



Modelling the effect of temperature variation on the seasonal dynamics of *Ixodes ricinus* tick populations

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ABSTRACT

Seasonal variation in temperature is known to drive annual patterns of tick activity and can influence the dynamics of tick-borne diseases. An age-structured model of the dynamics of *Ixodes ricinus* populations was developed to explore how changes in average temperature and different levels of temperature variability affect seasonal patterns of tick activity and the transmission of tick-borne diseases. The model produced seasonal patterns of tick emergence that are consistent with those observed throughout Great Britain. Varying average temperature across a continuous spectrum produced a systematic pattern in the times of peak emergence of questing ticks which depends on cumulative temperature over the year. Examination of the effects of between-year stochastic temperature variation on this pattern indicated that peak emergence times are more strongly affected by temperature stochasticity at certain levels of average temperature. Finally the model was extended to give a simple representation of the dynamics of a tick-borne disease. A threshold level of annual cumulative temperature was identified at which disease persistence is sensitive to stochastic temperature variation. In conclusion, the effect of changing patterns of temperature variation on the dynamics of *I. ricinus* ticks and the diseases they transmit may depend on the cumulative temperature over the year and will therefore vary across different locations. The results also indicate that diapause mechanisms have an important influence on seasonal patterns of tick activity and require further study.

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1. Introduction

The epidemiology of vector-borne diseases is sensitive to patterns of temperature and temperature variation (Pascual et al., 2006; Ogden et al., 2007; Estrada-Peña, 2009; Lafferty, 2009; Paaijmans et al., 2009). Tick-borne disease dynamics are particularly influenced by changing environmental conditions, especially variation in temperature (Randolph and Rogers, 2000; Ogden et al., 2007, 2008), because ticks have a long lifecycle and develop through multiple stages at a rate that is temperature dependent (MacLeod, 1932). Therefore, spatial and temporal variation in the abundance of tick populations shows a strong association with temperature, as well as vegetation type, humidity and soil water content (Randolph, 1997; Walker, 2001; Cadenas et al., 2007; Schwarz et al., 2009). The dynamics of temperate tick populations such as *Ixodes ricinus* and *Ixodes scapularis* are highly seasonal, because temperatures are too low during the colder months of the year to allow interstadial development and questing activity

(Randolph, 2004; Ogden et al., 2005). For example, the annual abundance distribution of questing tick populations in Europe and North America is typically concentrated in a small number of strong peaks that occur during the warmer part of the year (Gray, 1982; Walker, 2001; Randolph et al., 2002; Estrada-Peña et al., 2004; Ogden et al., 2005; Cadenas et al., 2007; Schwarz et al., 2009). The timing of the peaks varies between the different lifecycle stages, and the abundance of questing *I. ricinus* nymphs and adults often peaks in spring and autumn but not in summer (the warmest part of the year), while larvae are more likely to show a single mid-year peak in questing activity (Gray, 1982; Randolph et al., 2002; Estrada-Peña et al., 2004; Jouda et al., 2004; Schwarz et al., 2009).

Tick-borne diseases such as tick-borne encephalitis, Lyme borreliosis, louping ill and tick pyaemia persist due to transmission of the pathogen between tick lifecycle stages, whereby larvae and nymphs contract the disease by feeding on infectious hosts and then transmit the disease to susceptible hosts during subsequent blood meals as nymphs or adults. The temporal dynamics of different tick lifecycle stages, and how they depend on the climatic conditions to which the population is exposed, are therefore critical determinants of the patterns of disease outbreak. In particular, disease transmission is more likely to persist in environments

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in which the dynamics of the different active lifecycle stages are highly synchronous, especially for diseases that cause a brief period of host infectivity (Randolph et al., 2000; Laurenson et al., 2003; Ogden et al., 2008). The availability of susceptible hosts that are capable of transmitting the pathogen is also important to disease persistence, and the epidemiology of tick-borne diseases is typically complex and dependent on multiple host species (LoGiudice et al., 2003; Brunner and Ostfeld, 2008; Keesing et al., 2009).

Models of the seasonal dynamics of tick populations have been developed for a number of tick species in tropical and temperate environments (Gardiner et al., 1983; Randolph, 1997; Ogden et al., 2005). To represent observed seasonal patterns accurately, the tick lifecycle must be modelled in considerable detail, dividing the population into stages of eggs, larvae, nymphs and adults, and allowing the rate at which ticks develop from one stage to the next to depend on temperature. Important determinants of the seasonal patterns generated include the rate of temperature-dependent development, the assumptions made about density-dependent and density-independent mortality occurring in each lifecycle stage, the rate at which questing ticks find hosts, and the extent to which tick development and activity are delayed as a result of diapause (Gardiner et al., 1983; Randolph, 1997; Ogden et al., 2005).

Several studies suggest that a process known as morphogenetic diapause (Belozero and Naumov, 2002), whereby the interstadial development of tick lifecycle stages that become engorged relatively late in the year is delayed until the following year when temperatures start to increase, plays a large role in determining the seasonal patterns of questing tick abundance (Gardiner et al., 1983; Walker, 2001; Randolph, 2004; Sonenshine, 2005; Gray, 2008). Similarly, behavioural diapause, whereby there is a delay between emergence and questing activity (Gray, 1982; Belozero and Naumov, 2002; Randolph et al., 2002) is also thought to have a significant influence on seasonal tick dynamics (Walker, 2001; Randolph, 2004; Gray, 2008). Both models and field observations show that there is generally a greater degree of temporal overlap in the questing and feeding times of larvae, nymphs and adults of temperate tick populations than in those of tropical populations (Randolph et al., 2002; Randolph, 2004). In temperate environments, temperatures are not usually warm enough to allow progression through more than one lifecycle stage in a given year, and diapause acts to synchronise the onset of interstadial development and the time of emergence across the different lifecycle stages (Randolph, 2004). However the process of diapause, including its timing of onset, how long it lasts, and how it varies between different lifecycle stages and in different environments, is not well understood (Randolph and Rogers, 1997; Estrada-Peña et al., 2004; Randolph, 2004; Gray, 2008).

Warmer temperatures allow shorter interstadial development times and this can give rise to higher tick population abundance (Jouda et al., 2004; Schwarz et al., 2009; Gilbert, 2010). On the other hand conditions may be less favourable when temperatures are warmer leading to higher tick mortality, particularly as ticks are highly sensitive to desiccation (Cadenas et al., 2007). Moreover, whether higher temperature is associated with an increase in the risk of tick-borne disease depends on how increases in temperature affect the seasonal patterns of tick abundance and the degree of overlap in the times at which the different lifecycle stages are active (Randolph and Rogers, 2000; Ogden et al., 2008).

In this study an age-structured model of tick population dynamics was developed to explore the seasonal dynamics of *I. ricinus* populations over a range of temperature conditions. As a case study, a pattern of annual temperature variation similar to that observed in north-eastern Scotland was modelled. The model was used to explore how seasonal patterns in the abundance of different tick active life stages vary with differences in mean tempera-

ture and temperature variability. Finally, a simple susceptible-infectious-recovered (SIR) model of the dynamics of a tick-borne disease in a single host population was applied to explore the implications of temperature-driven changes in *I. ricinus* activity patterns for disease persistence.

2. Materials and methods

The model represented the *I. ricinus* lifecycle using a similar approach to that developed for other tick species by Randolph and Rogers (1997) and Ogden et al. (2005) (see Supplementary Fig. S1). All stages of the lifecycle were considered, namely eggs, larvae, nymphs and adults, as well as the progression of an individual within each of these stages, for example questing, feeding and interstadial development. The rate of interstadial development was assumed to depend on temperature (Randolph, 2004). The following sections describe firstly the model of temperature-dependent development which demonstrates how the time taken for interstadial development can vary for tick stages that complete development and emerge at different times of year. Secondly the population dynamic model used to estimate how the abundance of the cohorts of each life stage varies with time is presented. Finally, the model was extended to give a simple representation of the transmission of a tick-borne disease. All model parameters are given in Table 1.

2.1. Modelling temperature-dependent development

The durations of the lifecycle stages during which the development rate is temperature-dependent, including eggs developing into larvae, engorged larvae developing into nymphs, engorged nymphs developing into adults and engorged adults producing eggs (see Supplementary Fig. S1) were estimated using the degree-week accumulation model (Tuljapurkar and Caswell, 1997). This approximates the development rate of each life stage by an increasing function of temperature, and the total development time is determined by the cumulative temperature to which ticks are exposed during the development period. For each developmental stage, the weekly development rate, $f(T)$, was represented as a function of the mean temperature in a given week, T , by multiplying by 7 the daily development rate functions given in Randolph et al. (2002) which were fitted to data on Scottish *I. ricinus* ticks (Campbell (1948). The life history and development of the sheep tick *I. ricinus* in Scotland, under natural and controlled conditions. Ph.D., University of Edinburgh, UK). These functions are of the form $f(T) = aT^2 + bT + c$ where a , b and c are constants (Table 1). The value of $f(T)$ is the proportion of the total development of the lifecycle stage that occurs in a given week. Following Randolph et al. (2002), it was assumed that the development rate is independent of the time of year that the tick life stage begins development and that development stops below a certain threshold temperature T_0 , so that $f(T \leq T_0) = 0$ (Table 1). For a tick life stage that completes development and emerges at week w_i , the time at which it began development, w_j , is given by solving

$$\sum_{w=w_j}^{w_i} f(T_w) = 1 \quad (1)$$

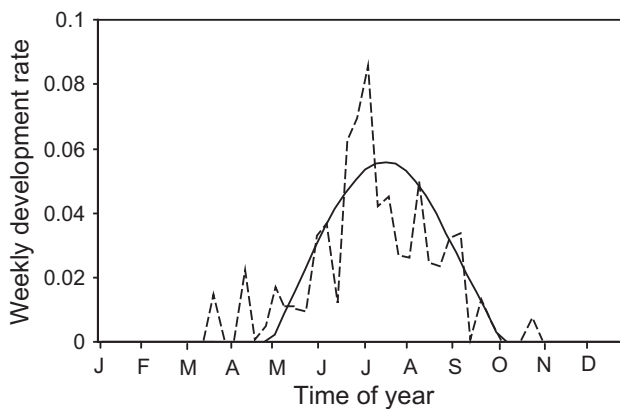
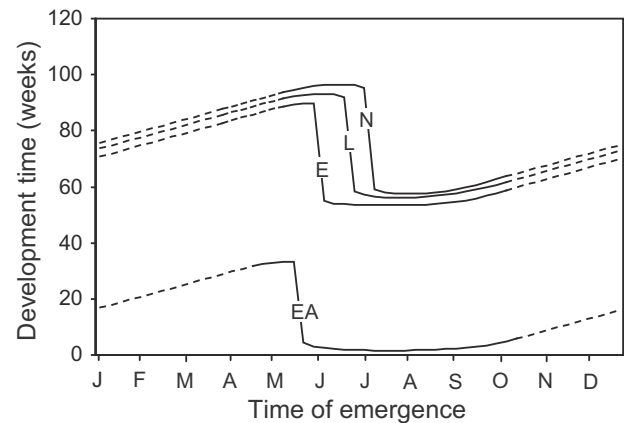
where T_w is the mean temperature for week w and the duration of interstadial development is $w_i - w_j$.

2.2. Temperature data for study locations

Patterns of annual variation in weekly temperature similar to those observed in Braemar, north-eastern Scotland (57° 0' N, 3° 24' W) were used to estimate tick development rates. This site

Table 1Parameters used in the model of the effect of temperature variation on the seasonal dynamics of *Ixodes Ricinus*.

Symbol	Definition	Value
a, b, c, T_0	Parameters determining the form of the temperature-dependent development rate function $f(T)$ (see text)	
	Eggs developing into larvae	−0.00001, 0.002, −0.019, 8.4
	Larvae developing into nymphs	0.00003, 0.00073, −0.007, 7.4
	Nymphs developing into adults	−0.000008, 0.0019, −0.016, 8.7
	Engorged adults producing eggs	0.0001, 0.01, −0.062, 8.7
t_E	Duration of the oviposition period	1 (week)
t_{HL}, t_{HN}, t_{HA}	Duration of the larval, nymphal and adult hardening periods	3 (week)
t_{FL}, t_{FN}, t_{FA}	Duration of larval, nymphal and adult feeding periods	1 (week)
t_{QL}, t_{QN}, t_{QA}	Maximum duration of larval, nymphal and adult questing periods	8, 12, 16 (week)
S_I	Weekly survival probability during interstadial development	
	Eggs developing into larvae	0.98
	Larvae developing into nymphs	0.98
	Nymphs developing into adults	0.99
	Engorged adults producing eggs	0.99
S_{HL}, S_{HN}, S_{HA}	Weekly survival probability during larval, nymphal and adult hardening	0.96
S_{QL}, S_{QN}, S_{QA}	Weekly survival probability of questing larvae, nymphs and adults	0.9, 0.8, 0.8
α, β	Parameters determining the form of density-dependent mortality of feeding tick life-stages (see text)	0.5, 0.049
$\lambda_0, \alpha_F, \beta_F$	Parameters determining the form of density-dependent fecundity of egg-laying adults (see text)	3000, 0.01, 0.04
p_L, p_N, p_A	Weekly host-finding probability for questing larvae, nymphs and adults	0.03, 0.3, 0.3
q	Proportion of ticks that feed after July that undergo diapause	0.8
T_q	Temperature below which questing ticks are not active	7 (°C)
H	Number of hosts	30
T_I	Duration of host infectivity	0.5 (week)

**Fig. 1.** Weekly development rate for engorged *Ixodes ricinus* larvae at different times of year at Braemar, north-eastern Scotland. The solid line shows the development rates calculated using 49 year mean weekly temperature and the dashed line shows the development rates calculated from weekly temperatures generated from normal random variation about the 49 year weekly mean with a standard deviation of 2 °C.**Fig. 2.** Development time for *Ixodes ricinus* life stages that complete development at different times of year, where weekly temperatures are equal to the long-term weekly mean for Braemar, north-east Scotland. Lines show the temperature-dependent development stages, E = eggs developing into larvae, L = engorged larvae developing into nymphs, N = engorged nymphs developing into adults, EA = engorged adults producing eggs. Dashed lines show times of year at which no development takes place.

was chosen owing to its proximity to areas that experience frequent outbreaks of louping ill, a viral disease transmitted by *I. ricinus*, which causes high mortality in hill-farmed sheep populations and in red grouse, *Lagopus lagopus scoticus*, an economically important game species (Laurenson et al., 2003). Weekly mean air temperature estimates for Braemar were obtained by cubic spline interpolation of the 49 year monthly mean air temperature data obtained from the UK Meteorological Office (<http://www.metoffice.gov.uk>).

For the purpose of validating the model, an average annual weekly mean temperature profile similar to that observed in Cwmystwyth, Wales (52° 4' N, 3° 50' W) was used, again by interpolating the long-term monthly mean data obtained from the UK Meteorological Office. This location is 30 km from the field site used by Randolph et al. (2002), and in the results section we compare seasonal patterns of tick activity generated for the Cwmystwyth temperatures with those observed by Randolph et al. (2002).

For the Braemar study site, Fig. 1 shows the weekly development rate of engorged larvae at different times of year. The development rate profile is bell-shaped, rising to a peak at the warmest time of year, and dropping to zero in the coldest times when temperatures are too low to allow development. Note that these development rate estimates may be higher than those obtained if soil temperature measurements had been used (Randolph, 2004). The effect of incrementing the mean temperature on tick population dynamics was examined by shifting the Braemar temperature profile, assuming that in each week of the year the mean temperature changed by an amount ΔT °C which was the same for all weeks. Normal random variation was also added to the weekly mean temperature, which generated considerable variation in the weekly development rates (Fig. 1), and the effect of such stochasticity on tick population dynamics was examined, as discussed in Section 2.3.3.

Fig. 2 shows the duration of interstadial development as a function of the time of year that the stage completes development and emerges given the weekly mean temperature profile for Braemar. For each life stage, ticks that emerge earlier in the year have taken a considerably longer time to develop than those that emerge later, when the development period is shorter by at least half a year (Fig. 2). This is because the ticks that emerge earlier in the year spent an extra winter in development, during which temperatures, and therefore tick development rates, are very low. At a certain point in the warmer part of the year there is a sharp drop in development times for a given tick life-stage (Fig. 2). At this point enough degree days have accumulated to allow all ticks with longer development periods to complete development and emerge, and ticks that emerge later in the year have completed shorter development periods. However this shorter development cycle may not be realised due to the onset of diapause causing a delay in the start of interstadial development, as discussed in Section 2.3.2.

2.3. Modelling tick population dynamics

To predict the number of ticks of a given life stage present at each week of the year, an age-structured matrix model that tracks the survival and development of each weekly cohort of ticks through the lifecycle stages was developed (see Supplementary Fig. S1). The model is similar to those developed for North American *I. scapularis* by Ogden et al. (2005) and for African *Rhipicephalus appendiculatus* by Randolph and Rogers (1997). As explained in Section 2.3.3, the model can track interannual stochastic variation in weekly temperature, allowing every cohort of ticks to experience different temperature conditions throughout their lifetime.

Parameter values for the model were obtained using data from the literature on the demographic rates and host-finding probabilities of *I. ricinus*, where available (Table 1; see Supplementary Table S1 for the data sources used). Throughout the periods of interstadial development, including eggs developing into larvae, engorged larvae developing into nymphs, engorged nymphs developing into adults and engorged adults producing eggs, the weekly survival probability was assumed to be constant. Therefore the total survival for each interstadial period depends on the development time, which is a function of the cumulative temperature as defined above. Each subsequent hardening phase was assumed to be of fixed duration, throughout which the survival probability was set to a constant value. Questing ticks were assigned a weekly probability of surviving and either finding a host or not finding a host. The amount of time individual ticks spend questing is therefore variable, but for each questing life-stage (larvae, nymphs, adults) there was assumed to be a maximum amount of time that questing could last before energy reserves became exhausted and the tick died. An effect of temperature on the weekly host finding probability was also incorporated, in accordance with observations of *I. ricinus* for which questing activity ceases in colder temperatures (Randolph, 2004; Gilbert, 2010). Following Ogden et al. (2005) and Randolph et al. (2002), if the temperature for a given week fell below a certain threshold, questing ticks had zero probability of finding a host.

2.3.1. Density-dependent mortality

Tick survival has been shown to be strongly related to tick density (Randolph, 1994a, b). Density-dependent tick mortality may occur when ticks are feeding on the host, owing to acquired host resistance (Randolph, 1994b) and grooming by the host (Ogden et al., 2005). This may also result in a density-dependent reduction in fecundity (Ogden et al., 2005). The model of Ogden et al. (2005) was used to estimate density-dependent mortality and fecundity of feeding ticks. For example, the weekly probability of mortality of feeding larvae in week w , μ_{LF}^w , is given by

$$\mu_{LF}^w = \alpha + \beta \ln((1.01 + z_{LF}^w)/H) \quad (2)$$

where H is the number of hosts, z_{LF}^w is the number of feeding larvae in week w and α and β are constants (Table 1). Mortalities of feeding nymphs and adults were calculated in a similar way. The fecundity of egg-laying adults, λ , was reduced by a factor that depended on density, and is given by

$$\lambda = \lambda_0 [1 - (\alpha_F + \beta_F \ln((1.01 + z_{ELA}^w)/H))] \quad (3)$$

where z_{ELA}^w is the number of egg-laying adults in week w and λ_0 , α_F and β_F are constants (Table 1).

2.3.2. Diapause

There is evidence that, in order to adapt to the seasonal variation of temperate climates, ticks regularly undergo periods of diapause, during which their rate of development is greatly reduced (Belozero and Naumov, 2002; Randolph et al., 2002; Randolph, 2004; Ogden et al., 2005; Sonenshine, 2005). Diapause is thought to be triggered by shortening day length experienced during the questing stage. Ticks that feed later than July have been observed to delay the onset of interstadial development until temperatures reach freezing point, ensuring that any significant development does not begin until the following year. This condition was incorporated into the model by specifying that a certain fraction, q , of questing larvae, nymphs and adults that obtain a blood meal in the months August–December delay the onset of interstadial development until the first day of the following year (Table 1).

2.3.3. Stochastic temperature variation

Based on the life-history processes detailed above, the model used to estimate the weekly abundance of ticks in each life stage is of the form

$$z^{w+1} = \mathbf{A}^w z^w \quad w = 1, \dots, W \quad (4)$$

where z^w is a vector containing the number of ticks in each age class in week w , and there are W weeks in the total time period of the simulation. The weekly transition matrix \mathbf{A}^w is $N - 1$ by N , where N is the total number of age classes. This matrix consists of elements $A_{n,n+k}^w$, which are the probabilities of ticks moving from age-class n to age-class $n + k$ in week w . For example, ticks in age-class n that survive and remain in the same life cycle stage move to class $n + 1$ in a weekly transition, whereas those that complete the current life cycle stage move to the first age class of the next stage. In contrast to previous age-structured models of tick population abundance (Randolph et al., 2002; Ogden et al., 2005), the transition matrix \mathbf{A}^w for a given week of the year differs for each year due to interannual stochastic temperature variation, applied as normal random variation about the long-term weekly mean temperature with standard deviation σ . The model keeps track of the development time lags over a series of years to generate seasonal patterns in tick abundance that reflect interannual temperature variation.

2.4. The effect of temperature variation on disease persistence

Ixodes ricinus transmits a number of medically and economically important diseases including tick-borne encephalitis, Lyme borreliosis and louping ill. A generic SIR model of the disease dynamics in the host population was incorporated, which is representative of the basic transmission process of a range of tick-borne diseases. The effect of varying patterns in the annual distribution of questing tick abundance, resulting from changes in mean temperature and temperature variability, on the persistence the disease was explored.

The host population was divided into categories of susceptible individuals that can become infected once bitten by an infectious

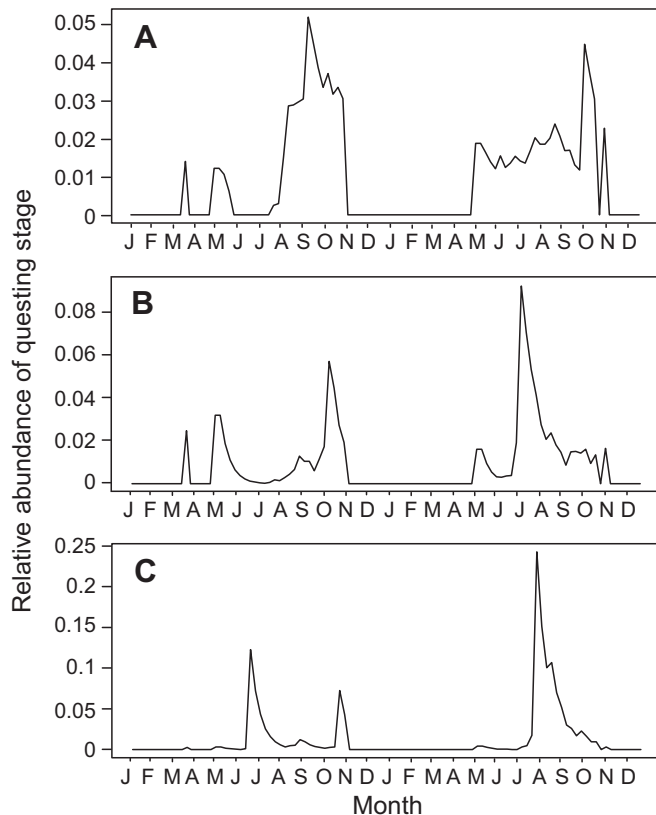


Fig. 3. Abundance of questing *Ixodes ricinus* life stages (A, larvae; B, nymphs; C, adults) at different times of year as a proportion of the total number of each stage questing in that year. Weekly mean temperatures are equal to the long-term weekly mean for Cwmystwyth, Wales. Weekly temperatures differ between years due to normal random variation about the weekly mean with standard deviation of 2 °C.

tick, infectious individuals that can transmit the disease to uninfected feeding ticks, and recovered individuals. For simplicity, the host population was assumed to be of constant size with annual generations. In the spring of each year (week 12), new, susceptible hosts replaced the current population at a constant rate of 50% per week over a 7 week period. This may represent a process of seasonal recruitment and mass mortality or culling of the previous generation of hosts. Hosts were assumed to be infectious for approximately half a week and recovered individuals had life-long immunity to the disease (Table 1). The disease transmission model could therefore be representative of the dynamics of louping ill in managed sheep populations in the United Kingdom (Sargison and Edwards, 2009).

It was assumed that all feeding tick stages (larvae, nymphs and adults) can contract the disease, and therefore that the infectious tick stages are feeding nymphs and adults. The proportion of feeding ticks that are infected in a given week was given by the proportion of infectious hosts multiplied by a half (because infectivity lasts for half a week). The proportion of hosts infected in that week was given by the number of infectious ticks per host. Interstadial transmission of the disease creates the potential for disease persistence without requiring reintroduction of the disease. A necessary requirement for persistence is that at least two different life stages feed at the same time, because hosts are infectious for less than a week.

The probability of disease persistence following the introduction of a single infectious host was calculated for each week of the year that the infection was introduced. This is a simple measure of the seasonally varying risk of disease persistence following

introduction, and is stochastic in this case owing to the normal random interannual variation in weekly temperatures. It can be interpreted as the probability that the basic epidemiological number for the disease, R_0 , is greater than 1 (Anderson and May, 1991). For each week of the year, this probability was calculated as the proportion of 100 simulations in which the disease persisted in the host population from the time of disease introduction in that week to the final year of the simulation, where the introduction was made in year 20 and the total length of the simulation was 50 years.

3. Results

Firstly, for the purpose of validating the model, the seasonal patterns in the abundance of questing ticks produced by the model for the Cwmystwyth annual temperature profile were compared with patterns observed by Randolph et al. (2002) for their nearby field study site. The effect of increments in mean temperature and different levels of interannual stochastic temperature variability on tick abundance dynamics were then examined for the Braemar study site. Finally, the implications of different seasonal tick activity patterns for the persistence of tick-borne diseases were explored.

3.1. Comparison with empirical observations

Patterns of abundance of questing larvae, nymphs and adults were generated using the long-term weekly mean temperature estimates for Cwmystwyth assuming that weekly temperatures vary between years due to normal random variation ($\sigma = 2$ °C). The results for two different years are shown in Fig. 3, where both years are greater than 20 years from the start of the simulation and are therefore independent of initial conditions. Seasonal patterns differed substantially between years, but there are two times of year at which abundance peaks typically occur: an early peak around spring (May–June) and a later peak around Autumn (August–October) (Fig. 3). This pattern agrees well with those observed in Wales (Randolph et al., 2002) and also in other parts of Great Britain (Gray, 1982; Walker, 2001) which show peaks in the abundance of questing lifecycle stages in either spring, autumn or both spring and autumn depending on the year of observation. While it is more common for questing larvae to show a dominant peak in abundance in the later half of the year, the observed peak abundance times for questing nymphs and adults in Great Britain are more variable (Randolph et al., 2002). For questing nymphs in particular the abundance is often highest in spring, although a dominant autumn peak does occur in some years (Gray, 1982; Walker, 2001; Randolph et al., 2002).

Both the model results in Fig. 3 and field observations show that the annual abundance distribution of questing nymphs and adults is more concentrated in the peak period than that of larvae (Randolph et al., 2002). This occurs because the engorged larvae and nymphs that begin interstadial development after July undergo diapause, delaying the onset of development until the following year, and therefore all emerging as respective nymphs and adults at a similar time.

3.2. The effect of varying mean temperature on seasonal tick activity patterns

Using the annual temperature profile for Braemar, the abundance of all tick age classes was calculated in each week of the year when the mean weekly temperatures were incremented by an amount ΔT °C, as described in the Section 2.2. Throughout this section no stochastic interannual variation in weekly mean tempera-

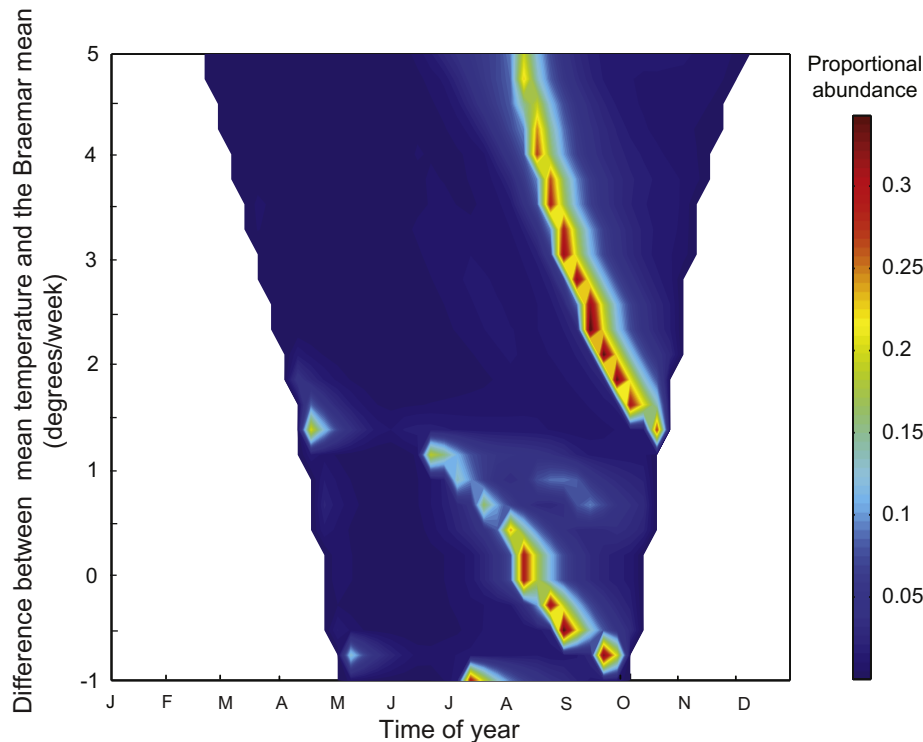


Fig. 4. The abundance of questing *Ixodes ricinus* nymphs at different times of year, as a proportion of the total number of nymphs questing in that year, for different deviations in the weekly mean temperature. The vertical axis shows the amount by which the temperature for each week of the year deviates from the 49 year weekly mean for Braemar, north-east Scotland.

ture was applied ($\sigma = 0$). Fig. 4 shows the seasonal pattern of the abundance of questing nymphs generated by allowing the model to converge to its equilibrium. At each temperature profile across a 6 °C range there is a dominant peak in abundance at a certain time of year. This agrees with empirical evidence that a single cohort of each life stage of *I. ricinus* is recruited each year (Randolph et al., 2002). As the mean temperature increases, the time of year at which this peak occurs varies in a systematic way, ranging from the earliest peak in April to the latest in November (Fig. 4). Similar patterns were produced for the abundances of questing larvae and adults (see Supplementary Figs. S2 and S3). This is because the predicted development times for ticks emerging from interstadial development at any given time of year are similar for emerging larvae, nymphs and adults (Fig. 2).

The variation in the timing of the abundance peak can be explained by the annual pattern of interstadial development times (for engorged larvae developing into nymphs) for the different temperature profiles (Fig. 5). For a given mean temperature profile, the position of the abundance peak corresponds to the time of year that development times switch from the longer cycle to the shorter cycle (Fig. 5). At this time, all developing nymphs that are on the longer cycle of development complete their development and emerge. As the mean temperature increases, development times become shorter and ticks on the longer development cycle emerge earlier in the year. This general pattern is consistent with observations of questing nymphs (and adults) in western Great Britain, which show that newly emerged questing ticks appeared sometime around autumn (August–October), and that they appeared earlier in the year at a warmer, southern site compared with a cooler site further north (Randolph et al., 2002).

When mean temperature rises above a certain threshold, there are enough degree days in a given year to shorten the maximum development time by one over-winter period (Fig. 5). The time of the peak in abundance of questing nymphs switches from early

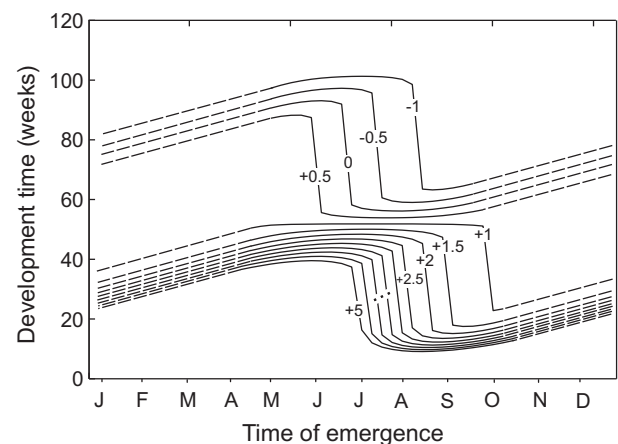


Fig. 5. Time for engorged *Ixodes ricinus* larvae to complete development and emerge as nymphs at different times of year, for different deviations in the weekly mean temperature. Line labels indicate the amount by which the temperature for each week of the year differs from the 49 year weekly mean for Braemar, north-east Scotland. Dashed lines show times of year at which no development takes place.

in the year (April–May) to late in the year (September–October) as this threshold is exceeded (Fig. 4). For all temperature profiles, there is a subsidiary peak in abundance early in the warm part of the year, occurring around May for cooler temperatures and in March for warmer temperatures. This corresponds to the time of year at which temperatures become warm enough for unfed, questing ticks to become active. Field observations indicate that the abundance at this time is often higher than the abundance peak that occurs at the time that the ticks emerge, especially for questing nymphs and adults. This may be because ticks that emerge in the later part of the year undergo behavioural diapause, delaying

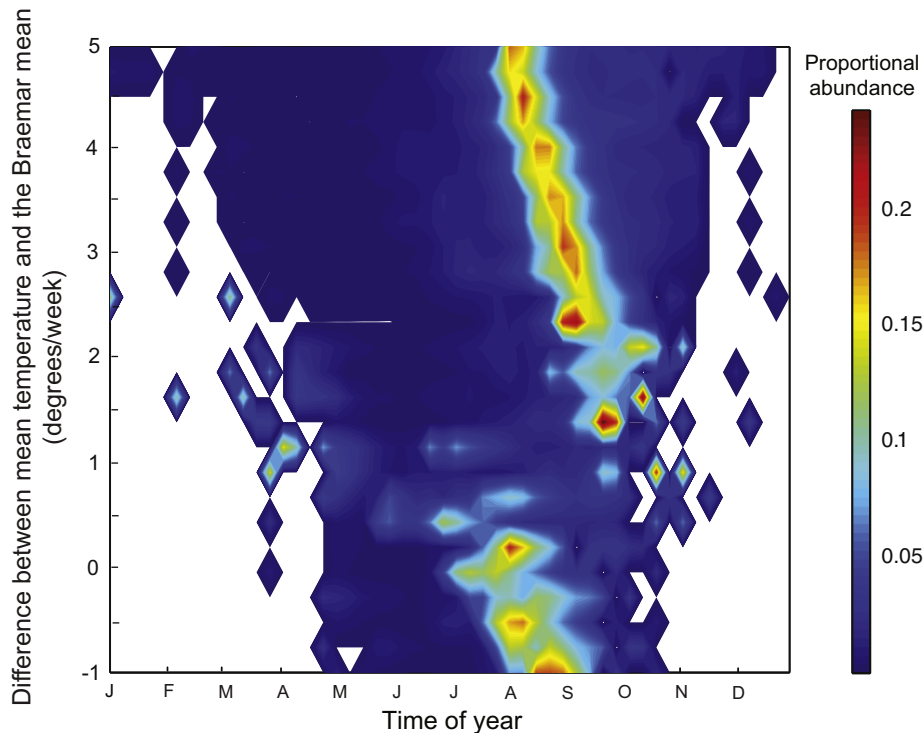


Fig. 6. The abundance of questing *Ixodes ricinus* nymphs at different times of year, as a proportion of the total number of nymphs questing in that year, for different deviations in the weekly mean temperature. The vertical axis shows the amount by which the mean temperature for each week of the year deviates from the 49 year weekly mean for Braemar, north-east Scotland. Actual weekly temperatures vary about the weekly mean due to normal random variation with a standard deviation of $\sigma = 2^\circ\text{C}$.

their questing activity until the following year (Belozarov and Naumov, 2002; Randolph, 2004).

3.3. The effect of stochastic temperature variation on seasonal tick activity patterns

The tick lifecycle can last up to 6 years (Gardiner et al., 1983), during which time development rates are likely to be considerably influenced by variation in environmental conditions, particularly variation in temperature. The effect of interannual stochastic variation in weekly temperature on the seasonal patterns of questing tick abundance was explored by adding to the weekly mean temperature a realisation of a normal random variable with mean of zero and a standard deviation of σ . Fig. 6 shows the effect of stochastic variation of $\sigma = 2^\circ\text{C}$ on the seasonal patterns in the abundance of questing nymphs.

At warmer temperatures, seasonal abundance patterns are similar to those observed in the absence of stochasticity (Fig. 6); dominant peaks in abundance occur at similar times to those in Fig. 4. At cooler temperatures the abundance distribution is more dispersed in the presence of stochastic temperature variation and there can be multiple peaks. Similar patterns for all temperature profiles were observed for questing larvae and adults (see Supplementary Figs. S4 and S5).

There are three reasons why the abundance distribution is less affected by stochasticity at warmer temperatures than at cooler temperatures. Firstly, development times are shorter at warmer temperatures and so a given level of stochastic temperature variation experienced during development has less effect on the emergence time. Secondly, development rates approach asymptotes at higher temperatures. Finally, when temperatures are warmer emergence times are more likely to be in the later half of the year (Fig. 6), and therefore the onset of interstadial larvae-nymph and nymph-adult development is synchronised by diapause (Randolph, 2004).

A comparison of Figs. 4 and 6 shows that when the cumulative temperature is close to the threshold above which the maximum development time decreases by one winter period (Fig. 5), the inclusion of interannual stochastic temperature variation causes high variability in the times of abundance peaks, and an increased likelihood of peaks in the first half of the year. This is because temperature stochasticity can lead to large changes in interstadial development times as the threshold is approached. Stochastic variation in temperature is therefore a potential explanation for field observations of questing *I. ricinus* throughout Europe, which show a dominant spring peak in some years but not in others (Randolph et al., 2002; Jouda et al., 2004; Gray, 2008).

3.4. The effect of temperature variation on disease persistence

The probability of disease persistence as a function of the week of introduction of a single infectious host was calculated as described in the Section 2.4. Fig. 7 shows the results corresponding to the annual temperature for Braemar and a temperature profile for which the weekly mean temperature is 2°C warmer than that for Braemar. For Braemar, the probability of persistence is high at the times of year when questing nymphs are abundant (Fig. 7A). This indicates that there is a strong degree of overlap in the times when the tick life stages feed throughout the warmer period of the year. This result was relatively unaffected by the degree of stochastic interannual variation in weekly temperatures (Fig. 7A). For the Braemar temperature profile, the emergence times of questing ticks are likely to be synchronous even in the presence of a high degree of stochasticity because there is a peak in emergence of questing nymphs, and similarly of questing larvae and adults, in the July–August period (Figs. 4 and 6). Therefore the feeding tick life stages enter diapause and undergo most of their development at similar times of year.

For the annual weekly temperature profile that is on average 2°C warmer than Braemar, the amount of stochasticity in weekly

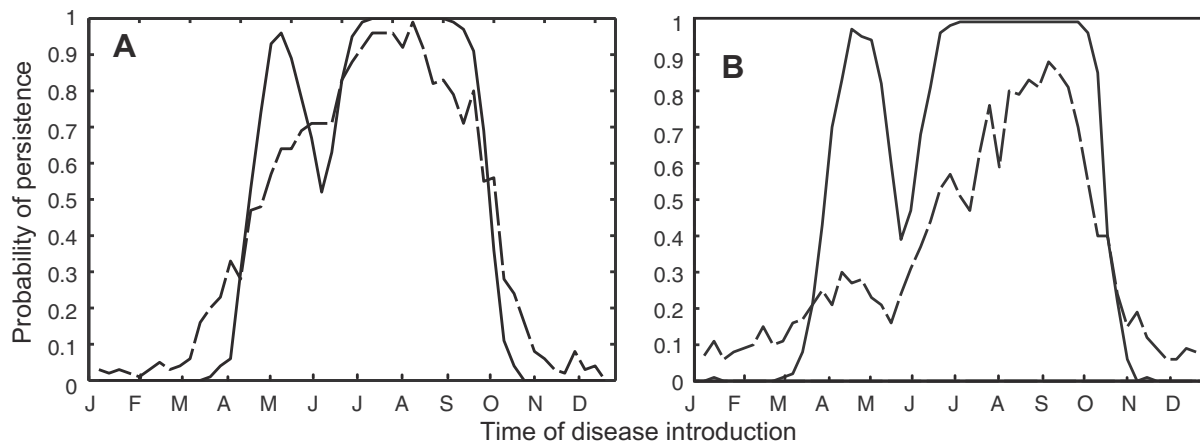


Fig. 7. The probability of disease persistence following introduction of a single infectious host as a function of the time of year that the introduction occurs. (A) Weekly mean temperature is given by the 49 year weekly mean for Braemar, north-east Scotland. B) Weekly mean temperature is 2 °C higher than the weekly mean for Braemar. Weekly temperature differs between years due to normal random variation. Solid lines and dot-dashed lines show cases where the interannual standard deviation in weekly temperature (σ) is 1 and 3 °C, respectively.

mean temperature considerably affects the probability of persistence, particularly when the infection is introduced in the earlier part of the year (Fig. 7B). Persistence probabilities are lower in the presence of greater stochastic variation in temperature because in this mean temperature range, temperature stochasticity causes the annual distribution of questing tick abundance to become more dispersed (Fig. 6). This occurs because the peak emergence time of questing ticks is relatively late in the year (September–October), thus a relatively cold year can shift emergence times to the early months of the year due to the delay caused by the winter period. Given that temperature-dependent development rates differ for each interstadial developmental stage (Fig. 2), it is possible that some developing life stages experience the delay while others do not. As a result, increasing stochastic variation in temperature leads to a lower probability of coincidence of the times that ticks of different life stages feed in high numbers, particularly since ticks that feed in the first half of the year do not undergo diapause.

These results indicate that the effect of increasing mean temperature on the probability of disease persistence depends on the temperature conditions at the site in question (specifically, the cumulative annual temperature) as well as the extent of the temperature rise. An increase in mean temperature of 2 °C, an amount that lies within the range of the projected effects of global warming on mean temperatures by 2080 in Great Britain (<http://ukclimate-projections.defra.gov.uk/content/view/826/500/>), can reduce the probability of persistence following disease introduction, depending on the level of between-year temperature variability and the effects of diapause on the seasonal dynamics of the tick population (Fig. 7).

4. Discussion

By application of an age-structured model of the seasonal dynamics of *I. ricinus* populations, we have shown a clear pattern in the times of year that ticks emerge from interstadial development to begin questing as mean temperature changes incrementally. This relationship depends on whether enough degree weeks accumulate in a given year to allow interstadial development to be completed in a single year. If temperatures are too cool for this to occur, the times of peaks in abundance vary more strongly with changes in mean temperature and emergence peaks can happen as early as the start of spring (around March). When temperatures are sufficiently warm to allow the threshold to be exceeded then peaks

in emergence usually occur in the later half of the year (July–September) and increasing mean temperature has less of an effect on the time of peak abundance. The timing of the peaks is well predicted by the annual profile of temperature-dependent development times and corresponds to the position of the mass-emergence event.

This broad pattern is robust to the inclusion of interannual stochastic variation in weekly temperature, although the annual distribution of emergence times becomes more dispersed, particularly for cooler temperature profiles. Further, this temperature stochasticity causes considerable variability in the peak emergence times when the annual cumulative temperature approaches the threshold described above.

Observations of wild tick populations in Great Britain show that moulting and emergence of nymphs and adults occurs in the later part of the year (July–October) (Randolph, 2004; Gray, 2008). This is the pattern predicted by the model for the majority of the temperature profiles used in the analysis (Fig. 4). However the field observations show that this peak emergence time does not always correspond to the time of year at which questing ticks are most abundant, particularly for the nymph and adult stages. Observations show that questing nymphs and adults are sometimes most abundant in spring, when the temperatures become warm enough to allow questing ticks to become active (Gray, 1982; Walker, 2001; Randolph et al., 2002). This has been attributed to a process of behavioural diapause, or a delay in the questing activity of newly emerged ticks until the year following emergence (Randolph, 2004).

The model did not incorporate a behavioural diapause mechanism because it would obscure the relationship between temperature and emergence times that has been shown. Further, there is a lack of empirical data demonstrating behavioural diapause in *I. ricinus*, when it occurs and which age-classes are affected (Randolph, 2004; Nuttall and Labuda, 2005). However, the results indicate that if ticks emerging in the later part of the year delay their questing activity until the following year, as empirical observations indicate (Sonenshine, 2005), a dominant peak of activity in spring would occur for a wide range of annual temperature profiles. Thus, in accordance with other studies (Belozero and Naumov, 2002), these results emphasise the need for further empirical study of diapause processes in tick populations.

Moreover, the results suggest that other factors that may also contribute to an early-year peak in questing tick abundance. For some temperature profiles the model predicts a peak in emergence

of questing ticks in the first half of the year (spring or early summer). As temperatures vary from year to year, it is possible that a location which has an autumn peak under average temperature conditions experiences a spring peak if recent temperatures are cooler than average. This is supported by the analysis of the effect of stochastic temperature variation on peak activity times, which also shows that early and late year peaks can occur in the same year because not all questing ticks can find hosts before temperatures drop below the questing activity threshold over the winter.

The association between changes in temperature and the dynamics of tick-borne diseases is potentially complex, because disease persistence depends on the times at which the different tick lifecycle stages feed and the availability of host species that can facilitate interstadial transmission (Randolph et al., 2000; Gray, 2008; Ogden et al., 2008). Disease transmission is inefficient when there is a long delay between the time that a tick contracts the infection and the time that the infection is transmitted to other tick generations, which is one explanation for the lower prevalence of Lyme disease in southern areas of the United States compared with higher latitude, cooler locations (Ogden et al., 2008). The model results show that for some average annual temperature patterns, disease persistence is more robust to temperature variation, whereas for other patterns disease transmission is more easily disrupted by temperature variability. For the later 'sensitive' annual temperature profiles, the cumulative annual temperature is close to the threshold required for interstadial development to occur in a single year. Therefore, if temperatures are colder than average, some tick life stages may not complete development until spring of the following year. If this occurs, then the peak in questing activity is shifted to a period of the year when diapause does not take place and the dynamics of the different active stages become less synchronous.

In our exploration of the effect of changes in mean temperature on tick population dynamics, it was assumed for simplicity that mean temperature changes by the same amount in each week of the year. In reality changes in average temperature across Great Britain that occur spatially, or due to the effects of global warming on a particular location, are likely to vary seasonally (<http://ukclimateprojections.defra.gov.uk/content/view/826/500/>). For example, most scenarios of the effects of global warming on temperatures in the British Isles predict that average summer temperatures will increase by more than average winter temperatures. However, our conclusions depend primarily on changes in the cumulative temperature over the year, and will be qualitatively similar when the difference in average weekly temperature is seasonally dependent.

The model also simplifies tick population dynamics and the process of tick-borne disease transmission by considering a single host population of constant abundance on which all tick lifecycle stages can feed. However tick burdens experienced by hosts are related to the density of different host species (Brunner and Ostfeld, 2008). Most tick-borne diseases can be transmitted by multiple host species, most of which are hosts for some but not all of three feeding life stages (larvae, nymphs and adults), and which differ in their capacity to transmit pathogens (LoGiudice et al., 2003; Keesing et al., 2009). This has been shown to have an important effect on disease dynamics and prevalence (Randolph et al., 2000; Gilbert et al., 2001; Laurenson et al., 2003; LoGiudice et al., 2003; Norman et al., 2004; Ogden et al., 2008). For example, the local absence of deer at the times of year when ticks quest in high numbers can lead to increased feeding on rodents, which increases the prevalence of tick-borne encephalitis because rodents are susceptible to the disease whereas deer are not, and therefore the deer function as 'dilution hosts' (LoGiudice et al., 2003; Perkins et al., 2006). This also emphasises the importance of the spatial dynamics of the host population to tick-borne disease

dynamics (Watts et al., 2009), an aspect which has hitherto received little attention.

In conclusion, this model highlights trends in the seasonal patterns of tick activity as mean temperatures vary across a continuous spectrum and demonstrates the effect of different degrees of interannual stochastic temperature variation. There is considerable uncertainty associated with many of the parameters of the age-structured tick population dynamic model (Randolph, 2004), and we do not aim to predict the dynamics of ticks and tick-borne diseases accurately for a particular place and time. Nonetheless, the model produces times of peak emergence of questing ticks that are consistent with observations of natural populations of *I. ricinus* throughout Great Britain. The results are therefore useful in understanding the role of different patterns of temperature variation in the dynamics of tick-borne disease systems. The results also emphasise that, in order to understand the effects of changing climate on the dynamics and prevalence of tick-borne diseases, detailed location-specific knowledge of tick population demography and its dependence on climatic conditions is necessary.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.ijpara.2010.12.012](https://doi.org/10.1016/j.ijpara.2010.12.012).

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