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Invited Review

A walk on the tundra: Host–parasite interactions in an extreme environment

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ABSTRACT

Climate change is occurring very rapidly in the Arctic, and the processes that have taken millions of years to evolve in this very extreme environment are now changing on timescales as short as decades. These changes are dramatic, subtle and non-linear. In this article, we discuss the evolving insights into host–parasite interactions for wild ungulate species, specifically, muskoxen and caribou, in the North American Arctic. These interactions occur in an environment that is characterized by extremes in temperature, high seasonality, and low host species abundance and diversity. We believe that lessons learned in this system can guide wildlife management and conservation throughout the Arctic, and can also be generalized to more broadly understand host–parasite interactions elsewhere. We specifically examine the impacts of climate change on host–parasite interactions and focus on: (I) the direct temperature effects on parasites; (II) the importance of considering the intricacies of host and parasite ecology for anticipating climate change impacts; and (III) the effect of shifting ecological barriers and corridors. Insights gained from studying the history and ecology of host–parasite systems in the Arctic will be central to understanding the role that climate change is playing in these more complex systems.

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1. Introduction

The Arctic is a vast, sparsely populated region that has captured the imagination and interest of explorers and scientists for generations. It is an environment of extremes and has been considered by many an inhospitable landscape and the last frontier to be explored. Despite the 'hardships' imposed by the environment, interconnected communities of wildlife, people, and pathogens have thrived in this dynamically changing ecosystem for millennia (Pitulko et al., 2004; Goebel et al., 2008; Stanford and Bradley, 2012). The current accelerating changes to the arctic climate are, however, unprecedented historically and are having profound impacts on the daily lives of the Arctic's indigenous peoples and the structure and function of arctic ecosystems. The recently released IPCC report highlights the dramatic abiotic impacts that climate warming is having across the Arctic: shrinking sea-ice and ice caps, melting permafrost, erosion, and an increased frequency in extreme weather events (IPCC, 2013). Consequences of these changes include shifting plant and animal communities and changing food webs (Post et al., 2013), altered animal behaviour and phenology (Post and Forchhammer, 2008; Post et al., 2009), increased heat stress (Ytrehus et al., 2008; van Beest and Milner, 2013), and changes in pathogen diversity and patterns of exposure for people and animals (Kutz et al., 2005, 2009; Burek et al., 2008; Hoberg et al., 2008, 2013).

Wildlife is an integral part of the lives of northerners, and recent changes in the health and behaviour of populations of fishes, birds, and mammals are negatively influencing the physical, social, cultural and economic health of many human communities. For example, recent widespread and steep declines of barren-ground caribou populations have led to hunting quotas being imposed on indigenous peoples in many regions of northern Canada. As caribou hunting is considered an aboriginal right, these new regulations have resulted in dissent and political backlash (Gunn et al., 2009; Festa-Bianchet et al., 2011; Nesbitt and Adamczewski, 2013). Die-offs of muskoxen and population declines in western parts of the Arctic Archipelago over the last 5 years have also led to considerable concern about the future of subsistence and commercial hunting of these animals in the Canadian Arctic. Several recent mortality events in muskoxen have been attributed to the zoonotic bacterium, *Erysipelothrix rhusiopathiae* (promedmail.org 2012; Canadian Cooperative Wildlife Health Centre www.ccwhc.ca), exacerbating concerns among people about the safety of these 'country foods'. More generally, with increasing awareness of emerging infectious diseases, northern residents are understandably expressing concern about the safety of foods that have historically been the cornerstone of their diets (Kutz, 2007; Brook et al., 2009; Meakin and Kurvits, 2009; Curry, 2012).

Demonstrating the biotic and abiotic linkages between climate-related drivers and disease emergence is complex (e.g., Brooks and Hoberg, 2006, 2007; Lafferty, 2009; Rohr et al., 2011; Brooks and Hoberg, 2013), but arctic ecosystems provide an intimate arena for understanding the impacts of climate change on host–parasite interactions (Kutz et al., 2005, 2009; Hoberg et al., 2008, 2013; Brooks and Hoberg, 2013). When compared to temperate and tropical regions, arctic ecosystems are characterized by relatively low species diversity (e.g., Callaghan et al., 2004a,b; Meltofte et al., 2013). Currently, anthropogenic disturbances, such as landscape change and introduced species, are also minimal. This allows scientists to track the impacts of climate change on a variety of species and ecological processes with a minimum of confounding factors.

There has been considerable progress in understanding host–parasite interactions in the Arctic over the last two decades. This has been fueled by a critical mass of scientists, wildlife managers, and concerned northern residents. The resulting integration of local knowledge, field biology, classical and advanced DNA-based diagnostic techniques in parasitology, new approaches in ecological modeling, and explorations of historical processes, have generated substantial baselines for parasite biodiversity and new ecological knowledge on host–parasite interactions, particularly for ungulates (e.g., Hoberg et al., 2008, 2013; Kutz et al., 2012; Verocai et al., 2012; Molnár et al., 2013a,b). Increasingly, the ecological, physiological and evolutionary mechanisms that determine the host–parasite interface are being examined and interpreted within historical biogeographic and phylogeographic frameworks (Waltari et al., 2007; Hoberg and Brooks, 2008, 2010; Galbreath and Hoberg, 2012; Hoberg et al., 2012). This synergy of ecology and history ultimately provides deeper insights into the historical and ongoing patterns and processes of faunal assembly that can help us anticipate and predict future impacts of climate change in the north.

In this article, we discuss the evolving insights into host–parasite interactions for wild ungulate species, specifically, muskoxen and caribou, in the North American Arctic. These interactions occur in an environment that is characterized by extremes in temperature, high seasonality, and low host species diversity and abundance. We believe that lessons learned in this system can guide wildlife management and conservation throughout the Arctic, and can also be generalized to provide insights into host–parasite interactions globally. We specifically examine the impacts of climate change on host–parasite interactions and focus on: (I) 'Its Hotter than you Think', the direct temperature effects on parasites; (II) 'Evasions and Invasions' the importance of considering the intricacies of host and parasite ecology for anticipating climate change impacts; and (III) 'The Times They are a-Changin', the effect of shifting ecological barriers and corridors (Fig 1).

2. The hosts

An appreciation of the biogeographic history of the hosts is central to our current and future understanding of parasite diversity and host–parasite interactions. Caribou (*Rangifer tarandus* sspp.) and muskoxen (*Ovibos moschatus* sspp.) are the dominant and most abundant ungulates across the Arctic. The diversification, population structure, and current geographic ranges for these ungulates and their parasites was largely determined by historical processes of episodic expansion and isolation in response to climate variation and alternating glacial-interglacial stages during the last 3 million years. In the late Pliocene (3 Ma; million years before present) and through the Pleistocene (2.6 Ma to 10 Ka; 1000 years before present), ungulate populations in Eurasia and North America were intermittently linked across the Bering Land Bridge (Hoberg et al., 2012); within North America, populations and species were episodically isolated in refugial zones of varying extent and duration, north (Beringia) and south of the continental Laurentide–Cordillera glaciers (e.g., Shafer et al., 2010) (Fig. 2). During the late Pleistocene, muskoxen and caribou were important species in a highly diverse and largely sympatric assemblage of ungulates in Beringia (e.g., Guthrie, 1982). The relative sympatry, diversity and vagility of these ungulates, and their patterns of geographic colonization during episodic periods of climate change in the late

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