Opinion

Climate change and parasitic disease: farmer mitigation?

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Global climate change predictions suggest that far-ranging effects might occur in the population dynamics and distributions of livestock parasites, provoking fears of widespread increases in disease incidence and production loss. However, several biological mechanisms (including increased parasite mortality and more rapid acquisition of immunity), in tandem with changes in husbandry practices (including reproduction, housing, nutrition, breed selection, grazing patterns and other management interventions), might act to mitigate increased parasite development rates, preventing dramatic rises in overall levels of disease. Such changes might, therefore, counteract predicted climate-driven increases in parasite challenge. Optimum mitigation strategies will be highly system specific and depend on detailed understanding of interactions between climate, parasite abundance, host availability and the cues for and economics of farmer intervention.

Climate change, parasite abundance and distribution

The rates of physiological processes in the majority of invertebrates are highly dependent on ambient temperature. Therefore, because most macroparasites have at least some life-cycle stages that are free in the environment or within poikilothermic intermediate hosts, increases in temperature as a result of global warming might be expected to have profound effects on the abundance of parasite populations, through higher rates of development and release of infective stages [1–3]. An increased number of generations and prolonged periods during which conditions are favourable for survival and transmission would be expected to increase potential parasite temporal availability [4,5]. Similarly, warmer temperatures might be expected to change the geographic distributions of many parasites [6,7].

The degree of damage to a host is strongly correlated with macroparasite abundance. Each individual parasite usually inflicts little damage, which is often judged to be subclinical [8]. The significance of such subclinical burdens might be mainly epidemiological, with parasitized hosts acting as a source of further infection. However, as intensity of infection increases, so does the degree of damage, to the detriment of animal health and production [9,10]. This leads to widespread assumptions that as a result of climate change, livestock will tend to suffer from increasing disease and production loss caused by parasites. Although this tendency might be inherent in many systems, insufficient scientific attention has been paid to the mechanisms that could mitigate such increases and how they can best be exploited. These are split into biological and anthropogenic factors.

Mitigating biological factors

Just as development rates of many parasites of veterinary importance increase with temperature, so do their mortality rates [1,11]. Furthermore, in addition to direct effects, temperature will also affect mortality indirectly through the action of predators, parasitoids, pathogens and competitors [12], whose development and abundance are also potentially temperature sensitive. Hence, the net effect of climate change could be complex and far from easily predicted. Depending on the effects of temperature on development and mortality at different stages of the life cycle, the outcome in terms of abundance of infective stages can vary dramatically, especially when seasonality is taken into account. Thus, for instance, in temperate areas with mild winters, increased year-round temperatures would lead to poorer overwinter survival of infective larvae of trichostrongylid nematodes [11,13], leading to lower levels of spring infection. This could be offset by accelerated and prolonged build-up of larvae later in the grazing season [14,15]. In areas with cold winters, however, overwinter larval survival could be increased at higher temperatures [16], although warming might paradoxically increase mortality because snow melt exposes larvae to harsher conditions [17]. In summer, higher temperatures might be expected to increase development, but this is not always the case in the field [18], possibly owing to decreased moisture [19]. The influence of desiccation on parasite dynamics, already strong in warm regions, is likely to grow as temperate climates change.

The net effect of warming on parasite infection levels, therefore, could be complex. Some nematodes, such as *Nematodirus battus,* suspend development above an upper temperature threshold [20]. This changes the timing of infective stage availability under projected warming scenarios, shifting the disease threat. Overall levels of disease might be decreased as a result, but if farmers are poorly prepared for changes in the timing of infection, control measures could nevertheless fail.

For arthropod ectoparasites, the differential effects of warming on mortality, development and transmission are expected to vary widely, depending on the species in question. For some species (e.g. the sheep nasal bot fly, *Oestrus*

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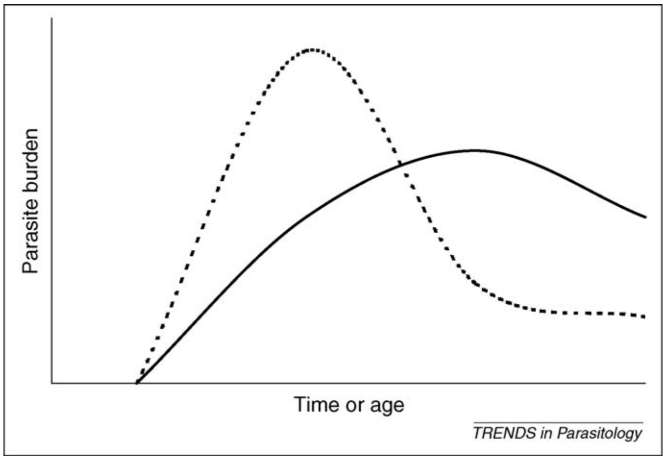


Figure 1. The peak shift. In systems in which acquired host immunity plays a prominent epidemiological role, infection tends to increase with host age to a peak and then decline (solid line). As parasite challenge increases, this peak tends to occur earlier and reach a higher level (dotted line), but infection levels in older age classes can actually decrease [41].

ovis, which overwinters as a hypobiotic larva within the host), warmer winters might allow year-round development, increasing parasite challenge and rendering temporally focused control difficult [21]. However, for other parasites (e.g. mange mites), higher temperatures are likely to decrease the survival of off-host stages, thereby reducing environmentally mediated transmission [22]. Similarly, for the blowfly agents of myiasis, such as *Lucilia sericata*, warmer winters might again allow year-round development but would probably strongly increase the mortality of post-feeding larval and pupal stages, which are resident in the soil [23]. Although genetic and behavioural differences exist between populations of various species in different climatic regions, nevertheless, broad changes in climate might lead to substantial shifts in the distribution and importance of particular parasites. Thus, for example, *L. sericata* is largely replaced as an important agent of myiasis in warmer Mediterranean or continental European regions by *Wohlfahrtia magnifica* [7]. The extent to which any such distributional changes might translate into increased challenge is hard to predict. However, because most arthropod parasites – as well as trematodes and some nematodes – are at least as limited by humidity as by temperature, effects of climate change will depend crucially on the interaction of both these climatic factors.

Even if the abundance of free-living parasite stages is increased, this need not necessarily lead to higher levels of infection, especially where host immunity is important (Figure 1). The role of immunity in the epidemiology of parasites of veterinary importance, therefore, is of key importance to the prediction of likely effects of climate change [4]. Changes in immunoepidemiology that alter the age at which peak parasite burdens typically occur can increase or decrease economic impacts, depending on timing in relation to the production cycle. Thus, exposure of lambs and calves to high levels of gastrointestinal nematode infection can decrease growth rates but yield rewards in terms of immunity to reinfection in replacement breeding animals. Selective breeding of animals with altered immune responses could be an effective mitigation strategy, although given associated metabolic and other costs, the optimal phenotype will not necessarily maximize expression of immunity [24,25].

Mitigating husbandry factors and rates of infection

Whatever its direct effects on parasite populations, climate change is likely to affect many aspects of animal husbandry, including the timing of reproduction and housing, nutrition, breed selection, and management interventions such as shearing. In addition, observed increases in disease incidence are likely to provoke intervention that could include altered husbandry practices, as well as chemical treatment (Box 1). It is important to remember that livestock face a range of parasitic and other diseases and interactions between them are common. Thus, for instance, increases in burdens of gastrointestinal nematodes in sheep are likely to increase susceptibility to myiasis through increased fleece soiling [26], irrespective of effects on *Lucilia* populations.

Changing patterns of grass growth might provoke altered grazing and housing patterns, with effects on the seasonality of parasite infection. Some parasites are transmitted more efficiently in housed or constrained livestock (e.g. lice [27]), whereas for those ingested with grass (e.g. gastrointestinal nematodes [1]), longer grazing seasons might be expected to promote infection. Increased abundance of infective nematode larvae on pasture in autumn will only result in disease if livestock are grazing at that time [15]. Temporary host absence through housing has a strong seasonal forcing effect on the dynamics of nematode infection in cattle [28], so changes in livestock management might be expected to have dominant effects on the epidemiology of this system, even without climatic effects on free-living stages. These are difficult to predict because management assumptions made in many relevant mathematical models are often too simple to reflect even the main interactions between husbandry and exposure [13,29]. On the other hand, more realistic models that include farm husbandry (see, for example, Ref. [30]) potentially suffer from lack of transparency and limited applicability outside the system in hand [29].

As well as increased temperature, altered rainfall patterns could affect both husbandry and parasite biology. Turn-out of cattle onto pasture in temperate areas, for example, requires reasonably dry pasture, as well as grass growth, potentially affecting exposure to nematodes at the start and end of the grazing season. The timing of transmission is important not only to the overall abundance of parasite populations but also, potentially, to the pathophysiological consequences of infection (which depend on host age, nutritional and immune status, and seasonality in the state of the free-living stages). Thus, type 2 ostertagiosis in cattle, caused by re-emergence of hypobiotic nematode larvae whose development was arrested in autumn [31], might increase in importance if autumn intake of larvae is increased. This could occur through rain-induced release of larvae from dried cowpats [32], combined with later grazing to take advantage of autumn grass growth. The climatic factors affecting management of livestock, therefore, are often as complex as those affecting the biology of their parasites and should be taken into account when predicting the effects of climate change on parasitic disease.

Box 1. Husbandry and sheep myiasis: a case study

Blowfly strike (ovine cutaneous myiasis) is a widespread and common seasonal problem in the UK, caused largely by the common greenbottle fly, *Lucilia sericata*. Strike affects almost all lowland sheep farms, and between half a million and one million sheep are struck each year [27]. Adult blowflies lay batches of up to 200 eggs in areas of the wool that are wet or soiled with faeces, so most strikes occur around the tail, anus and perineum. Anything that increases the amount of faeces that accumulates in the wool (such as an undocked tail, infection with parasitic gastrointestinal nematodes, diarrhoea or longer fleeces) can increase an animal's risk of being struck. The wound created by feeding maggots is a powerful attractant for more egg-laying female blowflies. As a result, multiple strikes occur quickly, and the feeding maggots cause considerable distress to the infested animal and, if untreated, rapidly result in its death.

A well-established stochastic simulation model of blowfly strike incidence in sheep can be used to investigate potential effects of changes in husbandry practice on strike incidence [42]. The model is based on two subcomponents. The first simulates the seasonal pattern of abundance of *L. sericata*, using quantified temperature-dependent development, mortality and oviposition rates [23,43]. The second uses the range of key factors known to increase the susceptibility of ewes and lambs to strike to estimate the proportion of a flock at risk each day [44]. The two components are then integrated to estimate a predicted strike rate per day. Key drivers in the model are the seasonal patterns of temperature and rainfall. However, parasitic nematode burdens and husbandry practices such as shearing and lambing dates, which are known to affect strike incidence, are also included. The model allows the effects of changes in climate or husbandry practices on strike incidence to be assessed.

During the period of adult activity, a characteristic pattern of strike incidence is observed. Initially, ewes are the most heavily struck age class because in spring and early summer, their long fleeces easily become wet and soiled, promoting high blowfly egg and larval survival. However, after shearing, ewe susceptibility is substantially reduced. Lambs initially have short fleeces, but after weaning in summer a combination of diarrhoea caused by gastrointestinal nematode infection and a growing fleece leads to soiling and rapidly increases their susceptibility to strike. Lamb strikes, therefore, predominate from mid-summer onwards, and ewe strikes are only of significance early in and at the end of the season (the latter depending on autumn temperatures).

The model shows that the incidence of strike at the start of the season is largely limited by fly abundance, whereas later in the year incidence is determined predominantly by the availability of susceptible hosts, with further increases in fly abundance later in the year making little difference to strike incidence.

The primary effects of increased temperature are to bring the date of first spring emergence of adult *L. sericata* forward to earlier in the year (a 2 °C increase in daily average temperature advances the spring emergence of the adult flies by 2–3 weeks) and to increase the rates of both fly population growth and mortality, with the net effect being increased peak fly population size. Larger fly populations result in a higher prevalence of strike, but the relationship between strike prevalence and fly abundance is non-linear because as the fly population increases, the system rapidly becomes limited by the availability of susceptible sheep.

Overall, higher temperatures are likely to increase strike incidence, particularly in ewes in early summer, but to have less direct effect on lamb strike incidence. However, shearing of ewes reduces susceptibility to strike substantially because it reduces fleece humidity and soiling [45]. Hence, a simple change in farm husbandry practice, to shear earlier, is likely to have a substantial effect on ewe strike incidence. Changing the shearing date from early June to early April largely eliminates any increase in ewe strike expected as a result of the higher temperatures and higher fly abundance (Figure I). Of course, the practicality of such a strategy depends on lambing dates because heavily pregnant ewes should not be sheared, and it is possible that a second shearing later in the season might also be necessary to prevent increased ewe strike in autumn because earlier fleece regrowth coincides with wetter weather. It is, therefore, evident that investigation of appropriate mitigation strategies must take into account animal management, as well as parasite biology.

This example illustrates how detailed information and understanding is required before effects of climate change on disease incidence in specific systems can be predicted and how basic changes in animal management and husbandry can mitigate expected effects. Similarly, further changes in shearing regimes and changes in lambing dates or worm management regimes could also be used to mitigate anticipated effects of climate change on blowfly strike in sheep.

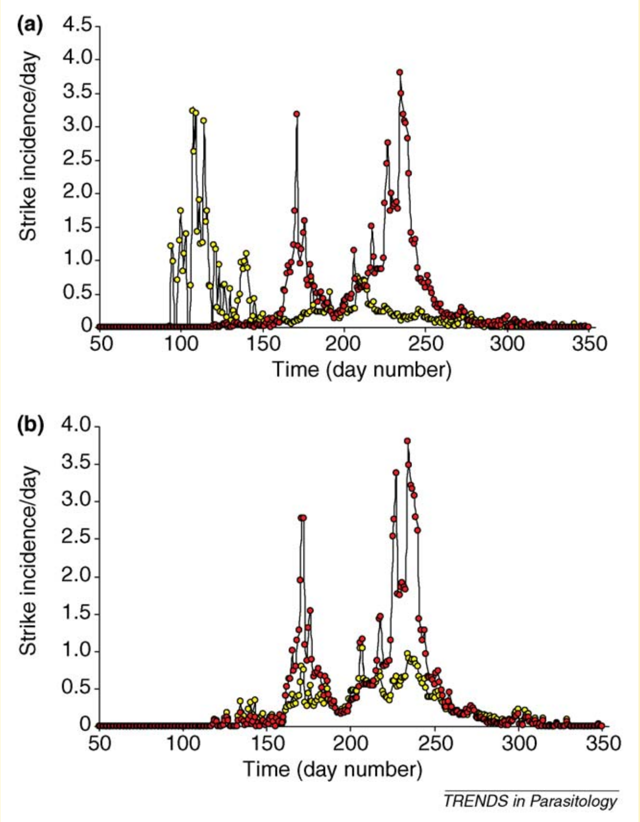


Figure I. Fly strike incidence per day predicted by a stochastic simulation model, where day 1 is the 1st of January, using daily temperature and rainfall data recorded SW England in 2003. Lambs were born on day 60 (1 March); no lambs were removed over the course of the year. No flock-level preventative insecticide treatment was applied to either ewes or lambs. **(a)** The pattern of strike incidence per day for a flock of 1000 ewes (yellow circles) and 1000 lambs (red circles) with ewe shearing in early summer (day 168). **(b)** Shearing brought forward to day 100.

Parasite adaptation to climate change and husbandry

The rapid development of anthelmintic resistance [33] is a reminder of the ability of parasites to adapt quickly in the face of selection pressures imposed by control efforts on farms. Much less attention has been given to likely parasite adaptations to climate change and to associated alterations in farm animal husbandry and non-chemical methods of parasite control. Thus, warming could, for instance, decrease the fitness benefit of developmental arrest in temperate winters and favour evolution towards year-round transmission [4]. Changes in the timing of infection could similarly alter the importance to parasite fitness of host immunity and competition with other parasites [34]. Little is known about the extent to which key parasite life-history traits are open to such selection and on what timescale epidemiologically important changes could develop

[35,36]. Studies on the free-living stages of *Haemonchus contortus* populations established in northern Europe [11] suggest that the relationships between temperature and development or survival are fairly stable in this species. Undoubtedly, however, changes in husbandry, including those aimed at mitigating the effects of climate change on parasitic disease, will drive evolutionary changes in parasite populations, further complicating predictions.

Modelling farmer intervention

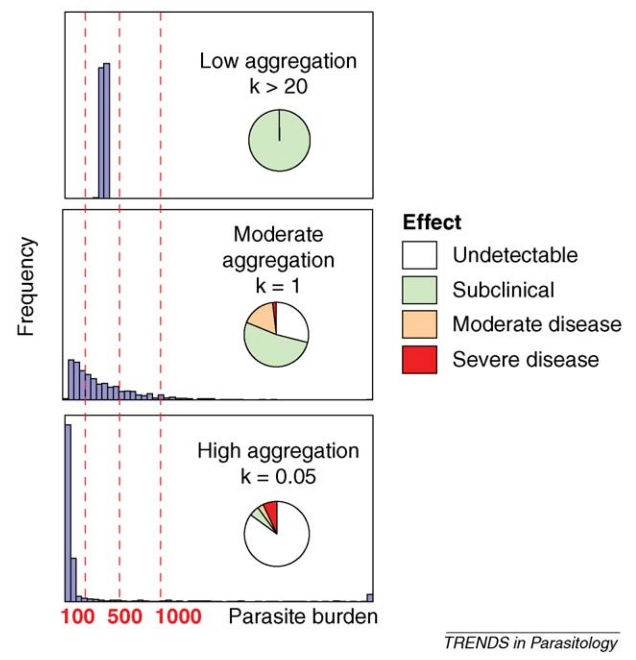
In the absence of antagonistic effects as a result of altered animal husbandry or limitation by host immunity, increased parasite abundance as a result of climate change might indeed lead to unconstrained increases in disease incidence and production loss. However, this is unrealistic, in that we would expect farmers to intervene before the effects of parasites on their livestock become overwhelming. This process is essentially density dependent, in that the strength of the effect on parasite populations through control would increase with parasite abundance. As such, farmer intervention might share some properties with other density-dependent processes in parasite population dynamics. Farmer intervention has particular properties, however, including a very pronounced trigger point based on observed effects, and, commonly, application of treatment to a group of animals irrespective of individual parasite burdens. By modelling this process, we might generate insights into likely farmer behaviour when faced with altered parasite epidemiology and how effective this will be in limiting the impact of disease. In particular,

Box 2. Parasite monitoring and risk management

Climate change could alter requirements for group-level antiparasitic treatment, either by accelerating the build-up of infection to dangerous levels or by changing the temporal distribution of risk and, therefore, optimum times for intervention. Because intensive chemical prophylaxis is inefficient and unsustainable, effective mitigation will rely on monitoring of parasite burdens and associated disease, such that responses through treatment or husbandry are efficiently targeted.

In practice, on-farm monitoring of parasite populations is often difficult and incurs costs to the farmer. In some cases, the first sign of a problem might be clinical disease in an individual animal, such as skin lesions and pruritis caused by lice or psoroptic mange or diarrhoea caused by gastrointestinal nematode infection. At this stage, it is likely that many other individuals are already infected and suffering from less obvious disease. The ability of clinical disease surveillance to detect parasite problems early enough to trigger effective action clearly depends strongly on the relationship between burden and disease but also depends, less obviously, on patterns of parasite aggregation (Figure I). For many (but not all) parasites, monitoring would better focus on apparently healthy animals, to detect increases in parasite populations before they cause excessive damage. Useful methods include grading anaemia in *Haemonchus* infection [46], on-farm systems for counting nematode eggs in faeces [47] and visual inspection for lice [48].

Increased risk of parasitic disease associated with climate change might necessitate increased investment by farmers in such proactive parasite monitoring. The resources so allocated will inevitably be diverted from other tasks, including treatment, and yet the optimization of investment in parasite monitoring has received little scientific attention. In other fields such as conservation [49,50] and control of invasive species [51], there is a clear trade-off between monitoring and action, which can signal the best path for risk mitigation. For example, the optimum density of traps for detecting invasive gypsy moths is highest for infestations with moderate growth rates because these are neither easy to detect nor easy to eradicate [51]. In this case, trap density is analogous to parasite monitoring effort, for example the frequency of faecal egg counting in nematode infections of livestock. In the farm situation, decisions must also be taken on the proportion of the group to examine. This will depend on parasite distribution. Thus, parallel studies on the detection of free-living animals suggest that when parasites are common, it is more useful to repeatedly sample a small number of animals, whereas for rare infections, less intensive surveillance of a larger proportion of the group would be a better strategy [50]. Repeated samples from a part of the group should give more information on temporal dynamics and signal appropriate treatment times at the group level, whereas cross-sectional sampling of a larger number of animals can underpin targeted selective treatment of individuals. Some preliminary attention has been paid to optimizing monitoring strategies for individual host–parasite systems [52]. Application of general rules for parasite distribution can be useful in this endeavour; for example, the negative binomial relationship leads to a simple prevalence-based method for monitoring sea louse abundance in fish [53]. However, greater documentation of the typical levels of aggregation found in livestock–parasite systems is needed, as well as deeper understanding of the mechanisms governing parasite distribution. If climate change alters parasite distribution, as well as abundance, this will affect the optimal design of monitoring strategies aimed at mitigating disease risk.



TRENDS in Parasitology

Figure I. Effects of parasite aggregation on the detection of disease in groups of livestock. Histograms represent frequency distributions of parasite burdens within a flock or herd, given an equal mean burden of 300, and varying levels of aggregation (as measured by negative binomial parameter k). It is assumed that infection is undetectable below a notional burden of 100 and detectable but of slight (i.e. subclinical) importance between 100 and 500, whereas burdens above 500 cause moderate (500–1000) or severe (>1000) disease (dotted lines and pie charts). At low levels of aggregation, burdens cluster close to the mean and all individuals have detectable subclinical infection. At very high levels of aggregation, however, few individuals have detectable levels of infection but those that do are likely to have high burdens and be severely affected. Moderate levels of aggregation make it easier to detect infection at the group level by proactive sampling because a high proportion of individuals carry detectable infection. By contrast, if monitoring is based on recognition of clinical disease, most notable infections will be detected at high levels of aggregation, but at more moderate levels, by the time overtly diseased individuals are detected, many more are already suffering from subclinical disease and associated production loss.

efficient monitoring of parasite infection and related disease will be crucial if farmers are to recognize and mitigate the risks to production (Box 2).

Advice on parasite control will be taken up only if it makes sense in the context of farm-level economics. Although the role of economics in the selection of parasite control strategies is a core part of farming and veterinary practice and has long been appreciated by parasitologists [37], scant scientific attention has been paid to this subject in recent decades because control has relied on routine chemical treatment. In dealing with the challenges of climate change, farmers' options for parasite control will be fewer, less simple and less effective than previously [38]. It is important that attention is given to the development of appropriate mitigation through better husbandry so that the response to higher parasite challenge is not simply one of greater insecticide or anthelmintic use, which might increase the rate of selection for resistance. Including farm economics, as well as the dynamics of diagnosis and intervention in models of parasite epidemiology, will increase the relevance of these models to control in the field. In other areas of biology, such as conservation, great advances have been made by extending 'pure' population dynamic models to include the behaviour and motivation of human exploitation (see, for example, Refs [39,40]). A similar shift in thinking, however uncomfortably this might sit with specialists in parasitology, would help to set changes in parasite population dynamics in their proper anthropological context. This is a necessary step if we are to determine to what extent changes in husbandry, whether provoked by increased parasitic disease or not, can compensate for direct effects of climate on parasite populations.

Concluding remarks

General predictions concerning the effects of climate change and, in particular, global increases in temperature on parasite epidemiology largely focus on increases in abundance or distribution owing to accelerated development of stages outside the definitive host. Although these predictions might in themselves be valid, actual effects in terms of the incidence of disease and production loss will be modulated by many factors. These include biological processes, such as host immunity, and farmer behaviour. Factors affecting the rate of detection of parasites and associated disease, thresholds for treatment and changes in husbandry are likely to strongly affect the nature of farmer responses to altered parasite epidemiology and their effectiveness. Interactions between these factors and parasite biology are very system specific. There is a need for research that considers likely effects of climate change and mitigation strategies in terms of the whole host–parasite system, including anthropogenic responses, and not just in terms of parasite population dynamics.

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