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The basic reproduction quotient (Q_0) as a potential spatial predictor of the seasonality of ovine haemonchosis

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Abstract. *Haemonchus contortus* is a gastrointestinal nematode parasite of small ruminants, which feeds on blood and causes significant disease and production loss in sheep and goats, especially in warmer parts of the world. The life cycle includes free-living immature stages, which are subject to climatic influences on development, survival and availability, and this species therefore exhibits spatio-temporal heterogeneity in its infection pressure based on the prevailing climate. Models that better explain this heterogeneity could predict future epidemiological changes. The basic reproduction quotient (Q_0) was used as a simple process-based model to predict climate-driven changes in the potential transmission of *H. contortus* across widely different geo-climatic zones, and showed good agreement with the observed frequency of this species in the gastrointestinal nematode fauna of sheep ($r = 0.81$, $P < 0.01$). Averaged monthly Q_0 output was further used within a geographical information system (GIS) to produce preliminary haemonchosis risk maps for the United Kingdom (UK) over a four-year historical span and under future climate change scenarios. Prolonged transmission seasons throughout the UK are predicted, especially in the south although with restricted transmission in peak summer due to rainfall limitation. Additional predictive ability might be achieved if information such as host density and distribution, grazing pattern and edaphic conditions were included as risk layers in the GIS-based risk map. However, validation of such risk maps presents a significant challenge, with georeferenced observed data of sufficient spatial and temporal resolution rarely available and difficult to obtain.

Keywords: basic reproduction quotient, geographical information system, *Haemonchus contortus*, risk maps, spatial prediction, climate change, epidemiology.

Introduction

Haemonchus contortus is a blood-feeding nematode parasite of the gastrointestinal (GI) tract of small ruminants that - along with other GI nematodes - causes substantial disease and production impact in livestock worldwide (Charlier et al., 2014a), especially in warm climatic regions. Adult worms are parasitic in the abomasum, and females lay eggs that pass out in the faeces, where they develop through first and second larval stages to the infective third larval stage (*L3*). The *L3* moves out of the faeces and onto the herbage, where it is ingested by a future host. Due to the warm and moist conditions required by the free-living stages for development and translation onto herbage (O'Connor et al., 2006), there is significant potential for spatial and temporal heterogeneity in the infection pressure of *H. contortus* based on prevailing climate and weather conditions. By understanding this heterogeneity, predictions of disease risk can be generated and potential effects of climate change on parasite ecology and epidemiology explored (Morgan and Wall, 2009; Van Dijk et al., 2010; Fox et al., 2012). In particular, successful mapping of *H. contortus* infection pressure could serve as an early warning system (EWS) for stakeholders, particularly farmers and their advisors; thus guiding effective and efficient strategic control plans (Van Wyk and Reynecke, 2011; Kenyon et al., 2009).

In practice, infection with *H. contortus* is likely to be complex and related to an array of management variables as well as climatic factors. Thus, although mathematical models of the population dynamics of *H. contortus* and its dependence on climate have been constructed previously (Smith, 1994), these tend to be

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limited in the extent to which they incorporate important management factors (Morgan, 2013), or alternatively include such factors but lack the transparency needed in order to separately explore effects of climate (Learmount et al., 2006). We take an alternative, simplifying approach. The strong influence of climate on the availability of infective *H. contortus* larvae, and the particularly high biotic potential of this species among the gastrointestinal nematodes of ruminants, is such that a simple index of climatic suitability for successful maturation of the free-living stages could itself be a useful predictor of transmission. The basic reproduction quotient (Q_0) was devised as such an index based on the widely used basic reproduction ratio (R_0) for micro-parasites (Roberts and Heesterbeek, 1993; Heesterbeek and Roberts, 1994). R_0 represents the number of hosts that are infected from each infected host, with $R_0 > 1$ signifying the potential for an epidemic to grow. Q_0 for macroparasites is similarly defined as the average number of adult female worms produced by one female worm in the absence of density-dependent constraints during its entire reproductive lifespan when introduced into a previously unexposed host population (Heesterbeek and Roberts, 1995). Q_0 therefore measures the maximum reproductive potential of a parasite between one generation and the next in the absence of any density-dependent constraint (Scott and Smith, 1994). As a threshold quantity, Q_0 is a simple estimate of the long-term trajectory of the parasite population (Anderson and May, 1991; Roberts, 1995). Similarly to R_0, Q_0 values less than unity indicate that environmental conditions are not conducive for persistence of the parasite population, should those conditions prevail. On the other hand, a Q_0 value ≥ 1 implies a tendency towards population growth in the absence of host immunity with resultant higher infection pressure. In effect, the Q_0 model should be able to identify conditions or factors that will affect the parasite's transmission potential (Grenfell and Dobson, 1995; Kao et al., 2000).

The present study aimed to explore the application of Q_0 as a predictor of spatio-temporal variation in transmission potential. Thus, the objectives were: first, to determine whether predicted Q_0 correlates with the observed occurrence of *H. contortus* infections in sheep across contrasting geo-climatic zones; second, to explore the spatial application of Q_0 in the form of maps at the national level using the United Kingdom (UK) as a case study; third, to dissect the components of Q_0 to identify and understand the role of different climatic variables in the predicted spatio-temporal variation of haemonchosis and, finally, to extend the model to identify the possible impacts of climate change on disease risk in future. The intention was to identify the potential for further development of Q_0-based approaches for this climate-sensitive parasite species.

Materials and methods

Assumptions of the Q_0 model

We aimed at developing a simple, dynamical Q_0 model, universally adaptable to any region, and only relying on climate drivers. The exclusion of management processes allows the present model to focus on how climate changes drive the availability of the free-living stages for host infection in space and time. Specific simplifying assumptions include the fact that the host population is grazed continuously on pasture, where all the free-living stages, particularly the infective *L3*, are evenly dispersed (Kao et al., 2000); there is no control regimen or grazing management; only free-living stages are affected by climate (Kao et al., 2000; Kahn, 2010) and the host population is assumed to be immunologically naive.

Model construction

The Q_0 model is deterministic and is calculated as follows:

$$Q_0 = \underbrace{\frac{\lambda}{2\mu_p}}_{\text{Term 1}} * \underbrace{\frac{d_e\, d_h}{(\mu_e + d_e)\,(\mu_{l3} + d_h)}}_{\text{Term 2}} * \underbrace{\frac{cH}{bA\mu_{lh} + cH}}_{\text{Term 3}} * \underbrace{pe}_{\text{Term 4}}$$

where λ represents the fecundity of females (eggs produced per female per day), which is divided by two to take account of the sex ratio; μ_p the mortality rate of adults in the host; d_e development rate from egg to *L3*; d_h the migration rate of *L3* from the faeces onto herbage; μ_e the mortality rate of eggs; μ_{l3} the mortality rate of *L3* in faeces; *c* the daily larval ingestion rate per host; *H* the host density; *b* the standing biomass; A the grazed area; μ_{lh} the temperature-dependent mortality rate of *L3* on pasture; and *pe* the establishment rate of *L3* (Rates are expressed per day, areas as hectares, and biomass and herbage intake in kg).

The breakdown of the model into four terms is useful for understanding the relation of Q_0 to phases of the parasite life cycle, thus:

(i) Term 1 = lifetime reproductive output.
(ii) Term 2 = probability of development to *L3* and successful migration of *L3* onto herbage.

(iii) Term 3 = probability of ingestion of *L3* by a susceptible host through grazing.
(iv) Term 4 = probability of establishment of *L3* once ingested and maturation to become a reproducing adult.

The model parameters are either constants, or vary dynamically with the climate (specifically temperature and rainfall). In order to assess the impact of rainfall limitation on the transmission of *H. contortus*, a variant of Q_0 was run based only on temperature, by removing rainfall-related constraints on larval development, survival and translation onto herbage. This nested derivative of Q_0 was represented as Q_{0t}. Parameter values were estimated by literature review. Further details on the construction of the model and the parameters used are given in the complementary supplement material (CSM).

Validation

To assess the reliability of Q_0 as a spatial predictor of *H. contortus* transmission across different geo-climatic regions, data on rainfall, temperature and haemonchosis burden were sourced across climatically diverse countries. Climatic variables were rainfall and temperature from the nearest available point (http://www.worldclim.org). Data on the haemonchosis burden in field populations of sheep or goats consisted of either *post mortem* recovery of adult worms (PM), recovery of *L3* from pasture (*L3*) or faecal egg counts with larval culture to characterise the specific proportion of *H. contortus* (FEC). These three haemonchosis indices were utilised in this study and taken to represent the proportion of the total counts that were *H. contortus* over all seasons sampled. The data search was designed to cover a broad range of eco-climatic zones based on the Koeppen-Geiger climate classification. Altogether, data were obtained for 25 different locations (see CSM). Q_0 was run to predict the overall average climatic conditions for *H. contortus* transmission at each location by using respective data on temperature and rainfall, at weekly or monthly resolution as available, and then averaged on an annual basis to arrive at mean annual model predictions. Where only monthly rainfall was recorded, it was assumed to be evenly distributed over the four weeks of the month. Mean Q_0 was compared with the proportion of *H. contortus* observed in order to test the ability of the model to distinguish between locations that had a propensity to support dominance of this species from those that did not.

Mapping Q_0 at the sub-national level

UK was used as a case study because of ready availability of climate data, and current concern around possible future impacts of climate change on ovine haemonchosis (Kenyon et al., 2009). A 25-km gridded monthly dataset for the whole of the UK for both temperature and rainfall was provided for the period 2003 - 2006 by the UK Met Office (UKCP09; available on request via the website). Future estimates of temperature and rainfall for the 2020s and 2080s were also obtained from the UKCP09 based on low and high projected emission scenarios (2020Lo, 2020Hi, 2080Lo, 2080Hi) (Murphy et al., 2009).

In order to compare the role of rainfall to that of temperature in generating transmission potential, Q_0 predictions (from both temperature and rainfall) and Q_{0t} predictions (from temperature alone) were calculated. Each version of Q_0 was then used as the only data-layer to construct a geographic information system (GIS)-based climate-driven haemonchosis risk map, using ArcMap version 10 (ESRI, Redlands, CA, USA) software.

Results

Output from the Q_0 model was first compared with observed level of *H. contortus* infection in small ruminants in different parts of the world, as broad-ranging point validation of model predictions regarding climatic suitability for development and transmission. Thereafter, the Q_0 model was applied on a spatial grid at the national scale (UK); before being subjected to exploration using future climate change scenarios.

Reliability test of Q_0 as a spatial predictor of H. contortus

Predicted annual average Q_0 was significantly correlated with the observed proportion of *H. contortus* in samples of adult worms, and larvae cultured from faeces and recovered from pastures (Pearson r_{25} = 0.81, P <0.01; Fig. 1). General differences in the proportion of *H. contortus* reported in different Koeppen-Geiger eco-climatic categories were reflected in predicted Q_0 (Fig. 2); thus, for example, tropical > temperate areas for both variables. Differences between locations with similar eco-climatic characteristics were also consistent with Q_0 in many cases; for example, Cuba > Ethiopia and Albany, Australia > Greece. This provides qualitative support for the ability of the model to predict broad differences in climatic suitability for transmission of *H. contortus*.

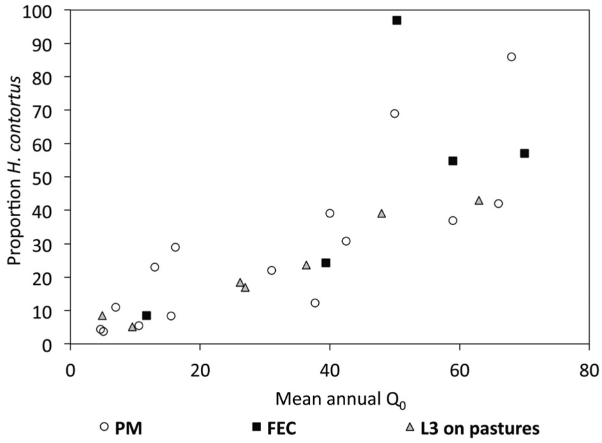

Fig. 1. Mean annual predicted Q_0 for *H. contortus* against the mean proportion of total parasite counts comprising *H. contortus* for 25 geo-climatic locations. Parasite counts were from *post mortem* recovery of adult worms (PM), faecal egg counts cultured to allow specific identification of larvae (FEC), and infective larvae recovered from pasture (L3).

Q_0*-based UK risk map*

For each year from 2003 to 2006, Q_0-based risk maps for the UK revealed that the summer months (June - September) constituted the highest climatic risk for ovine haemonchosis. This risk was predicted to decrease in autumn, as temperatures decreased, first in the north and then further south (shown in Fig. 3 for 2003, with other years 2004-2006 providing very similar patterns). In the whole of UK, the risk of *L3* development was predicted to be absent in the winter months (December - February). This general seasonal pattern agrees with that found in laboratory diagnoses of *H. contortus* infection in sheep in the UK (van Dijk et al., 2008), which provides qualitative validation of the model. The risk map for August 2003 indicated that there was reduction in the predicted haemonchosis risk in some parts of central-south and east England. Comparing Q_0, which included constraints on *L3* development and survival under low rainfall conditions, with Q_{0t}, in which this constraint was absent, identified that moisture limitation accounted for this apparent paradox (Fig. 4). In all other months and years examined, maps of Q_0 and Q_{0t} did not differ, indicating that moisture was not limiting to transmission in the model.

When projected climate change scenarios were applied to the Q_0 model, spatio-temporal distribution of risk changed substantially. Examples are shown in Fig. 5 for key months with respect to the 2003-2006 period and projected 2080s high emissions scenarios, which were representative of key predicted patterns. Rainfall limitation was predicted to increasingly suppress *H. contortus* transmission in the south of the UK in peak summer, while higher temperatures were predicted to support transmission in more northern regions. In other months, conditions were predicted to be better for transmission, leading to a prolongation of

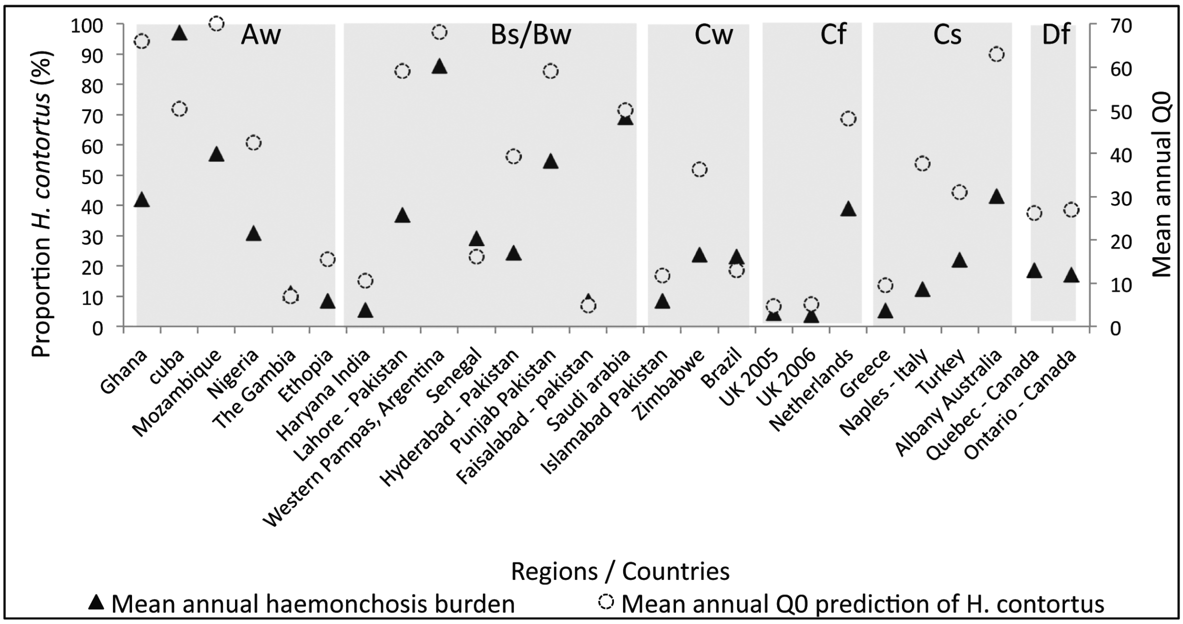

Fig. 2. Mean annual predicted Q_0 for *H. contortus* and the average proportion of total parasite counts comprising *H. contortus* for 25 geo-climatic locations (see Fig. 1 above). Locations are arranged based on the eco-climatic zones of the Koeppen-Geiger classification of climate, thus: Aw = tropical savannah; Bw = hot desert; Bs = hot semi-arid; Cw = subtropical; Cf = oceanic; Cs = Mediterranean; Df = continental.

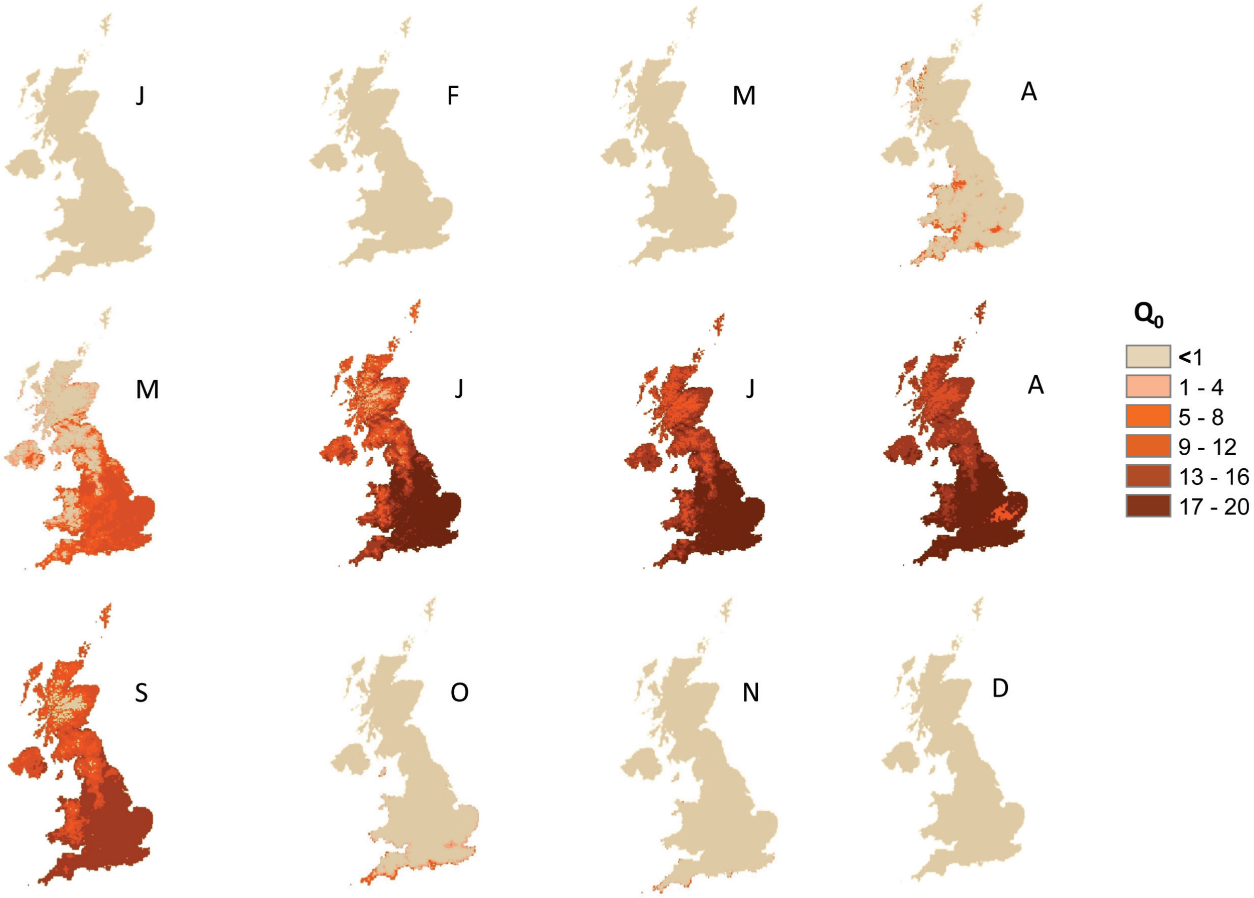

Fig. 3. Monthly GIS-based Q_0 risk map showing the geographic distribution and predicted relative risk of *H. contortus* infection pressure across the UK using climatic data from 2003.

the risk period throughout the country and the possibility of year-round transmission in the South, where Q_0 exceeded unity even in the coldest winter months of December and January. As in the historical time series, the period during which $Q_0 > 1$ was as much as four months longer in areas of the South than in northern Scotland under climate change scenarios.

Fig. 4. Comparison of the roles of rainfall and temperature in predicted *H. contortus* transmission potential across the UK using climatic data from August 2003. Q_{0t} represents a nested model of Q_0 that is unconstrained by moisture limitations on larval development, translation to pasture and survival.

Discussion

Knowledge and understanding of how climate supports or inhibits *H. contortus* transmission can provide a basis for farmers and their advisers to make farm decisions for strategic and sustainable parasite control. These decisions can help to keep *H. contortus* populations at an economically acceptable level in grazing sheep without encouraging selection for anthelmintic resistance through excessive treatment (Van Wyk and Bath, 2002; Van Wyk and Reynecke, 2011; Falzon et al., 2014). Essentially, information on spatio-temporal variation in climatic suitability for the availability of *L3* for infection of sheep, given pasture contamination with *H. contortus* eggs, should allow good farm management decisions to be made for cost-effective and sustainable control. Among parasites of sheep, *H. contortus* is a suitable candidate for such a climate-driven approach, since its ubiquity and high biotic potential mean that egg output is often high, and propagation of infection is largely driven by climate with rapid development of infective larvae under

Fig. 5. Comparison of predicted Q_0 under historic (2003-06 averaged) and projected future climates, using the UKCP09 high emissions scenario.

optimum conditions (O'Connor et al., 2006, 2008). This paper builds on earlier efforts to combine climate-driven aspects of nematode population dynamics into a simple model (Kao et al., 2000), extending such a Q_0 model to generate regional and sub-national predictions of propensity for transmission of *H. contortus*.

Results of the present study suggest that the Q_0 model shows promise as a spatial predictor of the climatic risk of ovine haemonchosis, notwithstanding its simplifying assumptions. Hence, the model was able to explain a substantial portion of the variation in the dominance of *H. contortus* in grazing sheep across different geo-climatic zones. Following the conclusions of Heesterbeek and Roberts (1994), Roberts (1995) and Kao et al. (2000), this promises that Q_0 can be used as part of risk assessments to determine the extent to which parasite control strategies should take specific account of *H. contortus* in specific regions in current and projected future climates.

The Q_0 model was adapted to a GIS in combination with gridded climatic datasets to consider how finer scale (sub-national) variations in climate could be harnessed to predict local risks of *H. contortus* transmission. Comparison of Q_0 and Q_{0t} suggests temperature rather than moisture limitation to be the main driver of the seasonal and regional variations in the observed haemonchosis risk across the UK. However, rainfall appeared to exert some limitation on the transmission potential of *H. contortus* in mid-summer in some years, especially in the south of the UK. This was predicted to become more common in future under current climate change scenarios. A similar pattern was predicted for blowfly strike caused by *Lucilia sericata*, by Rose et al. (2011). However, sporadic summer rainfall limitation on parasite transmission was projected to be compensated by a longer simulated transmission season in future, and increased risk especially in the North. This resonates with recent observations of spread of *H. contortus* in Scotland (Kenyon et al., 2009) and the general trend for increasing records of clinical haemonchosis across the UK (Van Dijk et al., 2008). This is also in tune with existing knowledge of the life cycle of this species, which among gastrointestinal nematodes has a relatively high thermal requirement for development (O'Connor et al., 2007; 2008; Kahn, 2010; Morgan and Van Dijk, 2012).

A limitation of the Q_0 approach is that dynamic changes in farm management are not considered, even though these are likely to be important factors in parasite epidemiology (Morgan and Wall, 2009) and on-farm management (Rahmann and Seip, 2006; Morgan and Van Dijk, 2012). For example, climatic risk might not translate into infection pressure if animals are housed and not grazing at the time. More sophisticated models are likely to be needed for a holistic understanding of parasite infection risk and suitable adaptation responses (Rose et al., 2015). Nevertheless, the simple models presented here could be useful to address strategic questions of the changing epidemiology of parasites in sheep, and to equip farmers with information on risk that could drive effective, targeted treatment (Kenyon et al., 2009; Charlier et al., 2014b). In this sense, transposing parasite prediction models onto GIS platforms offers hope for better links between climate-driven predictions of disease risk and control actions on the ground (Chanda et al., 2012).

While such platforms are increasingly within technical reach due to improvements in computer power and the availability of high-resolution climate data, parasitological data are rarely available, especially without bias (Musella et al., 2014). Moreover, bespoke studies at this scale to validate predictive spatio-temporal models of parasite risk are likely to be prohibitively expensive in most cases, and inherently limited when considering future climate change scenarios. Point validation of key predictions might be more feasible, using models to identify testable hypotheses. However, efficient and meaningful methods of testing model predictions are needed before they can be accepted more widely by stakeholders as useful tools in support of sustainable parasite control.

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Complementary supplement material: detailed definition and parameter estimates for the Q_0 model

The lifecycle model

The Q_0 model was based on the life cycle of *Haemonchus contortus* (Fig. 1). Four key biological processes drive the dynamics observed through time in the lifecycle model. They are: egg production by adult parasites, development of infective larvae (*L3*), chance of ingestion of *L3*, and establishment in the host following ingestion of *L3*. Arrows entering the box represent biological processes that lead to increases in the population of the stage in question, while the arrow leaving the box represent biological process that decrease stage-specific population. State variable abbreviations are given in Fig. 1.

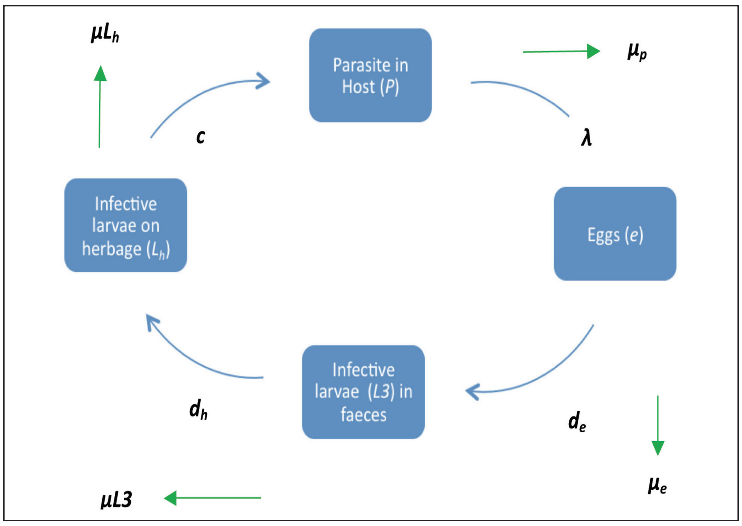

Fig. 1. Flow diagram illustrating the lifecycle model of *H. contortus*. *p* = parasite in host; *L3* = infective larvae in faeces; *c* = ingestion rate of herbage; λ = fecundity; *d* = development and migration rate; L_h =infective larvae on herbage; *e* = egg; μ = mortality rate for each stage.

Adult parasite burden in host (*P*)

The adults within the host lay their eggs and die at a constant rate, as we assumed we are dealing with naïve host population. The rate of change in the adult population in the host(s) is therefore described by:

$$P_t = P_{t-1}\ (1 - \mu_p) + L_{h(t-1)}\ cp_e \qquad \text{(eq. 1)}$$

where μ_p is is the mortality rate of adult worms in the host; λ the fecundity (eggs per female parasite per day); *c* the ingestion rate of herbage (kg per day); p_e the proportion of *L3* establishing; *t* the present time; and *(t-1)* the previous time step (one day).

Eggs (*E*)

The rate of change in the egg population through the time on pasture (per hectare) is described by:

$$E_t = E_{t-1}\ (1 - \mu_e - d_e) + P_{t-1}\ \lambda_h / 2A \qquad \text{(eq. 2)}$$

where *P* signifies adult parasites; *h* host number; *A* the area grazed (hectare); λ: fecundity (eggs per female worm per day); d_e the development rate of the deposited eggs; μ_e the mortality rate of the deposited eggs; *t* present time; and *(t-1)* the previous time step (one day).

Infective larvae in faeces (*L3*)

The rate of change in the population of *L3* in faeces (per hectare) is described by:

$$L3_t = L3_{t-1} (1 - \mu_{L3} - d_h) + E_{t-1}\, d_e \qquad \text{(eq. 3)}$$

where d_e signifies the development rate of the deposited eggs; μ_{L3}: the mortality rate of *L3* in faeces; d_h the migration rate of *L3* out of faeces onto herbage; *t* present time; and *(t-1)* the previous time step (one day).

Infective larvae on herbage (L_h)

The rate of change in population of *L3* on pasture (per kg herbage biomass) is described by:

$$Lh_t = Lh_{t-1} (1 - \mu_{Lh} - c_h / A) + L3_{t-1}\, d_h / b \qquad \text{(eq. 4)}$$

where d_h signifies the migration rate of *L3* out of faeces onto herbage; L_h infective larvae on herbage (number per hectare); μ_{Lh} the mortality rate of L_h; *c* the ingestion rate of herbage (kg per host per day); *b* herbage biomass (kg per hectare); *t* present time; (*t-1*) the previous time step (one day).

Parameter estimation

Field and laboratory studies that provided data on the effects of change in climate on the above parameters were surveyed. Linear or exponential or polynomial regression, as appropriate, was used to determine the slope, intercept, significance of relationship as well as the 95% confidence intervals (CI). The choice of regression for parameterization of any of the variable parameters was determined by which of the three regressions gave a good fit with the greatest statistical significance.

Parameter values

Mean fecundity rate - the daily egg production rate per female worm (λ)

The mean fecundity rate is the daily egg production rate per female worm. Since we are dealing with naïve hosts, studies that provided data on daily mean peak egg production per female worm were included in the estimation of λ (Table 1). λ = 6,431.

Table 1. Values of mean daily fecundity (λ) of *H. contortus* in naive host.

Source	λ	Range
Coyne et al., 1991a	6,582	
Coyne et al., 1991b	7,037	±1337
Gordon, 1958	7,500	5,000-10,000
Dineen and Wagland, 1966	6,334	5163-7504
Coyne and Smith, 1992	4,700	±632
Average	6,431	±1211

Adult worm mortality rate - the daily instantaneous rate per parasite per day (μ_p)

Since we assumed that we are working with a naïve host population, the best estimate for μ_p for the present model was determined from single infection studies with parasites counted at short intervals. Thus data presented in experimental results of Barger and Le Jambre (1988) and Coyne et al. (1991b) were included in parameterization of μ_p (Table 2). Altogether, nine replicates were sourced; they were averaged to arrive at 0.04 as the mean instantaneous mortality rate per worm per day (μ_p) with 95% confidence interval of ±0.037 (Table 2).

Table 2. Values of daily mortality rate of adult worm sourced from relevant studies.

Source	Replicare	Mortality rate	Range
Barger and Le Jambre, 1988	1	0.01	± 0.002
	2	0.036	± 0.005
Coyne et al., 1991a	1	0.0266	±0.0206
	2	0.0210	±0.0170
	3	0.0383	±0.0140
	4	0.0423	±0.0074
	5	0.0696	±0.0167
	6	0.0678	±0.0121
	7	0.0447	±0.0068
Average		0.04	±0.03673

Development rates - the instantaneous daily development rate (d_e)

In order to estimate d_e, studies providing data on the effect of temperature on successful development of 50% of the egg population to *L3* in faecal pellets, were used. Hsu and Levine (1977) reported time to 50% development of eggs to *L3* as a proportion of the maximum number of *L3* recovered. Rose (1963), on the other hand, reported minimum and maximum development times of egg to *L3*. From the data, we estimated d_e by as the mean development time from both minimum and maximum times. However, analysis of data from the former study indicates that the estimated mean times from Rose (1963) do not represent exactly the 50% development of the eggs to *L3*. Nevertheless, inclusion of data from Rose (1963) gave a more sensible model; hence its inclusion in estimating d_e (Table 3). For the present model, d_e for each data point = -ln (π); where π = proportion developed $^{(1/\text{time})}$.

Table 3. Parameter values for estimating daily instantaneous development rates; sourced from Rose (1963), Hsu and Levine (1977).

Temperature (Celsius)	Daily instantaneous development rate, d_e	Source
25.5	0.25	Rose, 1963
20.5	0.0667	Rose, 1963
15.5	0.0476	Rose, 1963
10.5	0.0333	Rose, 1963
20.5	0.12	Hsu and Levine, 1977
25.5	0.225	Hsu and Levine, 1977
30.5	0.235	Hsu and Levine, 1977
35.0	0.25	Hsu and Levine, 1977

Instantaneous development rates were used as estimated in Rose et al. (2015).

Table 3.1. Development rate of eggs - the instantaneous rate per parasite per day (d_e).

Source	Slope	Intercept	Linear Function	P-value	Confidence interval (CI)
Rose (1963) Hsu and Levine (1977)	0.011	-0.097	$y = 0.011T-0.097$ T = temperature	<0.01	Slope: ±0.00161 Intercept: ±0.0385

Migration rate of L3 - instantaneous daily migration rate (d_h)

For the present Q_0, changes in daily environmental conditions at the microclimate level of the herbage are considered crucial determinant of d_h. Data from Van Dijk and Morgan, (2011) were used for parameterization.

Table 4. Parameter values for estimating daily migration rates; sourced from Rose et al., 2015.

Temperature (Celsius)	Daily instantaneous migration rate (Number)
8	0.2458
10	0.2226
15	0.3352
20	0.2547
25	0.1784
33	0.1745

Daily mortality rate of eggs - the instantaneous daily mortality rate of eggs (μ_e)

Data from the studies of Todd (1976a) was used to estimate μ_e for the present model. The study specifically provided the lethal effects of temperature at the lowest and highest extremes that preclude egg development, thereby focusing only on mortality rates. In effect, this leaves a big gap between the two thermal extremes; however, this is not important for the present model, because within this temperature range, eggs would presumably develop before mortality becomes a limiting factor, provided that adequate moisture is available. Proportions of eggs surviving in faeces over time at each temperature were analysed based on the method used by Azam et al. (2012). μ_e for each data point was then estimated using the formula: $-\ln(\pi)$; where π is the proportion that died at each temperature point. All instantaneous rates at each temperature point were combined for the final regression (Table 5).

Table 5. Parameter values for estimating daily instantaneous mortality rates of eggs; sourced from Todd (1976a).

Temperature (Celsius)	Daily instantaneous mortality rates of eggs (number)
4	0.089
4.5	0.378
45	1

Importantly, only exponential regression of all instantaneous rates sourced from Todd (1976a) gave a good fit as well as a statistical significance ($P<0.05$,), hence the choice of the exponential regression for this parameter. It was also possible to reproduce μ_e based on the outcome of Todd (1976a). ANOVA ($F(1, 1) = 0.652$, $P <0.05$). $R^2 = 0.583$ (see Table 5.1).

Table 5.1. Mortality rate of egg - instantaneous rate per parasite per day (μ_e)

Source	Slope	Intercept	Exponential Function	P-value	Confidence interval (CI)
Todd et al., (1976a)	0.042	0.1514	$y = 0.1514e^{0.042T}$	<0.05	Slope: ±0.3655 Intercept: ±0.139

Mortality rate of infective larva in faeces - instantaneous daily mortality rate of L3 (μL_3)

Review of the available literature revealed studies by Todd (1976a,b) as the only relevant studies for estimating μL_3 for the Q_0 model. The two studies provided thermal effects from lowest to highest temperature extremes. Proportions of *L3* surviving in faeces over time at each temperature were estimated based on the methods described in Azam et al. (2012), and μL_3 for each data point was estimated using the formula: -ln (π), where π is the proportion of *L3* that died at each temperature point. All instantaneous rates at each temperature point were combined for the final regression (Table 6).

Table 6. Parameter values for estimating daily instantaneous mortality rates of infective larvae in faeces; sourced from Todd (1976a,b).

Temperature (Celsius)	Daily instantaneous migration rate of eggs (number)
5	0
20	0.16
20	0.175
25	0.06
30	0.165
30	0.18
45	1

Exponential regression of all rates sourced from Todd (1976a,b) gave a good fit with the most statistical significance and was able to reproduce μL_3 based on Todd (1976a,b). ANOVA (F (1, 5) = 9.295; P <0.01). $R^2 = 0.806$ (see table 6.1).

Table 6.1. Mortality rate of *L3* - instantaneous rate per parasite per day (μL_3)

Source	Slope	Intercept	Exponential Function	P-value	Confidence bonus
Todd et al., (1976a,b)	0.1082	0.005	$y = 0.005e^{0.1082T}$	<0.01	Slope: ±0.0227 Intercept: ±0.059

Mortality rate of L3 on pasture - instantaneous daily mortality rate of L3/pasture (μL_h)

Mortality rate of *L3* on pasture is the only parameter in the third term of Q_0 that is climate-driven; thus, the criteria for its estimation was based on including the effects of temperature (μL_{ht}) and rainfall (μL_{hr}).

The temperature parameter estimation on mortality of *L3* on pasture (μL_{ht}) was based on the outcome of studies by Grenfell (1985), who found that the maximum-likelihood estimates of larval mortality rates in faeces and on herbage had the ratio of 3:1. Thus the already estimated L_3 was divided by 3 to arrive at L_{ht} for the present model.

Effect of rainfall on mortality of *L3* on pasture (μL_{br}) accounts also for moisture effects as considered by Banks (1990) and Onyali (1990). Both regard the mortality of *L3* as a function of either dry or wet climate, when temperature is non-limiting. Their conclusion was that rainfall as a source of moisture or wetness exerts significant effect on mortality of *L3* on pasture.

We used a daily geometric survival probability formula (Kao et al., 2000) for daily survival probabilities for dry and wet microclimates on pasture as estimated from Banks (1990) and Onyali (1990). This was done using the t-distribution as explained earlier (Tables 7). The assumption was that if daily survival probability is close to 1, the mortality rate of *L3* on pasture can be determined by subtracting survival probability from 1 (Kao et al., 2000). That is, daily L_{br}, whether dry or wet microclimate = 1 – the daily survival probability. The estimated L_{br} was kept constant for each microclimate type, i.e. dry or wet.

Lack of rainfall in a week (Pweek<1mm)was considered as dry microclimate at the level of *L3* on pasture (Banks et al., 1990; Onyali et al., 1990; Rose et al., 2015) or wet otherwise (Pweek >1 mm).

Table 7. Daily survival probabilities for dry (S_d) and wet (S_w) microclimate at the level of *L3* on pasture, as estimated by Kao et al., (2000).

Source	S_d	S_w
Banks et al., 1990	0	0.873
Banks et al., 1990	0.737	0.937
Onyali et al., 1990	0	0.892
Average	0.246 ± 1.243	0.9006 ± 0.0959

Thus the daily μL_{bt} for dry microclimate = 1 - 0.246 = 0.754, while it = 1 - 0.9006 = 0.099 for wet microclimate.

Therefore, the daily mortality of *L3* on pasture (μ_{lh}) for dry microclimate = daily μL_{bt} + daily μL_{br} = (L_3/3) + (0.754) and for wet microclimate = daily μL_{bt} + daily μL_{br} = (L_3/3) + (0.099).

Standing biomass (b)

The standing biomass is a strong determinant of herbage intake rate per animal; therefore it provides basis to appreciate seasonality of *L3* transmission to grazing sheep. For the present Q_0, standing biomass was estimated as the mean of all data sourced and was set constant (Table 9).

Table 9. Values of standing biomass, *b* (kg of herbage per hectare).

Source	*b*	Comment
Nicol and Thompson, 1982	2000	Dried herbage was used in the spring season of New Zealand
Leathwick et al., 1992	1400	Dried herbage was also used from early summer to mid-winter in New Zealand
Average	1700 (1400-2000)	

Host density (stocking or host density per hectare (H)

We assumed that host density on pasture will remain constant in all climatic and environmental conditions, hence the estimated value for host density was set constant; it was estimated to be 17 (Table 10).

Table 10. Values of host density per hectare of pasture from relevant studies.

Source	*H*	Comment
Suarez and Busetti, 1995	14	Ewes and lambs in extensive farm system during study
White and McConchie, 1976	8.65	Merino wethers in semi-intensive farm system
Brown et al., 1985	11.75	Lambs in semi-intensive farm system
Barlow, 1985	11.25	Ewes and lambs in extensive farm system during study
Miller et al., 1998	8.33	Ewes and lambs in semi-intensive farm system
Waller et al., 1981	30 35	Ewes and lambs in extensive farm system during study
Average	17 (8-35)	

Herbage ingestion rate - herbage intake per weight in kg per host per day (c)

The *L3* population was assumed to be evenly spread over pasture. The herbage ingestion rate was estimated using the formula: daily herbage intake per sheep divided by the available herbage or standing biomass (Kao et al., 2000), and was set constant. Daily herbage or standing biomass = 1,700 (estimated from Nicol and Thompson, 1982; Leathwick et al., 1992) (see Table 9). Daily herbage intake was calculated as 2.975 from the estimates of Paton (1984) and Leathwick et al. (1992) (Table 11). Both rates were also set constant; hence, $c = 2.975 / 1{,}700 \approx 2.0 \times 10^{-3}$ $(2.13 \times 10^{-3} - 2.38 \times 10^{-3})$.

Table 11. Values of herbage intake per weight in Kg per host per day (Leathwick et al., 1992; Paton et al., 1984).

Source	Herbage intake (kg/day)	Comments
Leathwick et al., 1992	1.45 0.725	Lamb Lamb
Paton et al., 1984	0.8	Lamb
Total	2.975	

Probability of larval establishment - daily establishment rate of ingested L3 per ingested infective larvae (p_e)

Since we are working with naïve host populations, data for estimating p_e were sourced from single-infection experiments; however, very few published estimates are available. Barger and Le Jambre, (1988) and Coadwell and Ward, (1981) provide the only ones based on single infections; estimations from these studies were averaged to arrive at a constant p_e (Table 12).

Table 12. Estimates of probabilities of *L3* establishment within host (P_e); from results of single-infection experiments in non-immune sheep.

Source	Herbage intake/Kg/day	Comments
Barger and Le Jambre, 1988	0.59	×/÷ 1.2; single infections of group of sheep with doses of L3 (4,000-16,000)
Coadwell and Ward, 1981 (Barger and Jambre, 1988)	0.83	Lambs, single infection with 25,000 L3.
Average	0.71	Margin of uncertainty: ±0.05

Introduction of rainfall effects into the Q_0 model

Although there is lack of data on rainfall or moisture requirements for the survival and development success of the free-living stages of *H. contortus* we were able to include a workable rainfall function into the model. This was done by the heuristic deduction of rainfall rules from the relevant literature (Onyali et al., 1990; Banks et al., 1990; O'Connor et al., 2006; Wang, unpublished data). These rules provided the threshold of moisture requirement for the survival, development and migration success or failure of the free-living stages, given the time and overlapping cohorts. Essentially, the rainfall rules determine the effects of moist or drought conditions on the availability and transmission potential of the *L3* to grazing host.

Separation of the effects of rainfall from those of temperature in the Q_0 model

Additionally, we were able to utilize the sourced data on the effects of temperature on the availability of *L3* for sheep infection, to estimate all the temperature-driven parameters (Rose, 1963; Todd 1976a,b; Hsu and Levine, 1977; Barger and Le Jambre, 1988; Coyne 1991b; Wang, unpublished data). Thus, making it possible to run the model based only on temperature effects - Q_{0t}. This also gives the basic reproduction quotient model the capability to identify when and where moisture would limit or preclude transmissions of *L3* to the host. Moreover, the objective of a climate-based Q_0 necessitates the inclusion of rainfall effects in the model (Heesterbeek and Roberts, 1994; Robert, 1995; Kao et al., 2000). To this end, the estimation of temperature-based parameters and derivation of the rainfall rule made it possible to separate the effects of temperature from those of moisture on the free-living stages of *H. contortus*. Sources of validation data for the cross-regional comparison of Q_0 with observed haemonchosis are given in Table 13, which provide the data arranged chronologically according to the Koeppen-Geiger climate classification.

Table 13. Details of data sourced for the validation and reliability test of the Q_0 model across different geo-climatic locations.

Location (city country)	Koeppen-Geiger climate classification*	Methods for estimating haemonchosis level	Time period	Sources
Ghana	Tropical rainforest (Af) and Tropical savannah (Aw)	*Post mortem* recovery of adult worms	1994-95	Agyei, 1997
Cuba	Tropical savannah (Aw)	*L3* recovery from pasture	2000-01	Garcia et al., 2006
Mozambique	Tropical savannah (Aw)	Identification of *L3* by cultured faecal eggs	1978-79	Specht, 1982
Nigeria	Tropical savannah (Aw)	*Post mortem* recovery of adult worms	1987-88	Fakae, 1990
The Gambia	Tropical savannah (Aw)	*Post mortem* recovery of adult worms	1990-91	Fritsche et al., 1993
Ethiopia	Tropical rainy (Aw) and Hot semi-arid (Bsh)	*Post mortem* recovery of adult worms	2004	Sissay et al., 2007
Haryana, India	Steppe climates (Bs)	*Post mortem* recovery of adult worms	1977	Gupta et al., 1987
Lahore, Pakistan	Steppe climates (Bs)	*Post mortem* recovery of adult worms	2006-07	Qamar et al., 2009
Western Pampas, Argentina	Steppe climates (Bs)	*Post mortem* recovery of adult worms	1986-87	Suarez and Busetti, 1995
Senegal	Dry desert (Bwh) and Steppe climate (Bs)	*Post mortem* recovery of adult worms	1982-83	Vercruysse, 1985
Hyderabad, Pakistan	Dry desert (Bw)	Identification of *L3* by cultured faecal eggs	2004-05	Al-Shaibani et al., 2008
Punjab	Hot desert climate (Bw)	Identification of *L3* by cultured faecal eggs	Year not given	Jabeen et al., 2000
Faisalabad, Pakistan	Hot dry desert (Bwh)	*L3* recovery from pasture	2000-01	Iqbal et al., 2005
Saudi Arabia	Dry desert (Bwh)	*Post mortem* recovery of adult worms	1991-92	El-Azazy, 1995
Islamabad, Pakistan	Humid subtropical (Cwa; Cfa)	Identification of *L3* by cultured faecal eggs	2005	Chaudary et al., 2007
Zimbabwe	Temperate highland tropical (Cwb; Cwc)	*L3* recovery from pasture (on pasture)	1994	Pandey et al., 1994
Brazil	Maritime temperate (Cfb; Cfc; Cwa)	*Post mortem* recovery of adult worms	1981	Charles, 1989
United Kingdom	Temperate (Cfb; Cfc; Cwb; Cwc)	Identification of *L3* by cultured faecal eggs	2004-05	VIDA, Met Office
Netherland	Marine west coast (Cfb)	*L3* recovery from pasture (on pasture)	2001	Eysker et al., 2005
Greece	Mediterranean (Csa)	*L3* recovery from pasture (on pasture)	1997-98	Theodoropoulos et al., 1998
Naples, Italy	Mediterranean (Csa)	*Post mortem* recovery of adult worms	2005-06	Rinaldi et al., 2009
Turkey	Mediterranean (Csa)	*Post mortem* recovery of adult worms	Year not given	Tinar et al., 2005
Albany, Australia	Mediterranean climate (Csb)	*L3* recovery from pasture (on pasture)	1985	Besier and Dunsmore, 1993
Quebec, Canada	Humid continental mild summer (Dfb)	*L3* recovery from pasture (on pasture)	2007	Mederos et al., 2010
Ontario, Canada	Subarctic (Dfc; Dfb)	*L3* recovery from pasture (on pasture)	2007	Mederos et al., 2010

*Aw = tropical savannah; Bw = hot desert; Bs = hot semi-arid; Cw = subtropical; Cf = oceanic; Cs = Mediterranean; Df = continental.