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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

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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.

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 are highly dependent on weather and micro-climatic conditions (Khadijah et al., 2013a; Morgan and van Dijk, 2012; O'Connor et al.,

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2006, 2007, 2008; Reynecke et al., 2011; Rose, 1961, 1963; 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 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 evaluate 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.

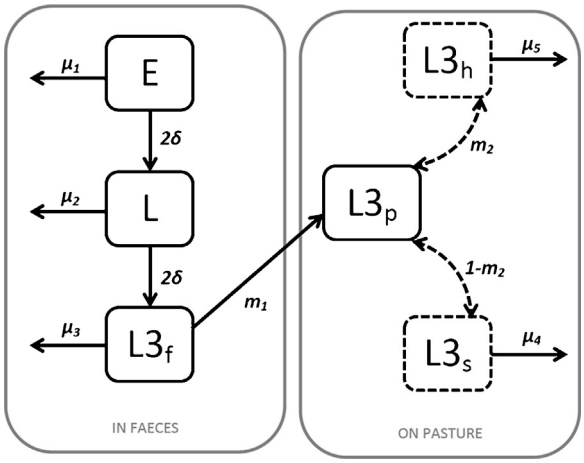

Fig. 1. Conceptual diagram of the GLOWORM-FL model framework. Parameter (lower case) and state variable (upper case) definitions are given in Table 1.

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 (Fig. 1). Eggs (E) develop to third stage larvae in the faeces ($L3_f$) 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).

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

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

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

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

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	–
δ	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

there is random movement between the soil and herbage (Van Dijk and Morgan, 2011). Therefore, L3 on pasture ($L3_p$) are assumed to reside in either the soil and vegetation mat layer ($L3_s$) or on herbage ($L3_h$). 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, dependent on a vertical migration parameter (m_2).

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

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

2.2. Parameter estimates

The model was parameterised for three trichostrongylid GINs that infect ruminants: *H. contortus, T. circumcincta* and *O. ostertagi* (Figs. 2–4; Table 2).

2.2.1. Temperature dependent development and mortality

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

Instantaneous daily rates were first estimated for each constant temperature from the reported time to 50% development (D50) or time to 50% mortality (M50) as $-\ln(0.5)/D50$ or $-\ln(0.5)/M50$. If these data were unavailable, rates were estimated in one of three ways: (1) using the proportion remaining at a single sampling interval, as $-\ln(\textit{proportion remaining})/\textit{days}$; (2) using the mean of the minimum and maximum development or mortality times, or (3) by linear regression of the transformed proportions of individuals developed or surviving over time as described by Azam et al. (2012). Where 100% mortality was observed within 24 h, an instantaneous 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., 1976a,b). 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 (Figs. 2 and 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 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 (Figs. 3 and 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

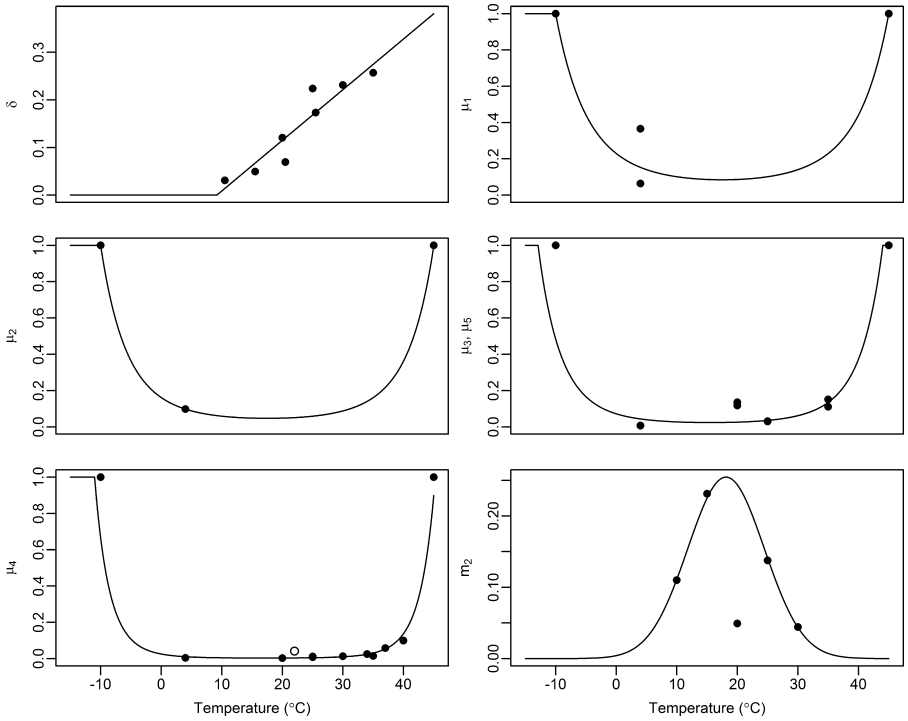

Fig. 2. Estimates of temperature-dependent life-history parameters for *H. contortus* (lines) based on analysis of data in the literature (closed circles). Parameter definitions are given in Table 1. Statistical output for linear models is provided in Table 2. Mortality of L3 in soil (μ_4) was estimated 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° 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.

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.

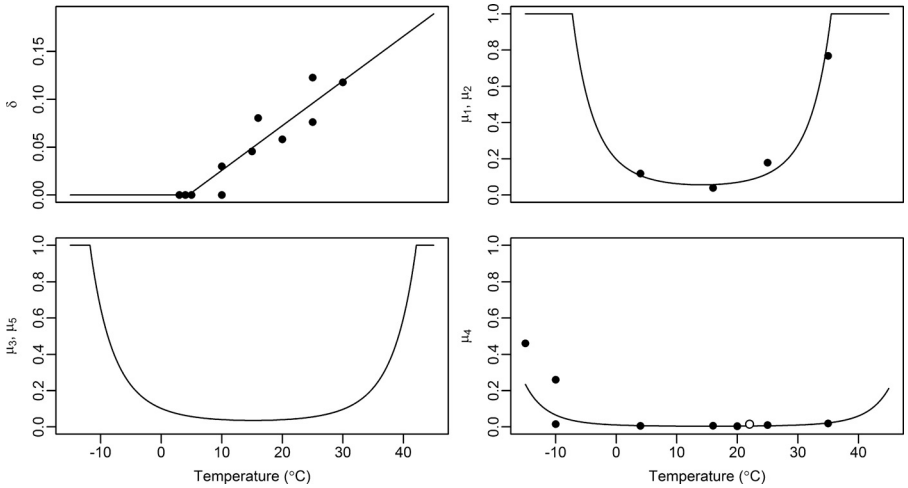

Fig. 3. Estimates of temperature-dependent life-history parameters for *T. circumcincta* (lines) based on analysis of data provided in the literature (closed circles). Parameter definitions are given in Table 1. Statistical output for linear models is provided in Table 2. Mortality of L3 in soil (μ_4) 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 Fig. 2.

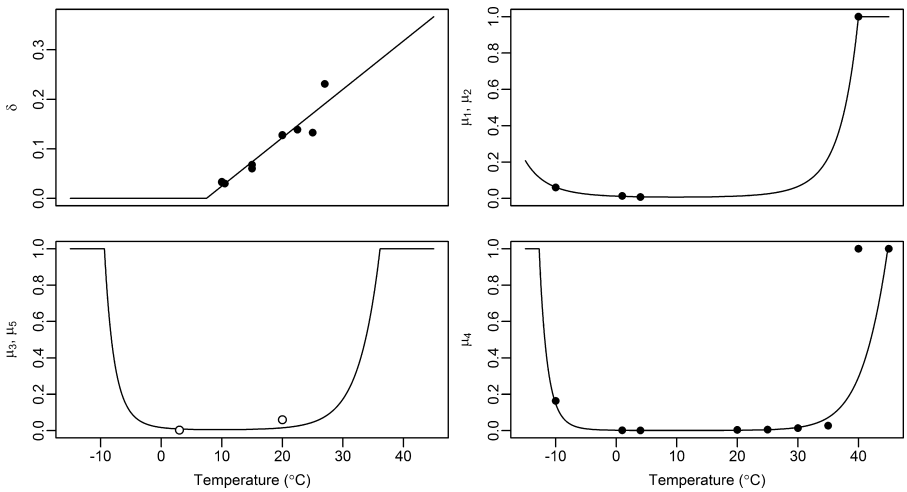

Fig. 4. Estimates of temperature-dependent life-history parameters for *O. ostertagi* (lines) based on analysis of data provided in the literature (closed circles). Parameter definitions are given in Table 1. Statistical output for linear models is provided in Table 2. Data points are not shown for the 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 Fig. 2.

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 h 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 72–96 h 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., 2007, 2008; 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 1.6 mm of simulated rainfall (Grønvold and Høgh-Schmidt, 1989) and from sheep faecal pellets following 2 mm of simulated rainfall (this study). Furthermore, horizontal migration rates of *H. contortus* were not significantly influenced by the amount of rainfall between 4 and 8 mm (Wang et al., 2014). Therefore, optimal moisture was defined as days where total precipitation ≥2 mm.

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 1.6–1.7 mm 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 3 g (∼6 pellets) were subjected to approximately 2 mm simulated rainfall and after 24 h 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. 0.14) 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

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
δ	*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	$-0.02085 + 0.00467T$ ($F_{1,10} = 76.57$, $p < 0.001$, $R^2 = 0.88$, $R^2_{adj} = 0.87$)	Crofton and Whitlock (1965), Crofton (1965), Pandey et al. (1989), Salih and Grainger (1982), Young et al. (1980a)
	Oo	$-0.07258 + 0.00976T$ ($F_{1,8} = 76.14$, $p < 0.001$, $R^2 = 0.90$, $R^2_{adj} = 0.89$)	Pandey (1972), Rose (1961), Young et al. (1980b)
μ_1	*Hc*	$\exp(-1.62026 - 0.17771T + 0.00629T^2)$ ($F_{2,3} = 4.65$, $p = 0.12$, $R^2 = 0.76$, $R^2_{adj} = 0.59$)	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)
μ_2	*Hc*	$\exp(-1.82300 - 0.14180T + 0.00405T^2)$ ($F_{2,1} = 1.723 \times 10^{31}$, $p < 0.001$, $R^2 = 1$, $R^2_{adj} = 1$)[c]	Todd et al. (1976a)
	Tc, Oo	As μ_1 above	–
μ_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,b)
	Tc, Oo	$10 \times \mu_4$	Pandey (1972), Persson (1974a)
μ_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)
μ_5	*Hc, Tc, Oo*	As μ_3 above	Grenfell et al. (1986), Van Dijk and Morgan (2011), Van Dijk et al. (2009)
m_1	*Hc*	$\begin{cases} 0.25, & P \geq 2 \\ 0, & P < 2 \text{ and } \sum_{i=-4}^{t} P_i/E_i < 1 \\ 0.051, & P < 2 \text{ and } \sum_{i=-4}^{t} P_i/E_i \geq 1 \end{cases}$	Present study; O'Connor et al. (2008), Wang et al. (2014)
	Tc	$\begin{cases} 0.21, & P \geq 2 \\ 0, & P < 2 \text{ and } \sum_{i=-7}^{t} P_i/E_i < 1 \\ 0.025, & P < 2 \text{ and } \sum_{i=-7}^{t} P_i/E_i \geq 1 \end{cases}$	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)
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*	$\begin{cases} 0.1, & \sum_{i=4}^{t} P_i/E_i < 1 \\ 0, & \sum_{i=4}^{t} P_i/E_i \geq 1 \end{cases}$	
	Tc	$\begin{cases} 0.1, & \sum_{i=7}^{t} P_i/E_i < 1 \\ 0, & \sum_{i=7}^{t} P_i/E_i \geq 1 \end{cases}$	

[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.

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 < 2 mm, 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 $0.051 \times 0.49 = 0.025$ (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 < 2 mm.

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

2.3. Model validation

Laboratory observations on the development success of *T. circumcincta* and *O. ostertagi* (Rossanigo and Gruner, 1995) and field observations on the development time and development success of *H. contortus* (Rose, 1963) and *O. ostertagi* (Rose, 1961) in a temperate region were used to validate model predictions of development and survival in faeces. Rossanigo and Gruner (1995) recorded the development success of various GIN species in faeces incubated at a range of constant temperature while maintaining optimal moisture conditions. Rose (1961, 1963) recovered L3 from faeces containing eggs that had been deposited at monthly intervals on pasture in South East England where the GINs were exposed to variable temperatures and moisture conditions. The model was initialised with 100 eggs and simulations were run using either the constant temperatures tested (Rossanigo and Gruner, 1995) or time series of daily air temperatures obtained for the study location. Meteorological data from Wisley weather station (Ordnance Survey grid reference: TQ062579), approximately 10 km from the Central Veterinary Laboratories, Weybridge, where Rose's (1963) observations were made, and 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, H. unpublished data) 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 60 km 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, $L3_p$, 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 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 $\pm(2 \times$ 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

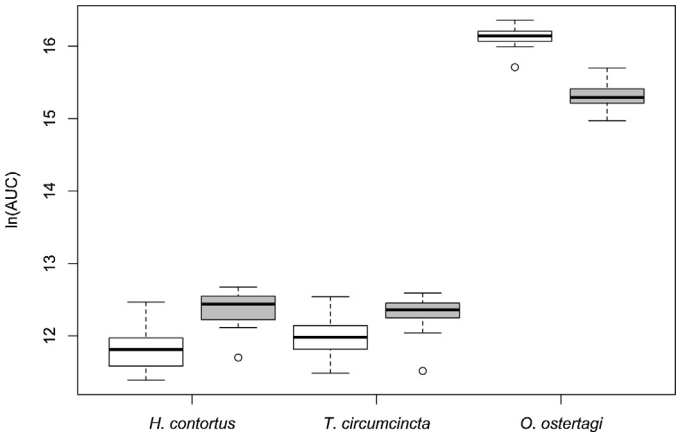

Fig. 5. Estimated annual AUC (Area Under the Curve) of the predicted numbers of L3 on pasture for *H. contortus*, *T. circumcincta* and *O. ostertagi* when using historical climatic data for the period 1969–1999 (white) and climatic data based on the RCP8.5 high emissions climate change scenario for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

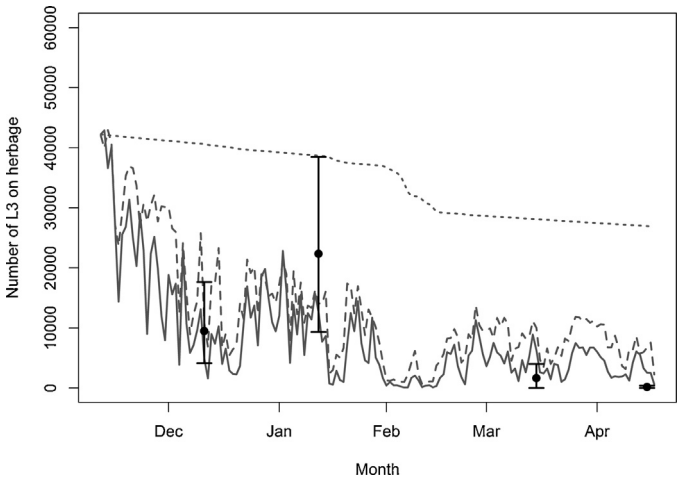

Fig. 6. The number of *H. contortus* L3 on herbage (L3 kg DM^{-1}) predicted using the GLOWORM-FL model and mean daily air temperature (dashed line) or fluctuating between the daily minimum and maximum temperature (dotted line) and the observed number (L3 kg DM^{-1}; points and error bars show mean and 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.

greenhouse gas emissions, a high rate of population growth, a dependence on fossil fuel and global CO_2 concentrations of ~950 ppm by 2100 (Van Vuuren et al., 2011). For comparison, record CO_2 concentrations of over 400 ppm 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 (Fig. 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 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 0–31.2 mm (Rose, 1963) and 0–23.2 mm (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 (Fig. 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 to 13.7 °C.

The GLOWORM-FL model, validated using observed numbers of *H. contortus* on pasture, outperformed a previously published, less complex model (Table 3; Fig. 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 0.03 mm (S.D. 1.09 mm) in mean daily rainfall is predicted under the RCP8.5 scenario, with an increase of up to 3.02 mm during the winter period and a decrease of up to 3.06 mm 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.*

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, H. (unpublished data)	*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, H. (unpublished data)	*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, H. (unpublished data)	*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, H. (unpublished data)	*Tc*	Pasture (Eq. (4))	Mean	1.17×10^{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, H. (unpublished data)	*Hc*	Smith (1990)	Mean	2.66×10^9	$F_{1,3} = 4.73$, $p = 0.12$	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 × the standard error of the slope coefficient.

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* ($W = 95$, $p < 0.001$; Fig. 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 (Fig. 7).

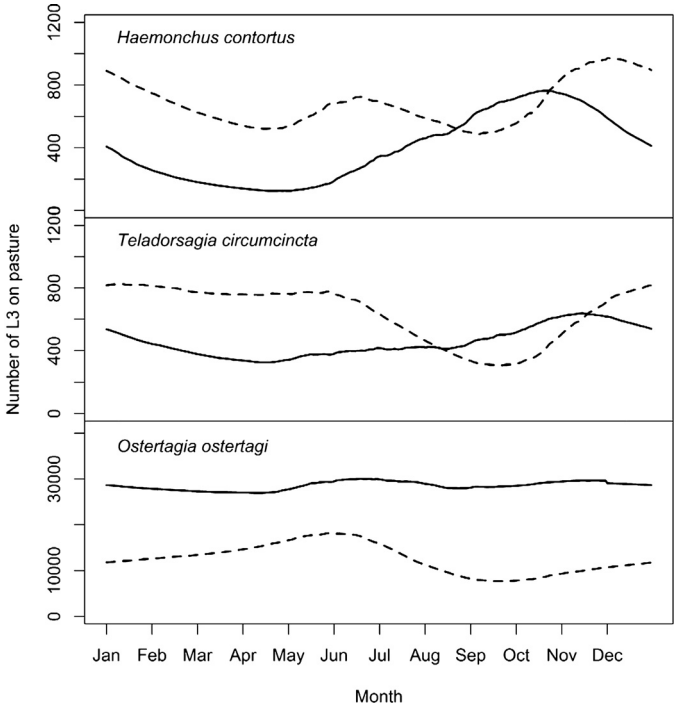

Fig. 7. The number of L3 on pasture (soil and herbage combined) predicted for *Haemonchus contortus* (top panel), *Teladorsagia circumcincta* (middle panel) and *Ostertagia ostertagi* (bottom panel) when using historical climatic data for the period 1969–1999 (solid line) and climatic data based on the RCP8.5 high emissions climate change scenario for the period 2070–2100 (broken line). Data shown are the disaggregated annual means from the 30-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.

A similar pattern of summer mortality is predicted for *O. ostertagi* (Fig. 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 recolonise herbage (Van Dijk and Morgan, 2011). For the same reason, the 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 (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 IPCC's RCP8.5 scenario. Climate-driven changes in the seasonal availability of L3 on pasture are likely to become increasingly important in the dynamics of GIN infection, particularly where host behaviour or farm management is slow to adapt in response to the change. In some cases, this may lead to an increase in disease (Van Dijk et al., 2008) whereas under different circumstances climate-driven changes may decrease exposure to infection. A better understanding of the seasonal dynamics of infection pressure will be key to the future of sustainable GIN control in livestock and could also benefit the management and conservation of wild ruminants.

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

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

An increase in temperature during the winter months was predicted, resulting in an increase in infection pressure for both *H. contortus* and *T. circumcincta* due to a corresponding increase in development rates. Development of *T. circumcincta* is possible throughout the year in South West England. In temperate regions *H. contortus* survival on pasture over winter is poor and there is very little development of eggs deposited on pasture as temperatures fall below the development threshold. However, *H. contortus* is able to survive the winter period as arrested larvae within the

host (Waller et al., 2004). The increase in temperatures predicted here for South West England, extends the period where the development of *H. contortus* is possible and could have significant short- and long-term impacts on the epidemiology of *H. contortus* in temperate regions. In the short-term, the increase in infection pressure 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 Gourbière (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 expected from factors such as trait variation (Troell et al., 2006; Van Dijk and Morgan, 2010), measurement error (Persson, 1974b) and uncertainty arising from model structure.

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

Discrepancies between meteorological observations and microclimatic conditions may account for the superior performance of simulations using mean daily air temperatures. Recent studies have demonstrated the importance of microclimatic factors in determining GIN abundance under controlled conditions (Khadijah et al., 2013b; O'Connor et al., 2008; Wang et al., 2014). In the field, temperature and moisture fluctuations in faeces may be buffered by the soil beneath and surrounding herbage. This buffering effect may also explain discrepancies between model predictions and observations, e.g. the model underestimated the time to development of *H. contortus* L3 observed by Rose (1963) during April and October regardless of whether minimum-maximum or mean temperatures were used. Soil temperature 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 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.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2014.11.033.

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