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Modelling the effects of recent changes in climate, host density and acaricide treatments on population dynamics of *Ixodes ricinus* in the UK

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Summary

1. A population model for the tick *Ixodes ricinus*, the most significant vector of pathogens in Europe, is used to explore the relative impact of changes in climate, host density and acaricide-treated hosts on tick abundance and seasonality.

2. A rise in temperature of the sort witnessed since 1989 speeds up the inter-stadial development of ticks, thereby reducing the cumulative effect of constant daily mortality rates and potentially raising population levels. The predicted earlier onset of tick-questing activity in the spring, due to stage-specific temperature thresholds, could increase contact between ticks and humans during recreational visits to the countryside in spring holidays. These tick population effects vary geographically with background climate.

3. The significant increase in deer abundance across Europe, including the UK, in recent decades is predicted to drive tick population increases, the effect varying with the initial density of hosts. In areas only recently colonized by deer, tick numbers are predicted to rise dramatically (given suitable climatic conditions). Where host densities are already high, however, further increases may reduce numbers of questing ticks; unfed ticks leave the questing population more rapidly, even though the overall tick population (and therefore pathogen transmission potential) increases.

4. Culling high-density deer populations as a control measure could, therefore, initially cause an apparent increase in questing ticks, with the predicted long-term population trajectory depending on the severity of the cull.

5. Conversely, the further addition of large hosts (e.g. sheep) would effectively reduce the number of questing ticks and therefore the risk to humans. If such sheep were treated with acaricide, tick populations are predicted to decrease rapidly, to an extent that depends on the relative abundance of wild (untreated) and treated hosts. Tick control in designated areas may be achieved by using sheep in this way as 'lethal mops', as used to occur in the past when sheep were regularly dipped.

6. *Synthesis and applications.* Both abiotic and biotic environmental changes witnessed recently could have contributed to apparent increases in tick populations, especially where these environmental factors were limiting in the past. The release of additional hosts treated with long-lasting acaricide is potentially an effective control strategy.

Key-words: climate change, deer density, geographical variation, *Ixodes ricinus*, population model, tick, tick control

Introduction

Arthropod-borne diseases are among the most significant causes of human mortality worldwide (Hill *et al.* 2005). An important element of disease risk is the distribution and abundance of the vector, both of which are liable to be directly affected by environmental change (Dobson 2009; Pascual & Bouma 2009). The likely impacts of future environmental change on diseases such as malaria and tick-borne encephalitis (TBE) have been investigated through statistical pattern-matching techniques that identify correlations between the recorded distribution of the vector and climatic variables, and use the resulting models to predict changes in distribution and/or abundance under projected future climate scenarios (Randolph & Rogers 2000; Rogers & Randolph 2000). This

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'top-down' approach has various advantages, including rapid implementation and the potential for utilizing existing spatial datasets that are often widely available, and must be favoured where complete biological data for the vector are lacking. The alternative 'bottom-up' approach, whereby the directly-measured effects of environmental conditions on vector development, feeding and reproductive success are incorporated into a population model, requires a solid and comprehensive understanding of the biology of the vector, but should produce more reliable, versatile and meaningful results (Ogden *et al.* 2005; Hay *et al.* 2006; Rogers & Randolph 2006). Such models may be used to produce either mapped estimates of distribution, based upon predicted population trajectories in individual grid cells (e.g. for the African tick *Rhipicephalus appendiculatus* (Randolph 2004)), or, more simply, simulations of population dynamics in a hypothetical environmental space under different scenarios.

The latter application effectively represents a strictly controlled environment in which the effects of individual factors may be assessed in isolation. In this paper we use the population model developed by Dobson, Finnie & Randolph (2011) to investigate the potential direct effects of changes in specific abiotic and biotic factors on the relative abundance and seasonality of the tick *Ixodes ricinus* (Linnaeus), one of the most widespread and multi-competent disease vectors in the northern hemisphere.

Climatic variables influence tick populations by dictating rates of development (via temperature) and mortality (via saturation deficit). Recent reports of extensions in the ranges of *I. ricinus*, putatively attributable to temperature increases having made new areas permissive for tick survival (Lindgren, Talleklint & Polfeldt 2000; Daniel *et al.* 2003; Holzmann *et al.* 2009), have fuelled speculation over the effects that climate change may have on tick distribution and hence future pathogen transmission (Danielova *et al.* 2008; Gray 2008; Gray *et al.* 2009), especially along latitudinal and altitudinal boundaries where temperature is typically limiting. Meteorological records show a consistent pattern of temperature change over the past 40 years throughout Europe north of c.42°N: against a background of quasi-decadel fluctuations (Pisoft, Kalvova & Brazdil 2004), a step increase in annual mean temperatures of up to c.1–2 °C in 1989, with consistently warm conditions but no upward trend since 2000 (Sumilo *et al.* 2007; Marty 2008; Ruckstuhl *et al.* 2008), rather than the smoothed continuous pattern commonly depicted by 10-year running means. The cause of the sudden warming is thought to be at least partly related to increased solar irradiance due to reduced aerosol concentrations (Wild *et al.* 2005). This is also seen in the UK (e.g. the Central England temperature series http://ukclimateprojections.defra.gov.uk/content/view/751/9).

The major biotic determinant of tick population dynamics is the abundance of vertebrate hosts, of which deer are quantitatively the most important for all tick stages including the reproductive adults. Accordingly, the oft-observed correlation between numbers of *Ixodes* spp. ticks and deer densities in Europe and North America confirms that deer are instrumental in maintaining robust populations of ticks (Wilson, Adler & Spielman 1985; Gray *et al.* 1992; Deblinger *et al.* 1993; Jensen, Hansen & Frandsen 2000; Rand *et al.* 2003), but detailed mechanistic analyses are lacking. When sampling vegetation for questing ticks, it is impossible to distinguish between those that have been removed from the population by mortality or quiescence/diapause and those removed by attachment to a host (Randolph & Steele 1985); field data relating tick abundance to host abundance are therefore difficult to interpret (Eisen, Eisen & Lane 2002).

In the UK, ticks are perceived to have increased in abundance in most areas over the past one or two decades, with a trend that largely coincides spatially and temporally with perceived increases in the density of deer, although the nature of the data collection prohibits firm conclusions (Scharlemann *et al.* 2008). The geographical range of deer species in the UK has expanded considerably between 1972 and 2007 (Ward, Etherington & Ewald 2008); native species of deer, red *Cervus elaphus*, fallow *Dama dama* and roe *Capreolus capreolus* occupied 2–4 times as many 10 km^2 cells in 2007 as in 1972, while introduced species, Chinese water deer *Hydropotes inermis*, sika deer *Cervus nippon* and Reeves' muntjac *Muntiacus reevesi* spread into 6–20 times as many cells. With no reliable estimates of absolute deer density within any part of their ranges, however, we were obliged to investigate the effects of arbitrary, yet realistic, changes described below, in line with the British Trust for Ornithology Breeding Bird Survey (BTO BBS) index of deer abundance (Battersby & Partnership, 2005) and estimated deer abundance in most European countries over the past several decades.

In this paper, we model the effects on tick populations of recent changes in climate and large host density independently. We then simulate scenarios of acaricide application on tick hosts to assess its efficacy as a control strategy. Present uncertainty of some parameter values in the model prevents reliable estimates of absolute tick abundance (Dobson, Finnie & Randolph 2011), so the effects are presented as changes in indices of tick abundance. In this way, the relative contributions of abiotic and biotic changes will become clearer, allowing land managers and livestock owners to assess the costs and benefits of manipulating host densities in attempts to control tick abundance.

Materials and methods

TICK POPULATION MODEL

The population model developed and described by Dobson, Finnie & Randolph (2011) is a modified stage-classified Leslie matrix (Leslie 1945) that predicts relative numbers of each tick instar (larva, nymph and adult) in each physiological state according to inputs of biotic and abiotic variables. In this paper, we present the numbers of questing ticks, an index of active ticks that are a subset of the full population.

CLIMATE

To evaluate the effects of changes in climate, we simulated tick populations based on daily climate data for 1970–2008. Long-term temperature and relative humidity data were downloaded from http://badc.nerc.ac.uk/data for meteorological stations at Hurn, Dorset

(−1·84°E, 50·78°N), close to the field site at Wimborne St. Giles (see Randolph *et al.* 2002), and Bala, Gwynedd (−3·58°E, 52·91°N), north of the field site in Powys, Wales. Microclimate data had been logged at the field sites during the period of tick observations (1996–2001). The model requires inputs of mean daily soil temperature (T_s – for tick development), saturation deficit (SD, 30 cm above-ground level to simulate mean questing position, calculated using relative humidity and temperature 30 cm above-ground level – T_q) and smoothed weekly mean of the daily maximum air temperature (an apparent cue for the onset of spring questing after behavioural diapause).

Calibrations between simultaneous mean daily temperatures from each meteorological station and its corresponding data logger were used to convert station readings to microclimate over the full 39-year period required, as follows. For the years where station and logger over-lapped, daily average series were produced where each day was given a value equal to the mean for that date across the full time period. Sine curves were fitted to these averaged series to produce idealized curves. The daily scale factors between the sine curves from the meteorological station and those from the data logger were calculated and used to produce T_s and T_q values from meteorological station mean air temperature (T_a) figures for 1970–2008. Relative humidity data from stations were similarly calibrated. Saturation deficit was calculated from the calibrated mean temperature (T_q) and relative humidity 30 cm above-ground level according to the equation in Randolph & Storey (1999). To allow tick population establishment, each model run was preceded by a 10-year period in which daily temperature and SD were averaged across 1980–89 to provide a single year of 'mean' conditions, which was looped 10 times.

HOST DENSITY

Effective host density is defined by the host contact rate experienced by each stage, which is represented as the probability that a tick in a questing position will make contact with a host. This fraction is separated into the relative contributions from large and small hosts: small hosts are programmed to feed 0% of adults, 55% of nymphs and 95% of larvae according to data in Talleklint & Jaenson (1994). Host contact values for the two sites were set at the levels used by Dobson, Finnie & Randolph (2011), specifically a daily probability of host contact varying between 0·07 and 0·11 for larvae to adults, respectively, at the Dorset site, and correspondingly 0·025 and 0·06 in Wales. This reflected the exceptionally high density of hosts, particularly deer and pheasants *Phasianus colchicus*, known to occur in the woodland site in Dorset, compared with the sparse host availability, mostly hill-grazing sheep, in Wales. Simulations were run under mean 1980–89 climatic conditions and the following variable host conditions: large host contact rates incrementally increased such that they doubled over 20 years and large host contact rates incrementally decreased such that they halved over 20 years. In all cases, the final conditions after 20 years were left constant for a further 10 years.

ACARICIDE

We consider two scenarios of acaricide application and assume in all cases that ticks die on contact with treated hosts (Steele & Randolph 1985; Pound, Miller & George 2000). This may not actually be the case given the reduced duration of effective acaricidal activity in current products, combined with normal practices of treating hill sheep only at times related to husbandry (e.g. lambing, shearing, mating). Rather than guess at the quantitative outcome of these factors, we present the ideal position, from which the real efficacy of acaricide treatment can be scaled accordingly. In the first scenario, a given proportion of existing large hosts are treated, simulated in the model by reducing on-host survival appropriately. In the second scenario, additional large hosts are added to the system, all of which are treated. In both scenarios, the effects of treating 10% or 50% of the original number of hosts were simulated.

Results

CLIMATE

The 39-year time series (1970–2008) reveal that mean annual temperatures at Hurn, Dorset, and Bala, Wales, showed quasi-decadel fluctuations and also a marked step increase around 1989, followed by consistently warm conditions but no upward trend since 1997 (Fig. 1), all of which are characteristic of most European temperature records. Seasonally, most of this warming occurred from January to early August, which includes early spring when temperatures cross the threshold for tick-questing activity, and also the period from April to July that is critical for the inter-stadial development of the majority of ticks and has shown a slight warming trend since 1997. During the present century, autumns have also been warmer. At the same time, there has been no consistent decrease in rainfall or relative humidity. An increase of 1–2 °C would not therefore increase maximum (summer time) saturation deficit as experienced by ticks within their woodland habitat to a level (>4 mm Hg) likely to cause increased mortality or decreased questing activity (Macleod 1935; Perret, Rais & Gern 2004).

Relative to the tick abundance predicted under mean 1980–89 conditions, tick populations were predicted to vary in response to the real fluctuations in temperature from 1970 to 2008 at both sites (Fig. 2). Within each site, predicted annual total indices of nymphs were positively correlated with soil temperature of the previous year, with annual means generally better than selected seasonal mean temperatures (e.g. April–July) as significant predictors (Fig. 3). There were, however, considerable differences between the sites in the effect of warming: although in Dorset, warmer initial conditions were followed by greater temperature increases (annual means by 0·69 °C from 1970–88 to 1989–99 and a further 0·30 °C to 2000–08) than in Wales (0·51 and 0·19 °C, respectively), and nymphal tick numbers increased by 7 and 36% over the same periods in Dorset, but by 77 and 159% in Wales (0·03 and 0·13 compared with 0·23 and 0·48 on the log scale in Fig. 2). Tick abundance was more variable from year to year in Wales, presumably reflecting temperatures that fluctuate closer to limiting levels. As expected from such a model with no inherent stochasticity, the abundance of each stage was strongly correlated with that of the previous developmental stage 1 year before, but again the tick population in Wales showed more variability in this respect (R^2 values 0·75 and 0·82 for nymphs-adults and larvae-nymphs in Wales compared with 0·99 and 0·92, respectively, in Dorset).

On average, the tick phenology was predicted to change after 1988, but again with site differences (Fig. 4). Under the

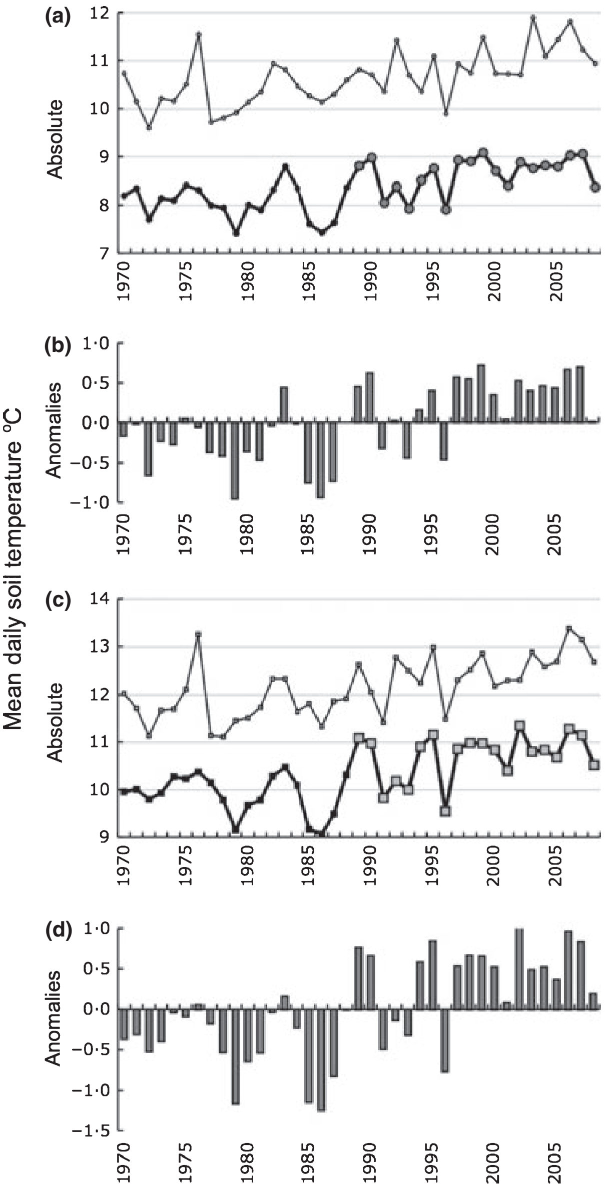

Fig. 1. Mean annual (thick line) and April–July (thin line) temperatures recorded at Bala, Wales (a) and Hurst, Dorset (c). Conditions before and after the step increase in temperature in 1989 are distinguished. (b) and (d) anomalies from the 1970–2008 mean for the above mean annual temperature series.

relatively cool conditions of Wales, warmer temperatures from 1989 allowed nymphs to start questing earlier, to reach their spring peak about a fortnight sooner, and show a more distinct second rise in the autumn; these changes continued with further warming from 2000. In Dorset, neither the timing nor the shape of either the spring or autumn nymphal peak changed significantly. For larvae, the timing of the spring peak barely shifted in Wales, but occurred about a fortnight earlier in Dorset. The degree of synchrony between larvae and nymphs, essential for the transmission of certain pathogens with short-lived infections in vertebrates, is very low at both sites and decreased further by 20% in Wales from 1970–88 to 2000–08, but increased by 36% in Dorset.

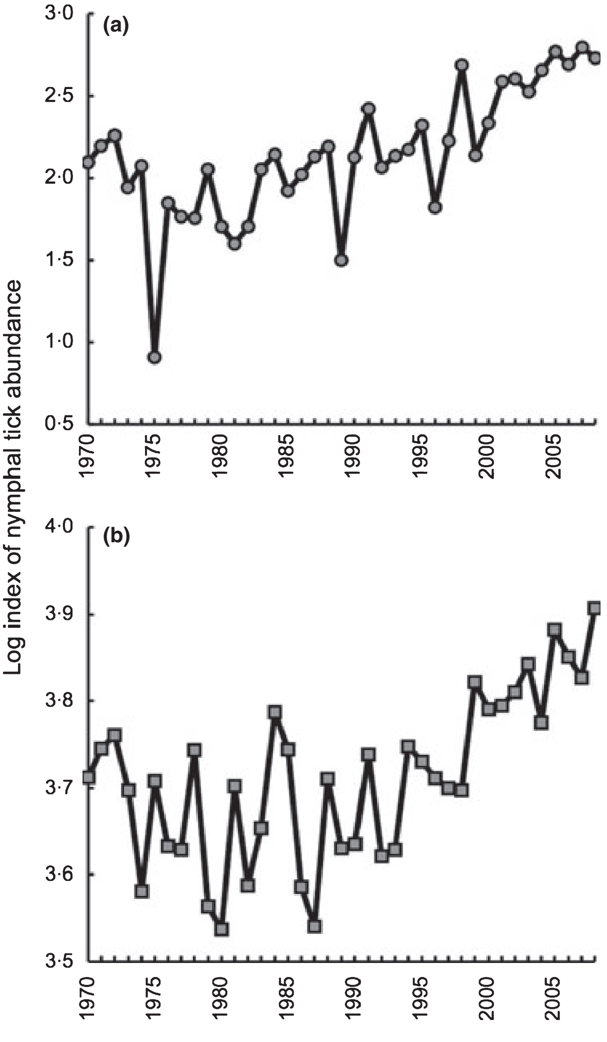

Fig. 2. Simulation of mean annual questing nymphal tick populations in Wales (a) and Dorset (b) under actual climate for 1970–2008. (NB different *y*-axis scales.)

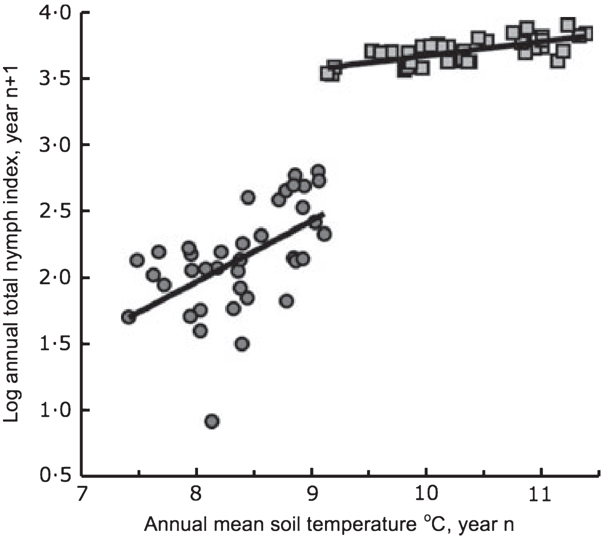

Fig. 3. Correlation of predicted log total annual numbers of nymphal ticks with mean annual soil temperatures of the previous year for Wales (○) and Dorset (□).

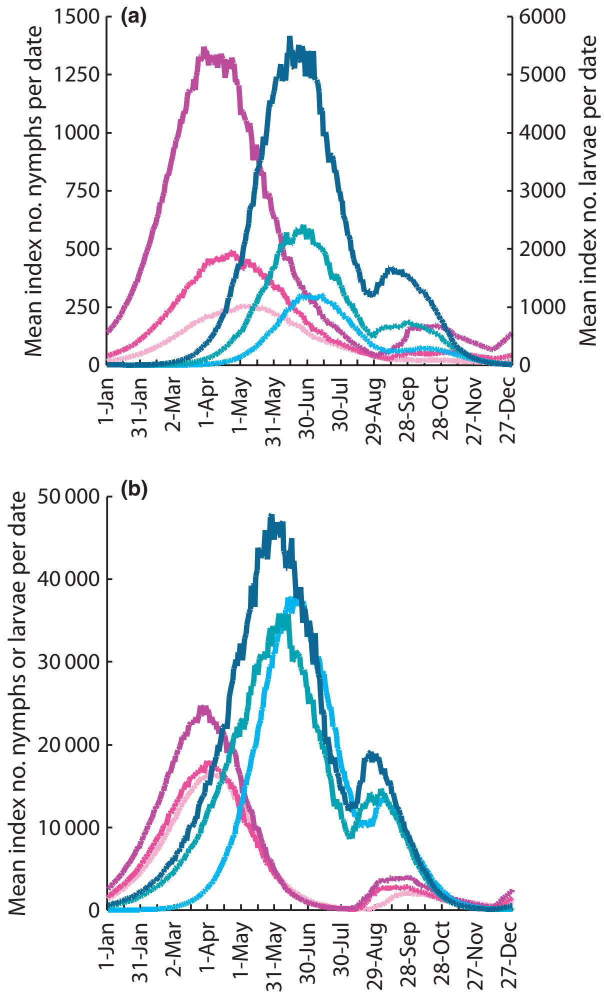

Fig. 4. Simulation of seasonal patterns of the mean daily abundance of questing nymphal ticks (pink) and larvae (aquamarine) for 1970–88 (pale), 1989–99 (middle) and 2000–08 (dark) for Wales (a) and Dorset (b).

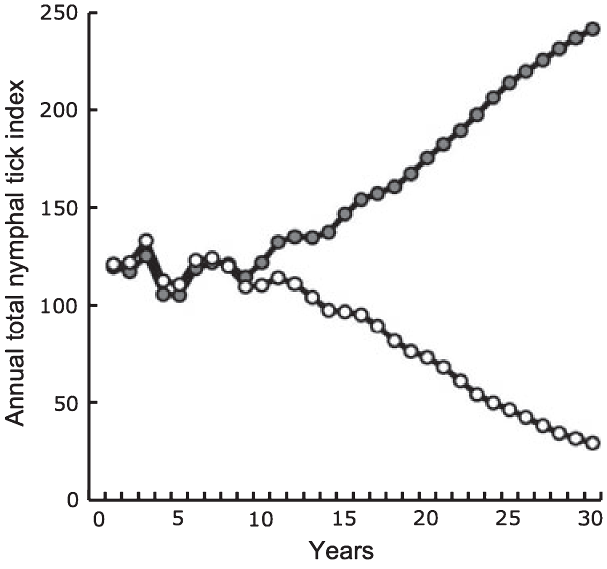

Fig. 5. Simulation of effects of doubling or halving the density of large hosts (deer) on the mean annual questing nymphal tick stock with initially low host contact rates (as in Wales).

HOST DENSITY

The effect of increased host density differed depending on the initial levels. In Wales (Fig. 5), an increase from the original low level caused little predicted change in nymph numbers over the first 10 years, but as host levels reached 1·4–2 times the initial level (years 10–20) the predicted questing nymph populations started to rise, reaching 47% increase by year 20. This increase continued over years 20–30, to reach a doubling of the original level and no levelling off, despite no further change in host densities. The impact of decreased host density also became apparent only after the first decade, and halving the abundance of large hosts reduced the questing nymphal population by 40% after 20 years and 76% after 30 years (Fig. 5). For the Dorset site, however, where initial host density values were considerably higher (see above), doubling the host density caused numbers of questing nymphs to decline by 16% after 30 years (Fig. 6a). Decreasing the host density also reduced the abundance of this tick stage (Fig. 6a), but only by 9%. The model shows, however, that, whereas in Wales, engorged adult densities (i.e. overall population fecundity) mirrored questing nymph densities, in Dorset, they changed independently of questing nymphs, reaching asymptotes at 30% above or below the original level when host densities were doubled or halved, respectively (Fig. 6b). Evidently questing ticks were simply removed at such a high rate when host contact rates were enhanced that their numbers were quickly exhausted each year. There was no apparent change in tick phenology.

ACARICIDE

Acaricide application at both sites caused a predicted drop in questing tick numbers (Fig. 7). Scenario 1 (acaricide applied to existing hosts) was slightly more efficient in reducing tick populations than scenario 2 (acaricide-treated hosts added to existing host assemblage), presumably because there were no counter-active positive effects of increased host density (above). Treating 10% of the host population was sufficient to reduce tick abundance within 4 years by about 50%, while treating 50% rapidly drove the tick population more or less to extinction. The efficacy of acaricide treatment, in terms of the proportional reduction in numbers of questing ticks after 30 years, was predicted to be similar at the two sites.

Discussion

In 73% of the locations covered by the 2006 UK survey of Scharlemann *et al.* (2008), ticks were perceived to have increased in abundance over the previous 5–10 years. The present study tests two potential causal factors, climate and host density. Temperatures at our UK sites exhibited a step-wise increase around 1989, in line with other parts of Europe (Sumilo *et al.* 2007; Marty 2008), which will have been generally favourable to tick populations as warmer temperature will

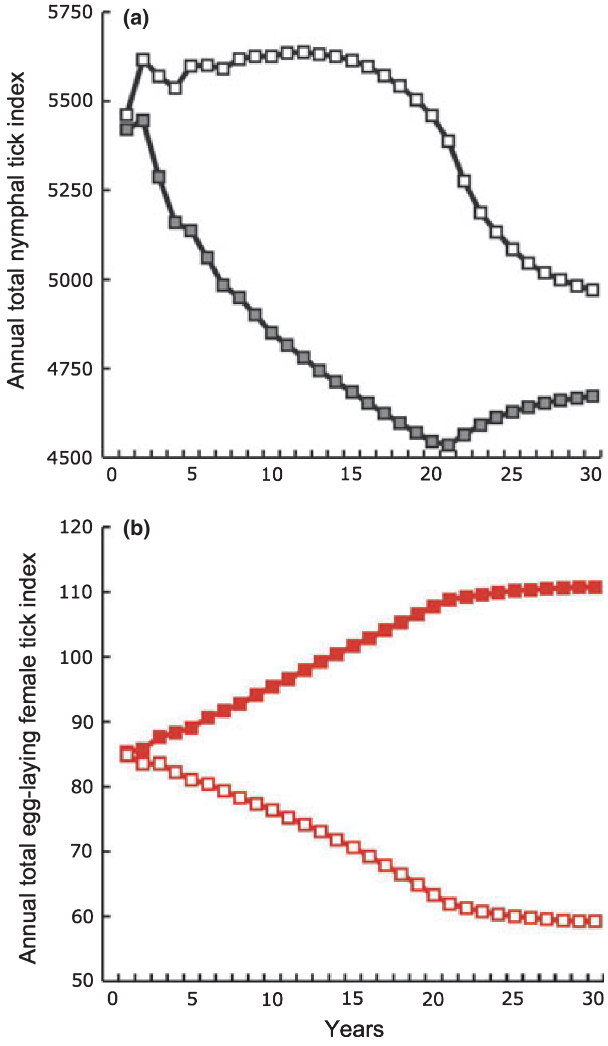

Fig. 6. Simulation of effects of doubling or halving the density of large hosts (deer) on the mean annual questing nymphal tick stock (a) and mean annual stock of post-engorgement adult ticks in a tick population (b) with initially high host contact rates (as in Dorset).

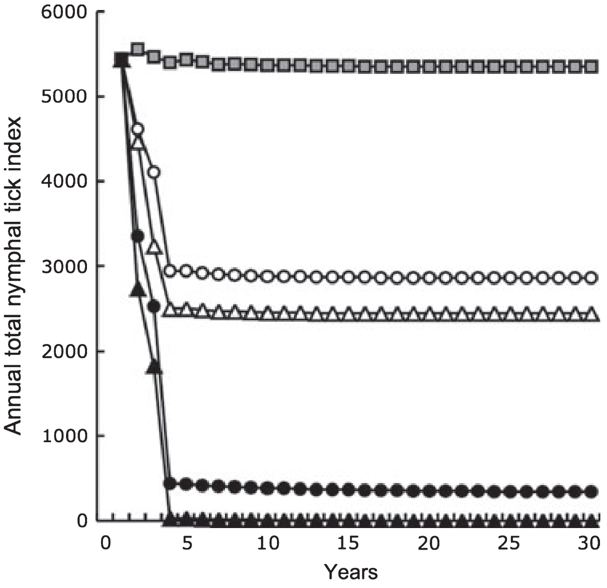

Fig. 7. Simulation of the effects of acaricide application on a tick population in Dorset, UK. Control (■); scenario 1 (△), acaricide is applied to 10% (open symbol) or 50% (filled symbol) of the existing large host community; scenario 2 (○), acaricide is applied to 10% (open symbol) or 50% (filled symbol) of newly added large hosts, quantified as the percentage of the pre-existing large host community.

speed the development of ticks from one stage to the next, thereby reducing the cumulative effect of constant daily mortality rates. The predicted population patterns suggest that more consistent temperatures from year to year, as seen post-1997, allow tick populations to build up. This is indicated by a) the initial decline in tick numbers from 1970, especially in Wales, once real temperature fluctuations drive the model after the initial uniform 10-year bedding-in period (Fig. 2) and b) the continuing increases in ticks post-2000 when mean annual temperatures did not increase, although mean April–July temperatures did show a slight upward trend. The predicted questing nymph populations responded more markedly to raised temperatures and were much more variable from year to year, under the more marginal conditions in Wales than in Dorset. There are two possible reasons for this. First, development rates of ticks increase nonlinearly with temperature, with lesser effects at higher temperatures (Randolph 2004). Secondly, density-dependent mortality (see a full description of the model in Dobson, Finnie & Randolph 2011) will have a greater stabilizing effect at the higher population levels and less harsh climatic conditions seen in Dorset. Most of the current range of *I. ricinus* in mainland Europe experiences warmer conditions during April–July than even the mildest parts of the UK, suggesting that the impact of climate warming on tick populations will be less marked there, but more significant at the latitudinal and altitudinal peripheries. At the same time, any more marked increase in summer time saturation deficit closer to critical levels at higher mainland temperatures could increase tick mortality associated with moisture stress, thereby dampening the predicted tick population increases as European climate changed over the past 20 years.

Any effect of warming conditions on reducing the average time taken to complete a full life cycle (thought to be at least 3 years in the UK – Randolph *et al.* 2002) will depend on whether ticks develop fast enough to escape from the constraints of daylength-induced overwinter diapause (both developmental and behavioural) (Belozerov 1982). Conversely, as seen in the 1970s in Wales, occasional unusually low spring or autumn temperatures can prevent ticks from completing their normal patterns of development and/or activity within the year, causing a sharp decline in numbers and a rebound the following year as delayed ticks emerge (apparent from dissecting the detailed outputs of the model). The prediction of altered phenology, such that the spring peak of questing ticks occurs earlier in the year (Fig. 4), arises from the empirically supported assumption in the model that emergence from behavioural diapause in the spring is triggered by the weekly mean of the daily maximum temperature; the observed threshold in the field is about 7 °C for adults and nymphs and 10 °C for larvae (Randolph 2004). A change in the timing of spring emergence has significant implications for pathogen transmission to humans when the vector is the one frequently encountered on recreational visits to the countryside, whose timing will be partly constrained by public holidays. Any management activities designed to reduce the risk of infection, such as the dissemination of information for awareness and self-protection, or cutting the vegetation back from the edge of maintained paths, may need to start earlier than in the past, before the spring holidays.

Our model suggests that under typical circumstances, greater host abundance can drive tick population increases, which might account for the perceived recent changes in tick abundance, including their appearance in new places (Scharlemann *et al.* 2008). Compared with temperatures, which have changed very little over the past 10 years, deer populations have expanded rapidly. Data on geographical range expansion of UK deer species between 1972 and 2002 show that roe deer *C. capreolus* increased by 2·3% per annum, fallow deer *D. dama* by 1·8%, red deer *C. elaphus* by 0·3%, Reeves' muntjac *M. reevesi* by 8·2%, sika deer *C. nippon* by 5·3% and Chinese water deer *H. inermis* by 2·0% (Ward 2005). Recent figures suggest an accelerated rate of increase between 2003 and 2007 in all species ranging from 5·2% p.a. for roe to 22·2% p.a. for Chinese water deer (Ward, Etherington & Ewald 2008). Range expansions are likely to follow increases in density in core areas, but unfortunately there exist few data on the real nationwide changes in numbers of these key tick hosts. The BTO BBS at 3139 1 km grid squares recorded an increase in their index of deer abundance of 55% for roe deer and 46% for muntjac from 1995 to 2002 (Battersby & Partnership, 2005). Although these figures are insufficient to give an indication of full changes in deer density, either locally or across the UK, it is clear that numbers of deer in the UK have increased significantly in recent decades in line with estimated densities across most of Europe. In areas that deer have only recently colonized, a doubling of large hosts for ticks is likely to be a very conservative estimate, and our predictions indicate that tick numbers could have risen dramatically in such places.

The finding that increasing host density from an initially high level may cause a decline in the questing tick population (Fig. 6a) should come as no surprise. Finite fat reserves mean that ticks can quest for a finite time period; typically, a certain proportion of the questing tick population will not come into contact with a host and will therefore perish (Randolph & Steele 1985; Randolph *et al.* 2002). Under these circumstances, a greater host contact rate will ensure that a higher proportion of the original cohort of ticks is fed, which will increase population fecundity (Randolph & Steele 1985). At some point, however, the host contact rate will become so high that all questing ticks can be expected to find a host before exhausting their fat reserves (i.e. the proportion of the cohort that finds a host will reach 1 and so be unable to go higher). Increasing the host density will hasten the removal of the questing tick population while only slightly increasing population fecundity (by shortening the average period over which ticks suffer mortality through moisture stress or predation). Thus, the evident reduction in this one phase – questing ticks – (Fig. 6a) masks an increased total population comprising all physiological phases, as demonstrated by the growing number of engorged adults (Fig. 6b), which will augment the transmission potential for tick-borne pathogens. In a tick population experiencing such high host density, a deer cull (for example) would initially cause an apparent increase (Rand *et al.* 2004), because the questing stages would not be removed so quickly from the vegetation. The long-term population trajectory would depend on the severity of the cull, but land managers wishing to instigate such a measure to control ticks should be advised that benefits may be seen in the longer term, after an initial period during which results may appear to be counter productive. Given approximate tick densities and host densities, our model would be able to predict the likely tick population trajectory under a given culling regime. Conversely, in a tick habitat with such high initial host densities, the further addition of large hosts (such as sheep) would effectively reduce the number of questing ticks and therefore the risk to humans.

Treating any additional hosts with acaricide would be even more effective. The predicted efficacy depended more on the proportion of the host population that was treated and less on whether those animals were already part of the host community or were simply added to it (scenario 1 or scenario 2). This has important management implications, because the treatment of wild hosts is clearly logistically highly demanding (Laurenson *et al.* 1997) (although less so when deer anoint themselves with acaricides via the corn-baited 4-poster devices used successfully, but at considerable cost, in the US – Pound, Miller & George 2000), whereas simply releasing treated (domestic) hosts into the area may be almost as effective. Indeed, in the past, when sheep were regularly dipped with long-lasting organophosphates against all manner of arthropod pests, including ticks, before their release onto the hills in the spring, they acted as 'lethal mops', picking up a large proportion of the ticks and killing them. Washing sheep at 2–3 monthly intervals with the acaricide Top Clip Gold Shield (Ciba Geigy) containing 60% w/v diazinon proved sufficient to reduce ticks by c.90% within 1 year in an enclosure on a Welsh hillside with low diversity of alternative vertebrate hosts (Randolph & Steele 1985). Treating domestic hosts has the additional advantage that the areas of ground over which they roam can be designated by fencing, such that the control measure is strictly focussed in the right place. Sheep are indeed being used in this way to protect grouse on Scottish moors where the value of shooting rights now far exceeds the value of sheep products, with the further advantage that such sheep may be treated at times independent of usual husbandry practices, if necessary.

It is apparent from this modelling exercise that both warming and increased host densities can result in greater tick populations. As with all complex systems, however, the responses of tick populations to simple changes in abiotic and/or biotic conditions vary depending on the initial conditions. The risk to humans and livestock of infection with tick-borne pathogens may change more markedly where the background environment is less favourable (lower temperatures and host densities). This is important along the environmental limits of tick populations, potentially allowing ticks to move up latitudinal and altitudinal gradients, as has been recorded recently in Sweden, the Czech Republic, Slovakia and Austria (Lindgren, Talleklint & Polfeldt 2000; Daniel *et al.* 2003; Holzmann *et al.* 2009; Lukan, Bullova & Petko 2010). In principle, this population model, developed here for two UK scenarios, could be rolled out across the broader range of conditions throughout the European distribution of *I. ricinus*, determining not only the relative change in abundance of ticks but also their potential to transmit various pathogens each with its own biological, and therefore environmental, prerequisites. In practice, however, this exercise awaits better data on microclimatic conditions experienced by ticks and better knowledge of the geographical heterogeneity of tick phenotype in relation to environmental factors.

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