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# Global warming is changing the dynamics of Arctic host–parasite systems

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Global climate change is altering the ecology of infectious agents and driving the emergence of disease in people, domestic animals, and wildlife. We present a novel, empirically based, predictive model for the impact of climate warming on development rates and availability of an important parasitic nematode of muskoxen in the Canadian Arctic, a region that is particularly vulnerable to climate change. Using this model, we show that warming in the Arctic may have already radically altered the transmission dynamics of this parasite, escalating infection pressure for muskoxen, and that this trend is expected to continue. This work establishes a foundation for understanding responses to climate change of other host–parasite systems, in the Arctic and globally.

**Keywords:** climate change; Arctic; Canada; parasitology; emerging disease

## 1. INTRODUCTION

### (a) *Arctic climate change and infectious diseases*

Recent anthropogenic climate change has altered physical and biological systems globally (McCarthy *et al.* 2001; Hassol 2004). Shifting patterns of abundance and distribution of pathogens, including metazoan and protozoan parasites, and the emergence of infectious disease in people, livestock and wildlife, are among the most important impacts of climate change (Epstein 1997; Daszak 2000; Kovats *et al.* 2001; McCarthy *et al.* 2001; Parmesan & Yohe 2003; Root *et al.* 2003). In the Arctic, where the effects of global climate change are already profoundly evident, dramatic alterations in host–parasite interactions are anticipated (Dobson *et al.* 2003; Hoberg *et al.* 2003; Hassol 2004; Kutz *et al.* 2004). Arctic species, including ungulates and their pathogens and the invertebrate vectors, have evolved under severe seasonal and environmental constraints (Strathdee & Bale 1998; Hoberg 2005), and the life history patterns of these species can be dramatically altered by even minor climatic perturbations (Graham *et al.* 1996). Thus, the Arctic serves as a sentinel, where studies to detect, understand and predict the responses of high latitude host–parasite systems to changing temperature can provide considerable insight into biotic implications of warming on a global scale. Empirical data necessary to evaluate the impacts of climate change on infectious diseases are, however, rare, and the few descriptive models available have focused on tropical or temperate ecosystems (Harvell *et al.* 2002).

### (b) *A model for the impacts of climate change on the ecology of arctic parasites*

To explore the impacts of climate change on host–parasite systems in the Arctic, we investigated the ecology of an important protostrongylid lung-dwelling nematode, *Umingmakstrongylus pallikuukensis*, in muskoxen from the Canadian Arctic (Kutz *et al.* 2001*a*, 2002). Prevalence of infection approaches 100% in the endemic region, and the parasite can cause respiratory compromise and predispose muskoxen to predation (Kutz *et al.* 2001*a*). Development from first-stage larvae (L1), shed in the faeces of the muskox, to third-stage larvae (L3), infective to the definitive host, occurs in a gastropod intermediate host. Infection follows ingestion of a gastropod containing L3, or L3 emerged from a gastropod (Kutz *et al.* 2001*a*). The slug *Deroceras laeve*, common in the region endemic for *U. pallikuukensis*, is an important intermediate host for this and other protostrongylids (Samuel *et al.* 1985; Kutz *et al.* 2001*b*).

Previously, we determined that rates of development of *U. pallikuukensis* from L1 to L3 in *D. laeve* on the arctic tundra can be predicted from a simple degree-day mathematical model (Kutz *et al.* 2002). This model incorporates hourly soil-surface temperatures, the threshold temperature (8.5 °C), the thermal constant (167 degree days (DD), the amount of heating above threshold required for development to L3 as determined in laboratory studies), and a maximum temperature set at 21 °C to account for microhabitat selection by slugs (Kutz *et al.* 2001*b*, 2002). In the present study, we apply this model to examine temporal and quantitative patterns of parasite development in the past, and in a future of climate warming. We assumed that the availability, survival and immunity of slugs, survival of L1 and L3, and all other climate parameters other than temperature remained constant. In this conservative model, these and other

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potentially relevant variables cannot be easily estimated in the absence of empirical data from this or other related host–parasite systems.

## 2. MATERIAL AND METHODS

### (a) *Historical patterns of larval development*

To estimate historical rates of larval development we used hourly air temperatures from the airport at Kugluktuk, Nunavut (67°50′N, 115°06′W; Environment Canada Meteorological Service) for the period 1978–2003 (hourly temperatures were not available for years prior to 1978). DD accumulated above the threshold of 8.5 °C were calculated as per Kutz *et al.* (2002) for each year from 1st May to 30th September. Hourly soil-surface temperatures, which are consistent predictors of development for *U. pallikuukensis* in slugs, are typically warmer than air temperatures in the early summer (up to 5 °C depending on year, month and time), but approximate air temperatures later in the summer (Kutz *et al.* 2002). Unfortunately, historical soil-surface temperatures were not available for this or any nearby site and, therefore, our predictions based on air temperatures may underestimate development rates in the early summer (for example, in 1998 from 10th June to 1st July, almost four times as many DD were accumulated based on surface (74DD) versus air (19DD) temperatures, but over the following three weeks only 1.2 times as many DD were accumulated at the surface (138DD) versus air (116DD)).

### (b) *Predicted effects of climate warming on patterns of larval availability*

(i) *Calculation of accumulated degree days for warming scenarios*

In the region where *U. pallikuukensis* is endemic, a climate warming scenario projects increases in mean temperature of $\geq 2$ °C by the 2020s, $\geq 4$ °C by the 2050s and $\geq 6$ °C (to a maximum of 8 °C) by the 2080s (Canadian Centre for Climate Modelling and Analysis Global Coupled Model 2, A21 Economic Regional Focus Simulation 1 http://www.cics.uvic.ca/scenarios/). We used the mean hourly air temperatures from 1978 to 2000 as a baseline and increased these hourly values by temperature increments of 1 °C to represent climate warming (note that although scenarios for warming indicate minimum temperatures will increase more than maximum temperatures, for the sake of simplicity this was not incorporated into our model). We then calculated the accumulated DD for each increase in temperature starting on 29th May. This date was used because this was the first day of the year on which DD were accumulated under the most extreme warming scenario of 8 °C.

(ii) *Calculation of numerical availability of L3 for warming scenarios*

We modelled L3 availability on a weekly basis throughout the summer under two different larval survival scenarios: (i) No L3 mortality—L3 were available in slugs or as emerged L3 and had 100% survival to October (note: emergence of L3 from slugs is a common phenomenon for this parasite and up to 100% of the larvae can emerge in a summer (Kutz *et al.* 2000)) and (ii) L3 mortality—L3 did not emerge and died when slugs died.

We assumed, for the purposes of this exercise, that cohorts of 10 slugs were infected on a weekly basis from 29th May to the end of September. Thus, cohort 1 was infected on 29th
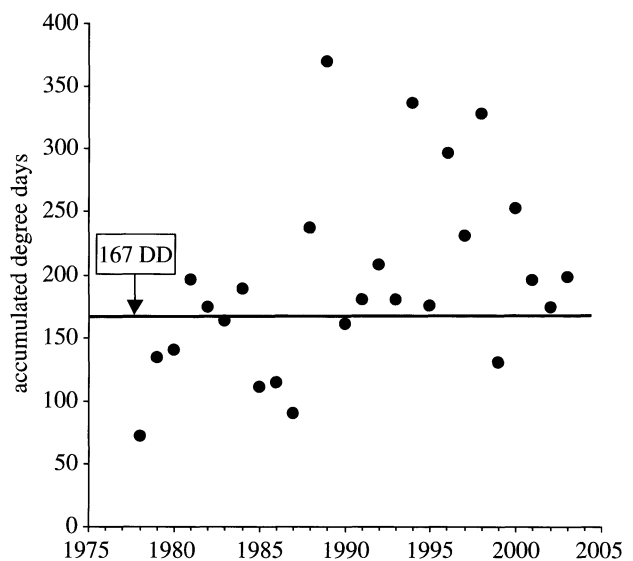
Figure 1. Annual accumulated degree days predicted near Kugluktuk, Nunavut for 1978–2003. Note that development to L3 (as indicated by accumulating at least 167DD) would be predicted in only 5 years from 1978 to 1990, but in 12 years from 1991 to 2003.

May and was not re-infected throughout the summer, cohort 2 was infected on 5th June and was not re-infected, and so forth. We also assumed that the infection dose and establishment rates among the different cohorts were the same. The weekly survival rates in our model were derived from a Cox regression of the average survival rates of infected slugs from Arctic field trials that took place from June through September in 1997 (Kutz *et al.* 2002). We used 13.6 as a constant for the number of L3/slug; this was based on the average number of L3/slug observed in experimentally infected slugs in these field trials (Kutz *et al.* 2002).

Under scenario (i) no L3 mortality, for each temperature increment we multiplied the slug survival rate for the date that the first L3 was available by 13.6 (L3/slug). The L3 present on that date were assumed to remain available until October even if slugs died, as the L3 would emerge and still be capable of completing the cycle. Under scenario (ii) L3 mortality, we assumed that L3 did not emerge from the slugs and were not available to muskoxen when slugs died. Therefore, calculations incorporated the weekly rates for slug survival (L3 availability in each cohort declined with time as slugs died). Under both scenarios, the L3 availability for a given date is the sum of L3 available from all cohorts on that date.

## 3. RESULTS

### (a) *Historical patterns of larval development*

Our model calculations for rates of parasite development from 1978 to 2003 indicate considerable inter-annual variability in the accumulated DD (figure 1). Only in some years were there sufficient DD (167) for development to L3 (a 1 year development cycle), and such years were more common from 1991 to 2003 (12 of 13), than from 1978 to 1990 (5 of 13; figure 1). When sufficient DD were accumulated in a single year for development to L3, the window for transmission of L3 from slugs ranged from 6 (1995) to 72 days (1996; table 1). In years when there were insufficient DD for development to L3, larvae would have had to over-winter in gastropods and

Table 1. Predicted availability of L3 near Kugluktuk, Nunavut from 1978 to 2003.

| year | date of first L3[a] | last date for slug infection[b] | last day for transmission by ingestion of infected slugs[c] | transmission period (days)[d] | degree days accumulated |
|---|---|---|---|---|---|
| 1978 | incomplete[e] | n/a[f] | 29-Sep | 0 | 71 |
| 1979 | incomplete | n/a | 27-Sep | 0 | 133 |
| 1980 | incomplete | n/a | 16-Sep | 0 | 140 |
| 1981 | 16-Aug | 10-Jul | 2-Oct | 47 | 196 |
| 1982 | 16-Aug | 23-Jun | 21-Sep | 36 | 174 |
| 1983 | incomplete | n/a | 3-Oct | 0 | 163 |
| 1984 | 17-Aug | 20-Jun | 28-Sep | 42 | 189 |
| 1985 | incomplete | n/a | 1-Oct | 0 | 111 |
| 1986 | incomplete | n/a | 28-Sep | 0 | 115 |
| 1987 | incomplete | n/a | 3-Oct | 0 | 90 |
| 1988 | 15-Aug | 8-Jul | 8-Oct | 54 | 237 |
| 1989 | 20-Jul | 25-Jul | 16-Sep | 58 | 369 |
| 1990 | incomplete | n/a | 28-Sep | 0 | 160 |
| 1991 | 16-Aug | 19-Jun | 21-Sep | 36 | 180 |
| 1992 | 11-Aug | 7-Jul | 18-Sep | 38 | 209 |
| 1993 | 19-Aug | 24-Jun | 23-Sep | 35 | 180 |
| 1994 | 20-Jul | 20-Jul | 25-Sep | 67 | 337 |
| 1995 | 21-Sep | 6-Jun | 27-Sep | 6 | 175 |
| 1996 | 16-Jul | 6-Jul | 26-Sep | 72 | 297 |
| 1997 | 4-Aug | 17-Jul | 30-Sep | 57 | 232 |
| 1998 | 26-Jul | 24-Jul | 5-Oct | 71 | 328 |
| 1999 | incomplete | n/a | 27-Sep | 0 | 130 |
| 2000 | 1-Aug | 18-Jul | 22-Sep | 52 | 253 |
| 2001 | 1-Sep | 13-Jul | 13-Oct | 42 | 195 |
| 2002 | 6-Sep | 9-Jun | 28-Sep | 22 | 173 |
| 2003 | 27-Aug | 5-Jul | 11-Oct | 45 | 198 |

[a] Based on infection of gastropods on 1st May.
[b] Last date that larvae infecting slugs could mature to L3 within that summer.
[c] Last date before 5 consecutive days with below freezing average daily temperatures.
[d] This denotes the transmission period for L3 in slugs and assumes that slugs become unavailable when temperatures go below freezing for 5 consecutive days; emerged L3 may still be transmitted beyond this period. (Last day for transmission − date of first L3.)
[e] Indicates incomplete development—larvae did not complete development to L3 within a single summer.
[f] L3 could not develop within a single summer, thus there is no last date for infection.

resume development to L3 the following year (a 2 year development cycle).

## (b) Predicted effects of climate warming on patterns of larval availability

Climate warming of as little as 1 °C above the 1978–2000 average shifted larval development from a 2 year cycle to a 1 year cycle (figure 2). Warming also expanded the period for transmission of L3 in slugs to muskoxen (defined as the time from when the first L3 became available in slugs to the last day before 5 consecutive days with average temperatures below 0 °C, when slugs are assumed to move deeper into the soil and begin hibernation) from 44 days (1 °C increase) to 105 days (8 °C increase; table 2). This is due to L3 becoming available 42 days earlier, and to a delay of 19 days in anticipated slug hibernation (table 2). Concomitantly, warming also allowed larval development to begin later in the summer and still be completed within the year (table 2). The accelerated development rates and expanded window for development and transmission also resulted in a considerable increase in numbers of infective L3 available to muskoxen in both scenario (i) no L3 mortality and scenario (ii) L3 mortality (figure 3a,b). Actual L3 availability is predicted to be within the range represented by the two scenarios in figure 3a,b.
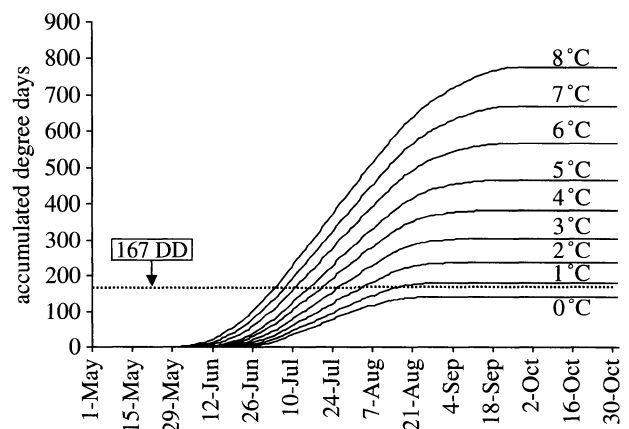


Figure 2. Predicted patterns of accumulated degree days with 0–8 °C increases above the 1978–2000 average, and assuming slugs are infected with L1 on 29th May. Note that as little as 1 °C increase results in accumulation of sufficient degree days for development to L3 in single summer.

## 4. DISCUSSION

Directional climate change has altered, and will continue to alter, distribution and phenology of a variety of taxa, and is predicted to have considerable impacts on the seasonal patterns of development and transmission of many pathogens in the Arctic and globally (Harvell et al.

Table 2. Predicted availability of L3 near Kugluktuk, Nunavut with climate warming from 1 to 8 °C.

| warming scenario (°C increase over 1978–2000 mean) | date for first L3[a] | last date for slug infection[b] | last day of transmission by slug ingestion[c] | transmission period[d] (days) | degree days accumulated |
|---|---|---|---|---|---|
| 0 | incomplete | n/a | n/a | n/a | 141 |
| 1 | 15-Aug | 30-Jun | 28-Sep | 44 | 181 |
| 2 | 03-Aug | 11-Jul | 29-Sep | 57 | 236 |
| 3 | 26-Jul | 20-Jul | 03-Oct | 69 | 305 |
| 4 | 20-Jul | 26-Jul | 11-Oct | 83 | 384 |
| 5 | 16-Jul | 02-Aug | 14-Oct | 90 | 466 |
| 6 | 11-Jul | 07-Aug | 15-Oct | 96 | 567 |
| 7 | 07-Jul | 12-Aug | 16-Oct | 101 | 670 |
| 8 | 04-Jul | 16-Aug | 17-Oct | 105 | 777 |

[a] Based on infection of gastropods on 29th May.
[b] Last date that larvae infecting slugs could mature to L3 within that summer.
[c] Last date before 5 consecutive days with below freezing temperatures.
[d] This denotes the transmission period for L3 in slugs and assumes that slugs become unavailable when temperatures go below freezing for 5 consecutive days; emerged L3 may still be transmitted beyond this period.

2002; Dobson et al. 2003; Parmesan & Yohe 2003; Kutz et al. 2004; Hoberg 2005). Our retrospective analysis for *U. pallikuukensis* suggests that, as a result of climate warming, L3 development has already shifted from a 2 year cycle to a predominantly 1 year cycle (figure 1). This nonlinear shift may have great ecological significance. For the 2 year cycles characteristic of 1978–1990, high over-winter mortality of slugs and developing larvae (Kutz et al. 2002) would have resulted in only a few L3 developing in the second year, and low-infection pressure for muskoxen. Unusually warm years during this period, such as 1988 and 1989, may have lead to a 'pulse' of L3 developing in a single summer, resulting in increased abundance of L3, a shift in temporal availability, and, possibly, disease outbreaks. Such a prediction is consistent with a linkage between unusually warm summer temperatures and periodic outbreaks of clinical disease for a related elaphostrongyline, *Elaphostrongylus rangiferi*, in reindeer in Finmark, Norway (Handeland & Slettbakk 1994). For the affected muskox population, a decline of 50% was observed from 1988 to 1994 (Fournier & Gunn 1998). Although this corresponded with the initial discovery of *U. pallikuukensis* in muskoxen, because of the remote nature of this population and the inherent costs and logistical difficulties associated with investigations in the Arctic, the role of the parasite in this decline was not determined.

From 1990 to 2003, the predicted pattern for larval development of *U. pallikuukensis* was one of multiple, consecutive, 1 year cycles. Based on our analyses of scenarios for climate warming, these 1 year cycles will be typical of the future (figure 2). These will extend the window of availability of L3 in slugs, augment numbers of L3 available (figure 3a,b), and could lead to increased intensity of infection in muskoxen, with adverse effects on their fecundity and survival. This is consistent with overall climate warming predictions for amplification of parasite populations through increased rates for development, reduction in generation times, and broadened seasonal windows for transmission (Hoberg et al. 2001).

The impacts of climate change on host–parasite interactions may differ depending on location within the parasite's 'climate envelope' (Sutherst 2001). For example, at the warmer southern and western extents of its current
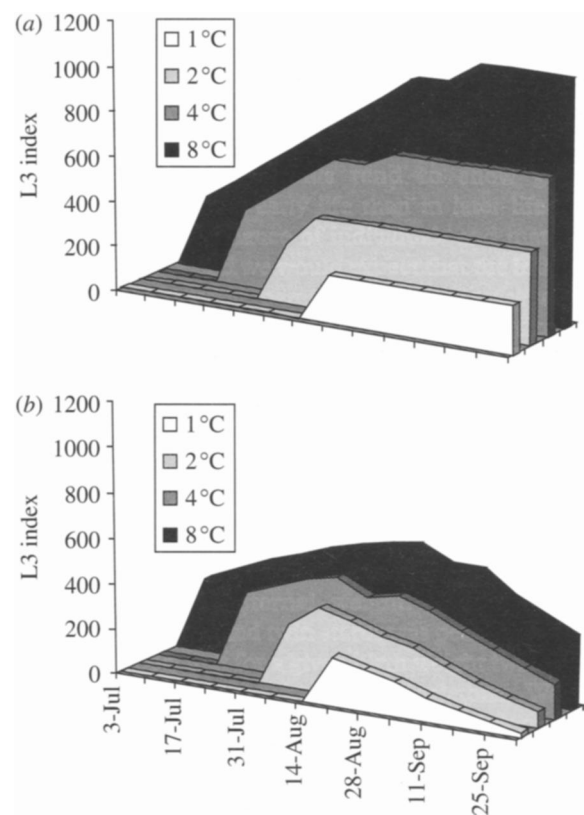


Figure 3. Predicted L3 availability (L3 index) in a single season under climate warming scenarios of 1, 2, 4 and 8 °C for assumptions (a) L3 are available in slugs or as emerged L3 and have 100% survival to October and (b) L3 do not emerge and die when slugs die.

range, *U. pallikuukensis* is well established, with a prevalence approaching 100%. Muskoxen in these areas of 'endemic stability' (Sutherst 2004) may tolerate moderately increased infection pressure resulting from warming. However, extremely high levels of L3 and an expanded temporal window of L3 availability, together with other stressors including habitat perturbation, interspecific competition, or severe weather events associated with climate change, may induce parasitic disease (Gulland 1992; Sutherst 2004). In contrast, at the northeastern edge of the range of *U. pallikuukensis*,

where cooler temperatures are currently a limiting factor, we might expect episodic range expansion (Kutz *et al.* 2002). In these cooler areas, we predict a pattern of primarily 2 year developmental cycles, with pulses of rapid larval development and accumulation associated with occasional warmer years, similar to the historical pattern (1978–1990). The resulting acute increase in infection pressure during warmer years may have significant implications for these muskox populations that have had little or no previous exposure (low-herd immunity), and may result in outbreaks of overt disease. Such disease outbreaks occurred in all age classes of caribou following the introduction of *E. rangiferi* to a naive population in Newfoundland (Ball *et al.* 2001).

Ecological disturbances associated with climate change may alter other biotic parameters that affect the epidemiology of *U. pallikuukensis*. For example, availability, survival and immunity of intermediate hosts, and survival of free-living larval stages are not incorporated into our model, but are important determinants of parasite persistence. *D. laeve*, an important intermediate host for *U. pallikuukensis*, has high phenotypic plasticity and survives in ecologically diverse habitats under a wide range of climatic conditions (Pilsbry 1948; Rollo & Shibata 1991). It will likely thrive in a changing climate, particularly in the north, where warmer and wetter conditions are anticipated (McCarthy *et al.* 2001). Importantly, larval stages in gastropods are buffered from the external environment because of microhabitat selection by these intermediate hosts, and consequently, survival and development rates of larvae are less likely to be impacted by climate variability and stochasticity (Saunders *et al.* 2002) than parasites with direct life cycles. Conversely, the free-living L1 and emerged L3 may be adversely affected by extreme temperatures, desiccation, ultraviolet radiation, and frequency of freeze–thaw cycles, all possible outcomes of climate change at high latitudes (Forrester & Senger 1963; Shostak & Samuel 1984; Hassol 2004). Climate-driven habitat perturbations are also predicted to influence habitat quantity and quality, nutrition, behaviour, immune function and patterns of geographic distribution and abundance of definitive hosts, sympatry with other ungulates, and the occurrence and emergence of an array of other parasites and pathogens (Hoberg *et al.* 2002, 2005; Hassol 2004). The final outcome for the health and persistence of muskox populations will depend on the interactions among these numerous climate-linked factors.

Our model has been validated by field studies on *P. odocoilei*, a phylogenetically distinct protostrongylid of Dall's sheep in a sub-arctic alpine habitat, and results indicate that possible effects of climate change in that system include parasite range expansion and amplification in endemic regions (Jenkins *et al.* in press). Our model is also directly applicable to other protostrongylid parasites of wild ungulates. For example, threshold temperatures and thermal constants have been determined for *E. rangiferi* and *Protostrongylus stilesi* (parasites of *Rangifer* and *Ovis*, respectively; Halvorsen & Skorping 1982; Samson & Holmes 1985) and could be incorporated into the model to develop testable hypotheses for current and future distribution and transmission patterns of these parasites. Application of the *U. pallikuukensis* model to these and other host–parasite systems will generate

insights into transmission patterns across a wide range of species, and will generate hypotheses exploring responses to climate change.

Climate change will alter biotic and abiotic conditions and dissolve ecological barriers, redrawing maps of current distribution of parasites and their hosts (Dobson *et al.* 2003; Hoberg 2005). The *U. pallikuukensis* model is a simple and conservative model that identifies and quantifies the effects of climate on critical life history stages of a nematode parasite, and explores responses of host–parasite assemblages to climate change. Such models, founded on empirical data, serve as powerful predictive frameworks for tracking of seasonal, annual and long-term changes in parasitic infections from local to global scales, and provide the foundation for developing more complex quantitative and comparative models for the epidemiology of pathogens in a changing climate.

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