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Climate change and infectious disease: helminthological challenges to farmed ruminants in temperate regions

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In the UK, recent mean temperatures have consistently increased by between 1°C and 4°C compared to the 30-year monthly averages. Furthermore, all available predictive models for the UK indicate that the climate is likely to change further and feature more extreme weather events and a trend towards wetter, milder winters and hotter, drier summers. These changes will alter the prevalence of endemic diseases spatially and/or temporally and impact on animal health and welfare. Most notable among these endemic parasites are the helminths, which have been shown to be very strongly influenced by both the short-term weather and climate through effects on their free-living larval stages on pasture. In this review, we examine recent trends in prevalence and epidemiology of key helminth species and consider whether these could be climate-related. We identify likely effects of temperature and rainfall on the free-living stages and some key parasite traits likely to determine parasite abundance under changed climatic conditions. We find clear evidence that climate change, especially elevated temperature, has already changed the overall abundance, seasonality and spatial spread of endemic helminths in the UK. We explore some confounders and alternative explanations for the observed patterns. Finally, we explore the implications of these findings for policy makers and the livestock industry and make some recommendations for future research priorities.

Keywords: endemic disease, parasite, ecology, adaptation, seasonality

Implications

A combination of passive surveillance, clinical observations and anecdotal evidence suggests that the epidemiology of the major helminth diseases of the UK livestock is changing. A detailed analysis of *post mortem* returns over the past 30 years reveals the most likely contributing factor to be climate change, in particular, changes in temperature and rainfall. This is manifested through altered overwinter survival of the free-living stages of these parasites and, where applicable, their intermediate hosts. Any change in the incidence, geographical distribution and seasonality of these important endemic parasites has obvious implications for disease control, animal productivity and welfare. We need improved diagnosis and early detection of livestock parasitic disease, coupled with increased awareness and preparedness to deal changing disease patterns.

Introduction

Climate change is arguably the greatest long-term challenge facing the human race today (IPCC, 2007). Increasing global temperatures will bring changes in weather patterns and rising sea levels, while altered rainfall patterns are predicted to increase the incidence of both drought and flooding events (Alcamo *et al.*, 2007). Among the most important effects of these changes will be the emergence and spread of infectious diseases, including those of animals (Khasnis and Nettleman, 2005; Vallat, 2008). In the UK, recent outbreaks of 'exotic' diseases, such as foot-and-mouth disease, avian influenza and bluetongue, have given stark indications of the potential impact of emerging infectious diseases of animals on national economies, animal welfare and human health.

The field of climate change and its effects on the dynamics of pathogens of veterinary importance has lagged well behind the climate change-focused research in other disciplines, to the extent that, in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), no animal pathogens were listed in an extensive overview by Rosenzweig *et al.* (2007). Published work has focused on the emergence of new diseases and the spread of disease vectors (e.g. Wittmann and Baylis, 2000; Colebrook and Wall, 2004; Randolph, 2004; Purse *et al.*,

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2005; Gould *et al*., 2006), but effects on endemic disease have hardly been addressed by robust science. Veterinarians have been urged to wake up to this fact in the veterinary press (Anon, 2007c).

This paper focuses on challenges ahead in the study of the effects of climate change on established infectious diseases, using parasitic worms affecting ruminants in the UK as an example. Parasitic helminths belonging to the classes Nematoda (roundworms) and Trematoda (flatworms) are ubiquitous on livestock farms. In temperate regions, arguably every single-farmed ruminant will be infected by one or more helminth species at some stage in its life. If the level of infection is high, this may lead to clinical disease and death of the animal. Exact numbers of deaths from these infections can only be guessed at as there is currently no active surveillance of helminth disease in the UK. Based on submissions to the main UK network of veterinary investigation laboratories, and published mortality rates, a conservative estimate would be thousands of sheep and hundreds of cattle per year. The total cost of helminth-induced subacute and chronic disease, presenting itself as anorexia, weight loss, diarrhoea, impaired reproduction, abortion and reduced milk yield and its prophylactic treatment eclipses mortality-related costs to the farming industry (Brunsdon, 1988; Ward, 2006; Louie *et al*., 2007). In the UK sheep industry, costs associated with gastrointestinal nematode infection related to reduced lamb growth rates plus treatment and prevention measures alone was estimated to be £84 million per annum (Nieuwhof and Bishop, 2005). Losses due to lungworm disease in 100-cow dairy herds have been calculated at £15 000 to 20 000 per outbreak (Woolley, 1997). Liver fluke infection affects farm income especially in terms of poor productivity, reduced milk yield and livers trimmed or condemned at slaughter. In the UK, costs of chronic infection in cattle alone have been estimated at £40 million per year (Bennett and IJpelaar, 2005).

Any effects of climatic change on helminths may be compounded by the rapid development and spread of anthelmintic resistance in parasites of sheep and, more recently, cattle (reviewed by Wolstenholme *et al*., 2004). The inexorable rise of parasite populations resistant to the few anthelmintic drugs available for their control poses a direct, ever increasing, threat to the sustainability of intensive livestock industries, including that of the UK (Waller, 1986; Jackson and Coop, 2000; Kaplan, 2004). Indeed, the recent emergence of multidrug resistant nematodes has been the final straw in driving several sheep enterprises out of business (Sargison *et al*., 2005). As we will discuss below, climate change may speed up the spread of anthelmintic resistance through parasite populations.

Climate change has the potential to increase the transmission intensity of highly pathogenic, ubiquitous parasites to levels uncontrollable by current management strategies. However, currently, research in the field has hardly progressed beyond describing perceived changes and speculation on causality. There is an urgent need to identify and quantify potential changes in parasitic challenge to animals to provide veterinarians and farmers with informed advice on the best practice for parasite control in food-producing animals in the coming decades. The study of the effects of climate change on parasites of livestock may also contribute very significantly to the wider study of climatic effects on disease transmission, and predicted overall growth or decline of a large number of other species.

Climate change may have short-term effects on parasites, which in turn will lead to parasite adaptation (Poulin, 2007; Skelly *et al*., 2007). At the same time, it may have effects on hosts and, in the case of farmed animals, on host management. These layers of complexity make it hard to predict the longer-term future accurately. One of the conclusions of the UK Government Foresight Project 2006 on infectious diseases was that 'we must understand how climate affects infectious diseases today before we can predict climate change's impacts of the future' (Brownlie *et al*., 2006). A pioneer of modelling the effects of global warming climate on infectious diseases, Professor D. J. Rogers, recently expressed his concern that, as future predictions cannot be disproved until the time comes, the work on models of responses of infectious diseases to climate change may 'reverse the trend of scientific enquiry' (Anon, 2007e). In light of the uncertainty presented by the differences in opinion on climate change scenarios between climatologists alone, this uncertainty seems a real danger indeed. There is an urgent need for the identification of methods to be deployed to build hypotheses that can be tested in the present. In order to predict the future, we will need realistic models based on the present and the past.

The bridging of gaps in our understanding of the effects of temperature and rainfall on the free-living stages of the parasites under study, therefore, forms an integral part of the study of future climate change. This review will start by exploring the likely changes in the abundance of these free-living stages. It will then focus on likely ways in which the parasites will adapt. The immediate climate-driven effects, and the parasite evolution that inevitably follows, will alter host–parasite interactions. Last, we will turn our attention towards ways to combat increased exposure of farmed ruminants to parasitic helminths, and attempt to guide future research priorities.

Helminth parasites

The major economically important helminth parasites affecting livestock in the UK are the gastrointestinal nematodes (roundworms) and the flukes (flatworms). The major nematode species infecting sheep are *Teladorsagia circumcincta, Nematodirus battus, Haemonchus contortus* and *Trichostrongylus* spp., and, in cattle, *Ostertagia ostertagi, Cooperia oncophora* and the lungworm, *Dictyocaulus viviparus*. Fluke, most notably the liver fluke, *Fasciola hepatica*, infects both sheep and cattle. The respective helminth groups have different transmission patterns, ecological requirements and dispersal strategies. However, they all possess free-living larval

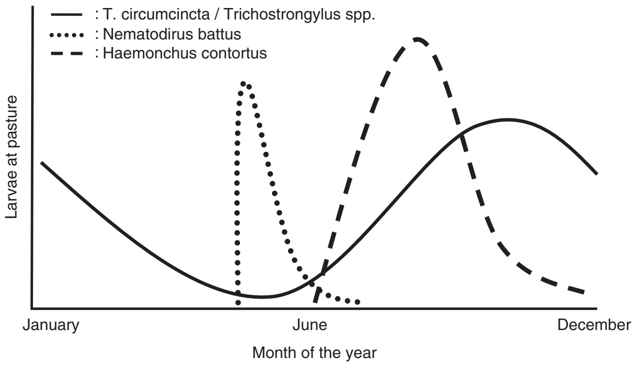


Figure 1 Schematic view of the traditionally observed seasonality of parasitic nematodes affecting sheep. *T. circumcincta* and *Trichostrongylus* spp. may overwinter at pasture and numbers of larvae decline in spring. During the lambing season, hypobiotic larvae overwintering in ewes mature and start to produce eggs; lambs increase pasture contamination levels over several worm generations. Although the epidemiology of *F. hepatica* is very different, the pattern of abundance of infectious metacercariae is similar to that of *T. circumcincta/Trich.* spp. larvae. However, *Fasciola* peak abundance is normally timed somewhat later in autumn. *N. battus* overwinters as infective larvae in the egg. In spring, a mass hatch of eggs is followed by a rapid decline of the larval population. The *H. contortus* population entirely overwinters in the adult host. Worms mature during the lambing season; Female adult worms are highly fecund and pasture contamination builds up rapidly. The relatively high temperature threshold for development of *H. contortus* and the inhibition of developing larvae in hosts in autumn result in a rapid fall in the number of larvae at pasture in autumn. As a result of climate change, these windows for parasite transmission are likely to shift and/or expand.

stages, which are directly affected by climatic factors, most notably temperature and rainfall. As a result, they display a seasonal pattern of infection in grazing livestock (e.g. Figure 1). Their seasonal and spatial prevalence can also be influenced indirectly through their invertebrate intermediate hosts (where appropriate) and the presence and movements of their definitive vertebrate hosts.

The eggs of the helminths involved must develop into infective stages, and migrate onto herbage, at pasture before transmission can occur. Assuming that hosts are present, the success rate of this non-parasitic phase is affected predominantly by climatic factors (as reviewed by O'Connor *et al.*, 2006) and, therefore, these parasites are likely to be highly sensitive to climate change. Increases in mean daily temperature as small as 1°C are thought to have significant effects on entire ecosystems (Fischlin *et al.*, 2007) and significantly increase development rates of nematodes (Kutz *et al.*, 2005). Global warming, therefore, has the potential to increase parasite-related losses in livestock dramatically.

Simultaneously, climatic changes influence a parasite's environment. Its longevity may be affected indirectly through alterations in the behaviour and abundance of predators and natural enemies of nematodes (Thieltges *et al.*, 2008). Patterns of herbage growth influence the probability of ingestion by a host (Morgan *et al.*, 2007). Changes in the rate of herbage growth can in turn influence the protein, energy, macroelement and trace element nutrition of ruminant hosts that graze on it, thus affecting the immune status of the host (Greer, 2008). In addition, stocking densities and the length of the grazing period are likely to be adapted to herbage availability (Menzel and Fabian, 1999). Such factors may well compound the direct effects of climate change on helminth parasites and make future parasite epidemiology very hard to predict. Until relatively recently, there was a seasonal pattern of parasite infection in livestock in the UK such that control strategies could follow a 'blueprint' based on predictable appearance of certain species at certain times of the grazing season. This is best exemplified by the seasonality of helminth parasites in sheep (Figure 1). This pattern of infection may well change as a result of climate change.

Parasites may thrive in a wide variety of climatic environments

Hypobiosis

Hypobiosis, or arrested larval development, is a particular feature of many nematode species and refers to the temporary, often seasonal, cessation in development at a precise point in the life cycle (Michel, 1974; Michel *et al.*, 1976). Arrest of larvae at early stages of in-host development ensures enhanced survival of parasite populations during adverse climatic conditions. A subsequent synchronised mass maturation of arrested larvae may be triggered and cause severe pathology and clinical disease. It has been predicted that, with warming, there may be selection against parasites entering an arrested stage and an increase in reproductive rate as a consequence of reduced density-dependent constraints (Hudson *et al.*, 2006).

High biotic potential

Successful transmission of these parasites is aided by synchronisation of the release of eggs or larvae onto pasture with weather-related suitability for development and survival of these stages plus the presence of the appropriate host species. The chances of at least a small part of the population successfully completing the life cycle is greatly enhanced by the high biotic potential of these parasites. For example, the nematode *H. contortus* is highly fecund, a single adult female can shed between 5000 and 10 000 eggs per day (Gordon, 1948; Levine and Todd, 1975). Infections normally comprise at least several hundred adults, so, once introduced, *H. contortus* can establish and rapidly increase levels of pasture contamination. Similarly, an adult liver fluke can shed 20 000 to 50 000 eggs per day, that is, approximately one egg every few seconds (Walker *et al.*, 2006). Fluke numbers are further multiplied by asexual replication within the snail intermediate host, such that each invading miracidium can give rise to upwards of 1000 infective cercariae. These parasites have adopted high-output strategies, which, at pasture, are normally combined with high loss rates of free-living stages. Such a strategy may increase the probability of establishment in new, suboptimal, environments. If climatic changes optimise the development of parasitic larvae, dramatic increases in the size of populations of these parasites may be expected and these are likely to lead to acute disease, and deaths in affected ruminants.

Genetic adaptation

Population genetic studies of several sheep and cattle nematodes, including *Ostertagia*, *Haemonchus* and *Teladorsagia,* reveal that these parasites are highly genetically diverse and, typically, have extremely large effective population sizes (Blouin *et al*., 1995). Furthermore, some liver fluke isolates have been shown to be triploid, which provides further options for genetic recombination and increased diversity (Fletcher *et al*., 2004). These parasites, therefore, appear to have the potential for high rates of true genetic change (microevolution). On top of this, the genotype of certain parasites has been shown to code for more than one phenotype (a trait known as phenotypic plasticity; Stearns, 1992; Poulin, 2007). Different expressions of the same genotype may be triggered by environmental conditions (Jarrett, 2008; van Dijk and Morgan, 2009) and, if certain phenotypes fare better when these conditions change, the proportion of the population expressing this phenotype is likely to increase. The proportion of larvae entering hypobiosis following certain climatic, or immunological, stimuli may be an example of phenotypic plasticity. This trait opens the door to very rapid adaptation to climate change (Davis *et al*., 2005; Visser, 2008).

Predicted climatic effects on parasite ecology

It is well established that the development and death rates of free-living stages are mainly driven by temperature and rainfall. Recent work has shown that UV light is highly detrimental to the longevity of infective nematode larvae and is likely to be a third important driver of larval abundance at pasture (van Dijk *et al*., 2009). With respect to climate change, UV levels are likely to remain relatively constant. However, if increases in temperature allow for transmission of parasites outside of windows of high UV activity, increases in parasite abundance may be higher than predicted from temperature alone (van Dijk *et al*., 2009). Therefore, UV intensity may have to be considered in predictions for the future and its effects further quantified at pasture. However, in this review, we will focus on temperature and rainfall.

Temperature

At temperatures below the maximum development threshold (the temperature above which parasites are adversely affected and development ceases), the development rates of eggs and early larval stages of helminths increase with increasing temperatures (Claxton *et al*., 1999; Hsu and Levine, 1977; Rose and Small, 1984). The economically important parasites have upper development thresholds approximating 30°C (Jehan and Gupta, 1974; Pandey *et al*., 1989; van Dijk and Morgan, 2009). The mean daily temperature, in temperate regions, rarely exceeds 25°C (Jenkins *et al*., 2007) and the effect of global warming on the free-living stages would appear to be easily predictable: these parasites would be expected to benefit from increased development rates, and perhaps a widening of the windows during which transmission is possible. The first papers on the effects of warming on parasite populations indeed suggest that small increases in temperature may lead to significant increases in developmental success of parasite populations (Kutz *et al*., 2005; Poulin, 2006). However, whether this will result in population growth is not easy to predict:

(1) Increases in mean temperatures may have contrasting effects on different stages in the life cycle. Alongside development rates of eggs and immature larvae, their death rates, and those of the infective larvae, also increase. Especially during the summer, the population, in terms of numbers of infective stages at pasture per time unit, will only increase in size if benefits to larval development outstrip a shorter life span. The sensitivity of larvae to increased temperatures differs between species (e.g. Boag and Thomas, 1985), and the degree to which species benefit from it may vary significantly. During the winter, the effects of warming on the survival of larvae, which have developed during the autumn, may again vary between different species. Larvae of all economically important nematodes survive for many months when kept at a temperature range of -2 to $+4$°C (Boag and Thomas, 1985; Troell *et al*., 2005; van Dijk and Morgan, 2008). *N. battus*, *T. circumcincta* and *Trichostrongylus* spp. appear to tolerate much lower temperatures very well (Andersen *et al*., 1966; Andersen and Levine, 1968; Ash and Atkinson, 1986; Pandey *et al*., 1993), whereas *H. contortus* appears sensitive to temperature drops below -3°C (Rose, 1963; Todd *et al*., 1976; Philip, 1983). Overwinter survival rates of the latter species may, therefore, be enhanced if fewer ‘extreme’ frost events take place. Similarly, increased, intramolluscan, overwinter survival of preinfective stages is likely for *F. hepatica* (Luzon-Pena *et al*., 1994).

 As all infective nematode larvae are surrounded by a cuticle, they cannot eat and have a finite energy reserve. If the temperature falls below the threshold for larval activity, approximating 5°C to 10°C (Wharton, 1981), these larvae curl up and remain immotile, thereby limiting the use of their energy reserves. The implications of this are that, if temperature rises above this threshold, larvae lose energy and ultimately die faster. Temperature increases in winter are likely to lead to increased larval activity, at times when few susceptible hosts are present at pasture, and therefore, decrease overwinter survival rates and the relative importance of the survival of these larvae in the year-to-year on-farm persistence of these parasites.

(2) Developmental temperature thresholds differ between species. The minimum temperature at which development

takes place varies between 4 and 5°C for *T. circumcincta* and *Trichostrongylus* spp. (Wang, 1967; Beveridge *et al*., 1989; Pandey *et al*., 1989) to 10°C to 12°C for *H. contortus*, *N. battus* and *F. hepatica* (Rowcliffe and Ollerenshaw, 1960; Gibson and Everett, 1976; van Dijk and Morgan, 2008). Obviously, global warming may only significantly extend transmission windows if the temperature increases above this threshold. For *T. circumcincta*, for example, with a development threshold close to average winter temperatures in temperate regions, developmental windows may significantly increase into the winter months, whereas for *H. contortus,* development during the coldest months may not be possible for many years to come. Development thresholds are likely to be strong determinants of parasite epidemiology and over-winter survival strategies in particular (van Dijk, 2008). To what extent they distinguish the strategies of parasites at pasture may be co-determined by the rate at which temperatures rise and fall in spring and autumn – if temperatures increase and fall very rapidly, then predicted differences in developmental windows of opportunity between species may be nullified.

(3) At above-development threshold temperatures, the change in the proportion of egg populations being able to develop as a result of temperature increases varies between species. For arctic-adapted species like *N. battus* and *T. circumcincta* (Hoberg *et al*., 1999; Hoberg, 2005), a large proportion of the population is able to develop at the lower threshold for development (Pandey *et al*., 1989; Rossanigo and Gruner, 1995; van Dijk and Morgan, 2008 and 2009). Although the larval development rates of these parasites increase with increasing temperatures, the increase in the proportion of the egg population being able to benefit from these increases is relatively small. Also, at temperatures over 25°C, the proportion of eggs being able to develop actually declines rapidly (Rossanigo and Gruner, 1995; van Dijk and Morgan, 2008). For tropic-adapted species like *H. contortus* (Hoberg *et al*., 2004), and *Trichostrongylus* spp., the proportion of eggs developing increases rapidly up to the optimum development temperature, which is higher than for the arctic-adapted species (Jehan and Gupta, 1974; Coyne and Smith, 1992; Rossanigo and Gruner, 1995). Therefore, at above development threshold temperatures, these species are likely to benefit more from temperature increases than arctic-adapted species.

(4) Some species, apart from temperature requirements for egg development, also have specific temperature requirements for the hatching of their eggs. The eggs of *N. battus* are thought to hatch when a cold spell (temperatures encountered during the winter) is followed by a temperature rise over 10°C in spring (Christie, 1962; Ash and Atkinson, 1986). Recent work has shown that the hatching of *N. battus* eggs is also bound by an upper temperature threshold of approximately 17°C (van Dijk and Morgan, 2008 and 2009). Therefore, alterations in spring temperatures may prevent the eggs of this parasite from hatching.

(5) Warming rates differ between months of the year and also between regions within the UK. Actual responses of different species of parasites to global warming may, therefore, differ considerably from predictions based on mean annual increases in temperature. Different species may benefit to different degrees in different regions.

(6) The life cycles of trematodes (e.g. *F. hepatica, Dicrocoelium dendriticum* and *Paramphistomum* spp.) involve intermediate hosts (Abrous *et al*., 1997 and 2000). Increases in temperature associated with climate change can have a significant effect not only on *Galba* spp. snail development, but also on the rate of development of the free-living stages of *F. hepatica* within the snail. Once infected, the rate of emergence of infective cercariae from snails has been shown to increase with increasing temperatures (Poulin, 2006). However, the snails have their own temperature thresholds for (breeding) activity, and development (Claxton *et al*., 1999; Hodasi, 1976). Temperature-driven increased abundance of the free-living stages infecting snails may not amount to an increased force of infection for the final host if the snail population does not benefit from climate change in a similar fashion (Mangal *et al*., 2008). Moreover, higher trematode burdens per snail may increase their mortality rates (Rondelaud *et al*., 2002). It has also been suggested that the size of individual snails may be more important than the total number of snails available for infection (Ollerenshaw, 1959; Yoder and Coggins, 1998). This would suggest that an influence of climate change on the availability of preferred food sources for the snail may also have an indirect effect on the parasite population. Indeed, Rondelaud *et al*. (2002) showed that cercarial production rates of snails vary with their food sources.

Moisture

As a result of climate change, periods of drought, followed by a limited number of days with heavy rainfall, have been predicted to become more frequent (Hennessy *et al*., 1997; Tapiador *et al*., 2007). Several studies have reported a positive correlation between rainfall and the emergence of trichostrongyloid larvae on herbage or the increase of worm burdens in tracer animals (e.g. Williams and Bilkovich, 1973; Bryan and Kerr, 1989; Stromberg, 1997). Such associations are most dramatic in semi-arid regions, where absence of rain may bring parasite transmission to a halt during the driest months and sharp peaks of larval emergence can be seen after periods of rainfall (Chiejina and Fakae, 1989; Onyali *et al*., 1990; Agyei, 1997; Sissay *et al*., 2007). Moisture is also prerequisite for both *Galba* spp. snails and the free-living miracidial and cercarial stages of *F. hepatica*, and the prevalence of fasciolosis is greatest following wet seasons (Andrews, 1999). However, even during dry seasons, suitable microhabitats probably exist on most UK farms for the maintenance of *F. hepatica* and consequent disease in certain cohorts of ruminant livestock (Skuce *et al*., 2008).

Development of nematodes

The development of eggs into infective *Trichostrongylus* spp. and *H. contortus,* larvae takes place in dung, which is passed with a certain moisture reserve. Development of these larvae has been shown to cease only during summers of 2 to 3 months drought accompanied by relative humidities as low as 20% and maximum mean monthly temperatures approximating 32°C (Onyali *et al*., 1990; Garcia Romero *et al*., 1997). On warm spring and summer days, such nematodes can reach the L3 stage even in dung, which becomes very desiccated before development is completed (Chiejina and Fakae, 1989).

The eggs of *N. battus*, and of the trematode *F. hepatica*, develop in the soil. Soil particles are normally surrounded by a layer of water, which is retained by forces of capillarity, osmotic pressure and gravity (Parkin, 1975). Studying the eggs of *N. battus*, Parkin (1975) showed that this parasite is able to take up water at osmotic pressures reflecting soil saturations between full water capacity and wilting point. Only eggs incubated in molar solutions appear not to be able to develop beyond the second larval stage while those incubated in salt solutions of strengths between 10^{-4} and 0.1 M manage to develop just as well as aqueous controls (Parkin, 1976). In temperate regions, the availability of water is, therefore, unlikely to be a crucial limiting factor in the developmental phase of these parasites.

Migration of nematodes

Infective larvae of most pathogenic nematodes develop in dung and then have to migrate out to pasture. *Ostertagia, Haemonchus* and *Cooperia* spp. proved not to be able to escape from cattle dung once it had become desiccated (Williams and Bilkovich, 1973; Chiejina and Fakae, 1989; Agyei, 1997). On dry, warm days, cattle faeces rapidly form a crust on the pat surface and it appears this crust, although it may protect them from further desiccation in the development stage, cannot be penetrated by L3. In the tropics, the sudden migration of these larvae, made possible by the arrival of the rainy season, may result in very sharp and dangerous peaks of larval emergence (Fakae and Chiejina, 1988; Chiejina and Fakae, 1989; Agyei, 1997). In temperate regions, it was also documented that drought-breaking rains may suddenly increase larval density on herbage 10-fold (Bryan and Kerr, 1989). Cattle faeces can clearly function as a reservoir of larvae during drought. Sheep pellets may trap larvae in a similar fashion (van Dijk, 2008). When heavy showers or even sustained periods of light rainfall follow a few weeks of drought, larval availability may suddenly reach dangerous levels. However, prolonged periods of drought may reduce the numbers of live larvae in the faecal depot quite rapidly (van Dijk, 2008). Also, in temperate regions, dew may be sufficient to allow for constant migration of larvae out of dung.

Several pasture-based studies (Skinner and Todd, 1980; Krecek *et al*., 1990; Niven *et al*., 2002) have suggested that a film of moisture is needed for the migration of larvae onto herbage, and this has become the established view among veterinary parasitologists. If this is indeed the case, larval migration is only possible either just after rains or when dew is found on grass leaves (Langrova *et al*., 2003). Studies by Callinan and Westcott (1986) suggested that relative humidity, and not necessarily free water, is the main driver behind larval migration. Extensive studies by Crofton (1948) and Rees (1950) suggested that gradients in relative humidity and temperature experienced by the larvae determined their migratory behaviour. Crofton (1948) proposed that larvae, above a certain temperature threshold, move continuously and randomly. However, when larvae move on a gradient of higher to lower relative humidities, they may stop and turn back. Such gradient-steered behaviour has been demonstrated for the free-living nematode *Caenorhabditis elegans* (Yamada and Oshima, 2003). Recent work proposed that UV light may also trigger larval movement away from damaging levels to more shaded areas of the lower grass stem (van Dijk *et al*., 2009). The theory of random, yet gradient-steered, movement explains why studies normally retrieve 90% of recovered larvae from the lower (cooler and more humid) 2.5 cm of the grass stems (Crofton, 1948; Rees, 1950; Silangwa and Todd, 1964; Callinan and Westcott, 1986) and also why studies retrieve a consistently low percentage of approximately 2% to 3% of larvae off herbage, a percentage which does not increase any further after the initial 24-h migration of larvae (Crofton, 1948; Rees, 1950; Silangwa and Todd, 1964; Callinan and Westcott, 1986; Langrova *et al*., 2003). Free water may not be needed for the migration of nematode larvae onto herbage and the migration of larvae is, indeed, likely to be a random process (van Dijk, 2008).

Trematodes

With regards to trematodes, adequate moisture supply has been shown to be essential for most stages in their life cycle: the survival of the eggs of both flukes and snails, the infection of snails by miracidia, the shedding of cercariae and the survival of encysted metacercariae (Kendall and McCullough, 1951; Ollerenshaw, 1959; Smith and Wilson, 1980). Below certain levels of soil moisture, parasite development is severely limited by the aestivation of snails (Kendall, 1949). Mathematical models of the ecology of parasites with pond-dwelling snails have ignored the influence of rainfall (Mangal *et al*., 2008). However, *Lymnaea* snails do not live inside water bodies but around their edges (Kendall, 1949; Ollerenshaw, 1959) and, therefore, models of *F. hepatica* will quite likely have to explicitly include a measure representing the soil moisture status. Defining the parameter that best describes soil moisture status, and quantifying its relation with the development and survival of both the parasite and the snail, poses a real challenge to furthering our understanding of the epidemiology of this parasite. Traditional models, attempting to forecast the risk of acute fasciolosis in autumn/winter, that have attempted to relate climatic conditions to disease incidence in sheep, incorporated total rainfall, transpiration and the number of rainy days (>1 mm rain; Ollerenshaw and Rowlands, 1959; Ross, 1970), but the effects of these parameters were not analysed in statistical models.

The likely effects of changing temperature and rainfall patterns can be summarised as follows. Although increases in mean temperature are likely to increase the development rates of the free-living stages, concurrent effects on death rates and effects on other stages of the life cycle make it hard to make a general prediction for overall population growth of parasites. Given the differences in temperature thresholds for development and hatching, and larval death rates, between species, it is likely that some species will benefit overall while others will not. Different species may benefit at different times of the year. Some species, most likely the arctic-adapted species, may only benefit short term, with a new plateau, or even collapse, of the population as temperature increases further. Meanwhile, in temperate regions, populations of especially tropically adapted species may continue to grow with further temperature increases leading to species shifts. Emergence patterns of larvae, which have developed in desiccated dung, may be altered by changes in rain patterns, but it is not clear to what extent. In contrast to the relative independence of nematodes on rainfall, soil moisture is thought to be an essential factor for all stages in the life cycle of *F. hepatica*. However, the influence of moisture parameters on fluke abundance has not been quantified.

The study of the behaviour of certain species in different geographical locations, representing different climatic environments, and the geographical origin of species, may yield important information on their future behaviour. Changes in parasite epidemiology may have to be studied at either a regional, or local scale. It will be difficult to assess the overall effect of multiple climate change-induced processes working on parasite populations simultaneously in any other way than through mathematical modelling. It will be a stern challenge to incorporate realistic climatic scenarios and climate stochasticity in these models, and extensive collaborations with climatologists are likely to be required.

Evidence for recent changes

In recent years, repeated suggestions of important changes in the epidemiology of helminths have been reported in the UK. First, reports suggesting an increased incidence of infection at pasture have surfaced. An increased incidence of parasitic gastroenteritis (e.g. Anon, 2004, 2005a and 2006a) has been signalled by the veterinary surveillance network. The incidence of fasciolosis (e.g. Anon, 2007d; Pritchard *et al*., 2005) and dictyocaulosis (David, 1997; van Dijk, 2004) appears to have increased significantly over the same period of time. At the same time, in recent years, different ages and species of animals have been affected by clinical disease. Pathogenic nematodes have traditionally caused disease in immunologically naive young animals, but, increasingly, adult animals also appear to be affected (van Dijk, 2004; van Dijk and Morgan, 2006; Sargison *et al*., 2007). Acute fasciolosis, associated with sudden death, is normally only witnessed in sheep, but was recently also described in calves (Anon, 2007b) and adult pigs (Anon, 2006b). Traditionally, rumen flukes (*Paramphistomum* spp.) were thought to be ubiquitous in the UK, yet rarely found in cattle grazing in the British Isles. Recently, diagnosing the presence of these parasites has become a routine event in veterinary surveillance laboratories in England, Wales and Ireland (Anon, 2008; Foster *et al*., 2008; Murphy *et al*., 2008).

Second, changes in the traditional seasonality of parasite abundance and disease have been described. Expansion of the transmission windows into the autumn of nematodes like *T. circumcincta* and *Trichostrongylus* spp. has been described (Anon, 2005b and 2007a). Concurrently, in Scotland, many cases of heavy infestations of lambs with *T. circumcincta* have been diagnosed in spring. Historically, as overwinter survival rates of larvae are considered to be too low, this had rarely been observed (Connan, 1986). Teladorsagiosis had, as a result of the periparturient relaxation of immunity in ewes in spring and subsequent autoinfection over several worm generations in lambs, normally been witnessed from late into the summer onwards (Sargison *et al*., 2002).

Third, within the UK, some helminth parasites appear to have expanded their transmission range spatially. The highly pathogenic, blood-feeding, nematode *H. contortus* was traditionally associated with the warmer south, whereas in Scotland, only the occasional outbreak related to the recent introduction of newly bought-in animals was diagnosed. Increasingly, evidence is mounting that the parasite is successfully completing its life cycle in Scotland and extending its geographical distribution (e.g. Anon, 2006c; Sargison *et al*., 2007). *F. hepatica* was, traditionally, mainly an inhabitant of the wetter western parts of the UK. However, subacute fasciolosis is increasingly diagnosed in the eastern parts of the UK, notably in East Anglia and eastern Scotland (Pritchard *et al*., 2005; Sargison *et al*., 2007).

Many of the above-described observed patterns were confirmed in a robust analysis of long-term surveillance data. van Dijk *et al*. (2008) analysed data on three different classes of gastrointestinal nematodes-affecting sheep. Over the past 5 to 10 years, the authors detected highly significant increases in GB annual diagnostic rates of *H. contortus*, *N. battus*, *T. circumcincta* and *Trichostrongylus* spp., approximately 4 to 5 times that of the levels experienced in the previous 20 to 25 years (see Figure 2) and coinciding with significant increases in mean temperature. For all species, there were signs that, in warmer environments, parasite transmission opportunities extended further into the autumn. In contrast to patterns described for Scotland above, for species such as *T. circumcincta* and *Trichostrongylus* spp., overwintering at pasture as larvae, significant decreases in

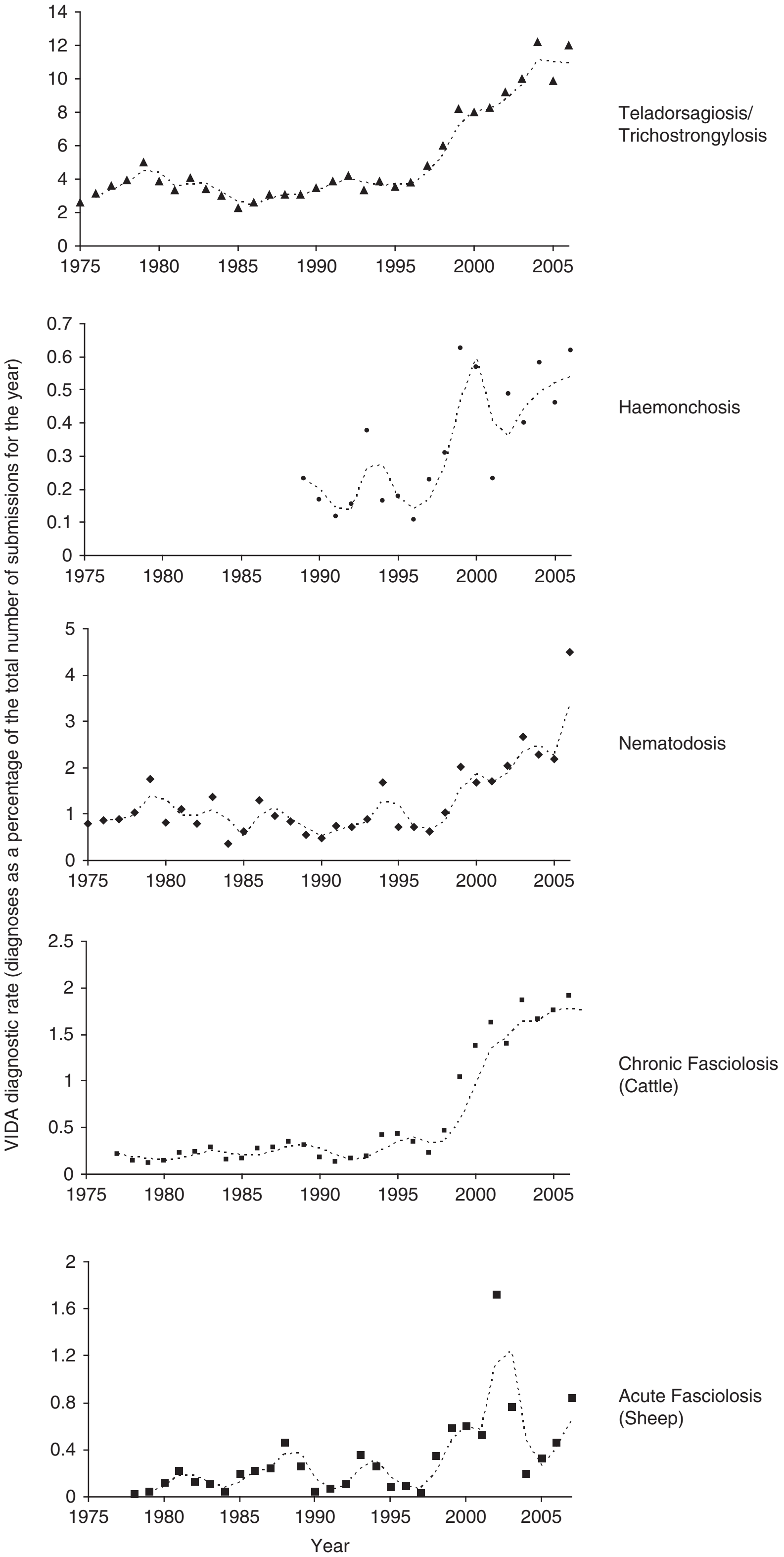
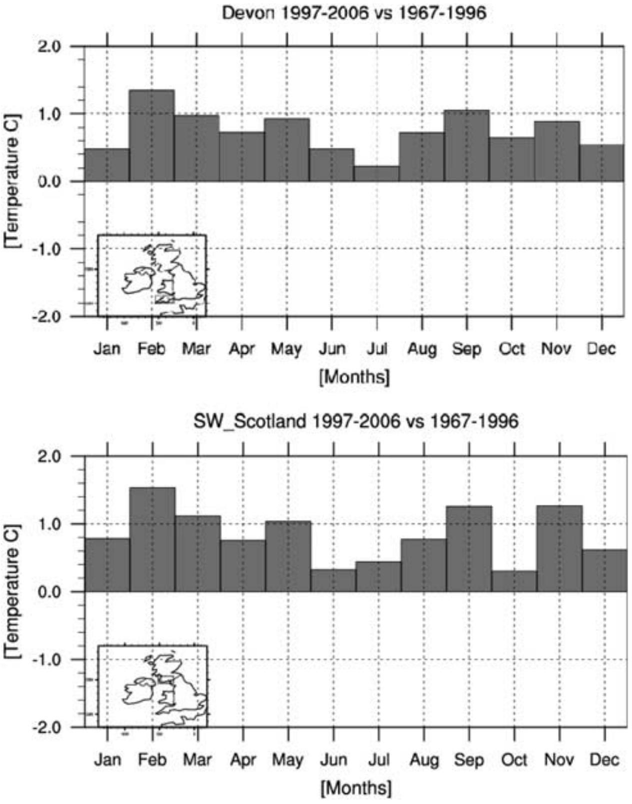


Figure 2 GB long-term trends in Veterinary Investigation Diagnosis Analysis (VIDA) recorded diagnostic rates of disease in sheep and cattle resulting from infections with helminth parasites. Trend lines drawn by exponential smoothing. Disease incidence, in all classes, shows a highly significant increase (Spearman's rho $\geqslant$0.450, $P \leqslant 0.005$) apparently starting in the late 1990s. Data sourced at VLA Weybridge.

observed spring disease frequency were observed. Most likely, this highlights that species in different regions, or even different localities within a region, may be affected by climate change in different ways (see Figure 3). Climate-related regional differences in grazing management may also have an important part to play.


Devon 1997-2006 vs 1967-1996

SW_Scotland 1997-2006 vs 1967-1996

Figure 3 Mean monthly mean temperature 1997 to 2006 as an anomaly of the previous 30 years, in two livestock-dense areas in the UK (Southwest Scotland and Devon). Warming not only occurs at different rates during different months of the year, there are also differences between regions within the UK. Overall the southwest of Scotland appears to be warming at a slightly faster rate. Such mean monthly differences may appear small yet represent a significant difference in degree-days (Hsu and Levine, 1977) available for development.

Regional differences in parasite epidemiology, a shift in the relative importance of the autumn months and an overall UK decrease in the abundance of infective larvae in spring can all be explained by above-mentioned predicted effects of global warming on the free-living stages of these parasites. The observed temporal shifts in parasite abundance may indicate that the benefits of increased development rates outstrip the disadvantages of increased death rates during some times of the year, but not in others. However, especially for *Haemonchus* and *Trichostongylus* spp., the parasite population would also be predicted to benefit from increased developmental opportunities in spring and early summer. It is very likely that this illustrates the simple fact that the abundance of parasites, apart from climatic factors, strongly depends on their opportunity for interaction with hosts, which will be further discussed below.

Confounding factors

A number of factors other than climate change may influence patterns of helminth parasitism in the UK livestock. Confounders may include the following:

Anthelmintic resistance

Recent surveys show that anthelmintic resistance is now widespread in large parts of the UK, affecting up to 80% of lowland sheep farms (Bartley *et al*., 2003), and numerous cases of multidrug resistance have been identified (Sargison *et al*., 2007). There are also reports of emerging resistance to triclabendazole, the drug of choice to treat fluke infections, in the west of Scotland (Mitchell *et al*., 1998; Brennan *et al*., 2007). However, as anthelmintic resistance has not been described in *N. battus*, it cannot explain the rise in the diagnostic rate of nematodirosis. Anthelmintic resistance alone can also not account for observed changes in temporal and spatial patterns of disease abundance in Great Britain. For example, for *H. contortus* and *N. battus*, significant increases in parasite abundance have been identified for the colder northern parts of GB, but not for the warmer southern parts (van Dijk *et al*., 2008). Anthelmintic resistance is likely to confound many of the observed changes but, currently, the rate of increase of the presence of resistant worm populations on farms cannot be quantified. Moreover, conversely, effects of anthelmintic resistance on disease rates may be confounded by climate change. Predicted changes to the UK weather are likely to lead to both longer grazing seasons and extended parasite transmission seasons which will, in turn, require increased anthelmintic treatment frequency thus compounding the problem. Climate change may also alter the proportion of the parasite population outside of the host, not exposed to the drug, at the time of anthelmintic treatment (the population *in refugia*; Martin *et al*., 1981; Sissay *et al*., 2006). For example, summer droughts may decrease the relative size of the pasture population of nematodes (Papadopoulos *et al*., 2001), thereby increasing the rate of build up of anthelmintic resistance at this time of the year.

Parasite evolution

As stated previously, helminth parasites typically have enormous biotic potential and are inherently genetically diverse. This provides them with the ability to adapt rapidly to changes in their environment (Gasnier *et al*., 2000). Important drivers for parasite evolution, apart from a changing climatic environment, include changing host–parasite interaction patterns, density dependence and competition between parasites (Poulin, 2007). Indirectly, on a farm, all of these (e.g. changes in grazing patterns, lambing season and the seasonal succession of worm species) are likely to be driven by the weather and, therefore, parasite evolution is unlikely to be a true confounder.

Farm management practices

Changes in the EU subsidy support and low-economic returns from livestock farming have generally resulted in reduced manpower and increasing flock sizes. Intuitively, this might be expected to make parasite control logistically more difficult to achieve or of lower priority. However, van Dijk *et al*. (2008), analysing census data, did not find indications that these factors have led to an intensification of sheep farming in the UK.

Motivation to submit samples
van Dijk *et al*. (2008) did not find evidence that submission rates to veterinary laboratories are correlated with farmers' income. Increased awareness of anthelmintic resistance may have increased the number of samples submitted for testing of effectiveness of treatments but, in the Veterinary Investigation Diagnosis Analysis database, such submissions are recorded under a separate category.

Animal movements
Parasitic pathogens may be introduced to new environments or onto new premises this way. For example, *H. contortus,* originally only endemic in the southern parts of England, appears to have been introduced to Scotland through animal movement. Robinson and Christley (2006) reported a slight upward trend in cattle movements in recent years. To our knowledge, analyses describing recent trends in the UK sheep movements are not available. It is unlikely that an increase in animal movements would result in upward trends for all species at approximately the same time.

After consideration of confounders, climate change is likely to be a driver behind the trends described above. However, the proportion of increase in diagnoses ascribed to anthelmintic resistance can currently not be estimated.

Changing host–parasite interaction

Apart from changes in the way parasites may utilise the host for overwinter survival (as discussed below), alterations in the seasonality of worm species are likely to lead to changes in the frequency and intensity of host contact and within-host encounter rates of different species of parasites. Predictions of future parasite epidemiology will, therefore, have to be co-shaped by host immunity and co-infection of hosts.

Host immunity
Lower-level, trickle-type, nematode infections are often tolerated by hosts, whereas mass invasions of the same parasites may invoke strong immune responses and an expulsion of all established worms (Behnke *et al*., 1992; Rothwell, 1989). Given these dose-dependent responses of hosts, climate-driven higher infections levels may not necessarily present the optimum strategy for population growth of parasites (e.g. Eriksen *et al*., 1992; Boes *et al*., 1998). Working with a natural host–parasite system, Hudson *et al*. (2006) even proposed that host immune systems may mitigate climate-driven effects on free-living stages altogether. However, the observed changes described above strongly suggest that this may not be the case for intensively farmed livestock.

Lower survival rates of larvae at pasture during warmer winters (Kao *et al*., 2000; van Dijk *et al*., 2008) are likely to lead to lower levels of infections, and immunity, in young animals in spring followed by a more rapid and prolonged build-up of infective larvae later in the grazing season. As a result, animals may be older when first encountering higher levels of infection and the effect of this on parasite populations is not clear. Similarly, little work has been carried out on the contribution of infections of older, immune, animals to the total on-farm population of parasites. Therefore, it is not known what role higher levels of infections of these animals in autumn would play in on-farm parasite epidemiology. However, it is likely that, in warmer autumns, higher numbers of ingested larvae will eventually hypobiose in these animals, leading to an increase in intensity of pasture contamination by adult animals in the following year. The uncertainty surrounding the effects of higher levels of infections of immune animals in autumn is compounded by evidence that the immune response of hosts is also influenced by seasonality and may wane during the autumn (Altizer *et al*., 2006; Cornell *et al*., 2008).

Co-infection
As a result of changes in seasonality, the transmission windows of two worm species traditionally overlapping may be separated. However, predicted expanding transmission windows for all species involved make an increase in the overlap of these windows a more likely prospect. If one parasite species limits the energy available to a host to mount an effective immune response (Medley, 2002) to another species, 'mutualism' might be observed between these species. Co-infections may also lead to an increased virulence of individual species (Alizon and van Baalen, 2008). However, if humoral and non-humoral immune responses against two species are very similar, the response to one species may also limit the establishment of the other (Lello *et al*., 2004). Recent work has suggested that, in the long-term, antigenically similar parasites cannot co-exist in one host (Alizon and van Baalen, 2008). Furthermore, one species may affect the other negatively by altering the physiological status of the intestine, for example, the pH (Mapes and Coop, 1973), or through competition for the same intestinal surface (Keymer, 1982; Boag *et al*., 2001).

T. circumcincta live in the abomasum of sheep, whereas *T. colubriformis* is an inhabitant of the small intestine. Under laboratory conditions, a dose-dependent synergistic effect has been described for concurrent infections with these species (Dobson *et al*., 1992; Steel *et al*., 1982; Sykes *et al*., 1988). When sheep were infected with high doses of both worms, their adult worm burdens and weight loss exceeded those expected from single species infections. Such positive effects of one worm species on the establishment rate of another have also been described for naturally infected, non-domesticated, animals (Lello *et al*., 2004). However, Jackson *et al*. (1992) reported a negative interaction between *T. circumcincta* and *T. vitrinus,* like *T. colubriformis*, an inhabitant of the small intestine. Similarly, Mapes and Coop (1973) showed how the abomasal parasite, *H. contortus,* suppressed the establishment of *N. battus* in the small intestine. At pasture, in groups of naturally infected lambs, the opposite was observed (van Dijk, J., unpublished data): high *H. contortus* egg outputs by lambs were heavily suppressed during the mass invasion of these lambs with *N. battus* larvae, but resumed once the lambs had managed to remove the resulting established *N. battus* worm burden. Negative interactions were also established between two abomasal parasites, *T. circumcincta* and *H. contortus* (Dobson and Barnes, 1995). It appears that the effects of co-infection of hosts cannot be easily predicted in terms of their location in the intestinal tract (crowding). Poorly understood physiological perturbations caused by one species may disrupt the other (Mapes and Coop, 1973; Dobson and Barnes, 1995). In single-species infections, it was shown that immune responses are necessary for density dependence (Paterson and Viney, 2002). This is likely to also be the case for multispecies infections. Thus, immune reactions against one, two or multiple species within one host may be depending on the density of the individual species (Conwill-Jenkins and Phillipson, 1971; Behnke *et al.*, 1992; Medley, 2002). An immune response may be targeted towards one species but be directed towards a different species, if the number of worms exceeds a certain threshold. For worms affecting livestock, such threshold levels are known neither for single nor for multispecies infections.

Parasite adaptation

Changes in overwinter survival rates of larvae at pasture and an extension of windows of opportunity for transmission are likely to drive adaptations of overwintering strategies of parasites. Alterations in the seasonality of species, leading to increased competition between species within the host, may select for worms developing a strategy to avoid co-infection. For *N. battus*, the hatching of eggs may become increasingly difficult in the future and the parasite is likely to have to explore alternative mechanisms for hatching (van Dijk and Morgan, 2008 and 2009). As temperature thresholds for development and hatching of larvae are strong determinants of the epidemiology of all helminths, it is likely that adaptations of these temperature thresholds would represent effective ways to influence the timing of appearance at pasture. Crofton (1965) and Crofton *et al.* (1965) showed that adaptation of developmental thresholds of *H. contortus* may indeed occur in the field. However, it was estimated that the observed divergence had occurred over hundreds of worm generations. Recent evidence indeed suggests that adaptations of temperature thresholds are very slow to occur (Troell *et al.*, 2005; van Dijk and Morgan, 2008 and 2009).

An alternative means to alter patterns of emergence at pasture include adaptations to the process of hypobiosis. This trait appears highly adaptable to local climate, as demonstrated by its absence in areas where development and transmission are secured all-year-round (El-Azazy, 1990; Waruiru *et al.*, 2001). Local environmental cues driving the hypobiotic process include temperature (Jacobs and Rose, 1990; Fernandez *et al.*, 1999), photoperiod (Langrova and Janskova, 2004; Lutzelschwab *et al.*, 2005), and drought (Giangaspero *et al.*, 1992; Ndamukong and Ngone, 1996). Interestingly, Langrova and Janskova (2004) suggested that the proportion of larvae arresting may also depend on the effects of these environmental cues on the hosts. Gaba and Gourbiere (2008) showed that the duration of hypobiosis is crucial to the success and stability of parasite populations. Alterations of the hypobiotic period may therefore be expected. Gaba and Gourbiere (2008) demonstrated that, if the timing of the arrest of development were to change as a result of climate change, the consequences for parasite populations are highly unpredictable.

van Dijk and Morgan (2008 and 2009) proposed that climate change may represent increased uncertainty in transmission opportunities of helminth parasites. They held this uncertainty responsible for apparent bet-hedging in *N. battus*. Instead of hatching in spring, as traditionally observed, this parasite appears to increasingly also hatch in autumn, leading to an observed significant rise in autumn disease in certain regions (van Dijk *et al.*, 2008). Apart from increases in climatic uncertainty, changing farm management practices may also represent increased uncertainty to parasites. Such uncertainty is likely to lead to parasites hedging their bets (Fenton and Hudson, 2002; Meyers and Bull, 2002), i.e., adopting more than one phenotypic strategy.

In conclusion, true genetic change (microevolution) is likely to be a slow process involving many parasite generations. However, changes in the phenotype distribution of parasites without a change in genotype (phenotypic plasticity), as well as dispersal to new, better-suited, habitats, can occur relatively rapidly, i.e., within years (Davis *et al.*, 2005; Visser, 2008). Therefore, parasite adaptation may rapidly lead to unexpected epidemiological patterns at pasture. It is of great, clinical, importance to determine which parasite traits are likely to be plastic.

Conclusions and recommendations

We found clear indications that climate change, apart from affecting the well-documented spatial spread of exotic diseases, has already changed the overall abundance, seasonality and spatial spread of endemic helminths in the UK. The observed changes are likely to be driven by the direct influence of temperature, and perhaps rainfall, on the free-living stages of these parasites. For the individual stages in the life cycles of these parasites, these influences have been studied in some detail. However, as it is still unclear which aspects of temperature (e.g. minimum, maximum, mean, falling and rising temperature fluctuations) best describe the effects on parasites, it will remain a challenge to quantify the effects of realistic warming scenarios. Also, especially with respect to snail-borne parasites like *F. hepatica,* it remains impossible to quantify the effects of rainfall-related parameters on the development and abundance of parasite and intermediate host. Climatic parameters, such as environmental temperature, often have contrasting effects on different stages of the life cycle. It may only be possible to get to grips with the effects of climate change on parasite population dynamics, and start to develop worm control strategies for the future, by taking all such effects into account simultaneously. Mathematical models are ideally placed to address these issues, especially when interfaced with Geographical Information Systems technology.

Observed recent changes in the epidemiology of nematodes, putatively related to climate change, can all be explained by the effects of temperature. It appears that, overall, for these parasites, the positive effects of extra development opportunities and increased development rates, through warming, outweigh the negative effects on environmental survival. However, the net effect of temperature on parasite dynamics is likely to vary between regions within the UK, between years and even between the months of the year.

Addressing the complexity in the population dynamics of the free-living stages is a challenge in itself. Changes in host–parasite dynamics and parasite–parasite competition within hosts, brought about by changes in seasonality, will go hand in hand with changes in the abundance of free-living stages. Currently, the effects of these factors are largely to be addressed in real pasture situations and the direction of their overall impact can only be guessed at. Add to this likely climate-induced changes in farm management (e.g. pasture management and parasite control policies; Morgan and Wall, 2009) and land use and it is clear that there is a mountain to climb before we can predict even the near future with any certainty. Moreover, changes that do not favour the persistence of parasite species on farms, as well as changes that do, will lead to parasite adaptation. There are already indications that parasites adapt rapidly to, for example, temperature changes. In order to be able to anticipate short-term adaptation, there is a need to describe parasite traits that are likely to be plastic, to understand their underlying genotypic and phenotypic mechanisms and work out expected rates of adaptation.

Helminth parasites are likely to be highly sensitive indicators of the effects of climate change on infectious organisms. On one farm, several or all parasite species are likely to be present. These species have different temperature-related thresholds and vital rates, moisture requirements and overwinter survival strategies. The study of such semi-controlled host–parasite systems, in particular the study of on-farm species shifts, may give vital information on infectious organisms and strategies that are likely to benefit from climate change. At the same time, farm management, which may change abruptly, poses rapid changes to the environment of these parasites and their hosts. Such environments may be ideally suited to study (rates of) parasite adaptation.

At this moment in time, measurable changes in the UK parasite epidemiology, likely to be at least in part related to climate change, have already taken place. Analysing these recent changes, therefore, may be a fruitful and reliable way of developing testable hypotheses on future parasite epidemiology. In order to be able to analyse these and future changes, it is vital to establish a baseline and to conduct parasite surveillance. Given the likely regional differences in parasite epidemiology, and responses to climate change, it is important to conduct this sort of surveillance at the appropriate scale. This also highlights the urgent need for laboratories involved in generating surveillance data to work along centrally agreed laboratory protocols and case definitions. Obviously, were such protocols to be agreed between countries and continents the impact of the surveillance undertaken would be dramatically increased.

Apart from analysing recent changes, another strategy that may give us vital clues on future parasite epidemiology is the study of parasites, which have already adapted to new environments. Once again, as some helminth species arrived here from the Tropics while others originated in the Arctic, these parasites are likely to provide useful models. Similarly, the study of the behaviour of endemic parasites at different latitudes may become increasingly important.

In short, we identify the following priorities for further research:

1. Improved diagnosis and active surveillance of parasitic helminth disease in the UK livestock.
2. Identification of the easily obtainable, essential, climatic parameters driving the abundance of the free-living stages of helminth parasites and quantification of their effects upon these stages. In particular, the effects of rainfall and humidity, likely to be essential for population growth of snail-borne parasites like *F. hepatica*.
3. Quantification of the overall effects of climatic changes on parasite dynamics. Once the effect of essential climatic parameters on free-living stages has been identified, the resultant effect can only be addressed in (mathematical) modelling frameworks. A clear challenge here will be to optimise the number of parameters to be included: too few and the models will give unrealistic output; too many and the models cannot be analysed. An explicit analysis of parameter uncertainty, after modelling parameters stochastically, is likely to assist in the optimisation process (Morgan *et al*., 2004). A second stern challenge is posed by the incorporation of the logistics of grazing strategies, and pasture use, in these models. Morgan *et al*. (2007), working with groups of migrating hosts, have shown that this is achievable.
4. Research towards better tests for anthelmintic resistance, as well as increased active surveillance for anthelmintic resistance, so that we can quantify its effects and take appropriate steps to manage its spread. If anthelmintic resistance cannot be measured in populations, it is unlikely that the true extent of the effects of climate change will ever be quantified.
5. Investigation of which traits of these parasites are likely to adapt rapidly, as well as likely rates of adaptation. The degree to which larval populations hypobiose, and perhaps the length of the period of arrested development, are examples of traits likely to adapt rapidly.
6. Investigation into the effect of infections of different age groups, in particular infections of older, partially

immune, animals in autumn on worm population dynamics.

7. Investigation into the effect of changing patterns of co-infection of hosts on the population growth of individual species. At realistic pasture levels of infection, for the pathogenic parasites concerned, very little is known about this subject.
8. Identification of likely adaptation of farm management to climate change. Are farmers currently adapting grazing, lambing and calving patterns? In terms of worm control, in the absence of clear guidance, how do farmers envisage to react to observed changes in the short term?
9. Continuing research into alternative strategies for parasite control, especially vaccination and rotational grazing, so that we have options for the control of endemic parasites that are more of a threat than ever as a result of climate change.

Climate change and the need to develop sustainable parasite control strategies pose a tremendous challenge to the livestock sector. It is likely that close collaboration between veterinary parasitologists, biologists, climatologists and modellers will be required to head these challenges. It appears all have their work cut out for some years to come.

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