

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

4 Hannah Rose^{1,2}, Tong Wang¹, Jan van Dijk³, Eric R. Morgan^{2,4}

5 ¹School of Biological Sciences, Life Sciences Building, University of Bristol, Tyndall
6 Avenue, Bristol, UK, BS8 1TQ

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

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

10 ⁴School of Veterinary Sciences, University of Bristol, Langford House, Langford,
11 Bristol, UK, BS40 5DU

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

13

14 **Abstract**

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

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

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

44

45

46 **1. Introduction**

47 Trichostrongyloid gastrointestinal nematodes (GINs) are a major cause of mortality
48 and morbidity in livestock (e.g. Allonby and Urquhart, 1975), threatening food
49 security via constraints on productivity (Fitzpatrick, 2013). Costs of GINs have been
50 estimated at 84 million pounds sterling (105 million Euros) annually for the sheep
51 industry in the UK alone (Nieuwhof and Bishop, 2007), although effects of infection
52 on farm economics can be complex and difficult to estimate (van der Voort et al.,
53 2013).

54 Adult trichostrongylid GINs inhabit the gastrointestinal system of a range of host
55 species including ruminants (Allonby and Urquhart, 1975; Morgan et al., 2005),
56 lagomorphs (Newey et al., 2005) and birds (Hudson et al., 1998). Eggs are
57 deposited in the environment in faeces, where they develop to infective larvae, which
58 then move onto herbage. Larvae are ingested by the host during grazing and
59 complete their life-cycle in the host (Anderson, 2000). The development, survival and
60 behaviour of the free-living stages and thus the availability of infective stages for
61 transmission is highly dependent on weather and micro-climatic conditions (Khadijah
62 et al., 2013a; Morgan and van Dijk, 2012; O'Connor et al., 2008, 2007, 2006;
63 Reynecke et al., 2011; Rose, 1963, 1961; van Dijk and Morgan, 2008, 2011). There
64 is evidence that recent increases in temperature in the UK have resulted in changes
65 in the phenology of GINs on pasture (Gethings et al. submitted) and in the incidence
66 of disease due to GIN infection (parasitic gastroenteritis) in livestock (van Dijk et al.,
67 2008). As a result, the potential impact of climate change on GIN-host dynamics is of
68 increasing concern (Rose et al., 2014; van Dijk and Morgan, 2010; van Dijk et al.,
69 2010).

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

81 Numerous gastrointestinal nematode models have been developed over previous
82 decades (reviewed elsewhere by Cornell, 2005; Roberts, 1995; Smith and Grenfell,
83 1994). Many are deliberately simple in order to explore model behaviour and system
84 dynamics (Cornell et al., 2004; Grenfell, 1992; Louie et al., 2005; Roberts and
85 Heesterbeek, 1995). Others include more biological detail in order to address
86 specific questions (Grenfell et al., 1987; Laurenson et al., 2011; Learmount et al.,
87 2006; Leathwick et al., 1995, 1992; Smith et al., 1987). However, climate-dependent
88 life-history parameters that determine the availability of infective stages on pasture
89 are often set at a constant rate (Laurenson et al., 2013). Furthermore, although
90 many models incorporate climate-dependence (Grenfell et al., 1987; Molnár et al.,
91 2013) and stage-specific mortality and development rates, to the authors' knowledge
92 no model explicitly incorporates movement of infective larvae between soil and
93 herbage nor addresses moisture-limitations on migration between faeces and
94 pasture (herbage and soil combined). Detail such as this will become increasingly

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

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

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

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

121

122 2. Materials and Methods

123 2.1 GLOWORM-FL model framework

124 The model framework is based on the general life-cycle of the free-living stages of
125 trichostrongylid gastrointestinal nematodes (Figure 1). Eggs (E) develop to third
126 stage larvae in the faeces ($L3_f$) via the pre-infective larval stages (L), and are subject
127 to stage-specific mortality rates (μ_i). As pre-infective larval stages (first stage larvae,
128 L1, and second-stage larvae, L2) are not separated, the model can be applied to
129 trichostrongylids that hatch as first stage larvae (e.g. *Haemonchus* spp.,
130 *Teladorsagia* spp. and *Ostertagia* spp.; Anderson, 2000), or second stage larvae
131 (*Marshallagia marshalli*; Carlsson et al., 2013).

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

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

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

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

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

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

142 Once on pasture, L3 can be recovered from both soil/mat layer and herbage. Although
143 Grenfell et al. (1986) included losses of L3 in soil due to soil moisture deficit or wash-
144 down during rainfall in their model, movement between soil and herbage was not
145 considered. Experiments have demonstrated the potential for bi-directional movement
146 of trichostrongylid L3 between soil and herbage (Krecek and Murrell, 1988; Rose and
147 Small, 1985) and that there is random movement between the soil and herbage (van
148 Dijk and Morgan 2011). Therefore, L3 on pasture ($L3_p$) are assumed to reside in either
149 the soil and vegetation mat layer ($L3_s$) or on herbage ($L3_h$). In order to simulate
150 random, bi-directional movement between herbage and the soil reservoir, substrate-
151 specific mortality rates (μ_4 , μ_5) are applied to the proportion of larvae estimated to
152 reside in soil and on herbage respectively, dependant on a vertical migration
153 parameter (m_2).

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

154 State variables and parameter definitions are listed in Table 1. The model was
155 implemented in R (R Core Team, 2013) using the *Isoda* function in the *deSolve*
156 package (Soetaert et al., 2010). *Isoda* uses an Adams-BDF (backward differentiation
157 formulae) adaptive integration method that detects the stiffness of the problem
158 throughout the simulation and switches between Adams and BDF integration
159 accordingly (Soetaert et al., 2010). The model returns daily output but the time steps
160 used for integration are not known prior to simulation when using the Adams-BDF
161 integration method. Therefore, time-series of variable climate-dependent rates e.g.
162 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 *Isoda* 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 $-\ln(\text{proportion remaining})/\text{days}$; 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.

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

193 Data were only used to estimate the mortality rates of pre-infective stages if the
194 temperatures were low enough to preclude development, or high enough that
195 mortality occurred prior to development to the next larval stage (e.g. Todd et al.,
196 1976). Development of L3 is arrested until they are ingested by the host. Therefore a
197 range of temperatures could be used to estimate the substrate-specific mortality
198 rates of L3.

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

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

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

222 **2.2.2 Moisture limitations and differences between host species**

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

232 **2.2.2.1 Moisture limitations on development success**

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

243 O'Connor et al. (2008) observed a significant decrease in the development success
244 of *H. contortus* where cumulative P/E fell below 1 within 4 days of deposition of eggs.
245 Khadijah et al. (2013a) recovered maximum *H. contortus* L3 from faecal pellets and
246 soil when simulated rainfall was applied between -1 and 2 days post deposition of
247 faeces containing eggs and concluded that faecal moisture 48-72 hours post
248 deposition was important for development success. No L3 were recovered from un-
249 watered controls. Similar data were not available for *T. circumcincta*. However,
250 Khadijah et al. (2013a) note that for *Trichostrongylus colubriformis*, faecal moisture
251 in the period 72-96h post deposition is important for development success. This
252 period is likely to be extended for *T. circumcincta* which is more resistant to
253 desiccation than *T. colubriformis*. A lower faecal moisture content (FMC) threshold
254 was observed for *T. circumcincta* development (yielding ≥ 1 L3 per 100 eggs) than *T.*
255 *colubriformis* (25% and 35% respectively; Rossanigo and Gruner, 1995). The critical
256 periods for *H. contortus* and *T. circumcincta* were therefore identified as 4 days and
257 7 days post deposition of eggs respectively (Khadijah et al., 2013b; O'Connor et al.,

258 2008). The cumulative P/E for development success is referred to as P/E_4 for *H.*
259 *contortus* and P/E_7 for *T. circumcincta*.

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

263 **2.2.2.2 Moisture limitations on the translation of L3 onto pasture**

264 Laboratory observations on the migration of *H. contortus* and *T. colubriformis* L3
265 indicate that, similar to development success, moisture limitations on horizontal
266 migration are mediated by faecal moisture content, which varies as a result of
267 interacting microclimatic factors (Khadijah et al., 2013a, 2013b; O'Connor et al.,
268 2008, 2007; van Dijk and Morgan, 2011). Few data were available to estimate the
269 temperature- and moisture-dependent horizontal migration rate of infective larvae
270 from faeces onto pasture. Therefore, data in the published literature were
271 supplemented with laboratory experiments to derive heuristic estimates for horizontal
272 migration under: 1) optimal moisture conditions (sufficient rainfall); 2) sub-optimal
273 moisture conditions (insufficient rainfall but sufficient FMC) and; 3) moisture-limiting
274 conditions (low FMC and insufficient rainfall).

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

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

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

298 The proportion of L3 that had migrated out of faeces was calculated as:
299 $\text{extra-pellet L3} / (\text{extra-pellet L3} + \text{intra-pellet L3})$, corrected for recovery efficiency.
300 Mean daily horizontal migration rates of 0.25 (S.D. 0.11) and 0.21 (S.D. 0.44) were
301 observed for *H. contortus* and *T. circumcincta*. FMCs prior to rainfall were 3-61% (*H.*
302 *contortus*) and 7-34% (*T. circumcincta*), increasing to 45-73% (*H. contortus*) and 39-
303 56% (*T. circumcincta*) after simulated rainfall.

304 *O. ostertagi* L3 were only observed on the surface of experimental pats that had
305 been watered (Grønvold and Høgh-Schmidt, 1989) suggesting that rainfall is
306 required to moisten the protective surface crust sufficiently to allow migration.
307 Therefore, estimates of horizontal migration of *O. ostertagi* under sub-optimal
308 moisture conditions were not considered. In contrast, small numbers of extra-pellet
309 *H. contortus* and *T. colubriformis* L3 have been recovered in the absence of rainfall
310 (O'Connor et al., 2008; Wang et al., 2014). Therefore a 4- and 7-day trailing
311 cumulative P/E rule was applied to *H. contortus* and *T. circumcincta* respectively to
312 characterise sub-optimal conditions, extrapolated from the observations of O'Connor
313 et al. (2008) and Khadijah et al. (2013b) on the effect of cumulative P/E on FMC and
314 development success. Sub-optimal days were defined as days where total
315 precipitation < 2mm, and trailing cumulative P/E ≥ 1. The species specific trailing
316 cumulative P/E values for migration are referred to as P/E₄ for *H. contortus* and
317 P/E₇ for *T. circumcincta*.

318 An estimated horizontal migration rate of 0.051 for *H. contortus* under sub-optimal
319 moisture conditions was derived from observations by O'Connor et al. (2008), where
320 30% of L3 migrated out of faeces within a 7 day period in the absence of rain but
321 following a period of simulated rainfall in the preceding 7 days. This is consistent with
322 the observed mean migration rate of 0.057 (S.D. 0.027) for *H. contortus* maintained
323 under high relative humidity of 98% and FMC of ~60% (Wang et al., 2014).

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

329 show that under optimal moisture conditions the instantaneous daily migration rate of
330 *T. circumcincta* is 49% that of *H. contortus*. Ninety-nine percent (S.D. 0.4) of *H.*
331 *contortus* L3 had migrated out of faeces within 7 days (Wang et al. 2014), compared
332 with 91% (S.D. 6.8) of *T. circumcincta* L3, giving instantaneous daily horizontal
333 migration rates of 0.71 and 0.35 respectively. Thus the estimated instantaneous daily
334 migration rate for *T. circumcincta* where moisture is sub-optimal is $0.051 \times 0.49 =$
335 0.025 (Table 2).

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

338

339 **2.2.3 Migration between soil and herbage**

340 Crofton (1948) observed seasonal patterns in the vertical migration of
341 *Trichostrongylus retortaeformis* L3 on pasture where fewer L3 were recovered from
342 the upper herbage layer in winter than in summer. It is likely that interacting climatic
343 and other abiotic variables including temperature, moisture, biomass composition
344 and light drive this seasonality (Amaradasa et al., 2010; Callinan and Westcott,
345 1986; Crofton, 1948; Dusenbery, 1989; Ogbourne, 1973; Rees, 1950; Saunders et
346 al., 2000; Silangwa and Todd, 1964; van Dijk et al., 2009). However, the majority of
347 studies have sampled only a superficial layer of soil (e.g. Crofton, 1948; Rees, 1950)
348 and therefore could underestimate the proportion of pasture L3 in soil relative to L3
349 on herbage. Mesocosm experiments (e.g. Callinan and Westcott, 1986; Knapp-
350 Lewitzke et al. in preparation) offer an alternative to ensure more complete sampling
351 of L3 in soil. The temperature-dependent proportion of trichostrongylid L3 expected
352 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,

377 Weybridge, where Rose's (1963) observations were made, were obtained from the
378 British Atmospheric Data Centre (badc.nerc.ac.uk). The same data were not
379 available for the time period of observations made by Rose (1961). Therefore,
380 meteorological data were obtained from the E-OBS gridded dataset (lat/lon:
381 51.355°N, -0.496°E; Haylock et al., 2008). Potential evaporation (mm/day) was
382 estimated from mean air temperatures using the Hamon method (Xu and Singh,
383 2001). Two simulations were run for each monthly deposit using mean daily
384 temperature and linear fluctuations between minimum and maximum daily
385 temperature to determine whether mean air temperature is sufficient to predict
386 development when temperatures are close to the minimum threshold for
387 development. Horizontal migration, m_1 , was set to 0 to prevent migration out of
388 faeces.

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

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

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

414 **2.4 Climate change simulations**

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

426 dependence on fossil fuel and global CO₂ concentrations of ~950ppm by 2100 (van
427 Vuuren et al., 2011). For comparison, record CO₂ concentrations of over 400ppm
428 were observed at the Mauna Loa observatory in May 2014 (Tans, 2014).

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

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

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

443

444 **3. Results**

445 **3.1 Model validation**

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

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

454 The model performed well when tested against field observations of *H. contortus* and
455 *O. ostertagi* development and survival in faeces (Table 3) demonstrating that the
456 models, parameterised using laboratory data, transferred well onto conditions
457 observed in the field. The range of mean air temperatures during the observation
458 periods was -3.9 to 24.7°C (Rose, 1963) and -2.5 to 23.2°C (Rose, 1961). The range
459 of total daily precipitation during the observation periods was 0-31.2mm (Rose,
460 1963) and 0-23.2mm (Rose, 1961).

461 The predicted dynamics and numbers of *H. contortus* and *T. circumcincta* L3 on
462 pasture fitted observations well, replicating the initial decrease in L3 density on
463 herbage followed by an increase, despite no further contamination of pasture (Figure
464 6; Table 3). This seasonal variability in L3 on herbage can be explained by the
465 vertical migration of L3 between soil and herbage; a model using only a temperature-
466 dependent mortality rate and not considering movement between the soil and

467 herbage was not able to replicate these dynamics. The range of mean daily air
468 temperatures during the observation period was -3.05 to 13.7°C.

469 The GLOWORM-FL model, validated using observed numbers of *H. contortus* on
470 pasture, outperformed a previously published, less complex model (Table 3; Figure
471 6).

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

478 **3.2 Climate change simulations**

479 At the chosen test location in South West England, UK, the HadGEM-ES model
480 predicts warmer wetter winters and warmer, drier summers during 2070-2100 under
481 the RCP8.5 high emissions scenario, compared with the historical period of 1969-
482 1999. A mean increase in mean air temperature of 4.57°C (S.D. 1.91°C) is predicted
483 by 2070-2100. The increase is greatest during the summer months with a maximum
484 of 8.65°C increase predicted during July and a minimum of 1.49°C increase
485 predicted during March. A mean decrease of 0.03mm (S.D. 1.09mm) in mean daily
486 rainfall is predicted under the RCP8.5 scenario, with an increase of up to 3.02mm
487 during the winter period and a decrease of up to 3.06mm during the summer period.
488 The change in seasonal temperatures and rainfall resulted in an increase in
489 predicted development rate throughout the year whereas mortality rates decreased
490 during the winter and increased during the summer. The pattern of moisture-

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

495 There was a significant predicted increase in annual infection pressure for both *H.*
496 *contortus* ($W=47$, $p<0.001$) and *T. circumcincta* ($W=95$, $p<0.001$; Figure 5) under the
497 RCP8.5 scenario compared with historical climatic data. Mean air temperature was
498 regularly higher than the predicted lower threshold for development of *T.*

499 *circumcincta* (4.46°C) when both historical and RCP8.5 data were used and
500 development was possible year round. However, the number of days where
501 development was possible increased from 328 to 360 (the HadGEM-ES model was
502 run on a 360 day year and therefore 360 represents the entire year). The increase in
503 temperatures predicted under RCP8.5 therefore resulted in increased development
504 rates year-round for *T. circumcincta*. In contrast, very little *H. contortus* development
505 is completed over winter when using historical climatic data as the mean air
506 temperature rarely rises above the predicted threshold for development of 9.17°C .

507 Therefore, the increase in temperatures predicted under RCP8.5 not only results in
508 an increase in development rate but also a lengthening of the season during which
509 development is possible. The period during which mean daily temperatures
510 exceeded the development threshold for *H. contortus* was extended by 3.3 months
511 from 188 days between March and September under historical climate to 258 days
512 between February and December under RCP8.5. A corresponding decrease in
513 mortality rates during the winter results in an overall increase in infection pressure
514 over the winter period, extending into early summer. Further increases in
515 temperatures during the summer result in increased mortality which offsets the

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

518 A similar pattern of summer mortality is predicted for *O. ostertagi* (Figure 7). When
519 using historical climatic data, there is a small increase in L3 on pasture during the
520 spring as temperatures exceed the predicted threshold for development of 7.44°C,
521 but the large number of L3 predicted on pasture is fairly consistent throughout the
522 year due to low mortality rates. However, there is a significant decrease in annual
523 infection pressure when using the RCP8.5 climatic data, compared with predictions
524 using historical data ($W=95$, $p<0.001$). The period during which mean daily
525 temperatures exceeded the development threshold for *O. ostertagi* was extended by
526 4.6 months from 216 days between March and October under historical climate to
527 347 days throughout the year under RCP8.5, but this is offset by significant
528 increases in mortality rates between May and November depleting the reservoir of
529 L3 in faeces and soil.

530

531

532 **4. Discussion**

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

551 An additional motivation for the development of the model was that characteristics
552 relevant to the epidemiology of GINs are similar between different livestock systems
553 and wild ruminants (Rose et al., 2014) and there is evidence of transmission where
554 livestock and wildlife meet or share ranges (Chintoan-Uta et al., 2014; Morgan et al.,
555 2007). There is therefore a need for a common framework that can be applied to a
556 range of GIN and host species. The GLOWORM-FL model framework was

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

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

577 GLOWORM-FL provides a tool to aid in the development of climate-based GIN
578 control methods. The model can be used to track pasture contamination and
579 evaluate the resultant climate-dependent infection pressure under a range of
580 management and climate scenarios. Here, its use is demonstrated using climatic
581 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.*

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

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

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

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

679 In some cases, linear regression of observations against model predictions was
680 significant, but the slope of the regression was marginally different from 1, indicating
681 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

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

709 The model was validated using observations made in a temperate region, with
710 temperatures ranging between - 4°C and 25°C. However, temperatures of up to
711 39.2°C were predicted under the RCP8.5 scenario and therefore some simulations
712 projected beyond the range of the conditions used for validation. *H. contortus* and *T.*
713 *circumcincta* simulations using climatic data for the RCP8.5 scenario showed that
714 high temperatures may result in counter-intuitive decreases in the availability of L3
715 due to a trade-off between increased mortality and development rates. Uncertainty in
716 climate change simulations due to projections outside of the range of observed data
717 could be reduced by repeating validation using data from regions with current
718 climatic conditions similar to those predicted under the chosen climate change
719 scenario.

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

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

736 **5. Conclusion**

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

745

746

747 **Acknowledgments**

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

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

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

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

765

766

767 **References**

- 768 Allonby, E.W., Urquhart, G.M., 1975. The epidemiology and pathogenic significance
769 of haemonchosis in a merino flock in East Africa. *Vet. Parasitol.* 1, 129–143.
- 770 Amaradasa, B.S., Lane, R.A., Manage, A., 2010. Vertical migration of *Haemonchus*
771 *contortus* infective larvae on *Cynodon dactylon* and *Paspalum notatum* pastures
772 in response to climatic conditions. *Vet. Parasitol.* 170, 78–87.
- 773 Anderson, R.C., 2000. Nematode parasites of vertebrates: their development and
774 transmission. CABI, Wallingford.
- 775 Azam, D., Ukpai, O.M., Said, A., Abd-Allah, G.A., Morgan, E.R., 2012. Temperature
776 and the development and survival of infective *Toxocara canis* larvae. *Parasitol.*
777 *Res.* 110, 649–656.
- 778 Callinan, A.P.L., 1978a. The ecology of the free-living stages of *Ostertagia*
779 *circumcincta*. *Int. J. Parasitol.* 8, 233–237.
- 780 Callinan, A.P.L., 1978b. The ecology of the free-living stages of *Trichostrongylus*
781 *axei*. *Int. J. Parasitol.* 8, 453–456.
- 782 Callinan, A.P.L., 1979. The ecology of the free-living stages of *Trichostrongylus*
783 *vitrinus*. *Int. J. Parasitol.* 9, 133–136.
- 784 Callinan, A.P.L., Westcott, J.M., 1986. Vertical distribution of trichostrongylid larvae
785 on herbage and in soil. *Int. J. Parasitol.* 16, 241–244.
- 786 Carlsson, A.M., Irvine, R.J., Wilson, K., Coulson, S.J., 2013. Adaptations to the
787 Arctic: low-temperature development and cold tolerance in the free-living stages
788 of a parasitic nematode from Svalbard. *Polar Biol.* 36, 997–1005.
- 789 Charlier, J., Höglund, J., von Samson-Himmelstjerna, G., Dorny, P., Vercruyssen, J.,
790 2009. Gastrointestinal nematode infections in adult dairy cattle: impact on
791 production, diagnosis and control. *Vet. Parasitol.* 164, 70–79.
- 792 Chintoan-Uta, C., Morgan, E.R., Skuce, P.J., Coles, G.C., 2014. Wild deer as
793 potential vectors of anthelmintic-resistant abomasal nematodes between cattle
794 and sheep farms. *Proc. R. Soc. B* 281, 20132985.
- 795 Collins, W.J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton,
796 T., Hughes, J., Jones, C.D., Joshi, M., Liddicoat, S., Martin, G., O'Connor, F.,
797 Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A., Woodward, S., 2011.
798 Development and evaluation of an Earth-System model – HadGEM2. *Geosci.*
799 *Model Dev.* 4, 1051–1075.
- 800 Cornell, S., 2005. Modelling nematode populations: 20 years of progress. *Trends*
801 *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 pattern 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., Hessele, 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 *Vétérinaires* 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.

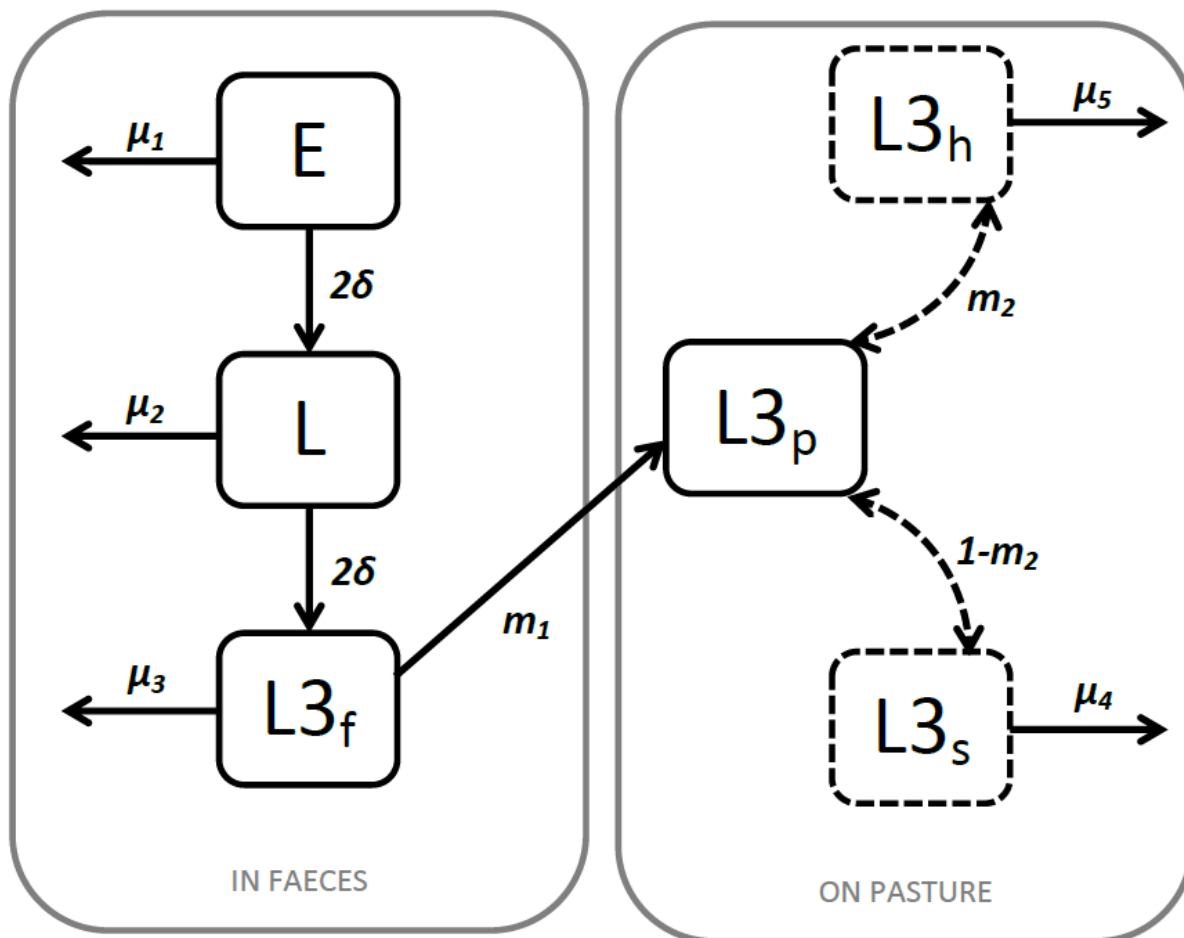
- 914 Newey, S., Shaw, D.J., Kirby, A., Montieth, P., Hudson, P.J., Thirgood, S.J., 2005.
915 Prevalence, intensity and aggregation of intestinal parasites in mountain hares
916 and their potential impact on population dynamics. *Int. J. Parasitol.* 35, 367–373.
- 917 Nieuwhof, G.J., Bishop, S.C., 2007. 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.

- 986 Soetaert, K., Cash, J., Mazzia, F., 2012. Solving Ordinary Differential Equations in R,
987 in: Gentleman, R., Parmigiani, G., Hornik, K. (Eds.), Solving Differential
988 Equations in R. Springer, New York, pp. 41–80.
- 989 Soetaert, K., Petzoldt, T., Setzer, R.W., 2010. Solving Differential Equations in R :
990 Package deSolve. R J. 2, 5–15.
- 991 Stear, M.J., Bishop, S.C., Doligalska, M., Duncan, J.L., Holmes, P.H., Irvine, J.,
992 McRirie, L., McKellar, Q.A., Sinski, E., Murray, M., 1995. Regulation of egg
993 production, worm burden, worm length and worm fecundity by host responses in
994 sheep infected with *Ostertagia circumcincta*. Parasite Immunol. 17, 643–652.
- 995 Sutherland, I.A., Leathwick, D.M., 2011. Anthelmintic resistance in nematode
996 parasites of cattle: a global issue? Trends Parasitol. 27, 176–181.
- 997 Tans, P., 2014. Weekly mean CO2 at Mauna Loa and historical comparisons [WWW
998 Document]. URL
999 ftp://aftp.cmdl.noaa.gov/products/trends/co2/co2_weekly_mlo.txt (accessed
1000 6.30.14).
- 1001 Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the
1002 experiment design. Bull. Am. Meteorol. Soc. 93, 485–498.
- 1003 Todd, K.S., Levine, N.D., Boatman, P.A., 1976. Effect of temperature on survival of
1004 free-living stages of *Haemonchus contortus*. Am. J. Vet. Res. 37, 991–992.
- 1005 Troell, K., Tingstedt, C., Höglund, J., 2006. Phenotypic characterization of
1006 *Haemonchus contortus*: a study of isolates from Sweden and Kenya in
1007 experimentally infected sheep. Parasitology 132, 403–9.
- 1008 Van der Voort, M., Charlier, J., Lauwers, L., Vercruyssen, J., Van Huylbroeck, G.,
1009 Van Meensel, J., 2013. Conceptual framework for analysing farm-specific
1010 economic effects of helminth infections in ruminants and control strategies.
1011 Prev. Vet. Med. 109, 228–35.
- 1012 Van Dijk, J., David, G.P., Baird, G., Morgan, E.R., 2008. Back to the future:
1013 Developing hypotheses on the effects of climate change on ovine parasitic
1014 gastroenteritis from historical data. Vet. Parasitol. 158, 73–84.
- 1015 Van Dijk, J., de Louw, M.D.E., Kalis, L.P.A., Morgan, E.R., 2009. Ultraviolet light
1016 increases mortality of nematode larvae and can explain patterns of larval
1017 availability at pasture. Int. J. Parasitol. 39, 1151–1156.
- 1018 Van Dijk, J., Morgan, E.R., 2008. The influence of temperature on the development,
1019 hatching and survival of *Nematodirus battus* larvae. Parasitology 135, 269–283.
- 1020 Van Dijk, J., Morgan, E.R., 2010. Variation in the hatching behaviour of *Nematodirus*
1021 *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

1042 Figure 1. Conceptual diagram of the GLOWORM-FL model framework. Parameter
1043 (lower case) and state variable (upper case) definitions are given in Table 1.

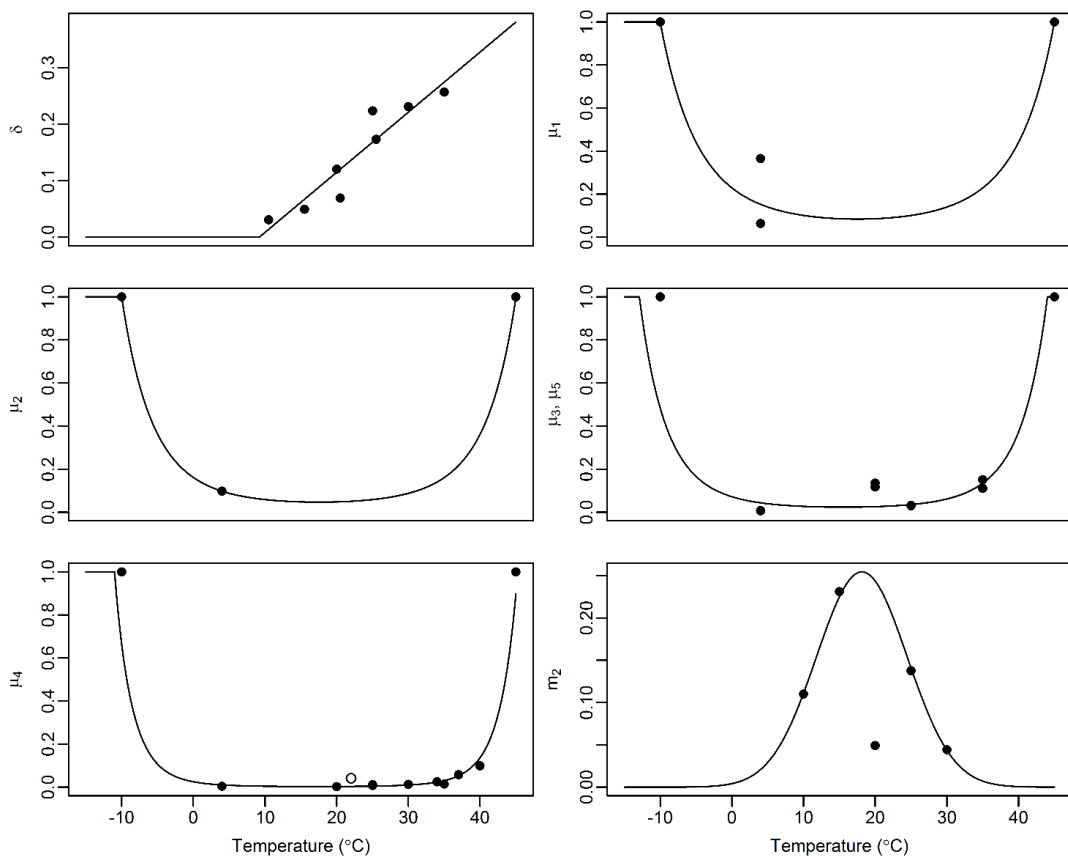


1044

1045

1046

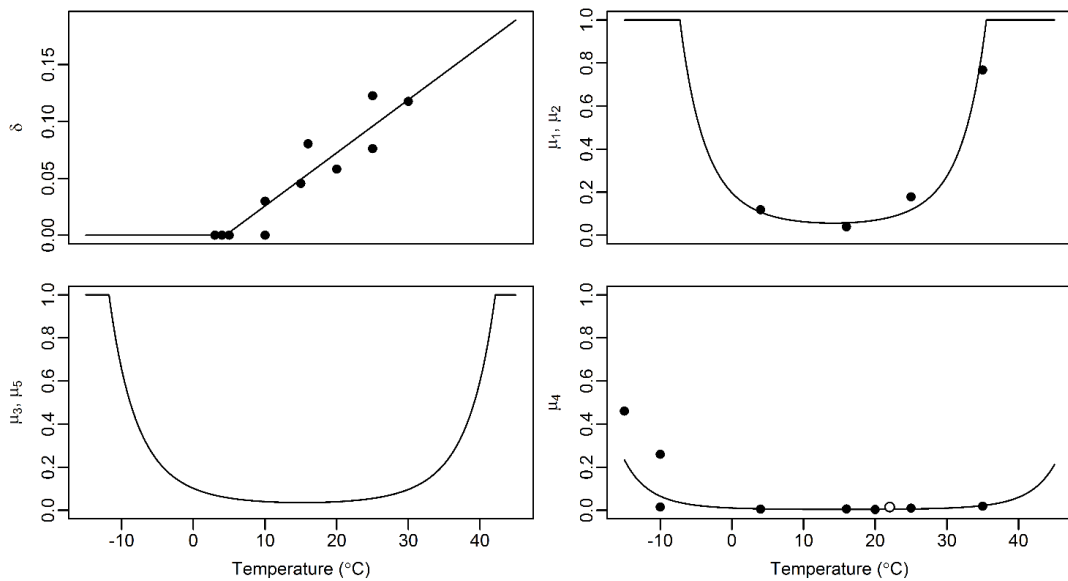
1047 Figure 2. Estimates of temperature-dependent life-history parameters for *H.*
 1048 *contortus* (lines) based on analysis of data in the literature (closed circles).
 1049 Parameter definitions are given in Table 1. Statistical output for linear models is
 1050 provided in Table 2. Mortality of L3 in soil (μ_4) was estimated from observations of L3
 1051 mortality in water. A point estimate of L3 mortality in desiccated soil at 20-24°C (van
 1052 Dijk and Morgan, 2011) is superimposed (open circle) for comparison. Data were not
 1053 available to estimate the mortality of L3 on herbage (μ_5), which was therefore
 1054 estimated using the mortality rate of L3 in faeces (μ_3). The data point at 20 degrees
 1055 was omitted from analysis of the vertical migration parameter (m_2) but is shown here.
 1056 A minimum threshold for development of 9.17°C is predicted.



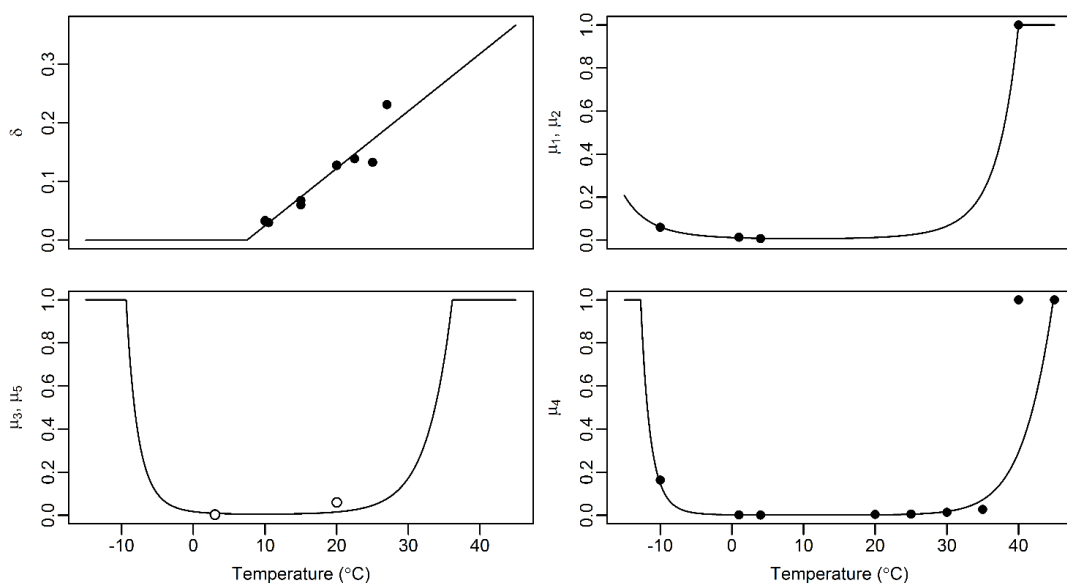
1057

1058

1060 Figure 3. Estimates of temperature-dependent life-history parameters for *T.*
 1061 *circumcincta* (lines) based on analysis of data provided in the literature (closed
 1062 circles). Parameter definitions are given in Table 1. Statistical output for linear
 1063 models is provided in Table 2. Mortality of L3 in soil (μ_4) was estimated from
 1064 observations of L3 mortality in water. A point estimate of L3 mortality in desiccated
 1065 soil at 20-24°C (van Dijk and Morgan, 2011) is superimposed (open circle) for
 1066 comparison. Data points are not shown for the mortality rates of L3 in faeces (μ_3)
 1067 and on herbage (μ_5) as no data were available to directly estimate these parameters.
 1068 These rates were therefore estimated from the mortality rate of L3 in soil (μ_4). A
 1069 minimum threshold for development of 4.46°C is predicted. The vertical migration
 1070 parameter is as shown in Figure 2.



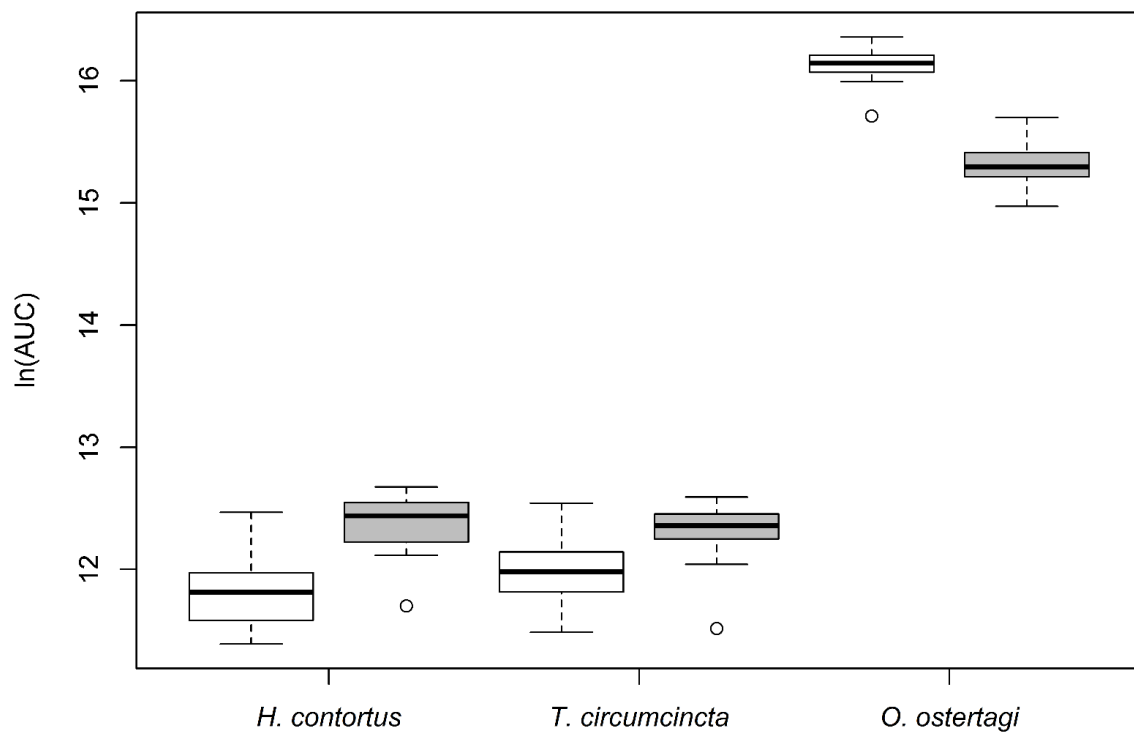
1073 Figure 4. Estimates of temperature-dependent life-history parameters for *O. ostertagi*
 1074 (lines) based on analysis of data provided in the literature (closed circles). Parameter
 1075 definitions are given in Table 1. Statistical output for linear models is provided in
 1076 Table 2. Data points are not shown for the mortality rates of L3 in faeces (μ_3) and on
 1077 herbage (μ_5) as no data were available to directly estimate these parameters. These
 1078 rates were therefore estimated from the mortality rate of L3 in soil (μ_4). Estimates of
 1079 mortality in faeces (μ_3) based on analysis of observations on *Cooperia oncophora*
 1080 and *O. ostertagi* mixed infections (open circles) are superimposed for comparison
 1081 (Persson, 1974a). A minimum threshold for development of 7.44°C is predicted. The
 1082 vertical migration parameter is as shown in Figure 2.



1083

1084

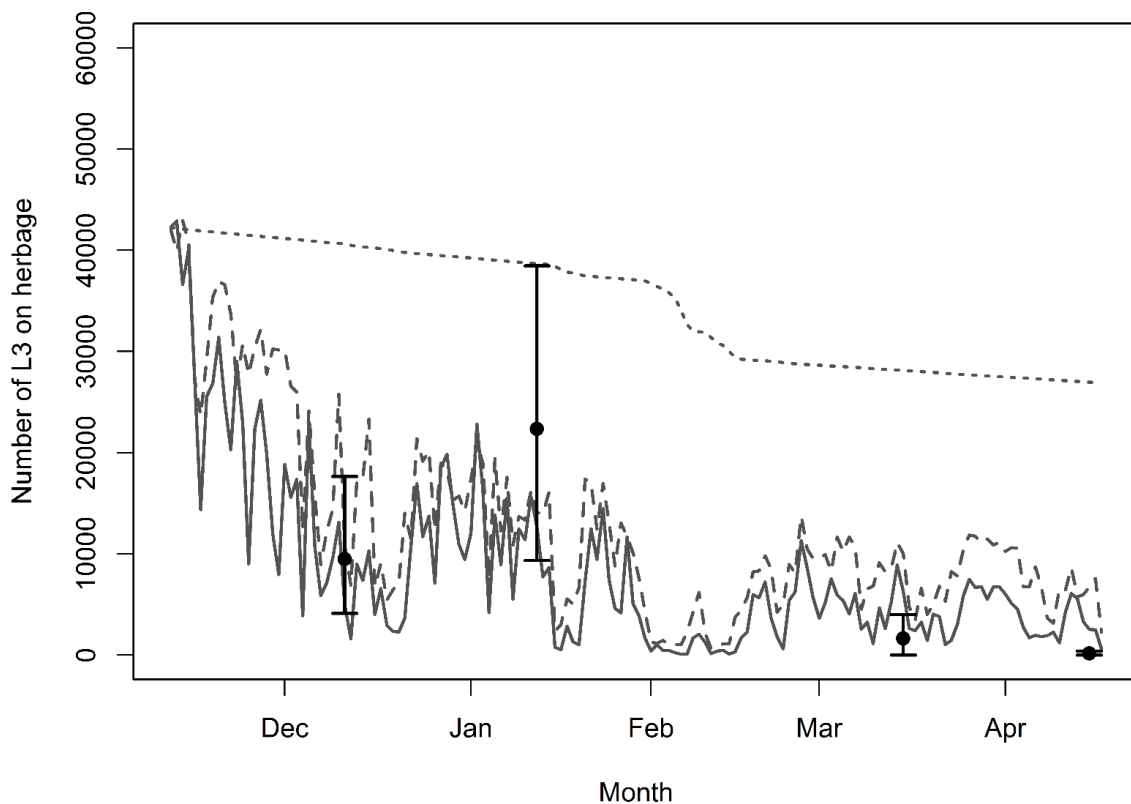
1085 Figure 5. Estimated annual AUC (Area Under the Curve) of the predicted numbers of
1086 L3 on pasture for *H. contortus*, *T. circumcincta* and *O. ostertagi* when using
1087 historical climatic data for the period 1969-1999 (white) and climatic data based on
1088 the RCP8.5 high emissions climate change scenario for the period 2070-2100 (grey).



1089

1090

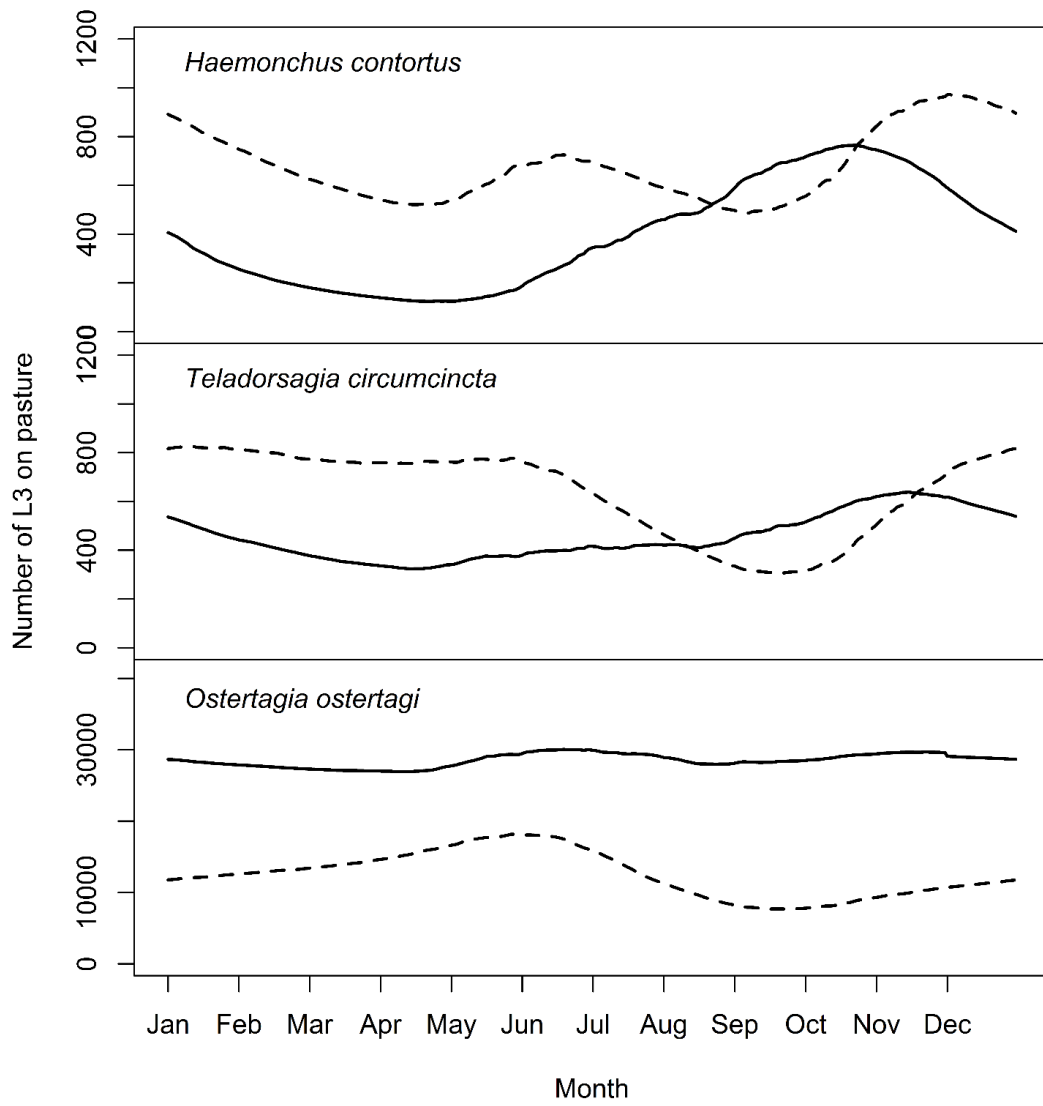
1091 Figure 6. The number of *H. contortus* L3 on herbage (L3 kg DM-1) predicted using
1092 the GLOWORM-FL model and mean daily air temperature (dashed line) or
1093 fluctuating between the daily minimum and maximum temperature (dotted line) and
1094 the number (L3 kg DM-1) observed by Wilkie et al. (submitted; points and error bars
1095 show mean and 95% confidence interval). Predicted numbers of L3 on herbage
1096 using a single mortality rate for L3 on pasture and no vertical migration (dotted line;
1097 Smith, 1990) are superimposed for comparison.



1098

1099

1100 Figure 7. The number of L3 on pasture (soil and herbage combined) predicted for
1101 *Haemonchus contortus* (top panel), *Teladorsagia circumcincta* (middle panel) and
1102 *Ostertagia ostertagi* (bottom panel) when using historical climatic data for the period
1103 1969-1999 (solid line) and climatic data based on the RCP8.5 high emissions climate
1104 change scenario for the period 2070-2100 (broken line). Data shown are the
1105 disaggregated annual means from the thirty year time-series. The first year of each
1106 time series was discarded. One hundred new eggs were input daily. Therefore no
1107 assumptions were made regarding management or intensity of infection in the host
1108 and the predicted dynamics are entirely climate-driven.



1109

1110

1111

1112 Table 1. State variable and parameter definitions

State variable/ Parameter	Definition	Units
<i>E</i>	Eggs	-
<i>L</i>	First stage (L1) and second stage (L2) larvae	-
<i>L3_f</i>	Third stage infective larvae (L3) in faeces	-
<i>L3_p</i>	Total L3 on pasture (soil and herbage combined)	-
<i>L3_s</i>	L3 in soil	-
<i>L3_h</i>	L3 on herbage	-
<i>σ</i>	Development rate from egg to L3	Instantaneous daily rate
<i>μ₁</i>	Egg mortality rate	Instantaneous daily rate
<i>μ₂</i>	L1 and L2 mortality rate	Instantaneous daily rate
<i>μ₃</i>	L3 mortality rate in faeces	Instantaneous daily rate
<i>μ₄</i>	L3 mortality rate in soil	Instantaneous daily rate
<i>μ₅</i>	L3 mortality rate on herbage	Instantaneous daily rate
<i>m₁</i>	Horizontal migration (translation) of L3 onto pasture	Instantaneous daily rate
<i>m₂</i>	Proportion of total pasture L3 on herbage	Proportion
<i>C</i>	Development success correction factor	Proportion

1113

1114

1115 Table 2. Parameter estimates derived from data in the literature and additional
 1116 laboratory experiments. ANOVA results are shown for the linear models fitted to
 1117 data from the literature to estimate temperature-dependent rates (see text).

Parameter	Species ^a	Estimate ^b	Data source
δ	<i>Hc</i>	$-0.09746 + 0.01063T$ ($F_{1,6}=43.5$, $p<0.001$, $R^2=0.88$, $R^2_{adj}=0.86$)	Hsu and Levine, 1977; Rose, 1963
	<i>Tc</i>	$-0.02085 + 0.00467T$ ($F_{1,10}=76.57$, $p<0.001$, $R^2=0.88$, $R^2_{adj}=0.87$)	Crofton and Whitlock, 1965; Crofton, 1965; Pandey et al., 1989; Salih and Grainger, 1982; Young et al., 1980a
	<i>Oo</i>	$-0.07258 + 0.00976T$ ($F_{1,8}=76.14$, $p<0.001$, $R^2=0.90$, $R^2_{adj}=0.89$)	Pandey, 1972a; Rose, 1961; Young et al., 1980b
μ_1	<i>Hc</i>	$\exp(-1.47135 - 0.11444T$ $+ 0.00327T^2)$ ($F_{2,3}=4.65$, $p=0.12$, $R^2=0.76$, $R^2_{adj}=0.59$)	Todd et al., 1976a
	<i>Tc</i>	$\exp(-1.62026 - 0.17771T$ $+ 0.00629T^2)$ ($F_{2,2}=6.27$, $p=0.27$, $R^2=0.93$, $R^2_{adj}=0.78$)	Pandey et al., 1993, 1989
	<i>Oo</i>	$\exp(-4.38278 - 0.10640T$ $+ 0.00540T^2)$ ($F_{2,1}=6.27$, $p=0.06$, $R^2=0.99$, $R^2_{adj}=0.99$)	Pandey, 1972
μ_2	<i>Hc</i>	$\exp(-1.82300 - 0.14180T$ $+ 0.00405T^2)$ ($F_{2,1}=1.723^{31}$, $p<0.001$, $R^2=1$, $R^2_{adj}=1$) ^c	Todd et al., 1976a
	<i>Tc, Oo</i>	As μ_1 above	-
μ_3	<i>Hc</i>	$\exp(-2.63080 - 0.14407T$ $+ 0.00463T^2)$ ($F_{2,9}=8.48$, $p=0.008$, $R^2=0.65$, $R^2_{adj}=0.58$)	Todd et al., 1976a, 1976b

	Tc, Oo	$10 * \mu_4$	Pandey, 1972; Persson, 1974a
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	$\begin{cases} 0.1, & \sum_{i=4}^t P_i/E_i < 1 \\ 1, & \sum_{i=4}^t P_i/E_i \geq 1 \end{cases}$	
	Tc	$\begin{cases} 0.1, & \sum_{i=7}^t P_i/E_i < 1 \\ 1, & \sum_{i=7}^t P_i/E_i \geq 1 \end{cases}$	

1118 ^a $Hc = Haemonchus contortus, Tc = Teladorsagia circumcincta, Oo = Ostertagia$
1119 $ostertagi$

1120 ^b $T = \text{temperature } (^{\circ}\text{C}), P = \text{total daily precipitation (mm)}, E = \text{total daily}$
1121 $\text{evapotranspiration (mm)}$

1122 ^c Note that the statistical significance here is an artefact of overfitting

1123

1124

1125 Table 3. Validation of simulations using data provided in the literature. Models are
1126 considered a good fit if regression through the origin is significant and the slope is
1127 not significantly different from 1. The error and R^2 are used to compare competing
1128 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	<i>Hc</i>	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	<i>Hc</i>	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	<i>Hc</i>	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	<i>Hc</i>	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	<i>Hc</i>	Pasture (eq. 4)	Min - Max	1.83 x 10 ⁸	F _{1,3} = 6.78, p=0.080	0.69 (0.59)	0.94 (0.22 – 1.67)
Wilkie et al. submitted	<i>Hc</i>	Pasture (eq. 4)	Mean	1.43 x 10 ⁸	F _{1,3} = 16.72, p=0.026	0.85 (0.80)	1.48 (0.76 – 2.20)
Rossani go and Gruner, 1995	<i>Tc</i>	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	<i>Tc</i>	Pasture (eq. 4)	Min - Max	1.03 x 10 ¹⁰	F _{1,3} = 9.91, p=0.051	0.77 (0.69)	1.26 (0.46 – 2.07)

Wilkie et al. submitted	<i>Tc</i>	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	<i>Oo</i>	Faeces (eq. 1-3; development success)	Constant	2050.2	F _{1,5} = 36.86, p=0.002	0.88 (0.86)	0.84 (0.57-1.12)
Rose, 1961	<i>Oo</i>	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	<i>Oo</i>	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	<i>Hc</i>	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)

1129 ^a *Hc* = *Haemonchus contortus*, *Tc* = *Teladorsagia circumcincta*, *Oo* = *Ostertagia*
1130 *ostertagi*

1131 ^b 95% confidence intervals were estimated as 2 x the standard error of the slope
1132 coefficient.

1133