.

An important management issue is now at hand with respect to muskox and sheep management in the Yukon and NT. The Mackenzie River currently separates the Alaskan muskoxen (*O. m. wardi*, west of the Mackenzie River), and the *U. pallikuukensis* infected muskoxen (*O. m. moschatus*, east of the Mackenzie River). Both populations are expanding their ranges (although not necessarily their population size, *i.e.*, see Reynolds *et al.*, 2002) and it may only be a matter of time before they come into contact. We know that at the very least the pulmonary parasite fauna differs between the two (*U. pallikuukensis* east of the river and *P. stilesi* west of the river) and we suspect that other differences in parasitic and viral fauna, and bacterial flora, are likely. Questions of importance include: (1) can *P. stilesi* be maintained in muskoxen in the absence of Dall's sheep? (2) are conditions and intermediate host availability suitable for *P. stilesi* to emerge east of the Mackenzie River? (3) will *U. pallikuukensis* emerge in

muskoxen west of the Mackenzie River? (4) are there additive effects of *P. stilesi* and *U. pallikuukensis*? (5) what other pathogens (parasitic, bacterial, and viral) are of concern? (6) what are the effects of introduction of these pathogens into naïve host populations? Clearly baseline knowledge of the pathogen diversity and life histories in both host populations is critical for understanding and addressing these issues.

TELADORSAGIA BOREOARCTICUS—A CASE OF “APPARENT” EMERGENCE OF A PARASITIC INFECTION AND “REAL” EMERGENCE OF A PARASITIC DISEASE DRIVEN BY A HIGH POPULATION DENSITY

“Apparent” emergence

Teladorsagia boreoarcticus, an abomasal nematode common in muskoxen across their range in Canada, was first described in 1999 (Hoberg *et al.*, 1999). This parasite is considered part of a “cryptic species complex” and is an excellent example of apparent emergence because of previous misidentification (*e.g.*, Divina *et al.*, 2002; Hoberg *et al.*, 2003). Historically, in surveys of Nearctic ruminants *T. boreoarcticus* had been identified as *T. circumcincta*, a nematode with an apparent cosmopolitan distribution in domestic sheep, other bovids, and some cervids (Hoberg *et al.*, 2001). Detailed morphological examination identified subtle differences between specimens of *Teladorsagia* in muskoxen and domestic sheep and subsequent examination of the ND-4 region of mitochondrial DNA revealed considerable genetic divergence. This led to the conclusion that *Teladorsagia* spp. in domestic sheep and muskoxen were distinct species (Hoberg *et al.*, 1999).

Teladorsagia boreoarcticus: an emerging disease

In recent years *T. boreoarcticus* has emerged as a cause of severe abomasal (the 4th stomach in a ruminant) disease in muskoxen on Banks Island, NT. Evidence is strong that this may be a new phenomenon. Muskoxen from Banks Island have been commercially harvested since the early 1980s. Throughout the years veterinarians and biologists have participated to varying degrees in the harvests and have collected a variety of samples for analysis. From 1982 to 1986 the viscera were examined and comments on abomasal parasitism indicated this to be mild to moderate (Tessaro *et al.*, 1984; Wobeser, 1984; Blake, 1985; Rowell, 1989). In addition, although low prevalences and intensities of two species of *Eimeria* (protozoan parasites) were found on fecal examination, no other gastrointestinal parasites were reported in the feces (Tessaro *et al.*, 1984).

In 1999, a study was initiated by RGAP to establish baselines for *T. boreoarcticus* in harvested Banks Island muskoxen and elucidate the life history, epizootiology, and effects of this parasite in muskoxen. Preliminary results indicate very high levels of infection relative to mainland animals and substantial abomasal pathology in the spring associated with mucosal larval stages. Pathology observed in April and May of 2001

was considerably more severe than that reported from the commercial harvests in 1982–1985. The current working hypothesis is that the pathology observed recently is associated with the emergence of hypobiotic larvae from the abomasal mucosa and that heavy infections in young females (2 and 3 yr old) may interfere with growth and restoration of body condition before the breeding season (J.N., S.J.K., unpublished data). Conception and pregnancy rates are sensitive to nutritional condition (Adamczewski *et al.*, 1998; J.N., unpublished data), consequently, high levels of parasitism resulting in poorer body condition may delay conception dates, reduce conception rates, and perhaps even postpone the age of first conception (J.N., unpublished data). Such effects on host fecundity may lead to fluctuations in the muskox population (*e.g.*, see May and Anderson, 1978; Hudson and Dobson, 1991; Dobson and Hudson, 1992; Grenfell, 1992; Gulland, 1992; Ives and Murray, 1997).

A high population density and climatic warming may be driving the emergence of *T. boreoarcticus* as a disease agent in muskoxen. On Banks Island the muskox population has grown at an exceptional pace, expanding from a few hundred animals in 1958 to approximately 65,000 non-calf animals in 1994 (Fournier and Gunn, 1998). During the last 10 years this population has fluctuated at high densities ranging from 65,000 in 1994, 46,000 in 1998, and 69,000 in 2001 (J.N., unpublished data). The very high densities in 1994 and 2001, approximately one muskox/km², are greater than that seen for muskoxen elsewhere in the world (J.N., unpublished data). The effective density is even higher because the animals concentrate in the river valleys and meadows, which represent approximately 30% of the island. The high population density leads to substantial environmental contamination with eggs and larvae of *T. boreoarcticus*, which may lead to increased exposure and transmission rates (*e.g.*, see Grenfell, 1992; Gulland and Fox, 1992; Arneberg *et al.*, 1998; Stien *et al.*, 2002).

Concomitant with the tremendous muskox population increase is a trend of increasing temperature and precipitation. Banks Island is in the Arctic Region as defined by Environment Canada. Temperatures in this region have been above normal in 14 of the last 20 years (11 of the last 11), and the amount of precipitation has been above normal in 20 of the last 20 years (Environment Canada, accessed 12 January 2004, http://www.msc-smc.ec.gc.ca/ccrm/bulletin/regional_e.cfm). In these warmer and wetter years larval development rates would increase and mortality of the larvae from desiccation should be reduced. These climatic conditions, conducive to parasite development and survival, probably work synergistically with the high population density in amplifying *T. boreoarcticus*, and perhaps other parasites (*e.g.*, *Eimeria*), in the muskox population (S.J.K., J.N., unpublished data).

DISCUSSION

Emerging parasitic infections and diseases are of importance in northern ecosystems and in some in-

stances, through both clinical and sub-clinical effects, may threaten the stability of wildlife populations. The three case studies presented in this paper demonstrate that climate warming, movement of animals, and increased population density, are all potentially important drivers for emergence of parasitic infections and diseases in the north. Baseline knowledge for parasite biodiversity, long-term monitoring programs, and detailed studies investigating the clinical and sub-clinical effects of parasitism on wildlife individuals and populations, are essential for detecting changes, predicting the impacts of various drivers of emergence, and developing appropriate management strategies.

Drivers of emergence

Climate change and variability. The unprecedented rate of climate warming in the central and western Canadian Arctic and Subarctic (1.3–2.0°C, 1948–2003), bring a strong sense of urgency to understanding the potential impacts on northern host-parasite assemblages. Climate and climate variability affect all components of the host-pathogen-environment triad, and have been implicated as important factors in the emergence of many diseases (*e.g.*, see Dobson and Carper, 1992; Patz *et al.*, 1996, 2000; Lindgren *et al.*, 2000; Mellor and Leake, 2000; Marcogliese, 2001; Harvell *et al.*, 2002; Dobson *et al.*, 2003; Parmesan and Yohe, 2003; Root *et al.*, 2003). Warmer conditions will increase rates of development of the free-living larval stages of parasites or those in poikilothermic intermediate hosts, thereby reducing time to infectivity, and may shift life histories from multi-year to single year cycles or even multiple generations per year. However, exceptionally warm or dry conditions may result in higher mortality rates of the free-living stages of parasites (especially for those with direct life cycles) and offset some of the effects of more rapid development rates. Warming may be of particular importance in northern regions because the life history patterns of most hosts and parasites are severely constrained by climatic conditions and these species are often at the latitudinal or altitudinal extreme of their range (Kutz *et al.*, 2001b; Hoberg *et al.*, 2002; Dobson *et al.*, 2003). Field and laboratory studies on *U. pallikuukensis* and *E. rangiferi*, and model projections for *U. pallikuukensis*, confirm the sensitivity of these northern systems to climate warming (Handeland and Slettbakk, 1994; Kutz *et al.*, 2002; Dobson *et al.*, 2003).

Climate warming will also relax constraints on southern hosts and parasites and allow for a northward expansion of both taxa. Potential outcomes of northward expansion are complex and difficult to predict, but may include colonization of naïve hosts as well as parasite-mediated competition (*e.g.*, see Tompkins *et al.*, 2002). The rate and synchrony of these latitudinal shifts of colonizing mammals and pathogens, and their overall impacts on endemic wildlife species, remain uncertain.

Translocation. Movement of animals and disease vectors is perhaps one of the most common causes of

disease emergence globally (Williams *et al.*, 2002; Daszak *et al.*, 2000; Fayer, 2000; Deem *et al.*, 2001; Harvell *et al.*, 2002). Although translocations of hosts by people account for the majority of the disease emergence associated with animal movement, dissemination and potential introduction of pathogens may also be mediated by natural means such as migration, dispersal, and range expansion of hosts (*e.g.*, convergence of populations of muskoxen from east and west of the Mackenzie River). Regardless of how animals move, they bring with them their complement of macro and micro-organisms. This can result in the transmission of pathogens from introduced to naïve resident animals, or from resident to naïve-introduced animals (Deem *et al.*, 2001). The colonization of muskoxen west of the Mackenzie River by *P. stilesi* is a direct result of the anthropogenic movement of muskoxen into an ecological niche that it had not occupied for over a century. This situation now can serve as a remarkable natural laboratory for exploring the health impacts of translocation and the potential for reciprocal host switching at an ecotone (Hoberg *et al.*, 2002).

Host density. Parasite abundance typically increases with host density (*e.g.*, May and Anderson, 1978; Dobson and May, 1986; Gulland and Fox, 1992; Arneberg *et al.*, 1998). Habitat reduction/fragmentation and population growth without room for range expansion all increase the probability for parasite transmission within and among species (for example see Lyles and Dobson, 1993; Deem *et al.*, 2001; Dobson and Foutopoulos, 2001). The stress and immune compromise associated with crowding, together with greater concentration of and subsequent exposure to infectious parasitic stages, can result in emergence of disease as well as enhanced opportunities for host switching with subsequent emergence of pathogens in new host species.

The high population density of muskoxen on Banks Island and a significant and prolonged warming trend are probably the key drivers for the high levels of parasitism in these animals. Ongoing research is examining the hypothesis that the clinical and sub-clinical disease associated with the abomasal parasitism may be an important regulating factor in this population. Other possible limiting and regulating factors, for example predation and habitat quality, do not appear to be important at this time. Predation by wolves is low (estimated at less than 5,000 animals/yr), and commercial and subsistence harvest remove approximately 1,000 animals per year (J.N., unpublished data). Further, habitat quality and standing biomass has remained constant through the population fluctuations of the 1990s (J.N., unpublished data). Abomasal parasitism in Svalbard reindeer, occurring at a much lower intensity than observed in these muskoxen, decreases fecundity and is considered an important regulating factor for Svalbard reindeer (Albon *et al.*, 2002). Similarly, *Trichostrongylus tenuis* is thought to have an important role in the regulation and stability of red grouse populations (Dobson and Hudson, 1992). Fur-

ther investigation of the role of abomasal parasitism, the impacts on forage intake (*e.g.*, see Gunn and Irvine, 2003) and the possible interactions with predation, climate, and habitat quality, in regulation or stability of the Banks Island muskox population is warranted.

Host-parasite systems as environmental indicators

Knowledge of pathogen biodiversity and associated disease is important not only for managing wildlife, but it also provides information about an ecosystem that may not otherwise be readily apparent. For example, the appearance of *P. stilesi* in muskoxen confirms that muskoxen and Dall's sheep have some degree of habitat overlap and indicates that the exchange of other pathogens between these two species is likely. This has obvious management implications with respect to translocation or natural range expansions of both species. Knowledge of distribution and abundance of parasites with complex life cycles also provides information about ecosystem continuity (Brooks and Hoberg, 2000). For example, the presence of *U. pallikuukensis* in an area confirms that a suitable gastropod intermediate host is also present and changes in parasite abundance may reflect changes in the gastropod intermediate host populations, which in turn may indicate otherwise undetected changes in their preferred mesic and wet sedge meadow habitats. Additionally, monitoring levels of *T. boreoarcticus* in muskoxen may indirectly provide information on muskox density, habitat use, and microclimatic conditions at the soil surface.

Baselines and monitoring

It is clear that for northern ecosystems we do not have adequate baseline knowledge for parasite diversity, distribution and, for most parasites, we know little about the life history, epizootiology, and effects on host populations. Our challenge now lies in establishing baselines, archives, and long term monitoring programs that will enable us to detect and respond to changes in the health or balance of these systems.

Recognition of emerging parasitic infections and diseases is dependent first on accurate identification of the parasites (Brooks and Hoberg, 2000). In the past, limitations in our ability to discriminate among morphologically similar species have led to errors in documenting host and geographic distribution. Increasingly, with the application of molecular techniques combined with careful morphological study, substantial genetic and subtle structural differences have become evident between apparently similar parasites in domestic and wild ruminants (*i.e.*, *T. boreoarcticus*) (Hoberg *et al.*, 1999, 2003; Divina *et al.*, 2000, 2002).

To predict and recognize impacts of climate and other change "Frequent and long-term sampling along transects to monitor the full longitudinal and altitudinal range of specific [vector] species, and their seasonal patterns . . ." (Kovats *et al.*, 2001, p. 1067) is necessary. Resources are insufficient to address all

hosts and parasites, so systems for study and monitoring, and sampling protocols, need to be strategically selected. Consideration needs to be given to the vulnerability of a species, population, or region to the health impacts of climate change; the importance of a species to ecosystem stability; how representative the host-parasite system is as an indicator of the overall health of the ecosystem; and feasibility (financial and logistic) of monitoring (e.g., see Brooks and Hoberg, 2000; Kovats *et al.*, 2001; Hoberg *et al.*, 2003). Monitoring can be approached using a variety of strategies including specific planned animal collections and cooperation with commercial or community harvests. Additionally, the education and training of youth and harvesters, with their subsequent participation as 'eyes on the land' for the early detection of change, is invaluable (A. Veitch, personal communication).

Predictive models

Predictive models, conceptual and mathematical, are important tools for understanding infection and disease emergence and epizootiology. Models may incorporate aspects of the life histories of the pathogens and hosts, and can be used to predict the role of a parasite in host population dynamics (e.g., see Ives and Murray, 1997), as well as the effects of climate change, translocation, changes in population density, and other disruptions. A simple model for predicting the development rates of *U. pallikuukensis* on the tundra provides an example of how models can expand our knowledge of the transmission dynamics in this host-parasite system (Kutz *et al.*, 2002). This model uses surface temperatures and parasite development parameters to predict larval development rates under different temperature conditions and may be used to predict years where outbreaks of disease associated with *U. pallikuukensis* would be expected. A similar approach to other parasites, for example *P. stilesi*, will enable us to predict whether temperature conditions are suitable for their establishment in other geographic regions or habitats. Such models facilitate and promote a pro-active approach to wildlife management aimed at predicting and mitigating the potential effects of emerging disease.

CONCLUSION

We anticipate that emerging infections and diseases in northern species will become more common as high latitude systems are further exploited, people and their domestic animals encroach on wildlife range, species expand their distributions, and as climate warming continues to drive change across a variety of habitats. Host and parasite communities are predicted to respond to warming and environmental change, but perhaps at differing rates. Impacts on wildlife and human health are inevitable, yet, at this point in time we lack the baseline knowledge and many of the tools to predict and detect these effects. An emphasis on education and awareness from the community to agency and government levels, a commitment to establishing baselines and strategic, long term monitoring programs,

and collaborative and interdisciplinary research is necessary to enable us to anticipate the occurrence and implications of infection and disease emergence in wildlife and people in the north.

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