Asynchrony in host and parasite phenology may decrease disease risk in livestock under climate warming: *Nematodirus battus* in lambs as a case study

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SUMMARY

Mismatch in the phenology of trophically linked species as a result of climate warming has been shown to have far-reaching effects on animal communities, but implications for disease have so far received limited attention. This paper presents evidence suggestive of phenological asynchrony in a host-parasite system arising from climate change, with impacts on transmission. Diagnostic laboratory data on outbreaks of infection with the pathogenic nematode *Nematodirus battus* in sheep flocks in the UK were used to validate region-specific models of the effect of spring temperature on parasite transmission. The hatching of parasite eggs to produce infective larvae is driven by temperature, while the availability of susceptible hosts depends on lambing date, which is relatively insensitive to inter-annual variation in spring temperature. In southern areas and in warmer years, earlier emergence of infective larvae in spring was predicted, with decline through mortality before peak availability of susceptible lambs. Data confirmed model predictions, with fewer outbreaks recorded in those years and regions. Overlap between larval peaks and lamb availability was not reduced in northern areas, which experienced no decreases in the number of reported outbreaks. Results suggest that phenological asynchrony arising from climate warming may affect parasite transmission, with non-linear but predictable impacts on disease burden. Improved understanding of complex responses of host-parasite systems to climate change can contribute to effective adaptation of parasite control strategies.

Key words: Climate change, non-linear, *Nematodirus battus*, nematode, epidemiology, spring, anthelmintic, sheep, food security, disease.

INTRODUCTION

Responses of parasites to increasing global temperatures include accelerated development rates, and altered seasonal dynamics of transmission (Kutz *et al*. 2005; Brooks and Hoberg, 2007; Morgan and Van Dijk, 2012), geographic expansion (Lawler *et al*. 2006; Kreyling *et al*. 2012) and even parasite extinction (Dobson and Carper, 1992; Brooks and Hoberg, 2007). In non-parasitic systems, there is increasing evidence that climate warming can drive changes in the phenology of many plants and animals (Parmesan and Yohe, 2003) and that such changes can lead to mismatch in the phenology of inter–dependent species, with profound and often non-linear effects on species and ecosystems (Visser and Both, 2005; Both *et al*. 2009; Singer and

Parmesan, 2010; Lof *et al*. 2012; Thackeray *et al*. 2013). In spite of the fact that the development and survival of the infective stages of many parasite species are strongly dependent on temperature (e.g. O'Connor *et al*. 2006) and that host presence and susceptibility are often highly variable, the question of such phenological mismatch has only recently been addressed in host-parasite systems (Klapwijk *et al*. 2010; Brown and Rohani, 2012; Paull *et al*. 2012; Paull and Johnson, 2014).

In livestock, knowledge of changes in the timing of parasite presence could provide a route to improved control, and enable adaptation to otherwise deleterious effects of climate change on infection pressure and production loss (Rivington *et al*. 2007; Morgan and Wall, 2009; Van Dijk *et al*. 2010). Attenuation of increased infection pressure by chemical means is unsustainable due to rapidly developing and widespread anthelmintic resistance (Kaplan and Vidyashankar, 2012; Rose *et al*. 2015a). Domestic

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livestock systems, in which many host factors are under the control of the farmer, provide opportune access to host and disease data that can be used to test predictions of phenological mismatches in transmission, which are generally hard to come by in natural systems. Uniquely, Great Britain has a long-established and consistent formal system for recording cases of livestock disease that are diagnosed in its regional network of veterinary investigation laboratories, which has underpinned studies to examine trends in the level and timing of parasitic disease in the national sheep flock, in order to evaluate and update control strategies (Van Dijk *et al.* 2008). These analyses have revealed regional differences and shifts in seasonality in clinical diagnoses ascribed to several gastrointestinal nematode species, including *Nematodirus battus*.

Nematodirus battus parasitizes the small intestine of ruminants, primarily sheep and can cause significant disease problems in grazing lambs in spring (Graham *et al.* 1984; Thomas, 1991). Eggs shed by infected lambs generally develop over summer, receive a chilling stimulus over winter and hatch the following spring when temperatures increase above 11·5 °C (Van Dijk and Morgan, 2008). The typical seasonal dynamics of nematodirosis (clinical *Nematodirus* sp. infection) have altered since its discovery and emergence in the 1950s, and there is now great variation in the timing of disease within and between years (Thomas, 1991; Van Dijk *et al.* 2008; McMahon *et al.* 2012).

Management practices can also have profound effects on the epidemiology of *N. battus*. The severity of disease at flock level is linked not only to parasite factors, e.g. the size and timing of the larval peak in spring, but also the intensity of grazing of susceptible lambs at this time, which is mainly governed by the date of lambing, and hence, in most flocks, by autumn photoperiod (Smith and Thomas, 1972). Empirical studies aiming to explain variation in the timing and severity of infections between years (Graham *et al.* 1984; Thomas, 1991; Van Dijk *et al.* 2008; McMahon *et al.* 2012) have focussed on temperature and taken no account of host availability. Since the lambing season is fairly consistent locally, the risk of disease is likely to change depending on the timing of larval emergence in relation to the age distribution of lambs, and hence their propensity to graze and ingest larvae (Smith and Thomas, 1972). Improved predictive understanding of the effects of climate on the hatching of *N. battus* larvae, from experiments under controlled conditions (van Dijk and Morgan, 2008), could help to identify and mitigate high disease risk arising from coincidence of host and larval availability. Empirical evidence of asynchrony in parasite transmission would also demonstrate the applicability of ecological principles elucidated in free-living systems to impacts of climate change on disease incidence in livestock.

The main aim of the present study was to determine the extent to which the effects of climate warming on the timing of parasite infective stage availability, in concert with patterns of susceptible host presence, are likely to affect the timing of disease. We use *N. battus* in British lambs as a model and build on recent empirical advances in understanding of parasite hatching behaviour, and on the availability of centrally recorded data on disease incidence. We hypothesize that a phenological mismatch may occur as a consequence of earlier-hatching larvae no longer being viable in large numbers at the time of peak spring grazing by lambs.

MATERIALS AND METHODS

Prediction of hatching dates from daily temperatures

A threshold-based model to predict the spatio-temporal variation in hatching dates of *N. battus* was developed based on conclusive experimental evidence that *N. battus* eggs require 7 days of experience between the lower and upper threshold temperatures of 11·5 and 17 °C to hatch, and that fluctuations outside of this range suspend hatching (Van Dijk and Morgan, 2008). Subsequent results on effects of humidity on hatching confirmed that temperature acts as the main driver of larval availability (Van Dijk and Morgan, 2012). Each 24 h period in which minimum ($T_{\min}$) and maximum ($T_{\max}$) temperatures were both within the hatching range of 11·5–17 °C counted as one full hatching day. When temperature passed outside the hatching range, the proportion of the day spent within the hatching range, P, was estimated by the following equation:

$$P = 1 - \frac{(T_{\max} - 17) + (11.5 - T_{\min})}{T_{\max} - T_{\min}}$$

The number of hatching days was summed until it reached 7 days, and the date on which this occurred in a particular year and location was defined as the hatching date. This simple model, equivalent to a degree-day model with adjustment for diurnal fluctuation above and below the hatching range, has been shown to predict the timing of egg appearance in lambs in spring on infected farms (Gethings *et al.* in review). The synchronous, rapid hatching of *N. battus* is such that this threshold-based model can capture the timing of peak infection risk, even though in reality larvae emerge over a number of days (Van Dijk and Morgan, 2008).

Trends in hatching date and diagnoses of nematodirosis over time

Scotland, South Wales and the North, Midlands, and South-West of England were selected for

analysis, corresponding approximately with catchment areas of selected veterinary investigation centres (Fig. 1; van Dijk *et al*. 2008; Morgan *et al*. 2012). For each region four locations were selected by random generation of British National Grid easting and northing coordinates, until four falling within the specified region were obtained. Temperature data for each point were extracted from the UKCP09 25 km^2 gridded observation datasets from the UK Meteorological Office for the period 1975–2006 (Perry *et al*. 2009). Gridded datasets of daily temperature values were only available until 2006. Hatching date was predicted separately for each location and averaged over the four selected locations within each region, to give a mean predicted hatching date in each year. For two regions over 4 years (Scotland 1975–1978 and South-West England 2000–2003), 10 locations were sampled at random and predicted dates compared with those generated using only four points: predicted hatching dates differed by an average of 2·6 (mode 1, range 1–6) days. Given a variation in hatching date between regions, and within regions between years, of well over 1 month (see results), this error was deemed acceptable and regional hatching dates predicted using the more efficient four-point algorithm.

The Veterinary Investigations Disease Analysis surveillance report (VIDA) is a compilation of data from recorded submissions made to the Animal Health and Veterinary Laboratories' Agency (AHVLA) Regional Laboratories and the Scottish Agricultural College Disease Surveillance Centres in Great Britain. Prior to 1999, causes of parasitic gastroenteritis (PGE) were coded based on the judgement of the clinical pathologist. Since 1999 diagnoses of PGE were similarly but more formally defined by common specific criteria. Hence, for a confirmed diagnosis of clinical *Nematodirus* sp. infection (nematodirosis), the following must be present: compatible clinical history and/or gross pathology and/or histopathology and either detection of significant numbers of adult or larval worms in the gastrointestinal tract, or detection of characteristic eggs in the feces. Recorded data detailing nematodirosis diagnoses from laboratory submissions in 1975–2006 were obtained from the Centre for Epidemiology and Risk Analysis (AHVLA, Weybridge). As there was minor disparity between regions as defined by the Ordnance Survey and region as defined by the VIDA database (van Dijk *et al*. 2008), the data were as far as possible aggregated so that data from lambing and climatic regions matched catchment areas of regional laboratories in the VIDA database (Fig. 1). Total number of clinical diagnoses was used for analysis without adjustment: neither total number of parasitological submissions nor the methods used in diagnosis changed substantially over the study period, and previous scrutiny for

Fig. 1. Regions of Great Britain as defined for lambing dates. Laboratory diagnoses were taken from the same areas except for South Wales (nested within Wales) and Midlands (nested within Midlands and South of England).

confounding bias considered this metric to be robust to other external influences such as sheep density and economic indicators (for a detailed discussion of the reliability of this dataset, see Van Dijk *et al*. 2008). Since diagnoses were reported at the level of laboratory catchment area, no data were available on exact farm location or other variables such as altitude, livestock numbers or management factors.

Trends in predicted hatching date, and number of diagnoses of nematodirosis, were analysed for each region using Pearson's product moment correlation of these variables against year. In order to test and quantify differences in typical hatching date at start and end of the 30-year period, paired samples *t*-tests were also conducted between the mean date of predicted hatch for 1975–1979 and 2002–2006 (5-year period averaged to smooth effects of weather in individual years). To evaluate whether timing of larval hatch influenced the incidence of nematodirosis in a given year, Pearson correlation was conducted on date of predicted hatch and total number of cases in each year, by region.

A One-Way Analysis of Variance was conducted to assess whether date of predicted hatch differed between regions. Differences between regions were assessed using Fisher's Least Significant Difference (LSD) *post hoc* test.

Data on the proportion of farms lambing in each month in different regions were previously gathered by means of a telephone questionnaire survey of 600 sheep farmers (of which 450 were in Great Britain, and the rest in Ireland) (Morgan *et al.* 2012). As December is regarded as early season lambing, it was considered the first month in a given year. Each month was divided into four equal periods in order to provide a 1-week resolution for overlap between lamb age and larval availability, and it was assumed that each month had a uniform frequency distribution of lambing across these periods. The predicted mean regional date of larval hatch for each year and the frequency distribution of lambing dates were used to estimate the proportion of lambs at risk in a particular year. All lambs born before the predicted mean date of hatching were deemed susceptible to infection, since they would have the opportunity to ingest significant quantities of grass while larvae were on the pasture, from the date of hatching until die-off, typically around 6–8 weeks later (van Dijk and Morgan, 2008; van Dijk *et al.* 2009; van Dijk & Morgan, 2010). This duration was based on laboratory observations of larval mortality rate, with 50% of larvae dying in 45 days at 20 °C, 15 days at 25 °C and 5 days at 30 °C (Van Dijk and Morgan, 2008); persistence into early summer following a spring hatch is therefore unlikely in most of the UK, though local conditions might sometimes allow this (Sargison *et al.* 2012). All lambs born on or after the date of predicted hatch were consequently deemed to be at low risk of developing nematodirosis, since larvae would normally have declined to very low levels by the time the lambs reached 4–8 weeks of age and began to graze significant quantities of grass.

Trends in the percentage of lambs at risk over time were analysed using Pearson correlation between year and the arcsine-transformed proportion of lambs at risk. To analyse whether the proportion of lambs at risk explained disease incidence in a given year, the arcsine-transformed proportion of lambs at risk in each year was correlated with the number of cases diagnosed for that region. Paired samples *t*-tests were also conducted between the mean predicted proportion of lambs at risk for 1975–1979 and 2002–2006. To test the suggestion by Ollerenshaw and Smith (1966) and Smith and Thomas (1972) that later larval hatching was associated with higher disease incidence, the predicted date of larval hatch was correlated with the arcsine-transformed proportion of lambs at risk. Because predicted proportion of lambs at risk was driven by lambing date in the model, and correlation is consequently not a fair statistical test, *P*-values were not

calculated, but the direction and size of the correlation were reported.

The peak month of lambing on each farm surveyed by Morgan *et al.* (2012) was compared for regional difference using the Kruskal–Wallis test and *post hoc* Mann–Whitney *U* tests with Bonferroni correction.

RESULTS

The average date of predicted hatch over the study period varied between regions and 5-year blocks by around 10 weeks ($F_{4,155} = 58\cdot364$, $P < 0\cdot001$; Table 1) The average predicted hatch dates over the entire period 1975–2006 differed significantly between regions (Fisher's LSD *post hoc* test, $P < 0\cdot001$), apart from South Wales and the Midlands ($P = 0\cdot189$), and in individual years ranged across 4 months between mid-February and mid-June (Table 1; Fig. 2). All regions except Scotland showed significant trends towards earlier predicted hatch between 1975 and 2006 (Table 2; Fig. 2). 5-year average predicted hatching date in these regions advanced by between 3 and 5 weeks (Table 1).

The South West of England experienced a significant reduction in the number of diagnosed cases over the 32-year period, while in Scotland there was a significant upward trend (Table 2). Trends in numbers of cases over time were not significant in other regions. There was a significant decrease in the mean number of cases between the periods 1975–1979 and 2002–2006 in the South West, significant increases in South Wales and in Scotland, and no significant differences in the Midlands or Northern England (Table 1).

The median month of lambing, as reported by telephone survey, differed significantly between regions ($H_6 = 41\cdot893$ $P = <0\cdot001$; Table 3), Sequential Mann–Whitney tests revealed that median lambing month in Scotland ($n = 52$) was significantly different to that in the Midlands and South ($n = 99$, $u = 1864$, $z = -2\cdot882$, $P = 0\cdot004$), Northern England ($n = 100$, $u = 1828\cdot5$, $z = -3\cdot138$, $P = 0\cdot002$) South West ($n = 100$, $u = 1957$, $z = -2\cdot560$, $P = 0\cdot010$) and Wales ($n = 99$, $u = 1\cdot521\cdot5$, $z = -4\cdot280$, $P = <0\cdot001$). No other regions were considered to be statistically different from each other in terms of median lambing date (2 D.F.; $P = 0\cdot984$).

Earlier hatching was associated with decreased proportion of lambs at risk in all regions except Scotland (Table 2). In the South West of England, an earlier average date of hatch was associated with a lower proportion of lambs at risk and both predictors correlated with a lower number of recorded cases. This relationship was not found in other regions (Table 2; Figs 3 and 4). Changes in the mean predicted percentage of lambs at risk between 1975–1979 and 2002–2006 varied by

Table 1. Spatio-temporal variation in the date of hatching of *N. battus* larvae and number of lambs at risk, as predicted by a mechanistic model of the temperature-dependent hatching of larvated eggs following winter chilling, and observed number of clinical diagnoses (Veterinary Investigations Disease Analysis surveillance data)

|		South West England	Scotland	South Wales	Midlands	Northern England
Date of predicted hatch	Mean 1975–1979	25-April	31-May	07-May	07-May	26-May
	Range (days)	20/4–4/5 (14)	26/5–6/6 (10)	30/4–16/5 (16)	26/4–14/5 (18)	17/5–6/6 (20)
	Mean 2002–2006	21-Mar	21-May	13-April	03-April	04-May
	Range (days)	22/2–15/4 (52)	17/5–27/5 (10)	9/4–26/4 (17)	26/3–21/4 (22)	28/4–17/5 (19)
	Paired samples *t*-test	$t(4) = 4·441$	$t(4) = 2·836$	$t(4) = 6·242$	$t(4) = 4·937$	$t(4) = 5·603$
		$P = 0·011$	$P = 0·047$	$P = 0·003$	$P = 0·005$	$P = 0·008$
Number of clinical diagnoses	Mean 1975–1979	24·2	38·2	17·4	22	17
	Range	15–39	26–65	5–41	13–37	9–36
	Mean 2002–2006	14·2	128	39	27	28·8
	Range	9–25	109–182	27–63	7–55	5–68
	Paired samples *t*-test	$t(4) = 6·086$	$t(4) = -11·231$	$t(4) = -3·407$	$t(4) = -0·711$	$t(4) = -1·770$
		$P = 0·004$	$P < 0·001$	$P = 0·027$	$P = 0·516$	$P = 0·151$
Lambs at risk (%)	Mean 1975–1979	96·4	100	100	99·1	100
	Range	93·6–100	–	–	97·7–100	–
	Mean 2002–2006	80	100	96·40	87·4	100
	Range	60–94	–	94·7–100	82·9–96·5	–
	Paired samples *t*-test	$t(4) = 3·413$	–	$t(4) = 3·891$	$t(4) = 4·000$	–
		$P = 0·027$		$P = 0·018$	$P = 0·016$	
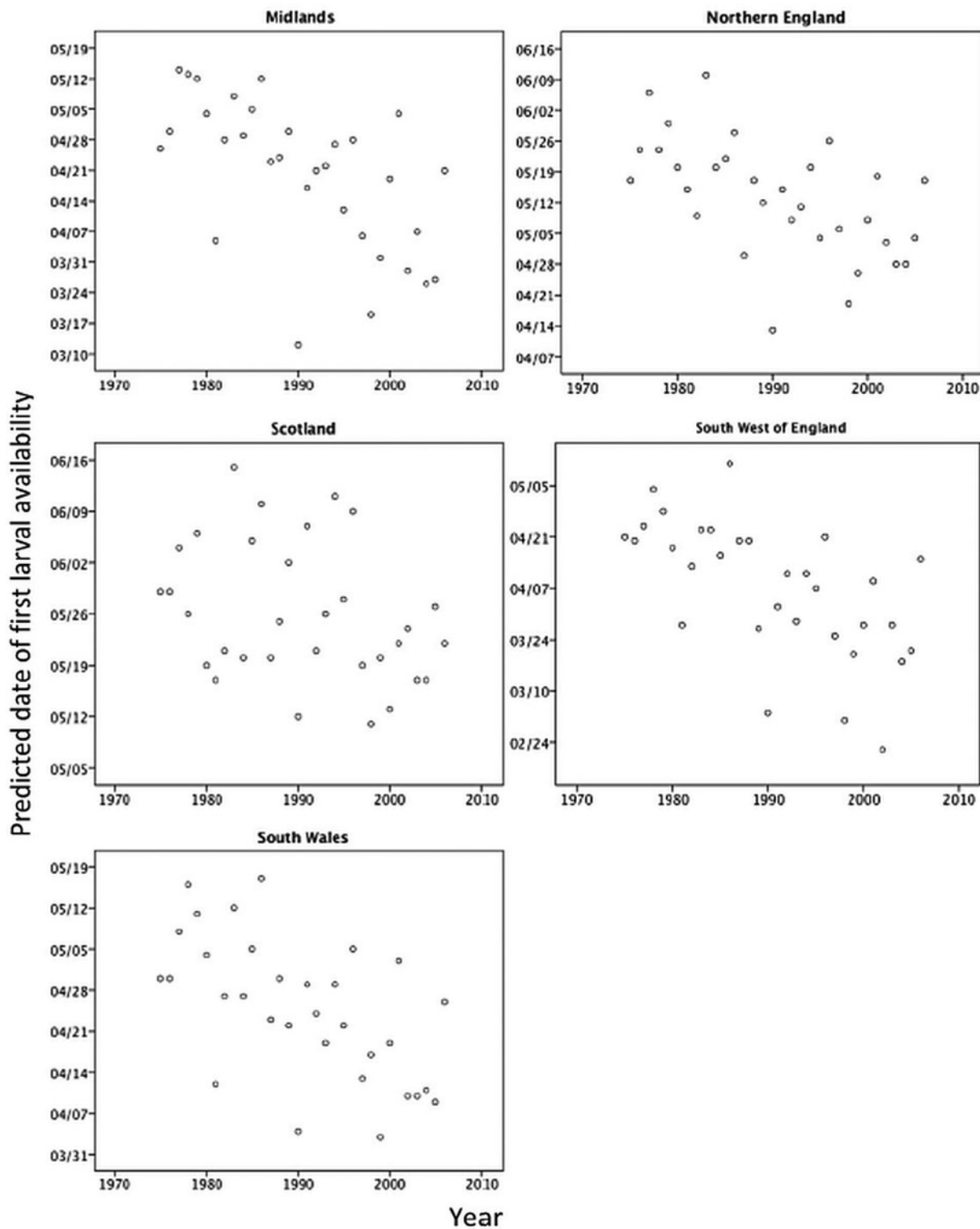
Fig. 2. Mean predicted date of first availability of *Nematodirus battus* larvae by region and year, as predicted by a mechanistic model of effects of temperature on accumulation of hatching experience in larvated eggs following winter chilling. For statistical analysis of correlations, see Table 3.

region ranging from −16·4% in the South West to 0% in Scotland and Northern England (Table 1; Fig. 4).

DISCUSSION

Global warming has driven earlier increases in spring temperatures, with demonstrated impacts on the distribution and phenology of free-living animals and pathogens (Visser *et al.* 1998; Altizer *et al.* 2006; Lawler *et al.* 2006; van Dijk *et al.* 2008; Polley and Thompson, 2009). Previously, the generally predictable conditions under which *N. battus* hatched in Great Britain meant that the incidence of disease was fairly consistent between years

Table 2. *Trends over time in* N. battus *disease predictors (hatching date, number of lambs at risk) and observed disease incidence (number of cases recorded in Veterinary Investigations Disease Analysis surveillance data), and correlation between disease predictors and observed cases, by region, 1975–2006.* r *= Pearson product moment correlation. Cells with significant correlations are highlighted in bold.* P*-values are omitted for the correlation between date of predicted hatch and percentage of lambs at risk, since these variables are dependent in the risk prediction model, and not statistically independent.*

		South West England	Scotland	South Wales	Midlands	Northern England
Predicted date of hatch over time	r	−0·616	−0·326	−0·597	−0·606	−0·563
	P value	**< 0·001**	0·069	**< 0·001**	**< 0·001**	**< 0·001**
Number of cases over time	r	−0·518	0·670	0·346	−0·038	0·228
	P value	**0·002**	**< 0·001**	0·053	0·836	0·210
Date of predicted hatch *vs* number of cases	r	0·468	−0·101	0·034	0·188	0·154
	P value	**0·007**	0·580	0·853	0·304	0·400
Percentage of lambs at risk *vs* the number of cases	r	0·513	0·205	−0·110	0·176	0·031
	P value	**0·003**	0·260	0·551	0·334	0·867
Percentage of lambs at risk over time	r	−0·601	0·302	−0·419	−0·540	−0·078
	P value	**< 0·001**	0·094	**0·017**	**0·001**	0·671
Date of predicted hatch *vs* percentage of lambs at risk	r	0·958	−0·058	0·793	0·967	0·542
	P value					

Table 3. *Lambing dates by region (*n *= 450 farms). To calculate mean and standard deviation (*S.D.*), December was coded = 1, January = 2 etc. Farmers were asked to identify the main month of lambing on their farm, and the mode, mean, earliest and latest months calculated per region*

Region	N	Earliest	Latest	Mode (Mean)	S.D.
South West England	100	December	June	February (2·96)	1·36
Wales	99	December	April	March (3·31)	1·03
Midlands and South	99	December	May	March (3·44)	1·35
Northern England	100	December	April	March (3·58)	1·21
Scotland	52	January	April	April (4·31)	0·96

(Smith and Thomas, 1972). In contrast, the results presented here reveal a phenological shift towards earlier egg hatching since 1975, in line with the advancement of spring. This predicted shift in hatching date appears to result in asynchrony between host and parasite availability in some regions. This is explained by earlier hatching of infective larvae, such that numbers decline through natural mortality before late-born lambs ingest sufficient grass to be exposed to substantial infection. The consequent predicted decrease in the number of lambs at high risk of infection is supported by lower numbers of recorded cases in the South West both over the study period, and in years in which hatching occurred sooner. Elsewhere in Great Britain where the advancement in hatch date was less pronounced (Scotland; Table 1 and Fig. 3) or where a broad temporal overlap of parasite and host availability was maintained in spite of earlier hatching (South Wales and the Midlands; Fig. 3), the change in the proportion of lambs at risk was small and there was no significant decrease in the number of observed cases of nematodirosis. This suggests that there may be a 'tipping point', at which the number of

lambs exposed to large numbers of infective larvae declines sufficiently to drive decreases in observed disease in milder springs, and under climate warming. Such non-linear effects of climate change on ecology have been described in other systems (Mooney *et al*. 2009) and in some cases can be explained by relatively simple mechanistic models (Andre *et al*. 2010). A need has been identified for more experimental manipulations to test ecological effects of climate change, which can drive mechanistic models capable of up-scaling to ecosystem level (Altizer *et al*. 2013; Kreyling *et al*. 2014). The present paper uses such an approach by applying experimentally-obtained parasite vital rates to predict regional effects on disease incidence in farm ecosystems.

Alongside a smaller advance in predicted hatching date in Scotland than in the south, our model predicts much less inter-annual variation in *N. battus* hatching date in Scotland than elsewhere in Great Britain, both under historical and recent climates. Thus, climatic conditions appear to continue to support a consistent mass hatch of larvae in spring, at a time that is well suited to infect the majority of
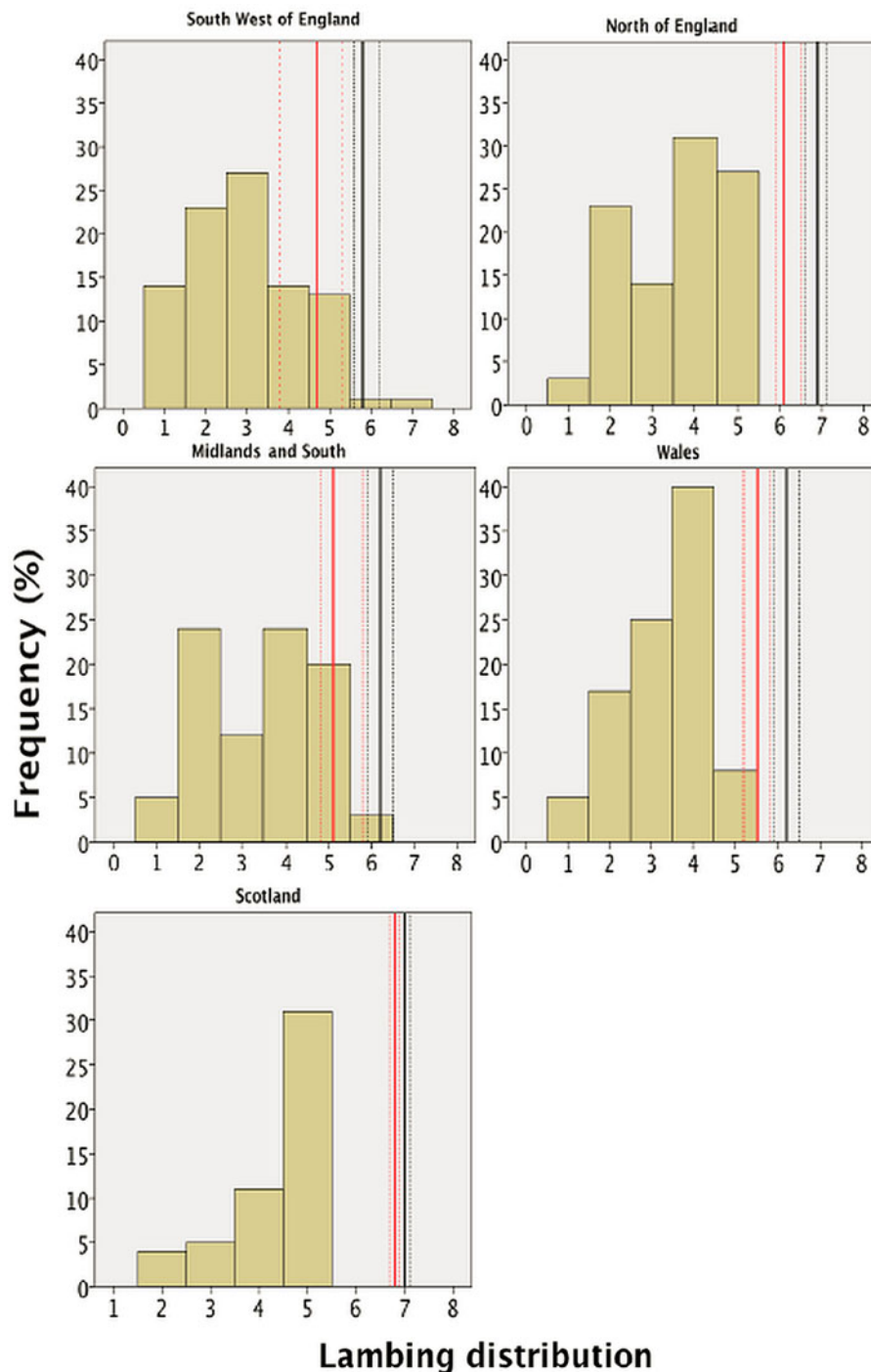
Fig. 3. The frequency distribution of peak lambing month between farms within the study regions (Morgan *et al.* 2012) and predicted mean date of hatching (solid lines) and range (dotted lines) of *Nematodirus battus* larvae in 1975–1979 (black, right) and 2002–2006 (red, left). Month 1 = December.

lambs, given their age and propensity to graze. In contrast, highly variable conditions for hatching in the South West lead, in some years, to poorer conditions for transmission. For a parasite that relies on year-to-year transmission between lamb crops for persistence, this could have disastrous consequences for population abundance and viability, in theory to the point of local extirpation. Interestingly, experimental comparison of hatching requirements between *N. battus* isolates from Scotland and the South West of England showed that in the south, not all larvated eggs required a chilling stimulus in order to hatch (Van Dijk and Morgan, 2010). This was proposed to confer an advantage when spring infection of lambs was unreliable, such that a proportion of larvae would have the opportunity to infect less susceptible, older sheep later in the year, mitigating the impact of bad (warm) spring conditions on genotype persistence. The effects of such a bet-hedging strategy on observed epidemiological
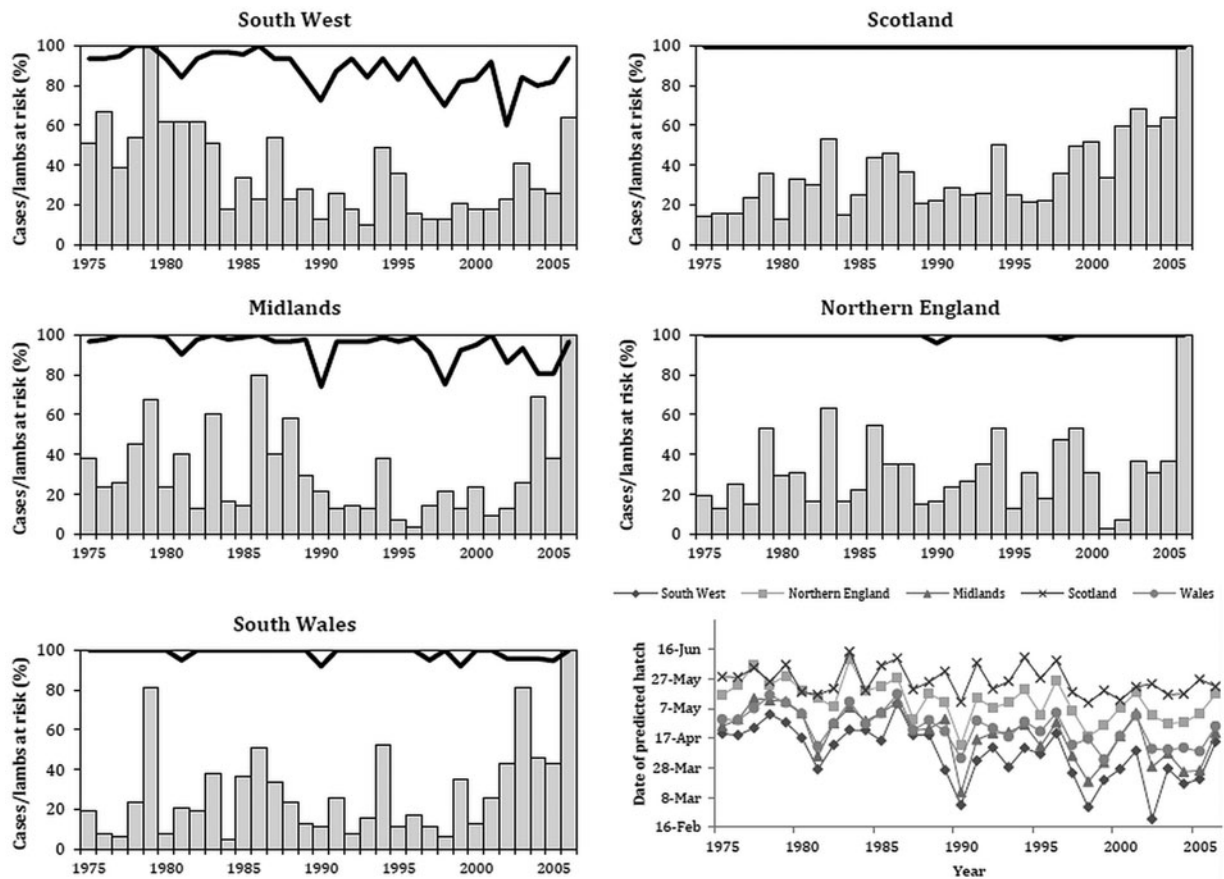
Fig. 4. Annual mean predicted percentage of lambs at risk (lines) and number of observed cases of nematodirosis recorded in the Veterinary Investigations Disease Analysis surveillance database (bars, standardized to the maximum recorded number) in the five study regions. The final panel shows the mean date of predicted hatch in each region over the studied period.

patterns under global warming, and the rate at which populations might change hatching behaviour, are key subjects for future study, with potentially important implications for the management of disease. As in many systems, the seasonal timing of key life history events could be subject to stronger selection pressure under climate change than patterns of thermal tolerance, and genetic drivers of seasonal timing deserve greater attention in climate change research (Bradshaw and Holzapfel, 2008). In *N. battus*, the status of the host as well as its presence could greatly modify the fitness consequences of altered phenology, with a tendency towards less precise temporal coincidence of larval hatch and lamb grazing potentially favouring lower burdens and less risk of pre-patent mortality and/or rapid development of strong immunity, and therefore paradoxically promoting parasite persistence.

Potential limitations of the approach presented here include simple assumptions concerning the relationship between diurnal temperature range and the accumulation of time spent within the hatching range, which were made in the absence of data to justify more complex representations of the experience of eggs near the soil surface. The model could

potentially be refined in the light of such data, as well as by more comprehensive sampling of regional climates to generate fully representative profiles. Nevertheless, the strong qualitative conclusions from this study are likely to hold after such refinements. Future adjustments in lambing dates to take advantage of earlier grass availability in spring could change assumptions of host availability in the current model, although these are likely to be constrained by unchanging autumn photoperiod, at least in the absence of technically demanding or costly strategies such as breed selection, hormonal intervention or artificial lighting regimes (Cameron *et al.* 2010). Similarly, changes in lambing dates over the study period could alter our interpretation of the data, although there is no evidence for systematic trends in lambing dates that could explain observed disease incidence, and given the constraints of photoperiod, such trends are unlikely to have occurred.

Adaptations through farm management have the potential to greatly alter outcomes of climate warming on parasitic disease systems in livestock (Morgan and Wall, 2009; Phelan *et al.* in review). For instance, the present study was unable to take

into account changes in the administration of anthelmintic treatments to lambs by farmers based on altered perceptions of the level and timing of disease risk. Such changes in management practices as a result of increased awareness could provide an alternative explanation of decreased disease incidence in the South West of England in the present study, although there is no reason to suppose that these would be restricted to a single region, much less the one region that appeared to experience a pronounced decrease in underlying risk. In any event, more research is needed on farmer attitudes and behaviour in relation to climate change risks, in order to inform animal health adaptation strategies (Morgan and Wall, 2009; Marshall *et al*. 2013; Skuce *et al*. 2013).

Predicting effects of climate change on ecosystems is complex, and it is increasingly obvious that, for parasites, accelerated development at higher temperatures does not necessarily translate to increased infection pressure. Even in Arctic systems, in which longer growing seasons can drive upward step changes in transmission dynamics (Kutz *et al*. 2005, 2013), maximum daily temperatures on solar irradiated tundra can take larval parasite stages beyond upper development thresholds, decreasing the availability of infective larvae (Hoar *et al*. 2012). This is predicted to favour spring and autumn peaks in larval availability, which depending on location and host movement patterns, could increase or decrease transmission. Generalized approaches that seek to characterize the optimal thermal niche of parasites (e.g. Molnar *et al*. 2013) are useful to predict broad effects of climate change on potential transmission, but accurate prediction of infection patterns in specific systems is likely to require integration of host factors. Thus, warmer temperatures favoured increased production of infective stages of gastrointestinal nematodes of rabbits, but not necessarily higher infection levels in the host, suggesting that the way in which hosts interact with available infective stages is crucial to net effects of climate change on infection (Hernandez *et al*. 2013). In a trematode-snail-amphibian system, striking non-linearities in the effects of climate warming were observed (Paull *et al*. 2012; Paull and Johnson, 2014). Higher temperatures led to earlier infective stage emergence, but decreased overlap between parasite and host presence, and consequently a marked decrease in infection levels and pathology (Paull and Johnson, 2014). Phenological mismatch appears to similarly explain present observations on *N. battus*, and such effects, therefore, appear capable of altering infection patterns in domesticated as well as natural animal systems.

The present results demonstrate that climate warming can drive paradoxically decreased transmission of parasites whose development is positively temperature-dependent, as a result of phenological mismatch between the availability of infective larvae and susceptible hosts, and that this can decrease observed disease incidence. Further, such events are likely to vary geographically, with, in the case of *N. battus*, the epidemiological and evolutionary implications being qualitatively different at regional scale. Improved understanding of the effects of climate and weather on the transmission of *N. battus* has the power to underpin forecasts of disease incidence and times of high risk, and to guide farmer practices, as for other nematode species (Rose *et al*. 2015*b*), though it appears that in this case forecasts would need to be produced on a regional basis. Effects of climate change later in the year could also affect transmission of *N. battus* through accelerated mortality at higher temperatures (Van Dijk and Morgan, 2008) or under increased solar irradiation (Van Dijk *et al*. 2009), or through altered opportunities for hatching in autumn. Furthermore, while decreased opportunities for transmission in spring might in the short term lead to attenuation of disease risk, it is likely that partial interruption of hatching in warmer climates will drive evolution of parasite life history to reconnect with host populations, for example through changes in hatching behaviour (Van Dijk and Morgan, 2010). The mechanisms and rate of such change are important targets for future research.

Although in this system there appears to be some attenuation of disease risk as a result of earlier larval availability under a warmer climate, its extent and consequences in this system are, therefore, very local, and liable to be modified by farm management practices. Lower risk from spring nematodirosis could be offset by higher transmission risk in autumn, while climate warming could drive concurrent increases in the transmission potential of other parasites: for example, *Haemonchus contortus* in Scotland (Kenyon *et al*. 2009; Bolajoko *et al*. 2015). While phenological mismatch does have the potential to affect parasite transmission and impacts on agricultural systems, models that capture farmer responses to climate change are needed to more fully understand and plan for the consequences of climate change on food production.

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