Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2011, **48**, 1017–1028 doi: 10.1111/j.1365-2664.2011.02003.x

A modified matrix model to describe the seasonal population ecology of the European tick *Ixodes ricinus*

Andrew D. M. Dobson[1], Thomas J. R. Finnie[2] and Sarah E. Randolph*[,1]

[1]*Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK; and* [2]*Health Protection Agency, Porton Down, Salisbury, SP4 0JG, UK*

Summary

1. The sheep tick *Ixodes ricinus* is the most multicompetent vector in Europe, which is responsible for significant diseases of humans and livestock throughout the northern hemisphere. Modelling the tick's complex seasonal dynamics, upon which pathogen transmission potential depends, underpins the analysis of tick-borne disease risk and potential tick control.

2. We use laboratory- and field-derived empirical data to construct a population model for *I. ricinus*. The model is a substantially modified stage-classified Leslie matrix and includes functions for temperature-dependent development, density-dependent mortality and saturation deficit–meditated probability of questing.

3. The model was fitted to field data from three UK sites and successfully simulated seasonal patterns at a fourth site. After modification of a single parameter, the model also replicated divergent seasonal patterns in central Spain, but any biological factors underlying this geographical heterogeneity have not yet been identified. The model's applicability to wide geographical areas is thus constrained, but in ways that highlight gaps in our knowledge of tick biology.

4. Sensitivity analysis indicated that the model was generally robust, particularly to changes in density-independent mortality values, but was most sensitive to changes in parameters related to density-dependent mortality.

5. *Synthesis and applications*. Vector population models allow investigation into the effects of individual environmental factors on population dynamics in ways not easily possible by experimental manipulation of *in situ* populations. Our model can be used to evaluate public health risk, tick management strategies and potential effects of future environmental change.

Key-words: climate dependence, ecology, *Ixodes ricinus*, population model, public health risk, seasonal dynamics, tick, vector-borne disease

Introduction

The sheep tick *Ixodes ricinus* (Linnaeus) is a haematophagous ectoparasite of considerable medical and veterinary importance. Its ubiquity within Europe and Eurasia, abundance and catholic use of vertebrate hosts make it an effective vector for a large number of bacterial, viral and protozoan infections. In the United Kingdom alone, it is responsible for transmitting the agents of Lyme borreliosis, human granulocytic anaplasmosis (HGA), babesiosis and Louping ill. Lyme borreliosis is the most common vector-borne disease of humans in the northern hemisphere and may also affect domesticated animals. A quantitative understanding of the complex life cycle of vector ticks must underpin any serious attempt to predict disease risk and investigate potential control strategies. Marked environmental seasonality and the consequent adaptive diapause commonly seen make modelling far more complex for temperate species than for tropical species. In the United Kingdom, peak abundance of *I. ricinus* nymphs and adults is seen in April/May, followed approximately 6 weeks later by the peak in larvae. All three stages display a lesser resurgence in numbers in late summer. These basic patterns vary geographically according to local environmental conditions, with significant consequences for the tick's vectorial capacity,

*Correspondence author. E-mail: sarah.randolph@zoo.ox.ac.uk

especially for pathogens with short duration of infectivity in the vertebrate (Randolph *et al.* 2000). The same is true of *I. scapularis* in North America (Ogden *et al.* 2007; Gatewood *et al.* 2009).

Each instar of *I. ricinus* (larva, nymph, adult female) takes a single blood meal from a separate vertebrate host. Larvae and nymphs typically feed for 2–4 days, whereas adult females require c.10 days and increase their body weight 100 times. The processes of development and moulting between instars takes several months, during which time ticks must survive on nutrients from this single meal. Microclimatic factors impose strong seasonal constraints on tick population dynamics, not least because most of the life span is spent off-host, either actively questing for hosts on vegetation or sheltering in moist microhabitats on the ground to avoid desiccation during development and seasonal diapause (Randolph 2004).

I. ricinus may undergo both behavioural and developmental (or morphogenetic) diapause (Belozerov 1982). Behavioural diapause is typically defined in the acarological literature as a preprogrammed period of functional inactivity in unfed ticks, whereas developmental diapause is a physiological state in which the ticks' bodies undergo biochemical changes, particularly related to a slowing of metabolic processes (Belozerov 1982; Randolph *et al.* 2002). Both forms of diapause allow ticks to minimise energy use during times when it would be climatically unfavourable to quest for hosts. In *I. ricinus* in temperate Europe, behavioural diapause occurs to variable degrees through autumn and winter and developmental diapause occurs as a precursor to development when ticks feed in late summer or autumn (reviewed in Randolph 2004).

In this paper, we present the first biological, process-based population model for *I. ricinus*. It incorporates all available empirical information on the biological processes that control *I. ricinus* populations, including environmental determinants of diapause initiation and cessation (Randolph 2004), and the probability of questing (Alekseev *et al.* 2000; Perret, Rais & Gern 2004), day-degree summation modelling of development (Randolph *et al.* 2002) and estimates of density-dependent mortality (Randolph 1997). The model is constructed using data from three separate field sites in the United Kingdom where detailed tick abundance and microclimatic variables were measured over a period of several years (Randolph *et al.* 2002), and tested against data from independent sites in the United Kingdom and in central Spain. A sensitivity analysis is conducted to assess the model's robustness to deviations in individual parameter values.

One of the most recent models of *Ixodes* spp ticks (Ogden *et al.* 2005) captured seasonality well and offered insights into potential range expansion of *I. scapularis* in Canada (Ogden *et al.* 2006), but none has been applied to *I. ricinus*. Our model is characterised by its distinct underlying mathematical approach, protracted egg-laying phenology, use of saturation deficit (as opposed to temperature) to mediate questing probability and simulation of development periods by incremental day-degree summation.

Materials and methods

MODEL DESCRIPTION

General

The tick model, which simulates relative numbers of ticks of each instar and physiological stage, is written in R language (R Core Development Team, 2005) and based around a stage-classified Leslie matrix (Leslie 1945; Caswell 2001), with some significant modifications. It moves by daily increments; ticks in each stage experience a daily probability of moving to the next stage (Fig. 1), although certain transitions incur fixed time delays to simulate such processes as feeding and post-eclosion cuticular hardening. Active processes such as temperature-dependent development and egg-laying, which take more than a single day to complete, are also simulated in multielement vectors outside the matrix.

Developmental diapause

Developmental diapause delays the onset of development if ticks experience shortening day length (Belozerov 1998) by feeding after a

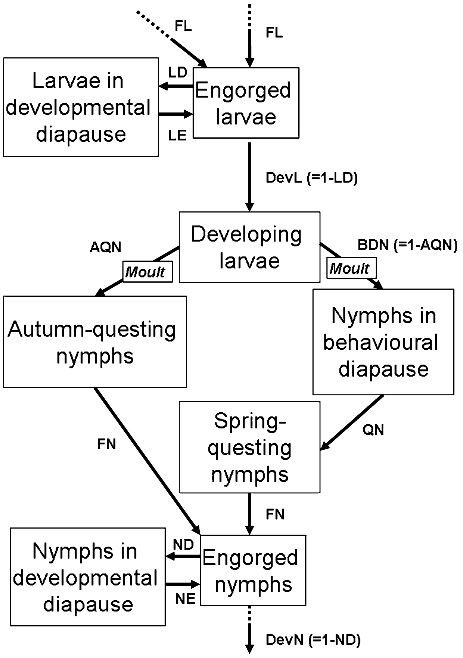

Fig. 1. Schematic outline of part of the model. The full model is repeated three times, once for each instar. Autumn questing and behavioural diapause (with subsequent spring questing) are mutually exclusive alternatives. Ticks enter developmental diapause if they have fed after a certain date in late summer (see text); thus, the proportions vary depending upon the development rate of the previous stage and the host contact rate. Labelled processes: FL, Larvae feeding (combines host encounter rate with probability of actively questing, mediated by saturation deficit); LD, Engorged larvae entering developmental diapause; LE, Larvae exiting developmental diapause; DevL, Engorged larvae beginning development; AQN, Developed nymphs questing in autumn (following a 20-day cuticular hardening period); BDN, Developed nymphs going into behavioural diapause in autumn (following a 20-day cuticular hardening period); QN, Nymphs exiting behavioural diapause to begin questing; FN, Nymph feeding (combines host encounter rate with probability of actively questing, mediated by saturation deficit); ND, Engorged nymphs entering developmental diapause; NE, Nymphs exiting developmental diapause.

certain date in late summer. Empirically, at three latitudinally graded sites across Europe, the observed date of diapause onset (see Randolph 2004 for details) coincided with the period (e.g. end of July, mid August, etc.) at which day length shortens at a maximal rate, measured according to when the centre of the sun dips 9° beneath the horizon ('tick twilight'). This is applied to the model. Because brief exposure to cold (at least 0 °C) breaks diapause (Campbell 1948) and development is determined by temperature above a threshold of c.7·5–9 °C (depending on the stage), as long as ticks have emerged from diapause before spring warming starts, the timing of emergence (onset of development) is not critical and is controlled by a Gaussian probability function that gradually releases ticks from 6 February onwards, a date chosen to accommodate these criteria adequately.

Development

Daily increments of development are modelled as a function of temperature with day-degree summation, using the following stage-specific equations derived by Randolph *et al.* (2002) from empirical observations of Campbell (1948), where T is daily mean temperature:

From egg to emerged larva:

$$Y = -0{\cdot}0000112T^2 + 0{\cdot}002305T - 0{\cdot}0185 \qquad \text{eqn 1}$$

From engorged larva to emerged nymph:

$$Y = 0{\cdot}0000303T^2 + 0{\cdot}000733T - 0{\cdot}00706 \qquad \text{eqn 2}$$

From engorged nymph to emerged adult:

$$Y = -0{\cdot}00000796T^2 + 0{\cdot}00193T - 0{\cdot}0161 \qquad \text{eqn 3}$$

Development is complete when the cumulative development reaches one, and eclosion at each instar is followed by a 20-day period of cuticular hardening.

Questing and behavioural diapause

Ticks with the potential to quest (i.e. not in diapause or development) are considered to be 'questing', although, importantly, this is a nominal state in the model and does not imply that they are necessarily actively questing for hosts. Probability of active questing is incorporated into the probability of contacting a host. The fat content of field ticks demonstrated that, whether or not they have undergone developmental diapause, ticks emerge for questing in a largely synchronised fashion each year in the late summer/early autumn (Randolph *et al.* 2002). These ticks then either quest at this juncture or undergo a period of behavioural diapause. It is not known what determines which individuals start to quest during the autumn rather than entering behavioural diapause, and here the choices are modelled as mutually exclusive. The proportions that go into either autumn questing (0·1) or behavioural diapause (0·9) were estimated by reference to the relative heights of spring and autumn peaks of abundance and are constant for all UK field sites described in this paper.

Ticks that undergo behavioural diapause over winter emerge to quest the following spring (Randolph *et al.* 2002), thought to be triggered by increasing temperatures; the threshold for onset of questing is set at a smoothed weekly average daily maximum temperature of 7 °C for nymphs and adults and 10 °C for larvae, in line with field observations (Perret *et al.* 2000; Randolph 2004). In years when this temperature index does not drop below 7 °C, the date of activity onset is set at 22 December, the shortest day; increasing day length is thought to stimulate questing where temperatures are sufficiently high (Randolph 2004). In reality, an increasing proportion of the tick population may start to quest as more of its microhabitat reaches the threshold temperature, so a Gaussian function is applied after the threshold date. The parameter values of this function were calibrated against field data so as to capture the timing and rate of spring appearance of questing ticks, but are nevertheless constant across the three UK field sites.

Host density and feeding probability

Effective host density is defined by the stage-specific host contact rate, represented as the probability that a tick in a questing position will make contact with a host (Table 1). This 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 limited empirical data from woodland habitats (Talleklint & Jaenson 1994), but on upland moorlands in the United Kingdom, large hosts (predominantly sheep) feed >90% of immature stages (Steele & Randolph 1985; Ogden, Nuttall & Randolph 1997). Here, we consider an individual's probability of finding a host, not the proportional rate of change in the questing population. Host contact rates were expected to vary between field sites, and values were scaled according to observed differences in tick density at the three sites used in model fitting (the only such site-specific parameter values).

A tick's feeding probability is calculated as the probability of its active questing (i.e. being positioned on the vegetation ready to respond to a passing host) multiplied by the host contact rate. The probability of active questing is modelled as a function of saturation deficit (SD) (eqns 4 and 5). Data on the effects of SD on the probability of questing by nymphs (also applied to larvae in lieu of anything more suitable) and adults are based on the proportion of ticks seen questing in field arenas over several months (Perret, Rais & Gern 2004) but do not account for tick mortality, so the data were first corrected, modelling mortality as an exponential decay curve. The SD values of Perret, Rais & Gern (2004) were calculated from relative humidity and temperature measured at a nearby meteorological station rather than by a data logger at the site. These values were adjusted using the relationships between relative humidity and temperature at the one of our field sites (Dorset) and a nearby meteorological station. The relationship between the corrected proportions of questing ticks and adjusted SD was used to generate the functions:

$$\text{Proportion of nymphs questing} = 0{\cdot}7393 \times e^{-0{\cdot}1054 * \text{SD}} \qquad \text{eqn 4}$$

$$\text{Proportion of adults questing} = 0{\cdot}7597 \times e^{-0{\cdot}1021 * \text{SD}} \qquad \text{eqn 5}$$

The feeding probability (F) for each stage can therefore be described by the generic equation:

$$F = pq * (shc + lhc) \qquad \text{eqn 6}$$

where
pq = the probability of questing
shc = small host contact rate
lhc = large host contact rate
Host contact rates for each stage, combined for both host sizes, are listed in Table 1.

The feeding period (3 days for larvae and nymphs, 10 days for adults) is incorporated into the model as a fixed delay. Density-dependent mortality is applied during this period.

Table 1. Model parameter values, specific for each field site only where shown. Values for the two validation sites are as per Exmoor

Parameter	Value
Density-dependent mortality	
Slope	
Larvae	0·219
Nymphs	0·7008
Adults	0·7008
Intercept	
Larvae	−1·45
Nymphs	−4·597
Adults	−4·597
Daily host contact rates	
Wimborne, Dorset	
Larvae	0·07325
Nymphs	0·0975
Adults	0·105
Exmoor, Somerset	
Larvae	0·0493
Nymphs	0·071
Adults	0·09
Powys, Wales	
Larvae	0·025
Nymphs	0·04
Adults	0·06
Constant daily mortality	
Questing	
Larvae	0·0068
Nymphs	0·0034
Adults	0·00136
Behavioural diapause	
Larvae	0·001428
Nymphs	0·000476
Adults	0·000408
Developmental diapause	
Larvae	0·001428
Nymphs	0·000476
Adults	0·000408
Development	
Larvae	0·001428
Nymphs	0·000476
Adults	0·000408
Eggs	0·02618
Proportion of ticks that quest in autumn	
Larvae	0·1
Nymphs	0·1
Adults	0·1
Curve controlling exit from behavioural diapause – peak height	
Larvae	0·05
Nymphs	0·125
Adults	0·2
Curve controlling exit from behavioural diapause – centre date	
Larvae	2nd August
Nymphs	4th August
Adults	4th August
Curve controlling exit from developmental diapause – peak height	
Larvae	0·2
Nymphs	0·2
Adults	0·2
Curve controlling exit from developmental diapause – centre date	
Larvae	1st April
Nymphs	1st April
Adults	1st April

Egg-laying

A fully engorged adult female *I. ricinus* is assumed to lay 2000 eggs (Gray 1981). Egg laying is modelled as this fixed number of eggs distributed over a 60-day period according to the egg-laying curve for *Rhipicephalus appendiculatus* (Randolph & Rogers 1997), shown in eqns 7 and 8. Adult females are removed from the model after laying, when they die.

$$\mathrm{ELV} = k((1-(\mathrm{e}^{-r1x(1,60)}))\mathrm{e}^{-r2x(1,60)}) \qquad \text{eqn 7}$$

$$k = 1000/\mathrm{sum}(\mathrm{ELV}) \qquad \text{eqn 8}$$

LV is a 60-element vector that contains the factors by which to multiply the 60-element laying adult vector to generate the correct number of eggs laid per female per day. The term $x(1,60)$ describes the vector elements 1–60; the number of eggs laid by each female varies as she moves sequentially down the vector. The constant k, which depends upon the values of $r1$ and $r2$, ensures that the maximum number of eggs laid over 60 days does not exceed 2000; the function is applied to adults of both sexes, so the maximum number of eggs is halved to account for a 50:50 sex ratio (eqn 8). The constants $r1$ and $r2$ determine the steepness of the climb ($r1$) and decline ($r2$) of the egg-laying curve; we use the same values as Randolph & Rogers (1997), who adjusted the values to fit the curve to that of Branagan (1973).

Mortality

Daily density-independent mortality rates are applied to all stages. Background rates are based upon field observations on ticks held in permeable containers in the Czech Republic (Daniel *et al.* 1976) and Ireland (Gray 1981), but were modified *post hoc* to ensure that they were low enough to allow population equilibrium at the climatically least favourable of the field sites used for validation (Powys, Wales; see below for description of sites). To this end, all the published mortality values were multiplied by a factor of 0·68.

Mortality rates were not available for unfed ticks in behavioural diapause, which may suffer lower predation from arthropod predators than engorged ticks (Gigon 1985; Samish & Alekseev 2001) and be less susceptible to freezing stress (Dautel & Knulle 1997), but may be more vulnerable to desiccation owing to their higher surface-area-to-volume ratio and the relatively low levels of deposition of waxy lipids in their cuticles (Yoder, Selim & Needham 1997). In the absence of empirical data, the most parsimonious solution is to assume equal background mortality and apply the same rates as for the engorged stages.

Mortality rates vary with the degree of desiccation stress determined by atmospheric SD but increase only when SD rises beyond approximately 3 mm Hg (Mount, Haile & Daniels 1997). This was virtually never recorded in the tick habitats monitored in the United Kingdom, so this term was omitted rather than relying on the only available empirical parameters and relationships derived for a different species (*I. scapularis*) on a different continent (N America).

In addition to the background daily mortality rate, questing duration is limited to 60 days in larvae and 120 days in nymphs and adults, whether or not preceded by behavioural diapause, according to the approximate maximum life span of unfed ticks imposed by the metabolic costs of questing (Steele & Randolph 1985).

Besides mortality through desiccation, starvation and predation, all ticks are likely to experience density-dependent mortality, potentially mediated via host immunity (Sutherst, Wagland & Roberts 1978; Randolph 1994; but see Ogden *et al.* 2002), host grooming (Levin & Fish 1998) and host avoidance of infested areas (Sutherst *et al.* 1986). In East and South Africa, relatively simple demographic processes and seasonal recruitment in tropical climates allowed density-dependent effects to be estimated for *R. appendiculatus* from the relationships between interstadial mortality indices (*k*-values) and tick density (Randolph 1997). For example, in South Africa, the overall density-dependent relationship showed a slope of 0·387 and intercept of −0·814 during the larva-to-nymph interstadial period and a slope of 1·24 and intercept of −2·579 during the nymph-to-adult period. These data came mainly from farms where cattle act as the dominant host. A more varied host assemblage might produce weaker density-dependent effects if some hosts are less likely to display tick avoidance, grooming and/or acquired resistance (Randolph 1979). Where rodents feed a greater proportion of ticks, less density-dependent tick population regulation might be expected than in a cattle-only system, owing to the rapid turnover of hosts relative to the timing of acquired immune response. Because the *I. ricinus* model was designed to simulate environments with diverse wildlife host assemblages (and because 'mortality' in the African study also included density-independent mortality, which is accounted for separately in our model), the slope of density dependence was set below one and the intercept below zero (i.e. a positive threshold tick density). Within these constraints, the slope and intercept for the larva/nymph transition were iteratively adjusted to produce matches with the observed data; the nymph/adult values were fixed to retain the same proportional relationship to the larva/nymph values as in Randolph's (1997) study, with the same values applied to the adult/egg transition in the absence of any other empirical data.

Density-dependent mortality is applied during the engorgement period according to the generic eqns 9 and 10 for the probability of survival (*S*); individual values for slope and intercept for the three stages are given in Table 1:

$$kv = (i + s(\log((qp + 1) * 100))) * y \qquad \text{eqn 9}$$

$$S = 10^{-kv} \qquad \text{eqn 10}$$

where kv = '*k*-value'; i = intercept of line of best fit in relationship between kv and log of population size (see Randolph 1997); s = slope of line of best fit in relationship between kv and log of population size; qp = active questing population; y = a scaling value inversely proportional to the host contact rate. Higher host contact rates (i.e. host density) should cause concomitant reductions in density-dependent mortality, because the on-host density of a fixed number of ticks is reduced when the host density is increased.

FIELD DATA

Primary data (density of each tick stage) for model construction came from standard sampling for *I. ricinus* by dragging a blanket over the ground, carried out at approximately fortnightly intervals between 1997 and 2000 at three sites in the United Kingdom: Powys, Wales, and Dorset and Somerset (Exmoor), south-west England (Randolph *et al.* 2002 for sites and methods). Data for independent model validation were provided by blanket sampling on Exmoor in a similar habitat to above at 3-weekly intervals from March 2008 to December 2009 (Dobson, Taylor & Randolph 2011) and for a site in central Spain where ticks were sampled monthly for 9 years (Estrada-Pena *et al.* 2004).

CLIMATE DATA

From April 1996 to May 2001 in Dorset, April 1997 to September 2001 on Exmoor and April 1997 to September 2000 in Wales, hourly temperature (ground level and 30 cm above) and relative humidity (30 cm above ground level) at the three field sites were recorded using automatic weather stations (based on Squirrel data loggers; Grant Instruments, Cambridge, UK). Hourly data were converted to daily minimum, maximum and mean figures. Saturation deficit at 30 cm above ground level was calculated from temperature and relative humidity (equation in Randolph & Storey 1999). One gap in the Dorset data owing to logger malfunction was filled by calibrated data from local meteorological stations. For model simulations, actual climate data for each site were preceded by a 10-year series in which each day was given a value equal to the mean for that date across the full observation period for that site; this allowed population establishment. Comparisons with observed data were based on model simulations using the actual data after these 10 years of mean values.

Exits from behavioural diapause are triggered by threshold values in the smoothed weekly average of the daily maximum temperatures taken from meteorological stations closest to the field sites and smoothed by loess interpolation.

Climate data (temperature and relative humidity at questing height) for the Exmoor test site were taken during the field visits. Comparisons between these values and those from a nearby meteorological station were used to calibrate the latter, which were used as the input in model testing. Weekly climate data recorded for the field data from central Spain (Estrada-Pena *et al.* 2004) were converted to daily values by simple linear interpolation.

MODEL EVALUATION

Empirical validation

Model outputs were generated for the three field sites according to their specific climate data. Other parameter values (Table 1) were held constant across all sites apart from host contact rates, which reflect estimated indices of varying host abundance. The goodness-of-fit between the predicted seasonal patterns of numbers of ticks of each stage and those observed on each date of field sampling over 3 years was assessed according to the R^2 value and slope of the regression line (Randolph & Rogers 1997). The same procedure was used to test simulations for the two independent field sites (Exmoor and central Spain). In both cases, host contact rates were specified as per the original Exmoor site. The two sorts of diapause prevent the estimation of interstadial development periods from observations on field populations. Therefore, we cannot compare the observed and predicted relationships between interstadial mortality rates and population density, as did Randolph & Rogers (1997). Simulations for the independent Exmoor site are shown for the years of data collection (2008–2009), but those for Spain (a 9-year series) are presented as mean values per sample/model day across all years, because of an observed strong upwards trend over the 9 years that was demonstrably unrelated to climate (Estrada-Pena *et al.* 2004).

Sensitivity

The sensitivity of model predictions to deviations in parameter values was investigated following a previous method (Randolph & Rogers 1997). Models were run with each parameter value in turn alternately increased and decreased by 50%, except where parameters consisted of dates (e.g. the centre date of the curve controlling exit from behavioural diapause), which were moved forwards and backwards by 14 days. The intercepts of the density-dependent mortality functions were not altered, because they merely pertain to the hypothetical unit of density of the model simulations, and are thus effectively arbitrary.

Models were run with each altered parameter in turn for a 13-year simulation using climate data from the Dorset data logger, with each day's values comprising the mean values from that date in each of the years for which data were recorded. Using only the final 5 years of simulations, the effect on R^2 values and slopes in regressions of each changed model against the final model was recorded. Changed models that returned mean population sizes lower than the final model give regression slopes between zero and one and are presented in Figs 7 and 8 as negative reciprocals to give equivalent magnitude of change as in models where means are higher (when slopes exceed one). A slope of 0·2 therefore becomes -5, indicating that the changed model's mean was five times lower than that of the final model.

Population growth rate calculations involving matrix eigenvectors (Caswell 2001) are not suitable for this model owing to the number of life-history events (notably density-dependent mortality and temperature-dependent development) that are modelled in vectors external to the main matrix, and which vary according to external inputs and/or population state.

Results

ABUNDANCE AND SEASONALITY AT PRIMARY FIELD SITES FOR MODEL CONSTRUCTION

Observed and predicted numbers of ticks of each stage at the three field sites (Figs 2, 3 and 4) and correlations between them (R^2 and slope values, Table 2) indicate that, with some exceptions (notably larval seasonality in 1997 at Dorset and Exmoor), the timing of appearance and decline of each questing stage was adequately predicted. Differing ratios of tick life stages at each site (probably due to variable sampling efficiency of each stage in different vegetation or host composition – see Discussion) were accommodated by varying multiplication factors. The absolute heights of the spring and autumn peaks were less precisely captured, probably because they are so sensitive to host abundance. Larvae in Wales are one exception to the good model fit, probably because the structure and exposure of the ground vegetation there were less amenable to sampling and less hospitable, respectively, for this tick stage; sample sizes were therefore very small (see Discussion). Despite the potentially greater stochastic effects of small numbers in each sample of adults (see *y*-axes on Fig. 4), the model fit for this stage was generally acceptable; the exception at Exmoor was entirely attributable to the anomalous peak of adults observed there at the end of 2000. An apparently anomalous reversal of spring and autumn peaks in the first year (Fig. 2) reduced the overall correlation for larvae at Exmoor despite the otherwise excellent match (see Discussion).

ABUNDANCE AND SEASONALITY AT INDEPENDENT FIELD SITES FOR MODEL VALIDATION

Predictions of tick seasonal abundance at the two independent field sites threw up some instructive results. Those for a different site on Exmoor at a later period (2008–09) gave a good match to the seasonal pattern but predicted higher absolute numbers of nymphs and adults (Fig. 5), as would be expected if host abundance were greater at this site than at the primary site for which the host contact rates were calibrated. (Based on local reports of deer abundance, this is likely but cannot be tested empirically.) In central Spain, however, the same parameter values failed to capture the seasonal timing of activity of larvae and adults (Fig. 6, left). This was rectified when the percentage of ticks that quest in autumn, rather than entering behavioural diapause, was changed from 10% for all stages as in the model for the United Kingdom, to 40% for larvae, 25% for nymphs, and 95% for adults. The model then captured the starkly different seasonal patterns seen in central Spain much more closely (Fig. 6, right).

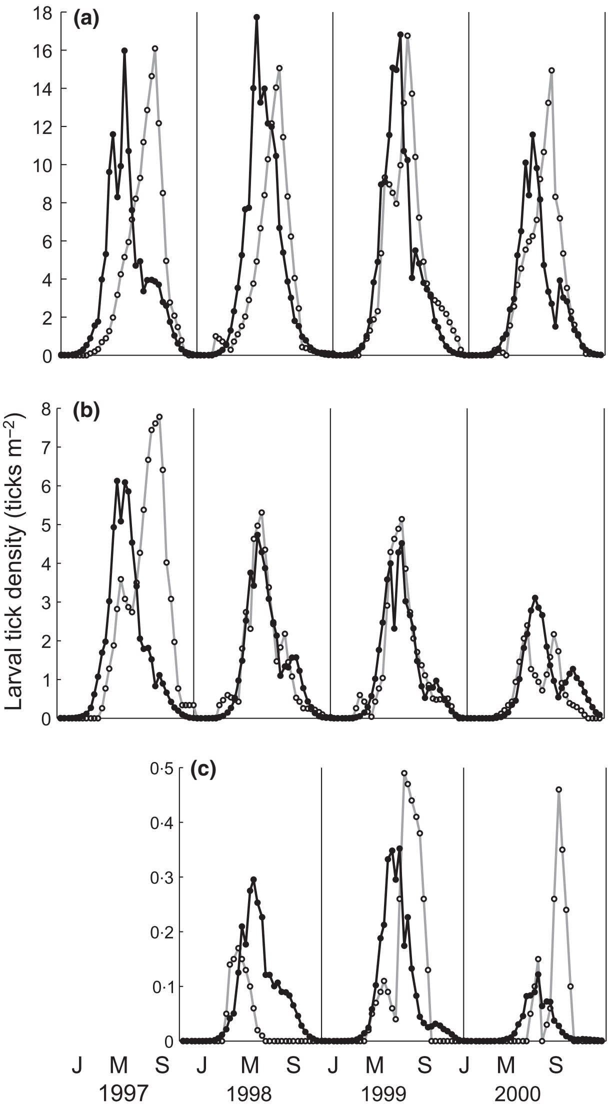

Fig. 2. Observed (○) and model simulations (●) of seasonal abundance of larval ticks at (a) Wimborne, Dorset, (b) Exmoor, Somerset, (c) Powys, Wales. Field data were smoothed to dekad intervals, and simulation data taken on concurrent dates. The predicted output is rescaled by the following factors: (a) ×1·16, (b) ×1·4, (c) ×0·16 (see text).

PARAMETER SENSITIVITY

Sensitivity results for simulations of nymph numbers (Figs 7 and 8) and extremely similar results for adults and larvae (not

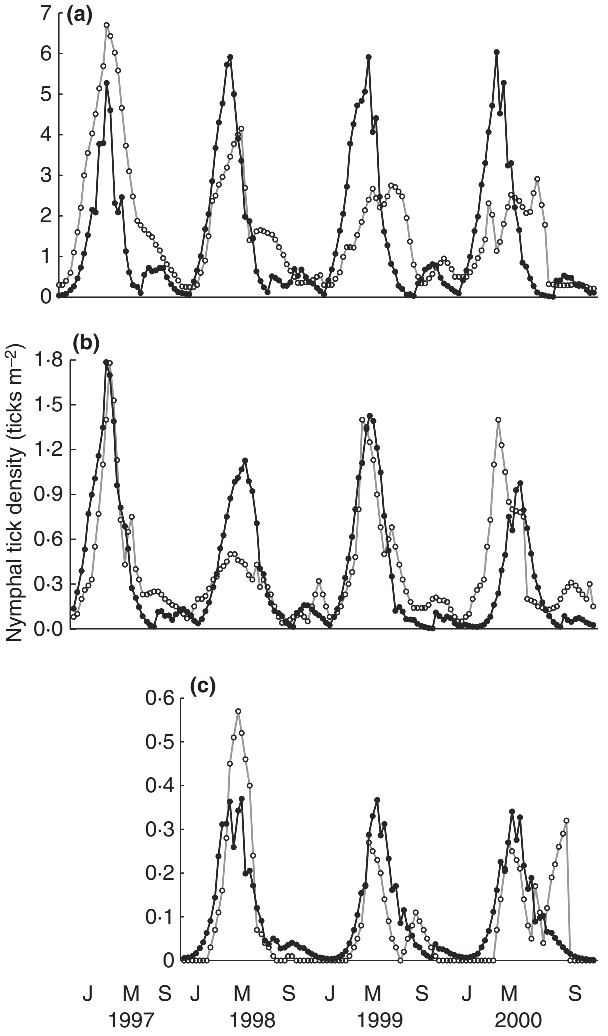

Fig. 3. Observed (○) and model simulations (●) of seasonal abundance of nymphal ticks at (a) Wimborne, Dorset, (b) Exmoor, Somerset, (c) Powys, Wales. Field data were smoothed to dekad intervals, and simulation data taken on concurrent dates. None of the predicted outputs was rescaled.

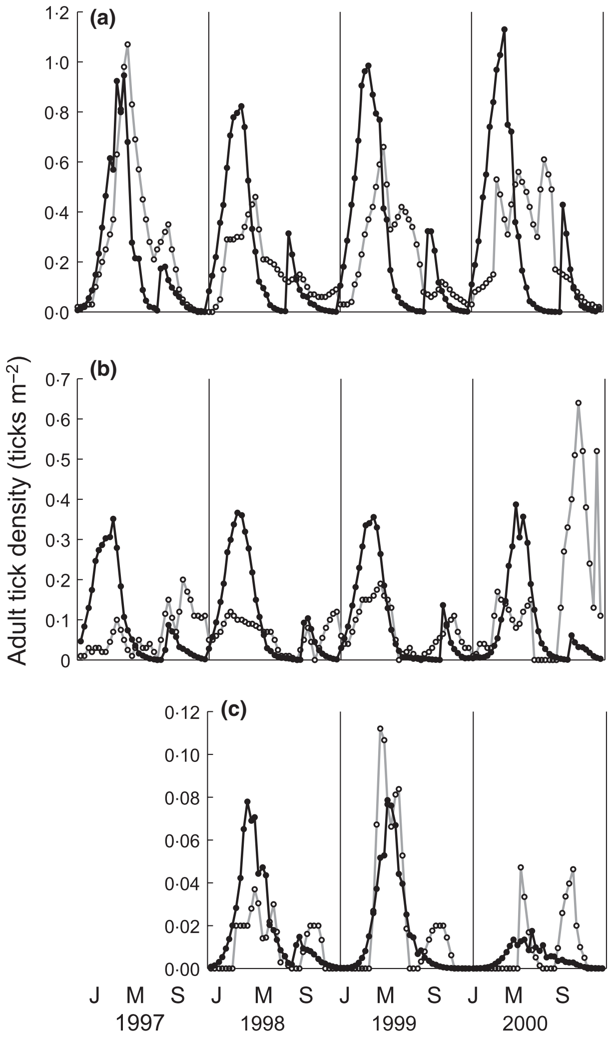

Fig. 4. Observed (○) and model simulations (●) of seasonal abundance of adult ticks at (a) Wimborne, Dorset, (b) Exmoor, Somerset, (c) Powys, Wales. Field data were smoothed to dekad intervals, and simulation data taken on concurrent dates. Observed adult numbers = 2 × females. The predicted output is rescaled by the following factors: (a) ×0·7, (b) not rescaled, (c) ×0·75 (see text).

shown) indicate a robustness of the final model to perturbations, as was seen for the African *R. appendiculatus* (Randolph & Rogers 1997); changes in host contact rates and parameters associated with density-dependent mortality had greater effects than changes in background daily mortality rates. Model simulations were, however, particularly sensitive to egg survival. In addition, changes in the curve dictating the spring-time onset of questing activity after behavioural diapause caused considerable deviation from observed seasonal patterns, but the reduced R^2 values were always $>0{\cdot}85$ of the original values (Fig. 7). Comparisons within groups of parameters (mortalities, autumn questing fractions, etc.) are more meaningful than between-group comparisons, given, for example, that a 50% increase in the fraction of ticks that quest in the autumn is only arbitrarily equivalent to a 50% increase in egg survival.

Perturbations to the slope of predicted/observed regressions caused by changes in density-independent mortality values were generally small and were in proportion to the initial values; the largest perturbation thus came from changes in egg survival (EgS), which had the largest starting value (0·02618).

Changes in density-dependent mortality parameters caused considerably more perturbations in the slope than in the R^2 values, indicating that such changes cause significant changes in equilibrium density but not in seasonal patterns. These large changes occurred when density-dependence was made more severe (up to 30-fold decrease in nymphal equilibrium population density by increasing the slope of the adult density-dependent mortality regression by 50%, almost certainly an unrealistic perturbation). These results match the assumptions made when choosing the density dependence parameters; the population is modelled as experiencing only moderate density dependence, such that any increase in its effect will immediately reduce population density, whereas decreases will have more negligible effects.

Table 2. R^2 values for correlations between predicted and observed tick abundances at each field site

	n	R^2	Slope
Wimborne, Dorset			
Larvae	144	0·353	0·507
Nymphs	144	0·303	0·656
Adults	144	0·198	0·909
Exmoor, Somerset			
Larvae	144	0·370	0·357
Nymphs	144	0·573	0·901
Adults	144	0·005	0·076
Powys, Wales			
Larvae	108	0·120	0·619
Nymphs	108	0·549	0·611
Adults	108	0·454	0·788
Exmoor, validation site			
Larvae	30	0·401	0·555
Nymphs	30	0·782	0·216
Adults	30	0·502	0·195
Spain, validation site*			
Larvae	108	0·294	0·0035
Nymphs	108	0·305	0·0023
Adults	108	0·044	−0·0022

*For the validation site in Spain, figures refer to the unmodified model, with the same proportions of ticks questing in the autumn as in the United Kingdom.

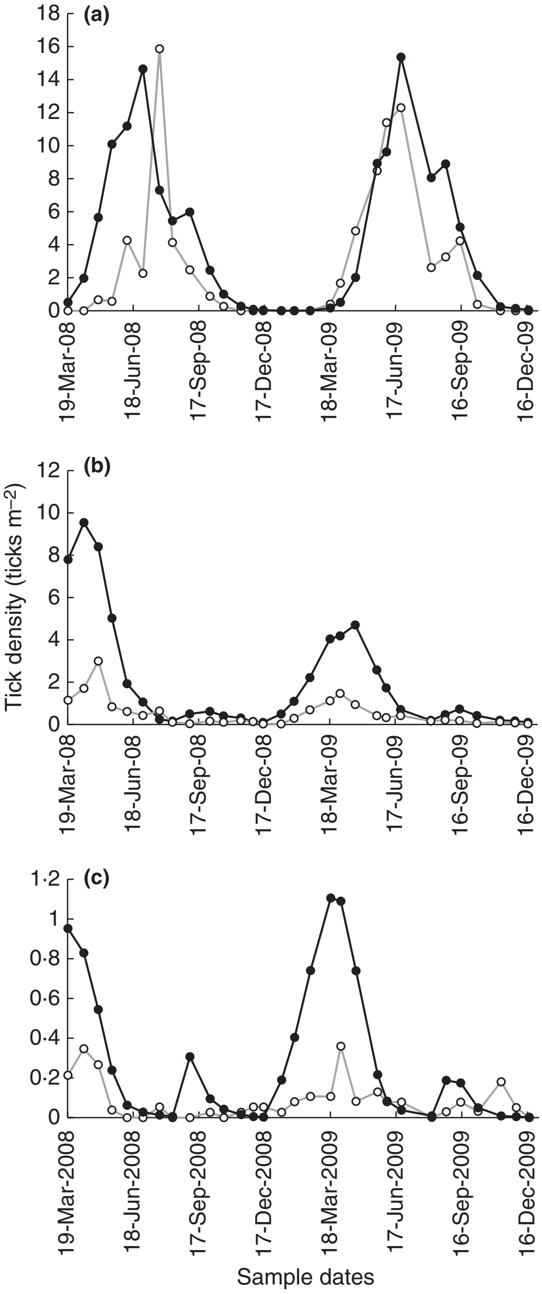

Fig. 5. Model simulations (●) and observed (○) numbers of larval (a), nymphal (b) and adult (c) ticks from an independent test site on Exmoor.

Discussion

This paper demonstrates the efficacy of the first process-based population model for *Ixodes ricinus*. At this early stage in its development, its function is less to predict seasonal dynamics and abundance across the tick's extensive range and more to test our understanding of the component population processes. In capturing the seasonal dynamics of *I. ricinus* in a north-western European climate, the model supports current ideas on the fundamental patterns of diapause, development and recruitment (Randolph *et al.* 2002).

Differences in goodness-of-fit between predictions and observations may be attributable to habitat features that determine how well field samples reflect reality. Both the primary and validation sites at Exmoor were open deciduous woodlands with an understorey of *Vaccinium* spp., which is ideal for sampling by blanket dragging, being pliable enough for the blanket to make contact equally with all parts of the vegetation throughout the year. In Dorset, the mixed deciduous/coniferous woodland, with ground cover of *Hyacinthoides non-scripta* and *Mercurialis canis*, allowed equally good sampling efficiency, despite some sparse *Pteridium aquilinum*. The Welsh site, in contrast, was an area of unimproved upland sheep grazing, comprising grasses of predominantly *Festuca*, *Agrostis* spp. and also much widespread *Molinia* spp., a substrate that strongly impedes the blanket's contact with lower parts of the vegetation where larval ticks quest. Additionally, the exposed nature of this latter site would render the tops of the vegetation unfavourable for larvae. This stage was, accordingly, significantly over-predicted by the model for this site. The adults in both Dorset and Wales were also slightly over-predicted, but this may reflect partly their relative rarity, and hence the greater element of chance in their observed abundance, and partly the greater likelihood of their being brushed off the blanket before being counted, owing to their greater size. The anomalous sudden peak of adults in 2000 at the Exmoor site is unexplained but not thought to indicate a significant change of conditions for questing adults. (The foot-and-mouth outbreak in 2001 prevented continuing fieldwork to explore any possible impact on future generations.) Differences between predicted and

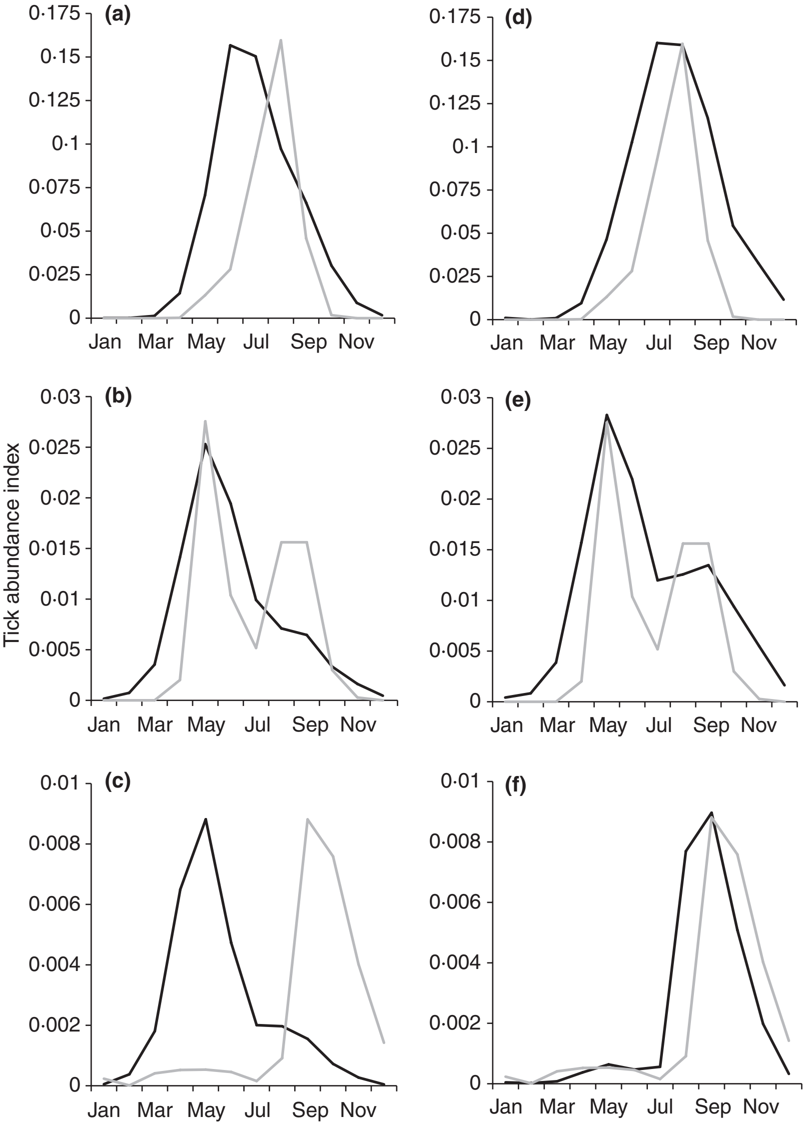

Fig. 6. Model simulations (black) and observed (grey) tick density per m^2 from central Spain recorded over 1994–2002 by Estrada-Pena *et al.* (2004). Models were run for all 9 years, but the figure shows mean values per sampling/modelling day across all years (see text). Model simulations were scaled to fit observations to aid visual interpretation. Left side (a), (b) and (c), model predictions for larvae, nymphs and adults, respectively, where host contact rates are set as per the Exmoor, United Kingdom, site, with no adjustment to the proportions of ticks showing autumn questing (10%) or overwinter behavioural diapause (90%). Right side, simulations with questing proportions altered to: (d) larvae – 40%, (e) nymphs – 25%, (f) adults – 95%.

observed peak tick numbers in the spring and autumn could result from seasonal variations in host abundance affecting the rates of both population growth and the removal of questing stages from the vegetation. The poor performance of the model in capturing larval seasonality at Dorset and Exmoor in 1997 (Fig. 2) may reflect a lag, to some extent, between climatic causes in 1 year and effects on ticks the following year. Simulated tick populations were first established using average climate conditions in the model before actual climate data were recorded on-site from 1997, so simulations in 1997 are likely to be less accurate than subsequent years.

The sensitivity analysis indicates that the predicted seasonal patterns are robust to realistic deviations in almost all parameters, so that knowledge of only approximate values within biological plausibility does not hinder the model's utility. The predicted population density, however, may be highly sensitive to exact values of egg survival, necessitating further laboratory experiments and field observations on this key life cycle stage.

An important function in the model is the fraction of moulted unfed ticks that, upon recruitment in the early autumn, quest immediately rather than enter behavioural diapause over winter and re-emerge the following spring. In north-western Europe, the majority do the latter (Randolph *et al.* 2002), so the ratio of questing to diapausing ticks is set at 1:9 for all stages in the UK model. Population seasonality was relatively insensitive to 50% changes in this parameter, but larger changes generated markedly different patterns. Indeed, the pattern recorded for *I. ricinus* in central Spain (Estrada-Pena

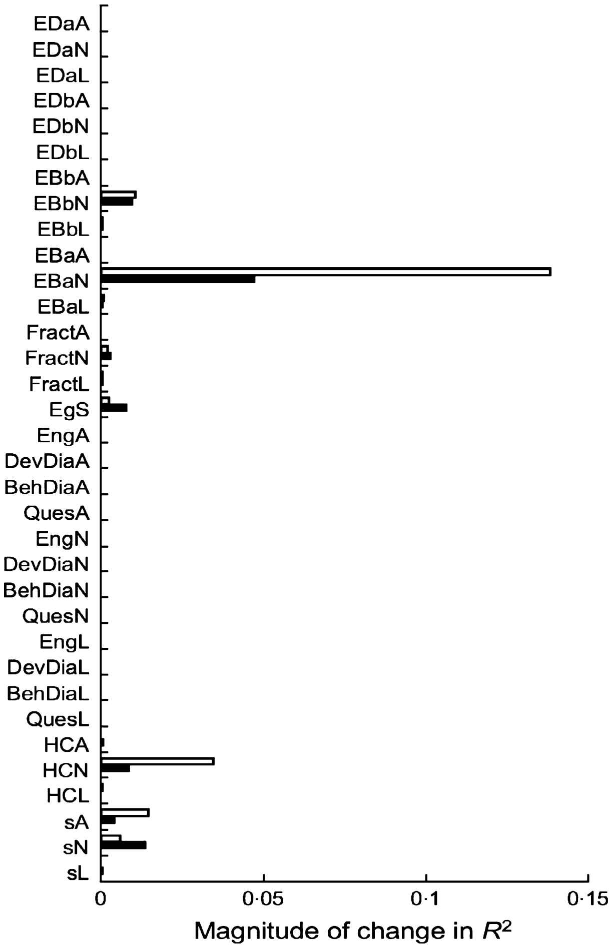

Fig. 7. Sensitivity analysis: reduction in regression R^2 value relative to final model after 50% increase (filled bars) or decrease (open bars) in parameter values. Parameter definitions: Controls on Gaussian function controlling exit from developmental diapause: EDbA, *Adult curve centre date*; EDaA, *Adult curve height*; EDbN, *Nymph curve centre date*; EDaN, *Nymph curve height*; EDbL, *Larva curve centre date*; EDaL, *Larva curve height*. Controls on Gaussian function controlling exit from behavioural diapause: EBbA, *Adult curve centre point*; EBaA, *Adult curve height*; EBbN, *Nymph curve centre point*; EBaN, *Nymph curve height*; EBbL, *Larva curve centre point*; EBaL, *Larva curve height*. Fraction questing in autumn: FractA, *Adults*; FractN, *Nymphs*; FractL, *Larvae*. Mortality values: EgS, Eggs; EngA, *Engorged adults*; DevDiaA, *Adults in developmental diapause*; BehDiaA, *Adults in behavioural diapause*; QuesA, *Questing adults*; EngN, *Engorged nymphs*; DevDiaN, *Nymphs in developmental diapause*; BehDiaN, *Nymphs in behavioural diapause*; QuesN, *Questing nymphs*; EngL, *Engorged larvae*; DevDiaL, *Larvae in developmental diapause*; BehDiaL, *Larvae in behavioural diapause*; QuesL, *Questing larvae*. Host contact rates: HCA, *Adults*; HCN, *Nymphs*; HCL, *Larvae*. Density-dependent mortality regression values: sA, *Adult slope*; sN, *Nymph slope*; sL, *Larva slope*.

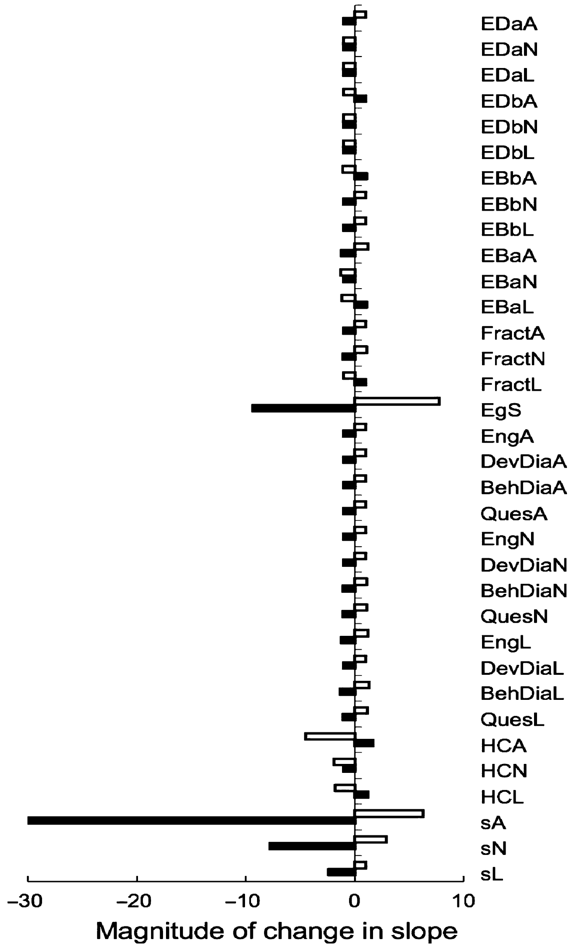

Fig. 8. Sensitivity analysis: change in regression slope relative to final model after 50% increase (filled bars) or decrease (open bars) in parameter values. Positive numbers are equal to the slope; negative numbers are equal to the negative reciprocal of the slope; thus, the axis reflects the factor by which slope is either multiplied or reduced. Parameter labels as in Fig. 7 legend.

et al. 2004) could only be captured by this model when 40% of larvae, 25% of nymphs and 95% of adults were set to quest in the autumn, with other parameter values unchanged. Crude analyses suggest that in northern Europe, this behavioural diapause may be triggered by responses to shortening day length (Randolph 2004), but the degree of variable genetic determination or phenotypic plasticity to allow ticks in geographically distinct environments to respond appropriately is entirely unknown. Ignorance of the degree of geographical phenotypic variation, as seen in *I. scapularis* (Keirans *et al.* 1996; Mount, Haile & Daniels 1997), limits the operation of any population model across the very extensive full range of *I. ricinus* without significant *post hoc* alterations to certain parameters. Observations on the behaviour of *I. ricinus* translocated to opposite extremes of its range would indicate whether geographical races act as discrete entities when considering population dynamics.

Evidently, a small number of climatic variables may satisfactorily explain spatial variation in seasonal patterns of tick numbers within the United Kingdom. Given the importance of these patterns to the transmission potential of some tick-borne pathogens (Randolph *et al.* 2000; Ogden *et al.* 2007; Gatewood *et al.* 2009), this model should be extended to include elements in the transmission cycle of one of the many pathogens vectored by *I. ricinus*. Such a model exists for Lyme borreliosis in North America in a simplified system involving a single host species (Ogden *et al.* 2007) and in a more complex host system (Mount, Haile & Daniels 1997).

To achieve the same predictability of overall abundance, however, host contact rates had to be varied within biologically reasonable limits, thereby indicating the importance of host abundance in determining tick abundance (Dobson & Randolph 2011). Unfortunately, this crucial biotic variable is highly variable in time and space and rarely quantified beyond crude relative indices. Indeed, a number of assumptions have been made that warn against using the model to make specific, quantitative predictions about absolute tick population size at equilibrium in different parts of the United Kingdom. We emphasise instead the model's utility for investigating the factors that influence tick density or for providing practical management recommendations where ticks pose an epidemiological and/or economic threat (Dobson & Randolph 2011).

Acknowledgements

We acknowledge the primary tick fieldwork carried out by Mick Peacey. This work was funded by the UK Department of the Environment and Rural Affairs (Defra) (project SE4105), the Research Councils' Rural Economy and Land Use (RELU) Programme (funded by the Economic and Social Research Council, Biotechnology and Biological Sciences Research Council and Natural Environment Research Council, with additional funding from Defra and the Scottish Executive Environment and Rural Affairs Department) (project RES-229-25-0007) and EU grant GOCE-2003-010284 EDEN. This paper is catalogued by the RELU Steering committee as RELU_ADR_002 and by the EDEN Steering Committee as EDEN0217 (http://www.eden-fp6project.net/). The contents are the sole responsibility of the authors and do not necessarily reflect the views of the European Commission.

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Received 4 January 2011; accepted 13 April 2011
Handling Editor: Eric Morgan