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Invited Review

Exploiting parallels between livestock and wildlife: Predicting the impact of climate change on gastrointestinal nematodes in ruminants

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ABSTRACT

Global change, including climate, policy, land use and other associated environmental changes, is likely to have a major impact on parasitic disease in wildlife, altering the spatio-temporal patterns of transmission, with wide-ranging implications for wildlife, domestic animals, humans and ecosystem health. Predicting the potential impact of climate change on parasites infecting wildlife will become increasingly important in the management of species of conservation concern and control of disease at the wildlife–livestock and wildlife–human interface, but is confounded by incomplete knowledge of host–parasite interactions, logistical difficulties, small sample sizes and limited opportunities to manipulate the system. By exploiting parallels between livestock and wildlife, existing theoretical frameworks and research on livestock and their gastrointestinal nematodes can be adapted to wildlife systems. Similarities in the gastrointestinal nematodes and the life-histories of wild and domestic ruminants, coupled with a detailed knowledge of the ecology and life-cycle of the parasites, render the ruminant-GIN host–parasite system particularly amenable to a cross-disciplinary approach.
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1. Introduction

Parasites are ubiquitous in wildlife and livestock and are an important component of ecological communities (Dobson and Hudson, 1986). Far from being "benign symbionts living in equilibrium with their hosts", parasites have a profound effect on host survival, fecundity and behaviour (Hudson and Dobson, 1995). There is mounting theoretical and empirical evidence that parasites play an important role in influencing host populations through impacts on survival and reproduction (Holmes, 1995; Hudson et al., 1998; Tompkins and Begon, 1999; Watson, 2013) and trophic equilibria (Grenfell, 1992). Parasitic infection and disease in wildlife and at the livestock–wildlife interface, therefore, has the potential to impede conservation efforts by restricting the ranges of host species (Dobson and Hudson, 1986) and threatening the persistence of species of conservation concern (Laurenson et al., 1998; Morgan et al., 2005; Page, 2013).

The Intergovernmental Panel on Climate Change (IPCC) concluded that "Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, sea level has risen, and the concentrations of greenhouse gases have increased" (IPCC, 2013). Global average surface temperatures increased by 0.85 °C between 1880 and 2012. However, the pattern of global warming is not spatially homogeneous. Analysis of observed surface temperatures estimates historic increases of up to 2.5 °C in parts of Canada, Brazil and Russia between 1901 and 2012 (IPCC, 2013). Changes in observed precipitation are more complex. Analysis of observed precipitation between 1951 and 2010 estimates historic decreases of up to 100 mm/year/decade in regions such as West Africa and contrasting increases of up to 100 mm/year/decade in regions such as Northern Europe (IPCC, 2013). Further temperature increases and changes in precipitation are predicted. Average surface temperatures could rise by more than 9 °C in the Arctic by 2081–2100 compared with the baseline period of 1986–2005 (IPCC, 2013).

Since many parasites have free-living stages and ectothermic intermediate hosts, their development and survival, and therefore, transmission dynamics, are inextricably linked with the environment (e.g. O'Connor et al., 2006). As a result, environmental perturbations caused by climate and associated anthropogenic and environmental change could have a profound impact on parasite phenology, host–parasite dynamics and host population dynamics (Kutz et al., 2005; van Dijk et al., 2010; Hoar, 2012; Altizer et al., 2013; Molnár et al., 2013). Declining numbers in a population of moose (*Alces alces andersoni*) in northwest Minnesota coincided with an increase in temperatures and lengthening of the annual growing season between 1960 and 2001. Pathogens, climate change and nutritionally deficient habitat were implicated as causative factors in the decline in numbers of moose (Murray et al., 2006). The authors concluded that this moose population is currently not viable and they emphasised the need to understand parasite dynamics in altered environments to predict and potentially mitigate negative changes in host–pathogen population dynamics.

Less is known about the effect of globalisation, policy and indirect effects of climate change on disease dynamics. It is possible to draw on observations of responses to recent environmental change and variability (e.g. McNeil et al., 2005; Moyes et al., 2011) to predict the impact of future changes. However, predicting the direction and magnitude of global change, and subsequently the impact on disease dynamics, is inherently difficult where drivers of change such as climate, anthropogenic pressures on land use, and policy interact. For example in the European Union agricultural land use, yield and on-farm provision for conservation and the environment are heavily influenced by the payment of subsidies under the Common Agricultural Policy and environmental constraints (Olesen and Bindi, 2002; Renwick et al., 2013). As a result, predictions are often centered on the impacts of climate change. A thorough understanding of the drivers of global change, host and parasite biology, ecology and distribution, and host–parasite dynamics, will be key to generating useful predictions of the likely impact of global change on wildlife and their parasite fauna.

2. Predicting the impact of climate change on parasite and host

The impact of climate change on parasites, hosts and parasitic disease is likely to be complex, particularly in multiple host/vector systems, at the edge of species' ranges, where species exhibit variability in key life-history traits that may act as a target for adaptation to climate change, and where there are non-linear interactions between climate and host/parasite response (van Dijk and Morgan, 2010; Rohr et al., 2011; Altizer et al., 2013). For example, species distribution models suggest that although increasing temperatures will result in the earlier spring emergence and later onset of diapause in blowfly (*Lucilia sericata*) in Great Britain, there may be a trade-off between increased development rates and temperature- and moisture-dependent mortality. This led to a decrease in the predicted probability of blowfly strike in sheep in regions where hot, dry summers are expected, resulting in two distinct periods of risk (Rose and Wall, 2011). A split transmission season under warming conditions is also predicted for *Ostertagia gruehneri,* an abomasal nematode of caribou, due to interactions between development and mortality rates at higher temperatures (Molnár et al., 2013). Predictions for climate change impacts on parasites are further complicated by concomitant changes such as: drug resistance in parasites of both livestock and wildlife (Chintoan-Uta et al., 2014); land use and habitat loss (Lafferty, 2009; Pascual and Bouma, 2009; Festa-Bianchet et al., 2011); host behaviour (Moyes et al., 2011), and; policy.

2.1. Modelling parasite and host dynamics under climate change scenarios

Empirical models such as species distribution models can be useful in identifying potential drivers of change (Pickles et al., 2013), particularly where detailed data and knowledge of the system are unavailable. For example, models can be constructed using distal (indirect) variables, such as precipitation, where proximal (direct) variables, such as soil moisture, are unavailable (Franklin, 2009). However, extrapolating beyond observed conditions to predict the impact of climate change relies on a number of assumptions, not least that correlations between variables remain constant under future conditions (Rose and Wall, 2011). Moreover, the response of host and parasite to change is often non-linear or threshold-dependent (Rohr et al., 2011). For example, there are species-specific optimal temperature and moisture requirements for the development and survival of the free-living stages of common gastrointestinal nematodes of ruminants. Above and below these optima the development success decreases (Rossanigo and Gruner, 1995).

Lafferty (2009) notes that factors other than climate, such as land use, play an important role in determining disease dynamics, and *"seasonality in disease does not necessarily indicate an effect of climate on disease"*. This is an especially pertinent point when considering the impact of climate change on parasites and infection dynamics, a system that exists and interacts on multiple scales and in multiple dimensions. In these systems, apparent correlations between climate, host and parasite life-history do not equate to causation (e.g. the seasonal arrest rate of nematode larvae and the peri-parturient rise in faecal egg counts in ewes; Lafferty,

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