GLOWORM-FL: a simulation model of the effects of climate and climate change on the free-living stages of gastro-intestinal nematode parasites of ruminants

Hannah Rose[1,2], Tong Wang[1], Jan van Dijk[3], Eric R. Morgan[2,4]

[1]School of Biological Sciences, Life Sciences Building, University of Bristol, Tyndall Avenue, Bristol, UK, BS8 1TQ

[2]Cabot Institute, University of Bristol, Cantocks Close, Bristol, UK, BS8 1TS

[3]Department of Epidemiology and Population Health, Institute of Infection and Global Health, University of Liverpool, Leahurst, Neston, Cheshire, UK, CH64 7TE

[4]School of Veterinary Sciences, University of Bristol, Langford House, Langford, Bristol, UK, BS40 5DU

Corresponding author: Email: hannah.rose@bristol.ac.uk Tel: +44 117 954 1383

Abstract

Gastrointestinal nematodes are important parasites of livestock and wildlife worldwide, causing mortality and morbidity, regulating host populations and threatening food security through reduced productivity of ruminant livestock. A significant part of the life-cycle of most GINs is completed outside of the host. GINs are therefore susceptible to changes in climate, and evidence of climate-driven changes in the phenology of GINs and the seasonal incidence of disease already exists. A modelling framework, GLOWORM-FL was developed to predict changes in the seasonal dynamics of the free-living stages of trichostrongylid GINs on pasture as a first step towards evaluating potential mitigation strategies. The general model framework was parameterised and validated for three GIN species that infect a range of ruminants worldwide: *Haemonchus contortus*, *Teladorsagia circumcincta* and *Ostertagia ostertagi*. The model builds significantly on previous models of GIN population dynamics by incorporating the behaviour of nematodes in response to climate variability, facilitated by recent advances in our understanding of the ecology of GINs. Simulations using historical and predicted future climatic data for a temperate region reveal the potential for an increase in annual infection pressure of *H. contortus* and *T. circumcincta* in small ruminants as increasing temperatures accelerate development and remove constraints on the development of *H. contortus* during the winter months. In contrast, a significant decrease in annual infection pressure is predicted for *O. ostertagi* in cattle due to accelerated development being offset by rapid mortality at higher temperatures. A similar trade-off is predicted during the summer months for *H. contortus* and *T. circumcincta* resulting in complex seasonal dynamics of the availability of infective stages on pasture. These changes could have significant impacts on the seasonal incidence and pathology of infection

by GINs. GLOWORM-FL therefore provides an important tool to predict the seasonal risk of transmission of GINs and will aid in the design of climate-driven, risk-based GIN control strategies.

Keywords: gastrointestinal nematode; climate change; population dynamics; nematode behaviour; ruminant; parasite ecology

1. Introduction

Trichostrongyloid gastrointestinal nematodes (GINs) are a major cause of mortality and morbidity in livestock (e.g. Allonby and Urquhart, 1975), threatening food security via constraints on productivity (Fitzpatrick, 2013). Costs of GINs have been estimated at 84 million pounds sterling (105 million Euros) annually for the sheep industry in the UK alone (Nieuwhof and Bishop, 2007), although effects of infection on farm economics can be complex and difficult to estimate (van der Voort et al., 2013).

Adult trichostrongylid GINs inhabit the gastrointestinal system of a range of host species including ruminants (Allonby and Urquhart, 1975; Morgan et al., 2005), lagomorphs (Newey et al., 2005) and birds (Hudson et al., 1998). Eggs are deposited in the environment in faeces, where they develop to infective larvae, which then move onto herbage. Larvae are ingested by the host during grazing and complete their life-cycle in the host (Anderson, 2000).The development, survival and behaviour of the free-living stages and thus the availability of infective stages for transmission is highly dependent on weather and micro-climatic conditions (Khadijah et al., 2013a; Morgan and van Dijk, 2012; O'Connor et al., 2008, 2007, 2006; Reynecke et al., 2011; Rose, 1963, 1961; van Dijk and Morgan, 2008, 2011). There is evidence that recent increases in temperature in the UK have resulted in changes in the phenology of GINs on pasture (Gethings et al. submitted) and in the incidence of disease due to GIN infection (parasitic gastroenteritis) in livestock (van Dijk et al., 2008). As a result, the potential impact of climate change on GIN-host dynamics is of increasing concern (Rose et al., 2014; van Dijk and Morgan, 2010; van Dijk et al., 2010).

Predicting climate-driven changes in the seasonal availability of free-living GIN infective stages is the first step to evaluating the potential impact of climate change on GIN infections in livestock and wildlife and developing sustainable strategies to control GINs and mitigate any increased transmission risk. These baseline predictions of infection pressure can then be integrated with patterns of host availability to evaluate the seasonal risk of transmission (e.g. Morgan et al., 2006). However, predicting the response of GINs to climate change is complicated by nonlinear relationships and interactions between climate, development and survival (Molnár et al., 2013), and the system necessitates parsimonious predictive models that balance sufficient biological detail with experimentally verifiable parameters (Morgan, 2013) and computational efficiency.

Numerous gastrointestinal nematode models have been developed over previous decades (reviewed elsewhere by Cornell, 2005; Roberts, 1995; Smith and Grenfell, 1994). Many are deliberately simple in order to explore model behaviour and system dynamics (Cornell et al., 2004; Grenfell, 1992; Louie et al., 2005; Roberts and Heesterbeek, 1995). Others include more biological detail in order to address specific questions (Grenfell et al., 1987; Laurenson et al., 2011; Learmount et al., 2006; Leathwick et al., 1995, 1992; Smith et al., 1987). However, climate-dependent life-history parameters that determine the availability of infective stages on pasture are often set at a constant rate (Laurenson et al., 2013). Furthermore, although many models incorporate climate-dependence (Grenfell et al., 1987; Molnár et al., 2013) and stage-specific mortality and development rates, to the authors' knowledge no model explicitly incorporates movement of infective larvae between soil and herbage nor addresses moisture-limitations on migration between faeces and pasture (herbage and soil combined). Detail such as this will become increasingly

important as increases in the frequency of extreme events such as drought and heavy rainfall are predicted into the late 21st century (IPCC, 2013).

The model framework presented here, GLOWORM-FL, builds on the work of Grenfell et al. (1987) and Smith (1990) by incorporating recent advances in our understanding of the behaviour and ecology of GINs on pasture to predict the climate-dependent seasonal dynamics of GIN infection pressure. The model provides a generic framework that can be applied to a range of GIN species. To demonstrate the flexibility of the framework and methods for data-driven parameter estimation, the model is parameterised and validated for three trichostrongylid GIN species - *Haemonchus contortus*, *Teladorsagia circumcincta* and *Ostertagia ostertagi* - and used to simulate the seasonal dynamics of the availability of infective stages on pasture under scenarios of likely climate change, independent of host factors.

The three species of GIN chosen here are of economic importance to the ruminant livestock industry worldwide, but also have a broad host range and infect free-ranging ruminants. The haematophagous abomasal nematode, *H. contortus* is highly pathogenic. Chronic infections in sheep may result in anaemia and death (Allonby and Urquhart, 1975). The abomasal nematodes *T. circumcincta* and *O. ostertagi* are responsible for significant production losses in the ruminant livestock industry (Charlier et al., 2009; Nieuwhof and Bishop, 2007). Anthelmintic resistance is increasingly widespread in all three species in livestock (De Graef et al., 2013; Kaplan and Vidyashankar, 2012; Papadopoulos et al., 2012; Sutherland and Leathwick, 2011) and has been recorded in *H. contortus* in wild deer (Chintoan-Uta et al., 2014). A better understanding of the population ecology of these parasites is

therefore needed to underpin the development of alternative control strategies against the backdrop of climate change and anthelmintic resistance.

2. Materials and Methods

2.1 GLOWORM-FL model framework

The model framework is based on the general life-cycle of the free-living stages of trichostrongylid gastrointestinal nematodes (Figure 1). Eggs (*E*) develop to third stage larvae in the faeces (*L3f*) via the pre-infective larval stages (*L*), and are subject to stage-specific mortality rates (μ_i). As pre-infective larval stages (first stage larvae, L1, and second-stage larvae, L2) are not separated, the model can be applied to trichostrongylids that hatch as first stage larvae (e.g. *Haemonchus* spp., *Teladorsagia* spp. and *Ostertagia* spp.; Anderson, 2000), or second stage larvae (*Marshallagia marshalli*; Carlsson et al., 2013).

$$\frac{dE}{dt} = -(\mu_1 + 2\delta)E + E_{new}C \quad (1)$$

$$\frac{dL}{dt} = -(\mu_2 + 2\delta)L + 2\delta E \quad (2)$$

$$\frac{dL3_f}{dt} = -(\mu_3 + m_1)L3_f + 2\delta L \quad (3)$$

As development from egg to L3 in faeces is divided over two stages, the development rate (δ) is doubled. The framework tracks numbers of overlapping cohorts of nematodes, and so new eggs deposited on pasture (E_{new}) join the pool of existing eggs.

Previous models of GIN free-living stages either model total L3 on pasture and implicitly assume that, once developed, L3 are available for transmission (Grenfell et al., 1987; Learmount et al., 2006), or separate L3 in faeces from L3 on pasture and apply a constant horizontal migration rate (Grenfell et al., 1986; Smith, 1990). Here,

L3 in faeces actively migrate from faeces onto pasture at a climate-dependent horizontal migration rate (m_1).

Once on pasture, L3 can be recovered from both soil/mat layer and herbage. Although Grenfell et al. (1986) included losses of L3 in soil due to soil moisture deficit or wash-down during rainfall in their model, movement between soil and herbage was not considered. Experiments have demonstrated the potential for bi-directional movement of trichostrongylid L3 between soil and herbage (Krecek and Murrell, 1988; Rose and Small, 1985) and that there is random movement between the soil and herbage (van Dijk and Morgan 2011). Therefore, L3 on pasture (*L3p*) are assumed to reside in either the soil and vegetation mat layer (*L3s*) or on herbage (*L3h*). In order to simulate random, bi-directional movement between herbage and the soil reservoir, substrate-specific mortality rates (μ_4, μ_5) are applied to the proportion of larvae estimated to reside in soil and on herbage respectively, dependant on a vertical migration parameter (m_2).

$$\frac{dL3_p}{dt} = -\mu_4\left((1-m_2)L3_p\right) - \mu_5\left(m_2\, L3_p\right) + m_1\, L3_f \quad (4)$$

State variables and parameter definitions are listed in Table 1. The model was implemented in R (R Core Team, 2013) using the *lsoda* function in the *deSolve* package (Soetaert et al., 2010). *lsoda* uses an Adams-BDF (backward differentiation formulae) adaptive integration method that detects the stiffness of the problem throughout the simulation and switches between Adams and BDF integration accordingly (Soetaert et al., 2010). The model returns daily output but the time steps used for integration are not known prior to simulation when using the Adams-BDF integration method. Therefore, time-series of variable climate-dependent rates e.g. temperature-dependent development rates, were generated prior to simulation and

163 introduced by interpolation using the *approxfun* function (Soetaert et al., 2012). New
164 eggs were deposited using the “events” argument of the *lsoda* function (Soetaert et
165 al., 2012). Model output is numbers of individuals per unit area e.g. per hectare, and
166 is therefore independent of herbage density.

167 **2.2 Parameter estimates**

168 The model was parameterised for three trichostrongylid GINs that infect ruminants:
169 *Haemonchus contortus, Teladorsagia circumcincta* and *Ostertagia ostertagi* (Figures
170 2-4; Table 2).

171 **2.2.1 Temperature dependent development and mortality**

172 Temperature-dependent instantaneous daily rates were estimated for development
173 from egg to L3 in faeces and stage- and substrate-specific mortality using data from
174 experiments that reported the proportions of individuals developed (for development
175 rates) or surviving (for mortality rates) at discrete intervals and at a range of constant
176 temperatures (Table 2).

177 Instantaneous daily rates were first estimated for each constant temperature from
178 the reported time to 50% development (D50) or time to 50% mortality (M50)
179 as *-ln(0.5/D50* or *-ln(0.5)/M50*. If these data were unavailable, rates were estimated
180 in one of three ways: 1) using the proportion remaining at a single sampling interval,
181 as *–ln(proportion remaining)/days*; 2) using the mean of the minimum and maximum
182 development or mortality times, or; 3) by linear regression of the transformed
183 proportions of individuals developed or surviving over time as described by Azam et
184 al. (2012). Where 100% mortality was observed within 24 hours, an instantaneous
185 mortality rate of 1 was applied.

Linear models were then fitted to the instantaneous daily rates at a range of temperatures, yielding a regression equation that could be used to estimate daily rates dependent on time-series of observed temperature data (Table 2). For development rates, which increase linearly as a function of temperature, simple linear regression was used. Mortality rates are highest at extreme high and low temperatures, therefore polynomial models were fitted to the log-transformed instantaneous mortality rates. Rates were limited between 0 and 1 where necessary.

Data were only used to estimate the mortality rates of pre-infective stages if the temperatures were low enough to preclude development, or high enough that mortality occurred prior to development to the next larval stage (e.g. Todd et al., 1976). Development of L3 is arrested until they are ingested by the host. Therefore a range of temperatures could be used to estimate the substrate-specific mortality rates of L3.

The mortality rate of L3 in soil (μ_4) for all GIN species was estimated using observations on the mortality of L3 in water, which for *H. contortus* and *T. circumcincta*, provided point estimates of instantaneous daily mortality rates similar to those reported by van Dijk and Morgan (2011) in soil at 20-24°C (Figures 2-3).

Exposure to UV irradiation increases the mortality of trichostrongyloid L3 in water (van Dijk et al., 2009) and the estimates of mortality in soil (Table 2; van Dijk and Morgan, 2011) are considerably lower than estimates of mortality on pasture (Grenfell et al., 1986). Therefore it is assumed that the mortality rate of L3 on herbage is higher than in soil, and the mortality of L3 in faeces (μ_3) was used as a proxy for L3 mortality on herbage (μ_5; Table 2).

No data were available to estimate the mortality of pre-infective larvae (μ_2) and L3 in faeces (μ_3) for *T. circumcincta* and *O. ostertagi*, Therefore the same mortality rate was used for eggs (μ_1) and pre-infective larvae (μ_2; Table 2). To estimate L3 mortality in faeces the temperature-dependent mortality of *O. ostertagi* in water (used to estimate μ_4) was compared with point estimates of mortality of *O. ostertagi* and *Cooperia oncophora* in cow manure (Persson, 1974a). The instantaneous daily mortality rates at 20°C and 3°C were estimated using Persson's data. As there was significant variability between sampling intervals the instantaneous mortality rate was calculated for each sampling interval and the mean estimated from these rates. Based on these analyses L3 mortality in soil is 4.9-18.5 times lower than in faeces. Therefore, in the absence of data to directly estimate the mortality rate of *T. circumcincta* and *O. ostertagi* L3 in faeces, it is estimated that $\mu_3 = 10\mu_4$, within the limits of 0 and 1 (Figures 3-4).

2.2.2 Moisture limitations and differences between host species

Moisture limitations on the availability of GIN infective stages are primarily mediated through changes in faecal moisture content (FMC; Mauleon and Gruner, 1984; Rossanigo and Gruner, 1995). There are significant differences in faeces structure and drying rates between host species. Sheep faecal pellets tend to dry rapidly following deposition, whereas the decrease in cow pat FMC is more gradual (Mauleon and Gruner, 1984). It is therefore necessary to not only parameterise the model for different nematode species, but also different host species. Here, we consider moisture limitations on *H. contortus* and *T. circumcincta* infecting sheep or other ruminants with a similar faecal pellet structure, and *O. ostertagi* infecting cattle.

2.2.2.1 Moisture limitations on development success

In addition to temperature limitations, development success (the proportion of eggs that develop to L3) is also a function of faecal moisture content (Rossanigo and Gruner, 1995). To impose faecal moisture limitations on development and mortality of *H. contortus* and *T. circumcincta* without explicitly modelling FMC, cumulative precipitation divided by cumulative potential evapotranspiration (referred to as cumulative P/E) is estimated for a species-specific critical period following deposition of eggs after O'Connor et al. (2008), who observed a strong positive relationship between cumulative P/E and the FMC of sheep faecal pellets. If cumulative P/E<1 then the number of new eggs (E_{new}) entering the pool of eggs in faeces is reduced by an amount specified by the correction factor parameter, *C*.

O'Connor et al. (2008) observed a significant decrease in the development success of *H. contortus* where cumulative P/E fell below 1 within 4 days of deposition of eggs. Khadijah et al. (2013a) recovered maximum *H. contortus* L3 from faecal pellets and soil when simulated rainfall was applied between -1 and 2 days post deposition of faeces containing eggs and concluded that faecal moisture 48-72 hours post deposition was important for development success. No L3 were recovered from un-watered controls. Similar data were not available for *T. circumcincta.* However, Khadijah et al. (2013a) note that for *Trichostrongylus colubriformis*, faecal moisture in the period 72-96h post deposition is important for development success. This period is likely to be extended for *T. circumcincta* which is more resistant to desiccation than *T. colubriformis*. A lower faecal moisture content (FMC) threshold was observed for *T. circumcincta* development (yielding ≥1 L3 per 100 eggs) than *T. colubriformis* (25% and 35% respectively; Rossanigo and Gruner, 1995). The critical periods for *H. contortus* and *T. circumcincta* were therefore identified as 4 days and 7 days post deposition of eggs respectively (Khadijah et al., 2013b; O'Connor et al.,

2008). The cumulative P/E for development success is referred to as P/E_4 for *H. contortus* and P/E_7 for *T. circumcincta*.

A protective surface crust forms on cow pats soon after deposition. It is therefore assumed that moisture is not limiting for GIN development within cattle faeces at lower FMCs (Rose, 1961).

2.2.2.2 Moisture limitations on the translation of L3 onto pasture

Laboratory observations on the migration of *H. contortus* and *T. colubriformis* L3 indicate that, similar to development success, moisture limitations on horizontal migration are mediated by faecal moisture content, which varies as a result of interacting microclimatic factors (Khadijah et al., 2013a, 2013b; O'Connor et al., 2008, 2007; van Dijk and Morgan, 2011). Few data were available to estimate the temperature- and moisture-dependent horizontal migration rate of infective larvae from faeces onto pasture. Therefore, data in the published literature were supplemented with laboratory experiments to derive heuristic estimates for horizontal migration under: 1) optimal moisture conditions (sufficient rainfall); 2) sub-optimal moisture conditions (insufficient rainfall but sufficient FMC) and; 3) moisture-limiting conditions (low FMC and insufficient rainfall).

Horizontal migration of GINs has been observed from cow pats following 1.6mm of simulated rainfall (Grønvold and Høgh-Schmidt, 1989) and from sheep faecal pellets following 2mm of simulated rainfall (this study). Furthermore, horizontal migration rates of *H. contortus* were not significantly influenced by the amount of rainfall between 4mm and 8mm (Wang et al., 2014). Therefore, optimal moisture was defined as days where total precipitation ≥ 2mm.

A daily horizontal migration rate of 0.06 (S.D. 0.057) applied for *O. ostertagi* based on the number of L3 recovered by Grønvold and Høgh-Schmidt (1989) from within and outside of cow pats after 1.6-1.7mm simulated rainfall was applied to pats with FMCs of 54-66%.

To estimate the daily horizontal migration rate for *H. contortus* and *T. circumcincta* faeces containing either *H. contortus* or *T. circumcincta* eggs provided by Moredun Research Institute, Edinburgh, UK were incubated at 20°C for 7 days and then allowed to dry at room temperature for varying amounts of time to obtain pellets with variable initial faecal moisture content (FMC). Three replicates of 3g (~6 pellets) were subjected to approximately 2mm simulated rainfall and after 24 hours L3 that had migrated out of faeces and L3 remaining in the faeces were recovered and enumerated (Wang et al., 2014). The recovery efficiency of extra-pellet and intra-pellet L3 were determined to be 84% (S.D. 3%) and 74% (S.D. 7%) respectively by placing a known number of L3 in the cup used to contain L3 that had migrated out of faeces (Wang et al., 2014) and seeding faeces with a known number of L3. The weight of each pellet was recorded before and immediately after the rainfall event, and after drying in an oven, to estimate the FMC at each stage.

The proportion of L3 that had migrated out of faeces was calculated as: extra-pellet L3/(extra-pellet L3 + intra-pellet L3), corrected for recovery efficiency. Mean daily horizontal migration rates of 0.25 (S.D. 0.11) and 0.21 (S.D. 0.44) were observed for *H. contortus* and *T. circumcincta*. FMCs prior to rainfall were 3-61% (*H. contortus*) and 7-34% (*T. circumcincta*), increasing to 45-73% (*H. contortus*) and 39-56% (*T. circumcincta*) after simulated rainfall.

O. ostertagi L3 were only observed on the surface of experimental pats that had been watered (Grønvold and Høgh-Schmidt, 1989) suggesting that rainfall is required to moisten the protective surface crust sufficiently to allow migration. Therefore, estimates of horizontal migration of *O. ostertagi* under sub-optimal moisture conditions were not considered. In contrast, small numbers of extra-pellet *H. contortus* and *T. colubriformis* L3 have been recovered in the absence of rainfall (O'Connor et al., 2008; Wang et al., 2014). Therefore a 4- and 7-day trailing cumulative P/E rule was applied to *H. contortus* and *T. circumcincta* respectively to characterise sub-optimal conditions, extrapolated from the observations of O'Connor et al. (2008) and Khadijah et al. (2013b) on the effect of cumulative P/E on FMC and development success. Sub-optimal days were defined as days where total precipitation<2mm, and trailing cumulative P/E≥1. The species specific trailing cumulative P/E values for migration are referred to as P/E_{-4} for *H. contortus* and P/E_{-7} for *T. circumcincta*.

An estimated horizontal migration rate of 0.051 for *H. contortus* under sub-optimal moisture conditions was derived from observations by O'Connor et al. (2008), where 30% of L3 migrated out of faeces within a 7 day period in the absence of rain but following a period of simulated rainfall in the preceding 7 days. This is consistent with the observed mean migration rate of 0.057 (S.D. 0.027) for *H. contortus* maintained under high relative humidity of 98% and FMC of ~60% (Wang et al., 2014).

To estimate the corresponding rate for *T. circumcincta* the instantaneous daily migration rate of *H. contortus* L3 estimated from data provided by Wang et al. (2014) was compared with the instantaneous daily migration rate of *T. circumcincta* estimated from an unpublished experiment conducted concurrently with the experiment of Wang et al. (2014) and using identical methods. These experiments

show that under optimal moisture conditions the instantaneous daily migration rate of *T. circumcincta* is 49% that of *H. contortus.* Ninety-nine percent (S.D. 0.4) of *H. contortus* L3 had migrated out of faeces within 7 days (Wang et al. 2014), compared with 91% (S.D. 6.8) of *T. circumcincta* L3, giving instantaneous daily horizontal migration rates of 0.71 and 0.35 respectively. Thus the estimated instantaneous daily migration rate for *T. circumcincta* where moisture is sub-optimal is 0.051*0.49 = 0.025 (Table 2).

Finally, a horizontal migration rate of 0 was applied for all GIN species on moisture-limited days where P/E<1 and total precipitation<2mm.

2.2.3 Migration between soil and herbage

Crofton (1948) observed seasonal patterns in the vertical migration of *Trichostrongylus retortaeformis* L3 on pasture where fewer L3 were recovered from the upper herbage layer in winter than in summer. It is likely that interacting climatic and other abiotic variables including temperature, moisture, biomass composition and light drive this seasonality (Amaradasa et al., 2010; Callinan and Westcott, 1986; Crofton, 1948; Dusenbery, 1989; Ogbourne, 1973; Rees, 1950; Saunders et al., 2000; Silangwa and Todd, 1964; van Dijk et al., 2009). However, the majority of studies have sampled only a superficial layer of soil (e.g. Crofton, 1948; Rees, 1950) and therefore could underestimate the proportion of pasture L3 in soil relative to L3 on herbage. Mesocosm experiments (e.g. Callinan and Westcott, 1986; Knapp-Lewitzke et al. in preparation) offer an alternative to ensure more complete sampling of L3 in soil. The temperature-dependent proportion of trichostrongylid L3 expected on herbage and in soil was estimated by fitting a second order polynomial regression

353 to the log transformed proportion of total *Teladorsagia* and *Trichostrongylus* spp. L3
354 recovered from herbage (Callinan and Westcott, 1986). In the absence of suitable
355 species-specific data, the same estimate was used for all trichostrongylid GIN
356 species, subject to validation. The observation at 20°C was omitted from analysis as
357 the decrease in L3 recovered from herbage was inconsistent with observations of L3
358 availability on pasture where the percentage of L3 recovered from herbage tends to
359 increase with increasing mean soil temperature between approximately 8-22°C
360 (Callinan, 1979, 1978a, 1978b).

361

362 **2.3 Model validation**

363 Laboratory observations on the development success of *T. circumcincta* and *O.*
364 *ostertagi* (Rossanigo and Gruner, 1995) and field observations on the development
365 time and development success of *H. contortus* (Rose, 1963) and *O. ostertagi* (Rose,
366 1961) in a temperate region were used to validate model predictions of development
367 and survival in faeces. Rossanigo and Gruner (1995) recorded the development
368 success of various GIN species in faeces incubated at a range of constant
369 temperature while maintaining optimal moisture conditions. Rose (1963, 1961)
370 recovered L3 from faeces containing eggs that had been deposited at monthly
371 intervals on pasture in South East England where the GINs were exposed to variable
372 temperatures and moisture conditions. The model was initialised with 100 eggs and
373 simulations were run using either the constant temperatures tested (Rossanigo and
374 Gruner, 1995) or time series of daily air temperatures obtained for the study location.
375 Meteorological data from Wisley weather station (Ordnance Survey grid reference:
376 TQ062579), approximately 10km from the Central Veterinary Laboratories,

Weybridge, where Rose's (1963) observations were made, were obtained from the British Atmospheric Data Centre (badc.nerc.ac.uk). The same data were not available for the time period of observations made by Rose (1961). Therefore, meteorological data were obtained from the E-OBS gridded dataset (lat/lon: 51.355°N, -0.496°E; Haylock et al., 2008). Potential evaporation (mm/day) was estimated from mean air temperatures using the Hamon method (Xu and Singh, 2001). Two simulations were run for each monthly deposit using mean daily temperature and linear fluctuations between minimum and maximum daily temperature to determine whether mean air temperature is sufficient to predict development when temperatures are close to the minimum threshold for development. Horizontal migration, m_1, was set to 0 to prevent migration out of faeces.

Field observations of *H. contortus* and other trichostrongylid (*Trichostrongylus/Teladorsagia* spp.) L3 over winter on naturally contaminated pasture in the absence of continued grazing by livestock (Wilkie et al. submitted) were used to validate the predicted dynamics of *H. contortus* and *T. circumcincta* L3 availability on herbage. Temperature data for the observation period were obtained from Yeovilton weather station (Ordnance survey grid reference: ST549231), approximately 60km from the farm where observations were made from the British Atmospheric Data Centre. The initial number of L3 recovered from herbage at the start of the observation period and the vertical migration parameter, m_2, were used to estimate the corresponding initial number of L3 expected in soil. All other initial values were set to 0. For each simulation the daily number of L3 on herbage is a product of the daily number of L3 on pasture, *L3p*, and the vertical migration parameter, m_2.

To determine whether the additional complexity of the pasture component of the GLOWORM-FL model was justified, simulations using an existing model for *H. contortus* (Smith, 1990) were also validated using Wilkie's (submitted) data as described above.

For each validation dataset and corresponding simulations, model fit was assessed using the residual sum of squares (RSS; Mayer and Butler, 1993) and linear regression through the origin. An intercept of 0 and slope of 1 would indicate perfect correspondence between model output and observations, therefore a regression through the origin with a slope that is not statistically significantly different from 1 indicates a good model fit. It is assumed that the slope is not statistically significantly different from 1 if the 95% confidence interval (estimated as the coefficient ±(2 x standard error of the coefficient) includes 1.

2.4 Climate change simulations

The validated model was run using mean daily temperature and total daily precipitation data from the atmospheric dataset provided by the Coupled Model Intercomparison Project Phase 5 (CMIP5; Taylor et al., 2012) to predict the potential impact of current climate change predictions on the seasonal availability of L3 on pasture (infection pressure). Simulations ran for 30-year time periods using either historical climatic data for the period 01/12/1969-30/11/1999 (representative of current climate) or a high emissions scenario (Representative Concentration Pathway 8.5; RCP8.5) for the period 01/12/2070-30/11/2100, from the HadGEM2-ES model output (ensemble r1i1p1) developed and run by the Met Office Hadley Centre (Collins et al., 2011; Martin et al., 2011). Characteristics of the RCP8.5 scenario include high greenhouse gas emissions, a high rate of population growth, a

dependence on fossil fuel and global CO_2 concentrations of ~950ppm by 2100 (van Vuuren et al., 2011). For comparison, record CO_2 concentrations of over 400ppm were observed at the Mauna Loa observatory in May 2014 (Tans, 2014).

Time series of mean daily air temperature and total daily precipitation were extracted for a grid cell in North Somerset in South West England, UK. This area is of particular interest as recent climate change has been associated with an increase in diagnoses of parasitic gastroenteritis in the region (van Dijk et al., 2008).

One hundred new eggs (E_{new}) were added daily to simulate a scenario of continuous grazing and host infection without making assumptions about management or seasonal changes in intensity of infection/nematode egg output. The first year of simulation was discarded as L3 accumulated on pasture throughout the first year. Output is presented as annual time series of daily mean numbers of L3 on pasture, calculated using the remaining 29-year output disaggregated into annual time series.

The area under curve (AUC) was calculated for each year using a trapezoid function in R to estimate the annual infection pressure under the historical and future climate scenarios. Wilcoxon rank sum tests were used to compare scenarios for each GIN species (Figure 5).

3. Results

3.1 Model validation

Overall the model was able to reproduce the observed development times, development success, and dynamics of L3 on pasture (Table 3), demonstrating the potential for a generic framework such as GLOWORM-FL to be adapted to suit different GIN and host species.

A slope marginally greater than 1 suggested that there was a tendency to under-predict the development success of *T. circumcincta* and *O. ostertagi* at constant temperatures between 5°C and 35°C compared with laboratory observations (Table 3).

The model performed well when tested against field observations of *H. contortus* and *O. ostertagi* development and survival in faeces (Table 3) demonstrating that the models, parameterised using laboratory data, transferred well onto conditions observed in the field. The range of mean air temperatures during the observation periods was -3.9 to 24.7°C (Rose, 1963) and -2.5 to 23.2°C (Rose, 1961). The range of total daily precipitation during the observation periods was 0-31.2mm (Rose, 1963) and 0-23.2mm (Rose, 1961).

The predicted dynamics and numbers of *H. contortus* and *T. circumcincta* L3 on pasture fitted observations well, replicating the initial decrease in L3 density on herbage followed by an increase, despite no further contamination of pasture (Figure 6; Table 3). This seasonal variability in L3 on herbage can be explained by the vertical migration of L3 between soil and herbage; a model using only a temperature-dependent mortality rate and not considering movement between the soil and

herbage was not able to replicate these dynamics. The range of mean daily air temperatures during the observation period was -3.05 to13.7°C.

The GLOWORM-FL model, validated using observed numbers of *H. contortus* on pasture, outperformed a previously published, less complex model (Table 3; Figure 6).

The performance of models using minimum and maximum or mean daily temperatures varied dependent on the validation dataset (Table 3) and in most cases both models gave similar output. However, models using minimum and maximum daily temperatures performed poorly against observation of *O. ostertagi* development in the field (Table 3). Therefore mean temperatures were used for all subsequent simulations.

3.2 Climate change simulations

At the chosen test location in South West England, UK, the HadGEM-ES model predicts warmer wetter winters and warmer, drier summers during 2070-2100 under the RCP8.5 high emissions scenario, compared with the historical period of 1969-1999. A mean increase in mean air temperature of 4.57°C (S.D. 1.91°C) is predicted by 2070-2100. The increase is greatest during the summer months with a maximum of 8.65°C increase predicted during July and a minimum of 1.49°C increase predicted during March. A mean decrease of 0.03mm (S.D. 1.09mm) in mean daily rainfall is predicted under the RCP8.5 scenario, with an increase of up to 3.02mm during the winter period and a decrease of up to 3.06mm during the summer period. The change in seasonal temperatures and rainfall resulted in an increase in predicted development rate throughout the year whereas mortality rates decreased during the winter and increased during the summer. The pattern of moisture-

limitation on development success and horizontal migration of *T. circumcincta* and *H. contortus* was similar under both scenarios. Although the patterns of change in life-history parameters were similar, the magnitude of change was species dependent, resulting in differing seasonal patterns of L3 on pasture.

There was a significant predicted increase in annual infection pressure for both *H. contortus* ($W=47$, $p<0.001$) and *T. circumcincta* ($W=95$, $p<0.001$; Figure 5) under the RCP8.5 scenario compared with historical climatic data. Mean air temperature was regularly higher than the predicted lower threshold for development of *T. circumcincta* (4.46°C) when both historical and RCP8.5 data were used and development was possible year round. However, the number of days where development was possible increased from 328 to 360 (the HadGEM-ES model was run on a 360 day year and therefore 360 represents the entire year). The increase in temperatures predicted under RCP8.5 therefore resulted in increased development rates year-round for *T. circumcincta*. In contrast, very little *H. contortus* development is completed over winter when using historical climatic data as the mean air temperature rarely rises above the predicted threshold for development of 9.17°C. Therefore, the increase in temperatures predicted under RCP8.5 not only results in an increase in development rate but also a lengthening of the season during which development is possible. The period during which mean daily temperatures exceeded the development threshold for *H. contortus* was extended by 3.3 months from 188 days between March and September under historical climate to 258 days between February and December under RCP8.5. A corresponding decrease in mortality rates during the winter results in an overall increase in infection pressure over the winter period, extending into early summer. Further increases in temperatures during the summer result in increased mortality which offsets the

increased development rate and results in a decrease in the number of L3 on pasture, below numbers predicted using historical data (Figure 7).

A similar pattern of summer mortality is predicted for *O. ostertagi* (Figure 7). When using historical climatic data, there is a small increase in L3 on pasture during the spring as temperatures exceed the predicted threshold for development of 7.44°C, but the large number of L3 predicted on pasture is fairly consistent throughout the year due to low mortality rates. However, there is a significant decrease in annual infection pressure when using the RCP8.5 climatic data, compared with predictions using historical data ($W=95$, $p<0.001$). The period during which mean daily temperatures exceeded the development threshold for *O. ostertagi* was extended by 4.6 months from 216 days between March and October under historical climate to 347 days throughout the year under RCP8.5, but this is offset by significant increases in mortality rates between May and November depleting the reservoir of L3 in faeces and soil.

4. Discussion

The model presented here consolidates advances in our understanding of the ecology and behaviour of gastrointestinal nematode free-living stages with the numerous existing models developed to simulate the population dynamics of GINs in ruminant livestock. Previous models were species-specific (Grenfell et al., 1986; Smith, 1990), restricted to livestock ruminants (Learmount et al., 2006), and constrained by the available data at the time they were developed. GLOWORM-FL builds significantly on these models to incorporate the active movement of GINs between substrates, and substrate-specific mortality rates, in addition to explicitly climate-dependent life-history parameters. Comparison of the output of GLOWORM-FL with an example of a preceding model that did not consider nematode behaviour with field observations confirmed that the additional complexity significantly improved model predictive performance. This is probably because the majority of L3 are sequestered in the soil at any one time (Callinan and Westcott, 1986; Silangwa and Todd, 1964; van Dijk and Morgan, 2011), and emerge onto herbage when climatic conditions allow. Therefore, soil should not be overlooked as a significant source of infection, acting as a reservoir for L3 that can recolonize herbage (van Dijk and Morgan, 2011). For the same reason, absence of L3 on herbage should not be interpreted as evidence for absence of GINs.

An additional motivation for the development of the model was that characteristics relevant to the epidemiology of GINs are similar between different livestock systems and wild ruminants (Rose et al., 2014) and there is evidence of transmission where livestock and wildlife meet or share ranges (Chintoan-Uta et al., 2014; Morgan et al., 2007). There is therefore a need for a common framework that can be applied to a range of GIN and host species. The GLOWORM-FL model framework was

parameterised and successfully validated using data available in the literature for three GIN species that are economically important parasites of livestock worldwide but also infect free-living ruminants (Morgan et al., 2005). Due to their economic importance, research on these species spans decades, thus providing sufficient data for parameter estimation. There were some gaps in the available data and therefore these species also provided an opportunity to demonstrate how the model can be successfully adapted by drawing on similarities between GIN species and robust validation exercises.

GINs are a global constraint on livestock production (Nieuwhof and Bishop, 2007; Perry and Grace, 2009). The increasing prevalence of anthelmintic resistance worldwide (Kaplan and Vidyashankar, 2012) and the threat of altered seasonal patterns of transmission due to climate change (Gethings et al. submitted; Molnár et al., 2013; van Dijk and Morgan, 2010; van Dijk et al., 2008) necessitate the development of alternative control strategies (Krecek and Waller, 2006). It may be possible to control the magnitude of exposure to GINs and therefore intensity of infection and production losses, for example by altering management practices to avoid grazing during periods of high risk or targeting treatments according to risk of exposure or suitability for development of free-living stages. To do this, understanding the population ecology of GINs and predicting the seasonal dynamics of infection pressure is fundamental.

GLOWORM-FL provides a tool to aid in the development of climate-based GIN control methods. The model can be used to track pasture contamination and evaluate the resultant climate-dependent infection pressure under a range of management and climate scenarios. Here, its use is demonstrated using climatic data representative of recent historical climate and climate expected under the

582 IPCC's RCP8.5 scenario. Climate-driven changes in the seasonal availability of L3
583 on pasture are likely to become increasingly important in the dynamics of GIN
584 infection, particularly where host behaviour or farm management is slow to adapt in
585 response to the change. In some cases, this may lead to an increase in disease (van
586 Dijk et al., 2008) whereas under different circumstances climate-driven changes may
587 decrease exposure to infection, as has apparently been the case for *Nematodirus*
588 *battus* infections in lambs in some parts of the UK (Gethings et al. submitted). A
589 better understanding of the seasonal dynamics of infection pressure will be key to
590 the future of sustainable GIN control in livestock and could also benefit the
591 management and conservation of wild ruminants.

592 Using historical climatic data, large numbers of *O. ostertagi* L3 were predicted year
593 round on pasture due to low mortality rates over winter and a turnover of L3 between
594 April and November when development rates increase and compensate for losses
595 due to the increased mortality rate. This suggests that the observed patterns of
596 ostertagiasis in calves in Europe (Williams et al., 1993), where peak worm burdens
597 are observed towards the end of the grazing season, are driven by cumulative
598 exposure to L3 on pasture and management or host factors as opposed to seasonal
599 variability in infection pressure (Höglund et al., 2013; Roberts and Grenfell, 1992).
600 Under the RCP8.5 climate scenario and a constant input of eggs, a decrease in *O.*
601 *ostertagi* infection pressure is predicted throughout the year due to significant
602 increases in predicted mortality rates depleting the reservoirs of infective stages in
603 faeces and on pasture. Although a reduction in the magnitude of exposure to
604 infective stages is favourable, there may also be an adverse impact on the
605 development of immunity through reduced exposure to L3 (Ploeger et al., 1995).
606 However, since the epidemiology of *O. ostertagi* infection is largely driven by

607 management and host factors (Höglund et al., 2013; Roberts and Grenfell, 1992),
608 altered management strategies in response to climate change may negate the
609 change in seasonal availability of L3 on pasture predicted here.

610 The seasonal incidence of *H. contortus* infection is primarily climate-driven, and the
611 pattern predicted here for South West England using the historical climatic data
612 broadly mirrors the seasonal diagnoses of haemonchosis in sheep in the region (van
613 Dijk et al., 2008). The implications of this for the control of haemonchosis in livestock
614 are that predicted changes in L3 on pasture are likely to result in similar changes in
615 the seasonal incidence of haemonchosis. The predicted pattern of infection pressure
616 for *T. circumcincta* when using historical climatic data also reflects patterns of
617 seasonal diagnoses (van Dijk et al., 2008), indicating a degree of climate-
618 dependence in the epidemiology of *T. circumcincta* infection in sheep in South West
619 England.

620 An increase in temperature during the winter months was predicted, resulting in an
621 increase in infection pressure for both *H. contortus* and *T. circumcincta* due to a
622 corresponding increase in development rates. Development of *T. circumcincta* is
623 possible throughout the year in South West England. In temperate regions *H.*
624 *contortus* survival on pasture over winter is poor and there is very little development
625 of eggs deposited on pasture as temperatures fall below the development threshold.
626 However, *H. contortus* is able to survive the winter period as arrested larvae within
627 the host (Waller et al., 2004). The increase in temperatures predicted here for South
628 West England, extends the period where the development of *H. contortus* is possible
629 and could have significant short- and long-term impacts on the epidemiology of *H.*
630 *contortus* in temperate regions. In the short-term, the increase in infection pressure
631 throughout the year will result in year-round transmission. In the long-term, *H.*

contortus may adapt in response to the reduced selection pressure for arrested development (hypobiosis) in the host, potentially resulting in a decreased propensity to arrest. Using a series of mathematical models, Dobson and Hudson (1992) showed that hypobiosis decreases the basic reproductive rate (R_0) of trichostrongylid nematodes. Gaba and Groubière (2008) built on the work of Dobson and Hudson and further demonstrated the potentially destabilising effect of hypobiosis on GIN population dynamics as the mortality rate of the free-living stages is decreased. Therefore, hypobiosis would not be favoured when climatic conditions render it unnecessary.

The predicted increase in the availability of *H. contortus* and *T. circumcincta* L3 on pasture during the spring under the RCP8.5 scenario is a concern as this coincides with peak lambing/kidding and peak parturition in many wild ruminants. Therefore, naïve individuals may experience a much greater challenge early in the grazing season under this scenario of climate change. Ewes experiencing a breakdown in immunity to gastrointestinal nematodes during pregnancy and lactation (Houdijk et al., 2001) will also experience a greater challenge . For example, an increase in *H. contortus* infection pressure during the spring could result in more acute haemonchosis in naïve individuals and increased pasture contamination early in the grazing season. These effects may be magnified by management and host factors. The current model considers a scenario of constant pasture contamination. However, pasture contamination may increase during the spring reproductive period due to the periparturient rise (PPR) in faecal egg counts observed in reproducing animals, which is due to the maturation of hypobiotic larvae resulting from a complex of factors thought to result in a reduction in immunity during pregnancy and lactation (Falzon et al., 2013; Gibbs and Barger, 1986; Houdijk et al., 2001).

A decrease in infection pressure is predicted during the summer months for all species tested as a result of a trade-off between increased development and increased mortality rates. As discussed for *O. ostertagi*, reduced exposure to L3 may impact on the development of immunity. However, these reductions may be dampened by increasing worm burdens in the host and therefore increased pasture contamination throughout the grazing season. Furthermore, there is potential for parasite adaptation in response to decreased transmission and the impact this has on host immunity. For example, nematode fecundity may be negatively associated with host immune response as suggested by the negative correlation between adult *T. circumcincta* length and immune response (mucosal and serum IgA against L3 and L4), and the positive correlation between worm length and number of eggs in (nematode) utero in artificially infected lambs (Stear et al., 1995). Integrating the GLOWORM-FL framework with models of the parasitic stages, host immunity (e.g. Grenfell et al., 1987) and parasite adaptation will allow the impact of changes in the seasonal exposure to L3 on the potential pathogenesis of infection and subsequent population dynamics of parasites on pasture to be explored.

Validation was successful for all three species tested, not only validating the model structure but also demonstrating that gaps in parameter estimates can be addressed using data from other species, that parameter estimates derived from laboratory observations perform well under conditions experienced in the field, and that data obtained from the nearest weather station can be used in the absence of local meteorological observations.

In some cases, linear regression of observations against model predictions was significant, but the slope of the regression was marginally different from 1, indicating systematic bias in the output. However, in most cases the error was within the range

682 expected from factors such as trait variation (Troell et al., 2006; van Dijk and
683 Morgan, 2010), measurement error (Persson, 1974b) and uncertainty arising from
684 model structure.

685 Simulations using mean daily temperature data outperformed those using minimum
686 and maximum data. Minimum and maximum daily temperature data were used to
687 test whether fluctuations above and below the development thresholds were
688 important in predicting the population dynamics free-living GINs. At certain times of
689 year the mean temperature may be above the threshold for development, but if the
690 minimum temperature falls below the threshold there is potential to over-predict the
691 development rate using only mean temperatures. Conversely, if the mean
692 temperature is below the threshold but the maximum falls above the threshold, then
693 models may fail to predict development at all. It was therefore surprising that
694 allowing temperatures to fluctuate between the minimum and maximum daily values
695 did not improve model performance.

696 Discrepancies between meteorological observations and microclimatic conditions
697 may account for the superior performance of simulations using mean daily air
698 temperatures. Recent studies have demonstrated the importance of microclimatic
699 factors in determining GIN abundance under controlled conditions (Khadijah et al.,
700 2013b; O'Connor et al., 2008; Wang et al., 2014). In the field, temperature and
701 moisture fluctuations in faeces may be buffered by the soil beneath and surrounding
702 herbage. This buffering effect may also explain discrepancies between model
703 predictions and observations e.g. the model underestimated the time to development
704 of *H. contortus* L3 observed by Rose (1963) during April and October regardless of
705 whether minimum-maximum or mean temperatures were used. Soil temperature
706 data were not available for use in these validation exercises but may better reflect

the microclimate around faeces. Where possible, further validation should also include soil temperature.

The model was validated using observations made in a temperate region, with temperatures ranging between - 4°C and 25°C. However, temperatures of up to 39.2°C were predicted under the RCP8.5 scenario and therefore some simulations projected beyond the range of the conditions used for validation. *H. contortus* and *T. circumcincta* simulations using climatic data for the RCP8.5 scenario showed that high temperatures may result in counter-intuitive decreases in the availability of L3 due to a trade-off between increased mortality and development rates. Uncertainty in climate change simulations due to projections outside of the range of observed data could be reduced by repeating validation using data from regions with current climatic conditions similar to those predicted under the chosen climate change scenario.

The development of parsimonious mechanistic models is inevitably a compromise between biological realism, complexity and the availability of data for parameter estimation. Here we have used observations on mortality of L3 in water to estimate mortality rates for L3 in soil. Although these estimates are similar to published observations of L3 mortality in soil (van Dijk and Morgan, 2011) and the model was able to predict the survival of L3 on pasture in a temperate region well, site-specific and temporal variations in soil conditions such as moisture content, pH and the presence of nematophagous fungi may affect the observed mortality rates and increase model uncertainty. Variations in faecal moisture and structural integrity of faeces in the field may also affect the population dynamics of GINs. Diarrhoea is commonly associated with infection by GINs such as *T. circumcincta* and *O. ostertagi* but can also be attributed to a range of other causative agents such as diet

and other gastrointestinal infections. As such it is difficult to characterise faecal consistency for inclusion in mechanistic models, but this potential source of variation should be noted, especially in the context of development success and horizontal migration of L3 between faeces and pasture.

5. Conclusion

A general model framework was developed to simulate the climate-driven population dynamics of the free-living stages of trichostrongylid GINs. Simulations using historical and future climatic data predicted significant changes in seasonal and annual infection pressure in the absence of host management, including a surprising decrease in infection pressure for *O. ostertagi*. Integration with management data, host behaviour and models developed to simulate the parasitic stages of these species, will enable the evaluation of GIN control options under a range of climate scenarios to identify long-term sustainable strategies.

Acknowledgments

The work was supported by funding from the FP7 GLOWORM project – Grant agreement N° 288975CP-TP-KBBE.2011.1.3-04, and carried out using the computational facilities of the Advanced Computing Research Centre, University of Bristol - http://www.bris.ac.uk/acrc/.

We acknowledge the E-OBS dataset from the EU-FP6 project ENSEMBLES (http://ensembles-eu.metoffice.com) and the data providers in the ECA&D project (http://www.ecad.eu). We are grateful to the British Atmospheric Data Centre and the Met Office for providing Met Office MIDAS Land Surface Station data (http://badc.nerc.ac.uk/).

We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the Met Office Hadley Centre climate modeling groups for producing and making available their model output. For CMIP the U.S. Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals.

Finally we would like to thank two anonymous reviewers for their helpful comments.

References

Allonby, E.W., Urquhart, G.M., 1975. The epidemiology and pathogenic significance of haemonchosis in a merino flock in East Africa. Vet. Parasitol. 1, 129–143.

Amaradasa, B.S., Lane, R.A., Manage, A., 2010. Vertical migration of Haemonchus contortus infective larvae on Cynodon dactylon and Paspalum notatum pastures in response to climatic conditions. Vet. Parasitol. 170, 78–87.

Anderson, R.C., 2000. Nematode parasites of vertebrates: their development and transmission. CABI, Wallingford.

Azam, D., Ukpai, O.M., Said, A., Abd-Allah, G.A., Morgan, E.R., 2012. Temperature and the development and survival of infective Toxocara canis larvae. Parasitol. Res. 110, 649–656.

Callinan, A.P.L., 1978a. The ecology of the free-living stages of Ostertagia circumcincta. Int. J. Parasitol. 8, 233–237.

Callinan, A.P.L., 1978b. The ecology of the free-living stages of Trichostrongylus axei. Int. J. Parasitol. 8, 453–456.

Callinan, A.P.L., 1979. The ecology of the free-living stages of Trichostrongylus vitrinus. Int. J. Parasitol. 9, 133–136.

Callinan, A.P.L., Westcott, J.M., 1986. Vertical distribution of trichostrongylid larvae on herbage and in soil. Int. J. Parasitol. 16, 241–244.

Carlsson, A.M., Irvine, R.J., Wilson, K., Coulson, S.J., 2013. Adaptations to the Arctic: low-temperature development and cold tolerance in the free-living stages of a parasitic nematode from Svalbard. Polar Biol. 36, 997–1005.

Charlier, J., Höglund, J., von Samson-Himmelstjerna, G., Dorny, P., Vercruysse, J., 2009. Gastrointestinal nematode infections in adult dairy cattle: impact on production, diagnosis and control. Vet. Parasitol. 164, 70–79.

Chintoan-Uta, C., Morgan, E.R., Skuce, P.J., Coles, G.C., 2014. Wild deer as potential vectors of anthelmintic-resistant abomasal nematodes between cattle and sheep farms. Proc. R. Soc. B 281, 20132985.

Collins, W.J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C.D., Joshi, M., Liddicoat, S., Martin, G., O'Connor, F., Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A., Woodward, S., 2011. Development and evaluation of an Earth-System model – HadGEM2. Geosci. Model Dev. 4, 1051–1075.

Cornell, S., 2005. Modelling nematode populations: 20 years of progress. Trends Parasitol. 21, 542–545.

802 Cornell, S.J., Isham, V.S., Grenfell, B.T., 2004. Stochastic and spatial dynamics of
803 nematode parasites in farmed ruminants. Proc. R. Soc. B 271, 1243–1250.

804 Crofton, H.D., 1948. The ecology of immature phases of Trichostrongyle nematodes:
805 I. The vertical distribution of infective larvae of Trichostrongylus retortaeformis in
806 relation to their habitat. Parasitology 39, 17–25.

807 De Graef, J., Claerebout, E., Geldhof, P., 2013. Anthelmintic resistance of
808 gastrointestinal cattle nematodes. Vlaams Diergeneeskd. Tijdschr. 82, 113–123.

809 Dobson, A.P., Hudson, P.J., 1992. Regulation and stability of a free-living host-
810 parasite system: Trichostrongylus tenuis in Red Grouse. II. Population models.
811 J. Anim. Ecol. 61, 487–498.

812 Dusenbery, D.B., 1989. A simple animal can use a complex stimulus patterrn to find
813 a location: nematode thermotaxis in soil. Biol. Cybern. 60, 431–437.

814 Falzon, L.C., Menzies, P.I., Shakya, K.P., Jones-Bitton, a, Vanleeuwen, J., Avula, J.,
815 Jansen, J.T., Peregrine, a S., 2013. A longitudinal study on the effect of lambing
816 season on the periparturient egg rise in Ontario sheep flocks. Prev. Vet. Med.
817 110, 467–80.

818 Fitzpatrick, J.L., 2013. Global food security: the impact of veterinary parasites and
819 parasitologists. Vet. Parasitol. 195, 233–248.

820 Gaba, S., Gourbière, S., 2008. To delay once or twice: the effect of hypobiosis and
821 free-living stages on the stability of host-parasite interactions. J. R. Soc.
822 Interface 5, 919–28.

823 Gibbs, H.C., Barger, I.A., 1986. Haemonchus contortus and other trichostrongylid
824 infections in parturient, lactating and dry ewes. Vet. Parasitol. 22, 57–66.

825 Grenfell, B.T., 1992. Parasitism and the dynamics of ungulate grazing systems. Am.
826 Nat. 139, 907–929.

827 Grenfell, B.T., Smith, G., Anderson, R.M., 1986. Maximum-likelihood estimates of
828 the mortality and migration rates of the infective larvae of Ostertagia ostertagi
829 and Cooperia oncophora. Parasitology 92, 643–652.

830 Grenfell, B.T., Smith, G., Anderson, R.M., 1987. A mathematical model of the
831 population biology of Ostertagia ostertagi in calves and yearlings. Parasitology
832 95, 389–406.

833 Grønvold, J., Høgh-Schmidt, K., 1989. Factors influencing rain splash dispersal of
834 infective larvae of Ostertagia ostertagi (Trichostrongylidae) from cow pats to the
835 surroundings. Vet. Parasitol. 31, 57–70.

836 Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M.,
837 2008. A European daily high-resolution gridded data set of surface temperature
838 and precipitation for 1950–2006. J. Geophys. Res. 113, D20119.

839 Höglund, J., Hessle, A., Dahlström, F., 2013. Calving season is a stronger
840 determinant of worm burdens in pasture-based beef production than the level of
841 residual larval contamination at turnout. Vet. Rec. 172, 472.

842 Houdijk, J.G.M., Jessop, N.S., Kyriazakis, I., 2001. Nutrient partitioning between
843 reproductive and immune functions in animals. Proc. Nutr. Soc. 60, 515–525.

844 Hudson, P.J., Dobson, A.P., Newborn, D., 1998. Prevention of population cycles by
845 parasite removal. Science (80-.). 282, 2256–2258.

846 IPCC, 2013. Summary for Policymakers, in: Stocker, T.F., Qin, D., Plattner, G.-K.,
847 Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M.
848 (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of
849 Working Group I to the Fifth Assessment Report of the Intergovernmental Panel
850 on Climate Change. Cambridge University Press, Cambridge.

851 Kaplan, R.M., Vidyashankar, A.N., 2012. An inconvenient truth: global worming and
852 anthelmintic resistance. Vet. Parasitol. 186, 70–78.

853 Khadijah, S., Kahn, L.P., Walkden-Brown, S.W., Bailey, J.N., Bowers, S.F., 2013a.
854 Effect of simulated rainfall timing on faecal moisture and development of
855 Haemonchus contortus and Trichostrongylus colubriformis eggs to infective
856 larvae. Vet. Parasitol. 192, 199–210.

857 Khadijah, S., Kahn, L.P., Walkden-Brown, S.W., Bailey, J.N., Bowers, S.F., 2013b.
858 Soil moisture influences the development of Haemonchus contortus and
859 Trichostrongylus colubriformis to third stage larvae. Vet. Parasitol. 196, 161–71.

860 Krecek, R.C., Murrell, K.D., 1988. Observations on the ability of larval Ostertagia
861 ostertagi to migrate through pasture soil. Proc. Helminthol. Soc. Wash. 55, 24–
862 27.

863 Krecek, R.C., Waller, P.J., 2006. Towards the implementation of the “basket of
864 options” approach to helminth parasite control of livestock: emphasis on the
865 tropics/subtropics. Vet. Parasitol. 139, 270–282.

866 Laurenson, Y.C.S.M., Bishop, S.C., Kyriazakis, I., 2011. In silico exploration of the
867 mechanisms that underlie parasite-induced anorexia in sheep. Br. J. Nutr. 106,
868 1023–39.

869 Laurenson, Y.C.S.M., Kyriazakis, I., Bishop, S.C., 2013. In silico exploration of the
870 impact of pasture larvae contamination and anthelmintic treatment on genetic
871 parameter estimates for parasite resistance in grazing sheep 1 2167–2180.

872 Learmount, J., Taylor, M.A., Smith, G., Morgan, C., 2006. A computer model to
873 simulate control of parasitic gastroenteritis in sheep on UK farms. Vet. Parasitol.
874 142, 312–329.

875 Leathwick, D.M., Barlow, N.D., Vlassoff, A., 1992. A model for nematodiasis in New
876 Zealand lambs. Int. J. Parasitol. 22, 789–799.

877 Leathwick, D.M., Vlassoff, A., Barlow, N.D., 1995. A model for nematodiasis in New
878 Zealand lambs: The effect of drenching regime and grazing management on the
879 development of anthelmintic resistance. Int. J. Parasitol. 25, 1479–1490.

880 Louie, K., Vlassoff, a., Mackay, a., 2005. Nematode parasites of sheep: extension of
881 a simple model to include host variability. Parasitology 130, 437–446.

882 Martin, G.M., Bellouin, N., Collins, W.J., Culverwell, I.D., Halloran, P.R., Hardiman,
883 S.C., Hinton, T.J., Jones, C.D., McDonald, R.E., McLaren, A.J., O'Connor, F.M.,
884 Roberts, M.J., Rodriguez, J.M., Woodward, S., Best, M.J., Brooks, M.E., Brown,
885 A.R., Butchart, N., Dearden, C., Derbyshire, S.H., Dharssi, I., Doutriaux-
886 Boucher, M., Edwards, J.M., Falloon, P.D., Gedney, N., Gray, L.J., Hewitt, H.T.,
887 Hobson, M., Huddleston, M.R., Hughes, J., Ineson, S., Ingram, W.J., James,
888 P.M., Johns, T.C., Johnson, C.E., Jones, A., Jones, C.P., Joshi, M.M., Keen,
889 A.B., Liddicoat, S., Lock, A.P., Maidens, A. V., Manners, J.C., Milton, S.F., Rae,
890 J.G.L., Ridley, J.K., Sellar, A., Senior, C.A., Totterdell, I.J., Verhoef, A., Vidale,
891 P.L., Wiltshire, A., 2011. The HadGEM2 family of Met Office Unified Model
892 climate configurations. Geosci. Model Dev. 4, 723–757.

893 Mauleon, H., Gruner, L., 1984. Influence de la déshydratation des fèces d'ovins sur
894 l'évolution des stades libres de strongles gastro-intestinaux. Ann. Rech.
895 Véterinaires 15, 519–528.

896 Mayer, D.G., Butler, D.G., 1993. Statistical validation. Ecol. Modell. 68, 21–32.

897 Molnár, P.K., Kutz, S.J., Hoar, B.M., Dobson, A.P., 2013. Metabolic approaches to
898 understanding climate change impacts on seasonal host-macroparasite
899 dynamics. Ecol. Lett. 16, 9–21.

900 Morgan, E.R., 2013. Detail and the devil of on-farm parasite control under climate
901 change. Anim. Health Res. Rev. 14, 138–142.

902 Morgan, E.R., Lundervold, M., Medley, G.F., Shaikenov, B.S., Torgerson, P.R.,
903 Milner-Gulland, E.J., 2006. Assessing risks of disease transmission between
904 wildlife and livestock: The Saiga antelope as a case study. Biol. Conserv. 131,
905 244–254.

906 Morgan, E.R., Medley, G.F., Torgerson, P.R., Shaikenov, B.S., Milner-Gulland, E.J.,
907 2007. Parasite transmission in a migratory multiple host system. Ecol. Modell.
908 200, 511–520.

909 Morgan, E.R., Shaikenov, B., Torgerson, P.R., Medley, G.F., Milner-Gulland, E.J.,
910 2005. Helminths of saiga antelope in Kazakhstan: implications for conservation
911 and livestock production. J. Wildl. Dis. 41, 149–162.

912 Morgan, E.R., van Dijk, J., 2012. Climate and the epidemiology of gastrointestinal
913 nematode infections of sheep in Europe. Vet. Parasitol. 189, 8–14.

914 Newey, S., Shaw, D.J., Kirby, A., Montieth, P., Hudson, P.J., Thirgood, S.J., 2005.
915 Prevalence, intensity and aggregation of intestinal parasites in mountain hares
916 and their potential impact on population dynamics. Int. J. Parasitol. 35, 367–373.

917 Nieuwhof, G.J., Bishop, S.C., 2007. Costs of the major endemic diseases of sheep in
918 Great Britain and the potential benefits of reduction in disease impact. Anim.
919 Sci. 81, 23–29.

920 O'Connor, L.J., Kahn, L.P., Walkden-Brown, S.W., 2007. The effects of amount,
921 timing and distribution of simulated rainfall on the development of Haemonchus
922 contortus to the infective larval stage. Vet. Parasitol. 146, 90–101.

923 O'Connor, L.J., Kahn, L.P., Walkden-Brown, S.W., 2008. Interaction between the
924 effects of evaporation rate and amount of simulated rainfall on development of
925 the free-living stages of Haemonchus contortus. Vet. Parasitol. 155, 223–234.

926 O'Connor, L.J., Walkden-Brown, S.W., Kahn, L.P., 2006. Ecology of the free-living
927 stages of major trichostrongylid parasites of sheep. Vet. Parasitol. 142, 1–15.

928 Ogbourne, C.P., 1973. Survival on herbage plots of infective larvae of strongylid
929 nematodes of the horse. J. Helminthol. 47, 9–16.

930 Papadopoulos, E., Gallidis, E., Ptochos, S., 2012. Anthelmintic resistance in sheep
931 in Europe: a selected review. Vet. Parasitol. 189, 85–88.

932 Perry, B., Grace, D., 2009. The impacts of livestock diseases and their control on
933 growth and development processes that are pro-poor. Philos. Trans. R. Soc.
934 London. Ser. B 364, 2643–2655.

935 Persson, L., 1974a. The survival of eggs and infective larvae of Ostertagia ostertagi
936 and Cooperia oncophora in solid cattle manure and urine. Zentralblatt für
937 Veterinärmedizin R. B 21, 677–691.

938 Persson, L., 1974b. A modified Baermann apparatus for the recovery of infective
939 nematode larvae from herbage and manure. Zentralblatt für Veterinärmedizin R.
940 B 21, 483–488.

941 Ploeger, H.W., Kloosterman, a, Rietveld, F.W., 1995. Acquired immunity against
942 Cooperia spp. and Ostertagia spp. in calves: effect of level of exposure and
943 timing of the midsummer increase. Vet. Parasitol. 58, 61–74.

944 R Core Team, 2013. R: A language and environment for statistical computing. R
945 Foundation for Statistical Computing, Vienna, Austria.

946 Rees, G., 1950. Observations on the vertical migrations of the third-stage larva of
947 Haemonchus contortus (Rud.) on experimental plots of Lolium perenne S24, in
948 relation to meteorological and micrometeorological factors. Parasitology 40,
949 127–143.

950 Reynecke, D.P., Waghorn, T.S., Oliver, A.-M.B., Miller, C.M., Vlassoff, A., Leathwick,
951 D.M., 2011. Dynamics of the free-living stages of sheep intestinal parasites on
952 pasture in the North Island of New Zealand . 2 . Weather variables associated
953 with development. N. Z. Vet. J. 59, 287–292.

954 Roberts, M.G., 1995. A pocket guide to host-parasite models. Parasitol. Today 11,
955 172–177.

956 Roberts, M.G., Grenfell, B.T., 1992. The population dynamics of nematode infections
957 of ruminants: the effect of seasonality in the free-living stages. IMA J. Math.
958 Appl. Med. Biol. 9, 29–41.

959 Roberts, M.G., Heesterbeek, J.A.P., 1995. The dynamics of nematode infections of
960 farmed ruminants. Parasitology 110, 493–502.

961 Rose, H., Hoar, B., Kutz, S.J., Morgan, E.R., 2014. Exploiting parallels between
962 livestock and wildlife: Predicting the impact of climate change on gastrointestinal
963 nematodes in ruminants. Int. J. Parasitol. Parasites Wildl.

964 Rose, J.H., 1961. Some observations on the free-living stages of Ostertagia
965 ostertagi, a stomach worm of cattle. Parasitology 51, 295–307.

966 Rose, J.H., 1963. Observations on the free-living stages of the stomach worm
967 Haemonchus contortus. Parasitology 53, 469–481.

968 Rose, J.H., Small, A.J., 1985. The distribution of the infective larvae of sheep gastro-
969 intestinal nematodes in soil and on herbage and the vertical migration of
970 Trichostrongylus vitrinus larvae through the soil. J. Helminthol. 59, 127–135.

971 Rossanigo, C.E., Gruner, L., 1995. Moisture and temperature requirements in faeces
972 for the development of free-living stages of gastrointestinal nematodes of sheep,
973 cattle and deer. J. Helminthol. 69, 357–362.

974 Saunders, L.M., Tompkins, D.M., Hudson, P.J., 2000. Spatial aggregation and
975 temporal migration of free-living stages of the parasitic nematode
976 Trichostrongylus tenuis. Funct. Ecol. 14, 468–473.

977 Silangwa, S.M., Todd, A.C., 1964. Vertical migration of trichostrongylid larvae on
978 grasses. J. Parasitol. 50, 278–285.

979 Smith, G., 1990. The population biology of the free-living phase of Haemonchus
980 contortus. Parasitology 101, 309–316.

981 Smith, G., Grenfell, B.T., 1994. Modelling of parasite populations: gastrointestinal
982 nematode models. Vet. Parasitol. 54, 127–143.

983 Smith, G., Grenfell, B.T., Anderson, R.M., Beddington, J., 1987. Population biology
984 of Ostertagia ostertagi and anthelmintic strategies against ostertagiasis in
985 calves. Parasitology 95, 407–420.

Soetaert, K., Cash, J., Mazzia, F., 2012. Solving Ordinary Differential Equations in R, in: Gentleman, R., Parmigiani, G., Hornik, K. (Eds.), Solving Differential Equations in R. Springer, New York, pp. 41–80.

Soetaert, K., Petzoldt, T., Setzer, R.W., 2010. Solving Differential Equations in R : Package deSolve. R J. 2, 5–15.

Stear, M.J., Bishop, S.C., Doligalska, M., Duncan, J.L., Holmes, P.H., Irvine, J., McRirie, L., McKellar, Q.A., Sinski, E., Murray, M., 1995. Regulation of egg production, worm burden, worm length and worm fecundity by host responses in sheep infected with Ostertagia circumcincta. Parasite Immunol. 17, 643–652.

Sutherland, I.A., Leathwick, D.M., 2011. Anthelmintic resistance in nematode parasites of cattle: a global issue? Trends Parasitol. 27, 176–181.

Tans, P., 2014. Weekly mean C02 at Mauna Loa and historical comparisons [WWW Document]. URL ftp://aftp.cmdl.noaa.gov/products/trends/co2/co2_weekly_mlo.txt (accessed 6.30.14).

Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. Bull. Am. Meteorol. Soc. 93, 485–498.

Todd, K.S., Levine, N.D., Boatman, P.A., 1976. Effect of temperature on survival of free-living stages of Haemonchus contortus. Am. J. Vet. Res. 37, 991–992.

Troell, K., Tingstedt, C., Höglund, J., 2006. Phenotypic characterization of Haemonchus contortus: a study of isolates from Sweden and Kenya in experimentally infected sheep. Parasitology 132, 403–9.

Van der Voort, M., Charlier, J., Lauwers, L., Vercruysse, J., Van Huylenbroeck, G., Van Meensel, J., 2013. Conceptual framework for analysing farm-specific economic effects of helminth infections in ruminants and control strategies. Prev. Vet. Med. 109, 228–35.

Van Dijk, J., David, G.P., Baird, G., Morgan, E.R., 2008. Back to the future: Developing hypotheses on the effects of climate change on ovine parasitic gastroenteritis from historical data. Vet. Parasitol. 158, 73–84.

Van Dijk, J., de Louw, M.D.E., Kalis, L.P.A., Morgan, E.R., 2009. Ultraviolet light increases mortality of nematode larvae and can explain patterns of larval availability at pasture. Int. J. Parasitol. 39, 1151–1156.

Van Dijk, J., Morgan, E.R., 2008. The influence of temperature on the development, hatching and survival of Nematodirus battus larvae. Parasitology 135, 269–283.

Van Dijk, J., Morgan, E.R., 2010. Variation in the hatching behaviour of Nematodirus battus: polymorphic bet hedging? Int. J. Parasitol. 40, 675–681.

1022 Van Dijk, J., Morgan, E.R., 2011. The influence of water on the migration of infective
1023 trichostrongyloid larvae onto grass. Parasitology 138, 780–788.

1024 Van Dijk, J., Sargison, N.D., Kenyon, F., Skuce, P.J., 2010. Climate change and
1025 infectious disease: helminthological challenges to farmed ruminants in
1026 temperate regions. Animal 4, 377–392.

1027 Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K.,
1028 Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M.,
1029 Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative
1030 concentration pathways: an overview. Clim. Change 109, 5–31.

1031 Waller, P.J., Rudby-Martin, L., Ljungström, B.L., Rydzik, A., 2004. The epidemiology
1032 of abomasal nematodes of sheep in Sweden, with particular reference to over-
1033 winter survival strategies. Vet. Parasitol. 122, 207–220.

1034 Wang, T., van Wyk, J.A., Morrison, A., Morgan, E.R., 2014. Moisture requirements
1035 for the migration of Haemonchus contortus third stage larvae out of faeces. Vet.
1036 Parasitol.

1037 Williams, J.C., Knox, J.W., Loyacano, A.F., 1993. Epidemiology of Ostertagia
1038 ostertagi in weaner-yearling cattle. Vet. Parasitol. 46, 313–324.

1039 Xu, C.-Y., Singh, V.P., 2001. Evaluation and generalization of temperature-based
1040 methods for calculating evaporation. Hydrol. Process. 15, 305–319.

1041

Figure 1. Conceptual diagram of the GLOWORM-FL model framework. Parameter (lower case) and state variable (upper case) definitions are given in Table 1.

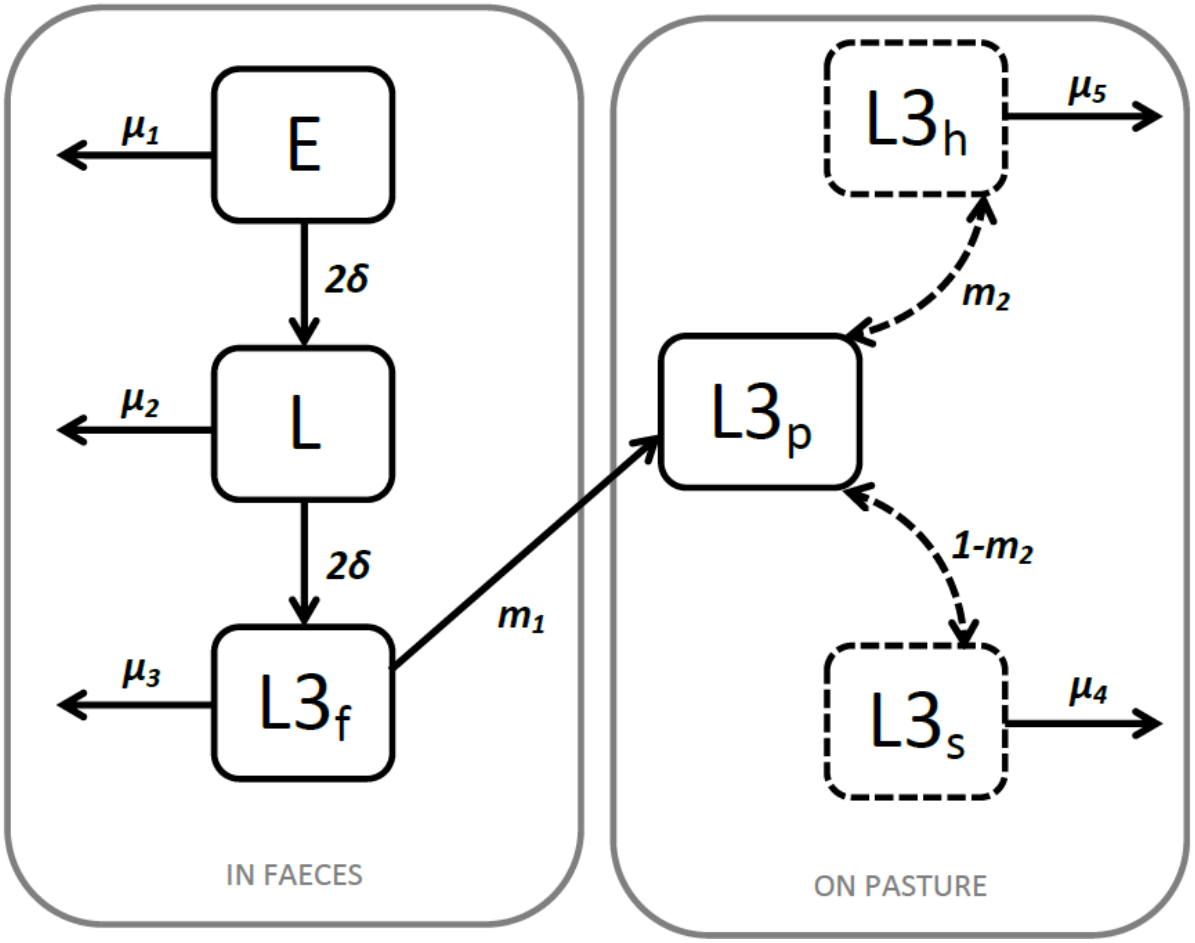
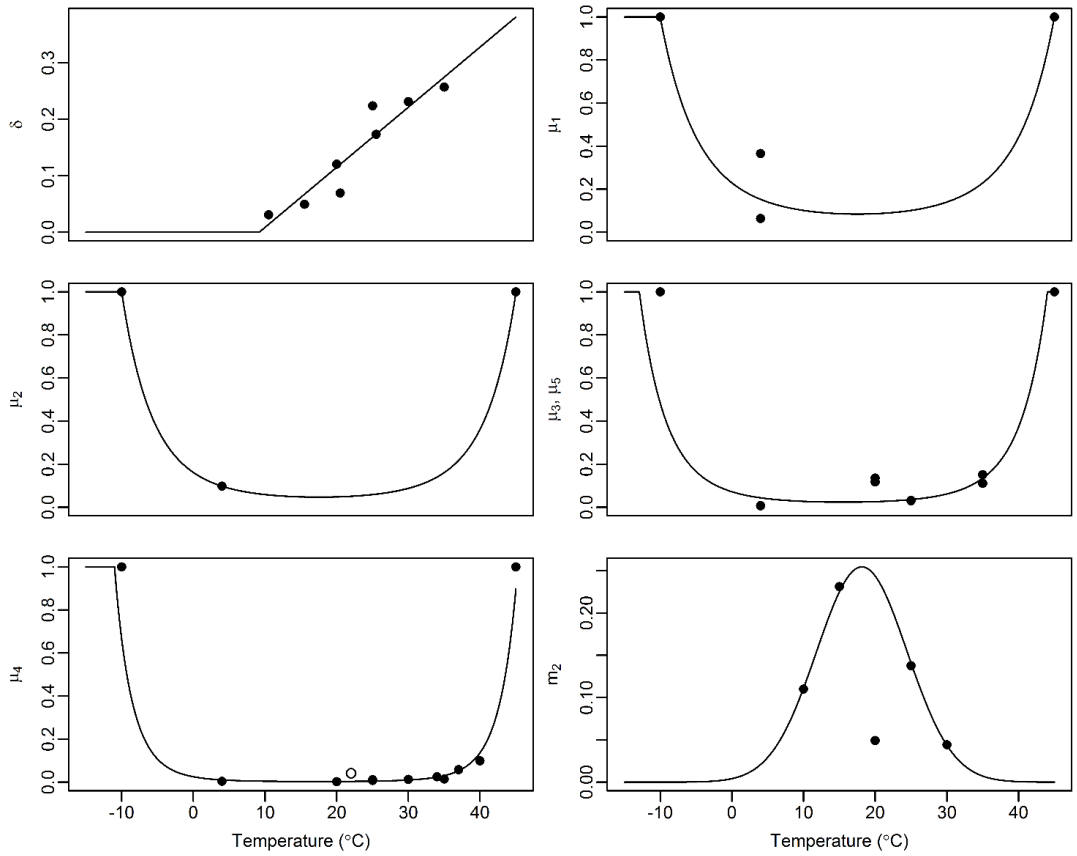
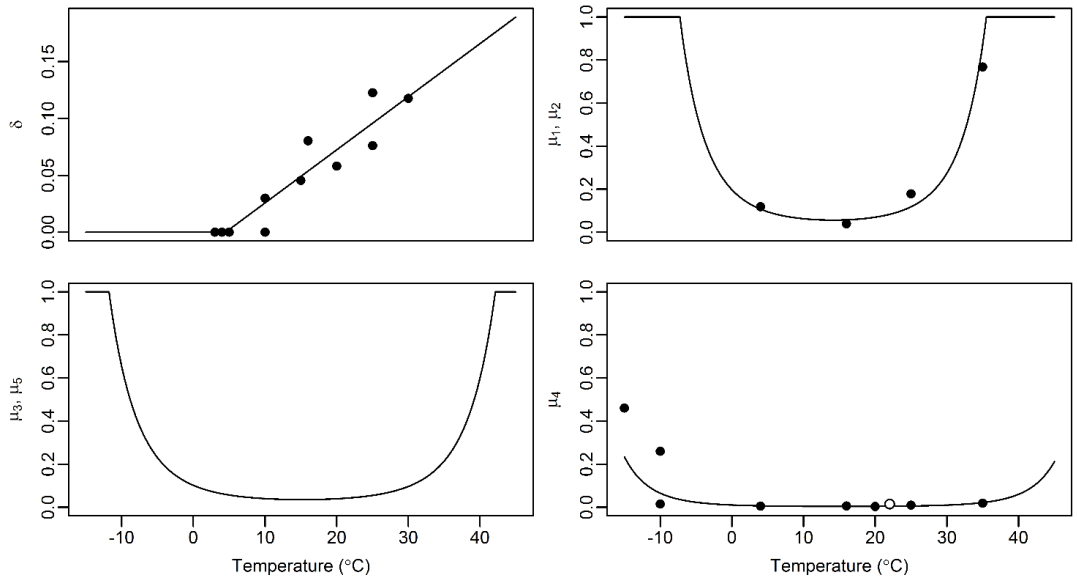


Figure 2. Estimates of temperature-dependent life-history parameters for *H. contortus* (lines) based on analysis of data in the literature (closed circles). Parameter definitions are given in Table 1. Statistical output for linear models is provided in Table 2. Mortality of L3 in soil (μ_4) was estimated from observations of L3 mortality in water. A point estimate of L3 mortality in desiccated soil at 20-24°C (van Dijk and Morgan, 2011) is superimposed (open circle) for comparison. Data were not available to estimate the mortality of L3 on herbage (μ_5), which was therefore estimated using the mortality rate of L3 in faeces (μ_3).The data point at 20 degrees was omitted from analysis of the vertical migration parameter (m_2) but is shown here. A minimum threshold for development of 9.17°C is predicted.



1059

Figure 3. Estimates of temperature-dependent life-history parameters for *T. circumcincta* (lines) based on analysis of data provided in the literature (closed circles). Parameter definitions are given in Table 1. Statistical output for linear models is provided in Table 2. Mortality of L3 in soil (μ_4) was estimated from observations of L3 mortality in water. A point estimate of L3 mortality in desiccated soil at 20-24°C (van Dijk and Morgan, 2011) is superimposed (open circle) for comparison. Data points are not shown for the mortality rates of L3 in faeces (μ_3) and on herbage (μ_5) as no data were available to directly estimate these parameters. These rates were therefore estimated from the mortality rate of L3 in soil (μ_4). A minimum threshold for development of 4.46°C is predicted. The vertical migration parameter is as shown in Figure 2.



1072

Figure 4. Estimates of temperature-dependent life-history parameters for *O. ostertagi* (lines) based on analysis of data provided in the literature (closed circles). Parameter definitions are given in Table 1. Statistical output for linear models is provided in Table 2. Data points are not shown for the mortality rates of L3 in faeces (μ_3) and on herbage (μ_5) as no data were available to directly estimate these parameters. These rates were therefore estimated from the mortality rate of L3 in soil (μ_4). Estimates of mortality in faeces (μ_3) based on analysis of observations on *Cooperia oncophora* and *O. ostertagi* mixed infections (open circles) are superimposed for comparison (Persson, 1974a). A minimum threshold for development of 7.44°C is predicted. The vertical migration parameter is as shown in Figure 2.

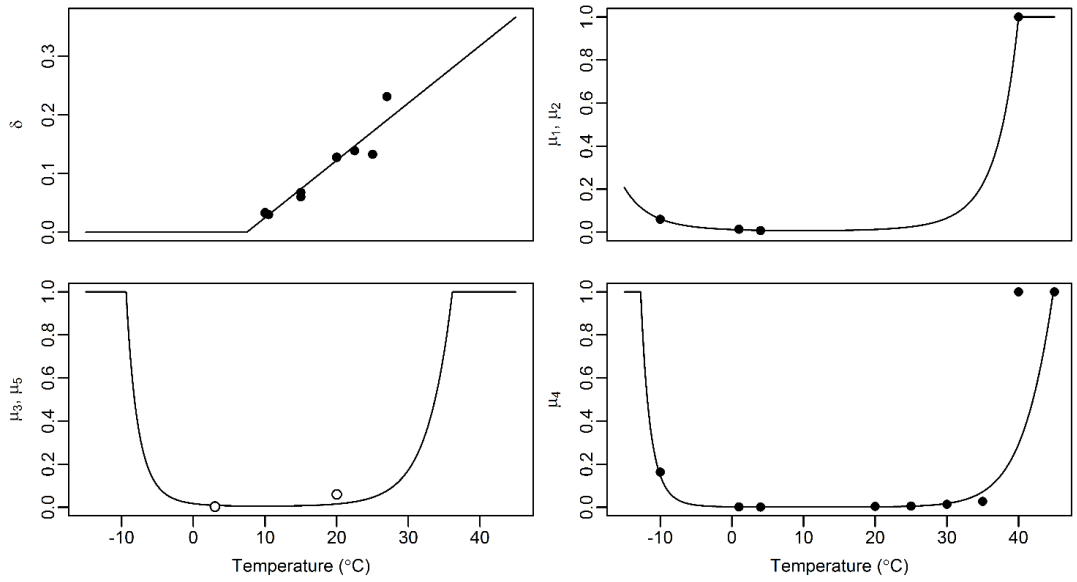


Figure 5. Estimated annual AUC (Area Under the Curve) of the predicted numbers of L3 on pasture for *H. contortus, T. circumcincta* and *O. ostertagi* when using historical climatic data for the period 1969-1999 (white) and climatic data based on the RCP8.5 high emissions climate change scenario for the period 2070-2100 (grey).

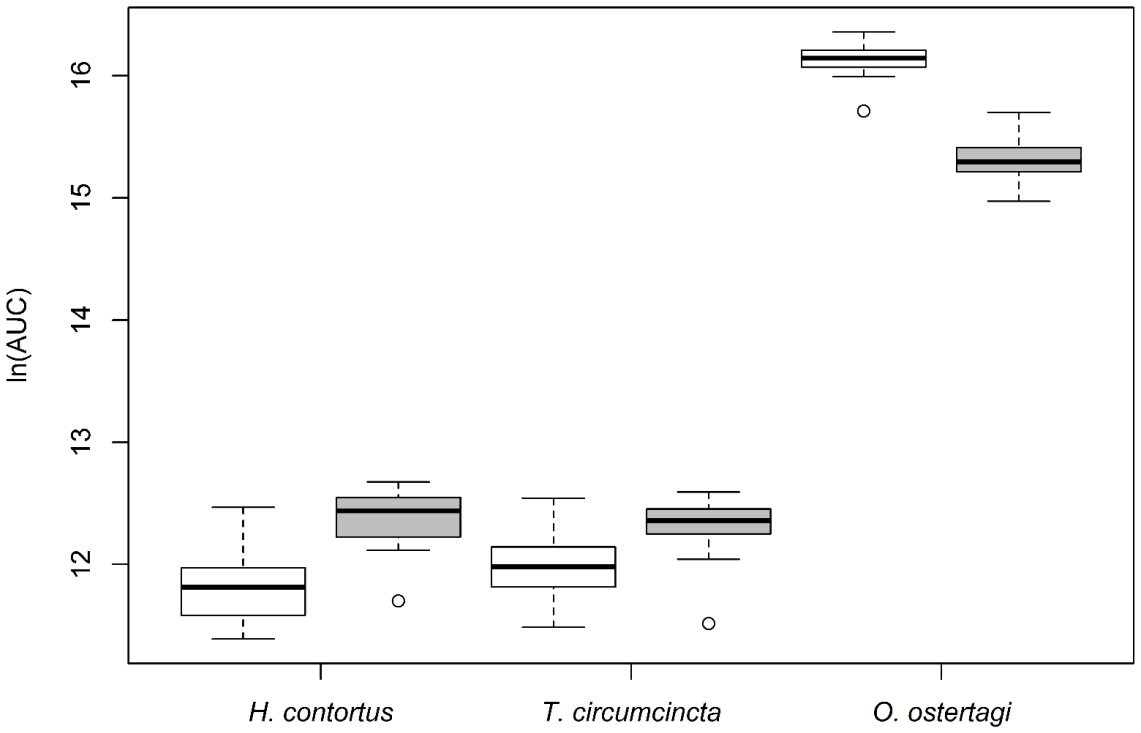


Figure 6. The number of H. contortus L3 on herbage (L3 kg DM-1) predicted using the GLOWORM-FL model and mean daily air temperature (dashed line) or fluctuating between the daily minimum and maximum temperature (dotted line) and the number (L3 kg DM-1) observed by Wilkie et al. (submitted; points and error bars show mean and 95% confidence interval). Predicted numbers of L3 on herbage using a single mortality rate for L3 on pasture and no vertical migration (dotted line; Smith, 1990) are superimposed for comparison.

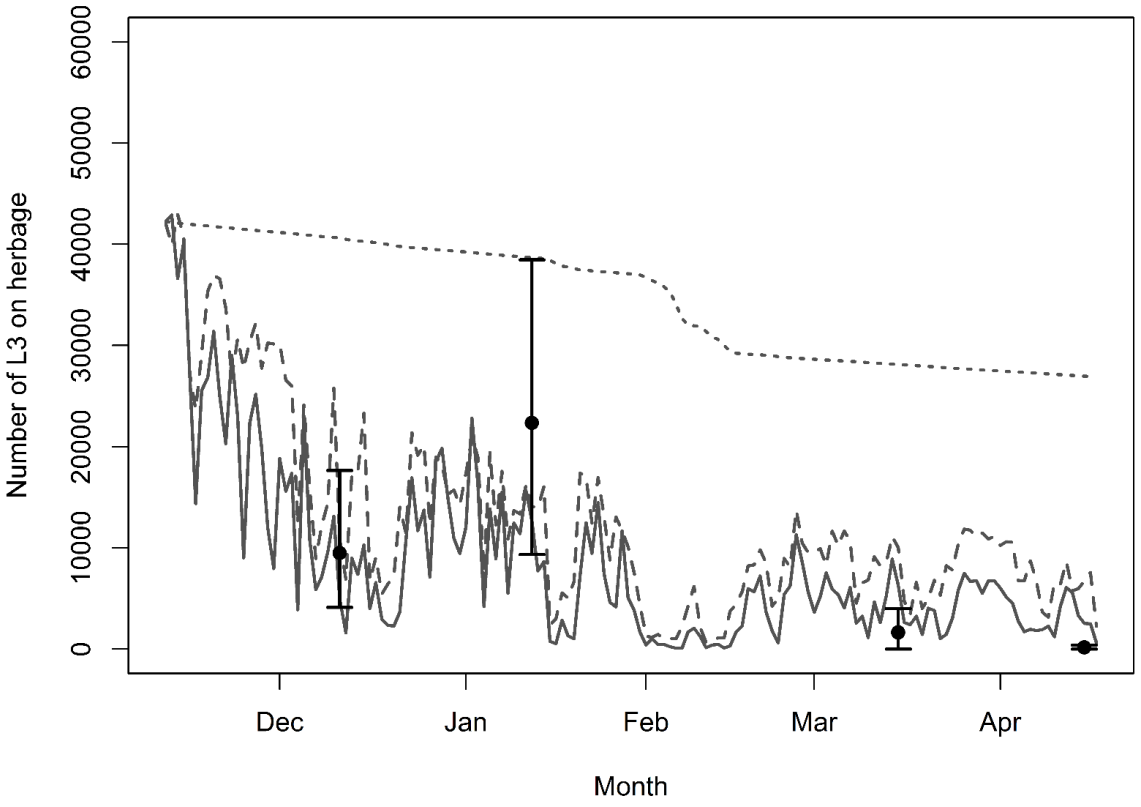
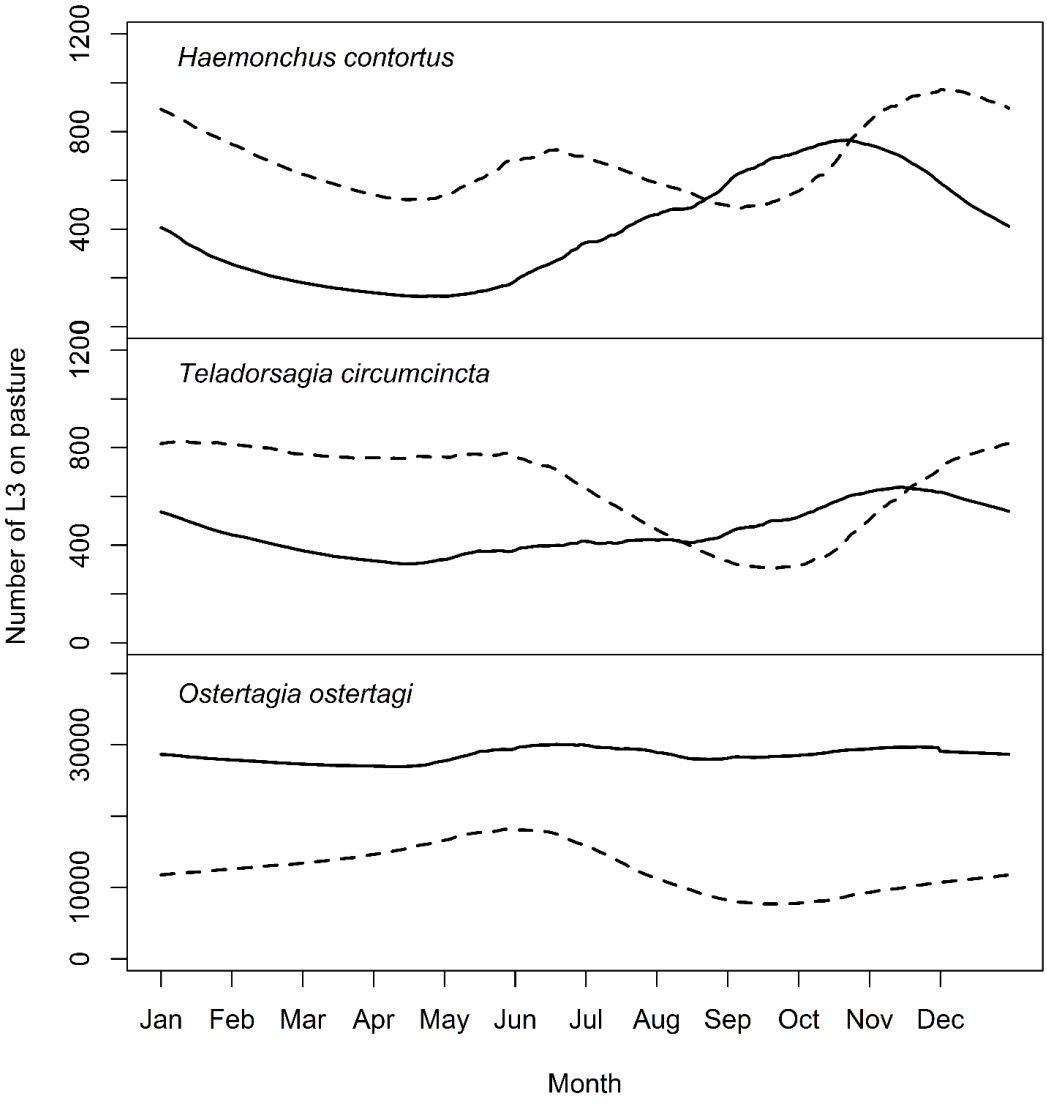


Figure 7. The number of L3 on pasture (soil and herbage combined) predicted for *Haemonchus contortus* (top panel)*, Teladorsagia circumcincta* (middle panel) and *Ostertagia ostertagi* (bottom panel) when using historical climatic data for the period 1969-1999 (solid line) and climatic data based on the RCP8.5 high emissions climate change scenario for the period 2070-2100 (broken line). Data shown are the disaggregated annual means from the thirty year time-series. The first year of each time series was discarded. One hundred new eggs were input daily. Therefore no assumptions were made regarding management or intensity of infection in the host and the predicted dynamics are entirely climate-driven.



1109

1110

1111

1112 Table 1. State variable and parameter definitions

State variable/ Parameter	Definition	Units
E	Eggs	-
L	First stage (L1) and second stage (L2) larvae	-
$L3_f$	Third stage infective larvae (L3) in faeces	-
$L3_p$	Total L3 on pasture (soil and herbage combined)	-
$L3_s$	L3 in soil	-
$L3_h$	L3 on herbage	-
σ	Development rate from egg to L3	Instantaneous daily rate
μ_1	Egg mortality rate	Instantaneous daily rate
μ_2	L1 and L2 mortality rate	Instantaneous daily rate
μ_3	L3 mortality rate in faeces	Instantaneous daily rate
μ_4	L3 mortality rate in soil	Instantaneous daily rate
μ_5	L3 mortality rate on herbage	Instantaneous daily rate
m_1	Horizontal migration (translation) of L3 onto pasture	Instantaneous daily rate
m_2	Proportion of total pasture L3 on herbage	Proportion
C	Development success correction factor	Proportion

1113

1114

Table 2. Parameter estimates derived from data in the literature and additional laboratory experiments. ANOVA results are shown for the linear models fitted to data from the literature to estimate temperature-dependent rates (see text).

Parameter	Species[a]	Estimate[b]	Data source
$\boldsymbol{\delta}$	*Hc*	$-0.09746 + 0.01063T$ ($F_{1,6}$=43.5, p<0.001, R^2=0.88, R^2_{adj}=0.86)	Hsu and Levine, 1977; Rose, 1963
	Tc	$-0.02085 + 0.00467\mathrm{T}$ ($F_{1,10}$=76.57, p<0.001, R^2=0.88, R^2_{adj}=0.87)	Crofton and Whitlock, 1965; Crofton, 1965; Pandey et al., 1989; Salih and Grainger, 1982; Young et al., 1980a
	Oo	$-0.07258 + 0.00976\mathrm{T}$ ($F_{1,8}$=76.14, p<0.001, R^2=0.90, R^2_{adj}=0.89)	Pandey, 1972a; Rose, 1961; Young et al., 1980b
$\boldsymbol{\mu_1}$	*Hc*	$\exp(-1.47135 - 0.11444T + 0.00327T^2)$ ($F_{2,3}$=4.65, p=0.12, R^2=0.76, R^2_{adj}=0.59)	Todd et al., 1976a
	Tc	$\exp(-1.62026 - 0.17771T + 0.00629T^2)$ ($F_{2,2}$=6.27, p=0.27, R^2=0.93, R^2_{adj}=0.78)	Pandey et al., 1993, 1989
	Oo	$\exp(-4.38278 - 0.10640T + 0.00540T^2)$ ($F_{2,1}$=6.27, p=0.06, R^2=0.99, R^2_{adj}=0.99)	Pandey, 1972
$\boldsymbol{\mu_2}$	*Hc*	$\exp(-1.82300 - 0.14180T + 0.00405T^2)$ ($F_{2,1}$=1.723[31], p<0.001, R^2=1, R^2_{adj}=1)[c]	Todd et al., 1976a
	Tc, Oo	As μ_1 above	-
$\boldsymbol{\mu_3}$	*Hc*	$\exp(-2.63080 - 0.14407T + 0.00463T^2)$ ($F_{2,9}$=8.48, p=0.008, R^2=0.65, R^2_{adj}=0.58)	Todd et al., 1976a, 1976b

	Tc, Oo	$10 * \mu_4$	Pandey, 1972; Persson, 1974a
$\boldsymbol{\mu_4}$	*Hc*	$\exp(-3.68423 - 0.25346T + 0.00740T^2)$ ($F_{2,8}$=50.76, p<0.001, R^2=0.93, R^2_{adj}=0.91)	Jehan and Gupta, 1974; Todd et al., 1976b
	Tc	$\exp(-4.58817 - 0.13996T + 0.00461T^2)$ ($F_{2,12}$=43.55, p<0.001, R^2=0.88, R^2_{adj}=0.86)	Gruner and Suryahadi, 1993; Jasmer et al., 1987; Pandey et al., 1993; Rossanigo and Gruner, 1996
	Oo	$\exp(-6.388 - 0.2681T + 0.01633T^2 - 0.00016T^3)$ ($F_{3,5}$=28.81, p=0.001, R^2=0.95, R^2_{adj}=0.91)	Pandey, 1972
$\boldsymbol{\mu_5}$	*Hc, Tc, Oo*	As μ_3 above	Grenfell et al., 1986; van Dijk and Morgan, 2011; van Dijk et al., 2009
$\boldsymbol{m_1}$	*Hc*	$\begin{cases} 0.25, & P \geq 2 \\ 0, & P < 2\ AND \sum_{i=-4}^{t} P_i/E_i < 1 \\ 0.051, & P < 2\ AND \sum_{i=-4}^{t} P_i/E_i \geq 1 \end{cases}$	Present study; O'Connor et al., 2008; Wang et al., 2014
	Tc	$\begin{cases} 0.21, & P \geq 2 \\ 0, & P < 2\ AND \sum_{i=-7}^{t} P_i/E_i < 1 \\ 0.025, & P < 2\ AND \sum_{i=-7}^{t} P_i/E_i \geq 1 \end{cases}$	Present study; O'Connor et al., 2008; Wang et al., 2014
	Oo	$\begin{cases} 0.06, & P \geq 2 \\ 0, & P < 2 \end{cases}$	Grønvold and Høgh-Schmidt, 1989

$\boldsymbol{m_2}$	*Hc, Tc, Oo*	$\exp(-5.48240 + 0.45392T - 0.01252T^2)$ ($F_{2,1}$=442.9, p=0.034, R^2>0.99, R^2_{adj}>0.99)	Callinan and Westcott, 1986
C	*Hc*	$\begin{cases} 0.1, & \sum_{i=4}^{t} P_i/E_i < 1 \\ 1, & \sum_{i=4}^{t} P_i/E_i \geq 1 \end{cases}$	
	Tc	$\begin{cases} 0.1, & \sum_{i=7}^{t} P_i/E_i < 1 \\ 1, & \sum_{i=7}^{t} P_i/E_i \geq 1 \end{cases}$	

[a] *Hc = Haemonchus contortus, Tc = Teladorsagia circumcincta, Oo = Ostertagia ostertagi*

[b] T = temperature (°C), P = total daily precipitation (mm), E = total daily evapotranspiration (mm)

[c] Note that the statistical significance here is an artefact of overfitting

Table 3. Validation of simulations using data provided in the literature. Models are considered a good fit if regression through the origin is significant and the slope is not significantly different from 1. The error and R^2 are used to compare competing models.

Data source	Species[a]	Model component tested	Temperature data used	Error (residual sum of squares)	Linear regression	R^2 ($R^2_{adjusted}$)	Slope (95 % CI[b])
Rose, 1963	*Hc*	Faeces (eq. 1-3; D50)	Min - Max	1093.5	$F_{1,6}$ = 12.21, p=0.013	0.67 (0.62)	2.18 (0.93 – 3.43)
Rose, 1963	*Hc*	Faeces (eq. 1-3; D50)	Mean	1097.5	$F_{1,6}$ = 9.561, p=0.021	0.61 (0.55)	1.93 (0.68 – 3.17)
Rose, 1963	*Hc*	Faeces (eq. 1-3; development success)	Min - Max	31.28	$F_{1,11}$ = 28.53, p<0.001	0.72 (0.70)	1.28 (0.80 – 1.76)
Rose, 1963	*Hc*	Faeces (eq. 1-3; development success)	Mean	105.74	$F_{1,11}$ = 11.91, p=0.005	0.52 (0.48)	0.49 (0.20 – 0.77)
Wilkie et al. submitted	*Hc*	Pasture (eq. 4)	Min - Max	1.83×10^8	$F_{1,3}$ = 6.78, p=0.080	0.69 (0.59)	0.94 (0.22- 1.67)
Wilkie et al. submitted	*Hc*	Pasture (eq. 4)	Mean	1.43×10^8	$F_{1,3}$ = 16.72, p=0.026	0.85 (0.80)	1.48 (0.76- 2.20)
Rossanigo and Gruner, 1995	*Tc*	Faeces (eq. 1-3; development success)	Constant	1679.10	$F_{1,9}$ = 86.9, p<0.001	0.91 (0.90)	1.54 (1.21 - 1.86)
Wilkie et al. submitted	*Tc*	Pasture (eq. 4)	Min - Max	1.03×10^{10}	$F_{1,3}$ = 9.91, p=0.051	0.77 (0.69)	1.26 (0.46- 2.07)

Wilkie et al. submitted	*Tc*	Pasture (eq. 4)	Mean	1.17 x 10^{10}	$F_{1,3}$ = 17.84, p=0.024	0.86 (0.81)	1.75 (0.92-2.58)
Rossanigo and Gruner, 1995	*Oo*	Faeces (eq. 1-3; development success)	Constant	2050.22	$F_{1,5}$ = 36.86, p=0.002	0.88 (0.86)	0.84 (0.57-1.12)
Rose, 1961	*Oo*	Faeces (eq. 1-3; D50)	Min – Max		$F_{1,11}$ = 26.9, p<0.001	0.71 (0.68)	21.03 (12.9 – 29.1)
Rose, 1961	*Oo*	Faeces (eq. 1-3; D50)	Mean		$F_{1,11}$ = 98.51, p<0.001	0.90 (0.89)	0.62 (0.50 – 0.75)
Wilkie et al. submitted	*Hc*	Smith (1990)	Mean	2.66 x 10^{9}	$F_{1,3}$ = 4.73, p=0.12	0.61 (0.48)	0.28 (0.02-0.53)

[a] *Hc = Haemonchus contortus, Tc = Teladorsagia circumcincta, Oo = Ostertagia ostertagi*

[b] 95% confidence intervals were estimated as 2 x the standard error of the slope coefficient.