

An empirical quantitative framework for the seasonal population dynamics of the tick *Ixodes ricinus*

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Abstract

The wide geographic and climatic range of the tick *Ixodes ricinus*, and the consequent marked variation in its seasonal population dynamics, have a direct impact on the transmission dynamics of the many pathogens vectored by this tick species. We use long-term observations on the seasonal abundance and fat contents (a marker of physiological ageing) of ticks, and contemporaneous microclimate at three field sites in the UK, to establish a simple quantitative framework for the phenology (i.e. seasonal cycle of development) of *I. ricinus* as a foundation for a generic population model. An hour-degree tick inter-stadial development model, driven by soil temperature and including diapause, predicts the recruitment (i.e. emergence from the previous stage) of a single cohort of each stage of ticks each year in the autumn. The timing of predicted emergence coincides exactly with the new appearance of high-fat nymphs and adults in the autumn. Thereafter, fat contents declined steadily until unfed ticks with very low energy reserves disappeared from the questing population within about 1 year from their recruitment. Very few newly emerged ticks were counted on the vegetation in the autumn, but they appeared in increasing numbers through the following spring. Larger ticks became active and subsequently left the questing population before smaller ones. Questing tick population dynamics are determined by seasonal patterns of tick behaviour, host-contact rates and mortality rates, superimposed on a basal phenology that is much less complex than has hitherto been portrayed. © 2002 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

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1. Introduction

Ixodes ricinus lives in a wide range of temperate environmental conditions throughout Europe, approximately from 10°W (Ireland) to 45°E (Ural mountains, Russia) and from 60°N (Sweden) to 30°N (Egypt). The abiotic prerequisite for tick population survival is high humidity (>c. 85 RH%) in microhabitats at ground level (Daniel et al., 1998), but temperature conditions vary considerably across this geographic range. As tick development rates and host-questing activity are temperature-dependent, there is geographic variation in the seasonal population dynamics of each life stage (larvae, nymphs and adults) of *I. ricinus*, which in turn has a major impact on the transmission dynamics of the many pathogens of medical or veterinary significance vectored by this tick species (Randolph, 1998; Korenberg, 2000; Randolph et al., 2000; Ogden et al., 2002). These

include piroplasms (*Babesia* spp.), spirochaetes (*Borrelia* spp.), rickettsia (*Ehrlichia* – now called *Anaplasma* – spp.) and viruses (tick-borne encephalitis and louping ill viruses), many of which have changed in distribution or abundance over the past decade (Suss and Kahl, 1997, 1999; Randolph, 2001). A climate-driven population model for *I. ricinus*, similar to the one for the African tick *Rhipicephalus appendiculatus* (Randolph and Rogers, 1997), would allow process-based predictive risk mapping for any of these infections, responsive to changes in climate both spatially and temporally. Before that can be achieved, the existing qualitative descriptions of tick seasonal population dynamics must be replaced by a quantitative framework. We must relate rates of the tick demographic processes of recruitment (development and activation) and loss (host attachment, temporary quiescence and death) to the correct abiotic and biotic driving forces. In addition, the natural cues for the onset and termination of diapause (Belozeroz, 1982) must be identified precisely.

Qualitative models of the life cycle of *I. ricinus* to account for the common, but not universal, bi-modal seasonal pattern of tick abundance (reviewed in Steele and

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Randolph, 1985) have become increasingly complex since the 1950s. Based on tick development periods and activity observed under quasi-natural field conditions (Lees and Milne, 1951; Cerny, 1958; Chmela, 1969; Cerny et al., 1974; Daniel et al., 1976; Gray, 1982, 1985), the common scenario is one of two cohorts, a spring and an autumn population, with a certain amount of exchange between the two (Lees and Milne, 1951; Donnelly, 1976; Gray, 1982, 1985, 1991; Walker, 2001). Furthermore, temperature-dependent development rates are envisaged to vary with cohort (Gardiner and Gettinby, 1981). We examined the validity of this complexity by modelling the natural phenology (i.e. seasonal cycle of development) of *I. ricinus* and then testing the predictions against the pattern of seasonal changes in the fat contents of questing ticks. Predictions of the timing of emergence of unfed ticks from the previously engorged stage, and thereby their potential recruitment into the questing population, depend upon knowing the duration of inter-stadial periods under natural field conditions. We combined known temperature-dependent tick development rates with temperatures recorded in the field to estimate these periods.

Fat is a non-renewable source of energy derived from each blood meal, that can be used as a marker of physiological ageing in the field. After emergence, fat is used to fuel the tick's locomotory and physiological activity involved in movement up vegetation stems to quest, and down again to moist conditions at the base of the vegetation to restore their fluid content by passive and active uptake of atmospheric water (Knulle and Rudolph, 1982; Needham and Teel, 1991; Sonenshine, 1991). Its natural rate of usage therefore varies with seasonal activity and climatic conditions (Steele and Randolph, 1985; Randolph and Storey, 1999), allowing a distinction between the calendar age and physiological age of ticks. Previous studies, almost all in northwest Russia, have used histological or anatomical examination to group field-collected *Ixodes* ticks into age grades (reviewed in Uspensky, 1995; Walker, 2001). This approach is appropriate to dissect the relatively uniform, unimodal patterns of seasonal dynamics of *Ixodes persulcatus* and *I. ricinus* there, but is not sufficiently precise for the more variable, complex patterns characteristic of *I. ricinus* in warmer temperate zones (Korenberg, 2000). Here we use an exceptionally detailed long-term set of observations on the seasonal abundance and absolute fat contents of ticks, and contemporaneous microclimate at three contrasting field sites in the UK, to establish a simplified, generic framework for the geographically variable phenology of *I. ricinus*.

2. Methods

2.1. Field studies

The three study sites formed a transect across a climatically variable part of the range of *I. ricinus*: (1) on the

Wimborne St. Giles estate, near Wimborne, Dorset (50°54'N, 1°56'W, 60 m above sea level), an area of deciduous and coniferous woodland with an under-storey of bracken; (2) west of Porlock in the Exmoor National Park, Somerset (51°12'N, 3°39'W, 350 m above sea level), an area of rather sparse deciduous woodland dominated by oak (*Quercus* sp.) with an under-storey dominated by *Vaccinia* sp.; and (3) on Mynydd Mallaen west of Llanwrtyd Wells, Powys, Wales (52°4'N, 3°50'W, 420 m above sea level), an area of upland sheep grazing (mainly *Agrostis*, *Festuca* and *Molinia* spp. with *Vaccinia* sp.). The densities of host-seeking ticks of all stages were counted every 2–4 weeks over 1995–2000 (Dorset), 1997–2001 (Exmoor) or 1997–2000 (Wales), by dragging a 1 m² white woollen blanket over the ground for 5 m and counting all the attached ticks, repeated 20 times to give a total sample area of 100 m².

On each sample occasion in Exmoor and Wales, rodents were live-trapped over one night, using a transect of 50 pairs of Longworth traps set 15 m apart. They were examined in the field (without anaesthesia) for ticks, for comparison with the abundance of questing larval ticks, and then released.

From April 1996 to May 2001 in Dorset, April 1997 to September 2001 on Exmoor and April 1997 to September 2000 in Wales, automatic weather stations (based on Squirrel data loggers supplied by Grant Instruments, Cambridge) recorded the following microclimatic factors at hourly intervals: temperature at three levels, on the soil and at 30 and 50 cm above ground level; relative humidity (RH) at 30 cm above ground level; rainfall, or in Dorset and Exmoor the amount of precipitation reaching the ground beneath the canopy; and irradiation from the sun.

2.2. Lipid analysis

From March 1997 to June 2000, the fat contents of 4,382 nymphs and 1,490 adults were measured. When very few ticks were available from the standardised sampling, additional ticks were collected for fat analysis so that, with very few exceptions, at least 10 adults (usually more) and 30 nymphs were analysed on each sample occasion during the tick's questing season; when ticks were abundant, subsamples of c. 50 nymphs were analysed. The ticks were killed instantly on collection from the field by exposure to ethyl acetate vapour within glass tubes. In the laboratory, they were held in desiccators until being processed individually as follows: dehydrated in a vacuum oven at 70 °C for 24 h, weighed on a micro-balance to the nearest 0.1 µg, washed in three 24 h changes of chloroform to remove the lipid, re-dried in the oven at 70 °C for 24 h, and finally re-weighed to give the lipid-free weight (commonly called reduced dry weight, RDW) from which the lipid content was calculated.

2.3. Estimation of tick inter-stadial periods

Temperature-dependent rates of *I. ricinus* development under constant conditions were derived from Campbell's unsurpassed laboratory observations (Fig. 1) (Campbell,

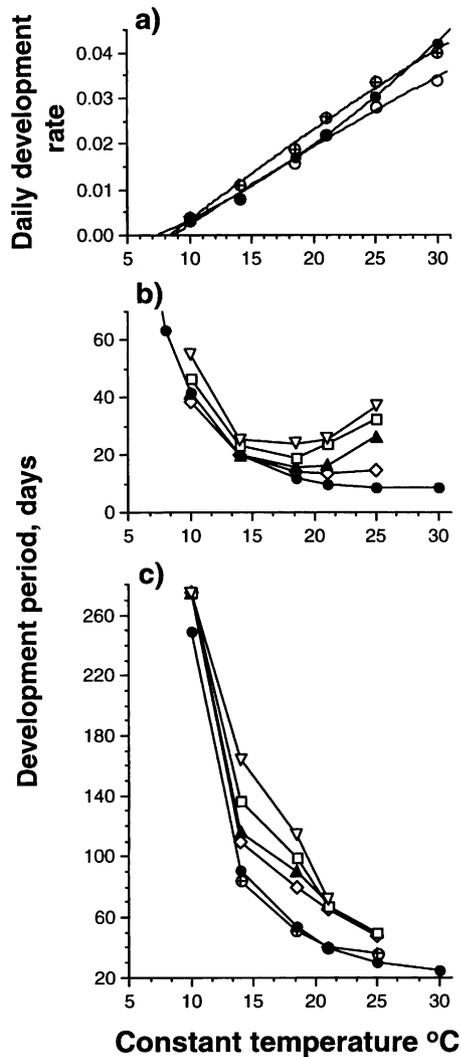


Fig. 1. (a) Mean temperature-dependent daily development rates for ticks (*Ixodes ricinus*) that fed in the spring; (\oplus) from egg to emerged larva: $Y = -0.0000112X^2 + 0.002305X - 0.0185$, $r = 0.997$; (\bullet) from engorged larva to emerged nymph: $Y = 0.0000303X^2 + 0.000733X - 0.00706$, $r = 0.999$; (\circ) from engorged nymph to emerged adult: $Y = -0.00000796X^2 + 0.00193X - 0.0161$, $r = 0.996$. (b) Mean temperature-dependent pre-oviposition periods and (c) egg development periods for females that fed in the spring (\bullet), July (∇), August (\square), September (\blacktriangle), October (\diamond), or were exposed after feeding to 0°C (\oplus). All data from Campbell (1948).

J.A., 1948. The life history and development of the sheep tick *Ixodes ricinus* Linnaeus in Scotland, under natural and controlled conditions. PhD thesis, University of Edinburgh, Edinburgh). For these observations of several hundred ticks of each stage at each temperature, the standard deviation was almost always 5–10% of the mean. Inter-stadial development periods in the field were modelled using recorded soil temperatures and a refinement of the day-degree summation method that was applied to the African tick *R. appendiculatus* (Randolph, 1997). As tick development periods decrease non-linearly with increasing temperature (Fig. 1), daily mean temperatures will tend to under-esti-

mate development periods. Therefore, the natural diurnal temperature cycle to which ticks are exposed was taken into account by using an hour-degree summation. To reduce the hourly temperature records to a manageable data set, mean diurnal hourly records were computed over 10 day periods, i.e. to give three decadal mean diurnal cycles per month. Campbell's (1948) constant temperature mean development rates were applied to each hour of these decadal means to predict the fraction of total development achieved per 10 days (adjusting for months with 31 or 28 days) (Fig. 2). Thus, for example, we predicted that 12–13% of larval-nymphal development would occur in Dorset over each 10 day period in July 1999, but only 4–6% in October. The total duration of the development period was found by summing the 10 day periods until development was complete. As a first approximation, ticks are assumed to take an average of c. 20 days to find a host (Randolph and Steele, 1985) (and are assumed to be counted on the vegetation on average half-way through this period), and to require a period of c. 20 days to harden off before they quest as the next stage. These periods, plus the c. 10 day feeding period of females, were added to the development period to give the total minimum duration of the mean inter-stadial period. Given the variance of Campbell's (1948) original observed development rates, for 95% of ticks these modelled inter-stadial periods are accurate to within ± 18 –43 days (i.e. ± 2 SD, where SD is 10% of the mean) over the periods of 3–7 months of non-zero development rates during spring to autumn each year (Fig. 2). This degree of accuracy is quite sufficient for the conclusions of this paper.

Both in the laboratory under constant conditions (Campbell, 1948; Kemp, D.H., 1968. Physiological studies on hard ticks Ixodidae. PhD thesis, University of Edinburgh, Edinburgh) and under quasi-natural field conditions (Chmela, 1969; Cerny et al., 1974; Daniel et al., 1976, 1977; Gray, 1982), the inter-stadial periods of *I. ricinus* may be prolonged

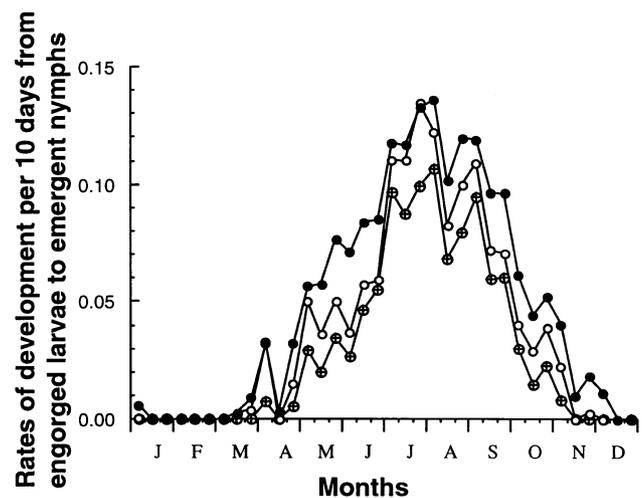


Fig. 2. Seasonal variation through 1999 in *Ixodes ricinus* larva-to-nymph development rates per 10 days at the three study sites in the UK, Dorset (\bullet), Exmoor (\circ) and Wales (\oplus).

by a variable delay in the onset of development (commonly called ‘morphogenetic diapause’; Belozarov, 1982). The delay is longest in those ticks which feed in the field in late July/early August and diminishes progressively from July-fed to October-fed ticks (Fig. 1b,c). Any ticks exposed to a brief period of 0 °C show non-delayed development, similar to those fed in the spring (i.e. pre-July) (Fig. 1c). This diapause was incorporated as follows: for the larval-nymphal, nymphal-adult and egg-larval periods, the observed delay is such that for any tick feeding after mid-July, development would not start until late October at the earliest, by which time field temperatures are so low that virtually no development occurs until the following spring (Fig. 2). Pre-oviposition periods are much briefer so that even July-fed females may start their delayed egg laying within 3–4 weeks of engorgement. These eggs, however, then suffer a delay, effectively taking them over winter before embryonic development begins. Over-winter development periods may thus be modelled without any precise knowledge of the cues for the onset and duration of diapause.

3. Results

3.1. Seasonal variation in numbers of questing and feeding ticks

Although superficially similar from year to year, there was in fact considerable annual variation in seasonal patterns of questing activity, illustrated here by the longest series of sample data, from Dorset (Fig. 3). Unfed larvae started questing from April/May and accumulated on the vegetation until their abundance declined precipitously

from peak levels that may occur from late June until September. Seasonal numbers of nymphs and adults, which tended to mirror each other closely, were also variable from year to year: both stages increased in early spring from very low over-winter levels, then declined from peak levels anytime after early May or late July, and showed minor brief resurgence from September to November.

Records from Exmoor and Wales (Fig. 4) show similar degrees of temporal variability, and also highlight the geographical variation. At Exmoor there was a more marked mid-summer decline in all tick stages, particularly for adults, which emphasised a more distinct autumn period of tick activity (exceptionally marked for adults in 2000). This latter feature was seen most clearly in Wales, although no larvae appeared in the autumn of 1998.

Apart from very occasional nymphs, only larvae were seen feeding on rodents in Exmoor and Wales. The seasonal pattern in infestation levels followed that of questing larvae except that the decline from peak numbers commonly occurred 1–2 months earlier on rodents than on the vegetation (Fig. 5). Commonly, when larvae were scarce in the autumn, rodents picked up relatively more than were counted on the blanket (in Wales in 1999, most of the large number of questing larvae were seen on only one out of the 20 blanket drags, both in August and September, i.e. came from a single clump).

3.2. Predictions of timing of developmental recruitment of each tick stage

Predictions of the earliest potential onset of questing by hardened-off emergent ticks (based on mean development rates) show remarkable consistency between sites, years and

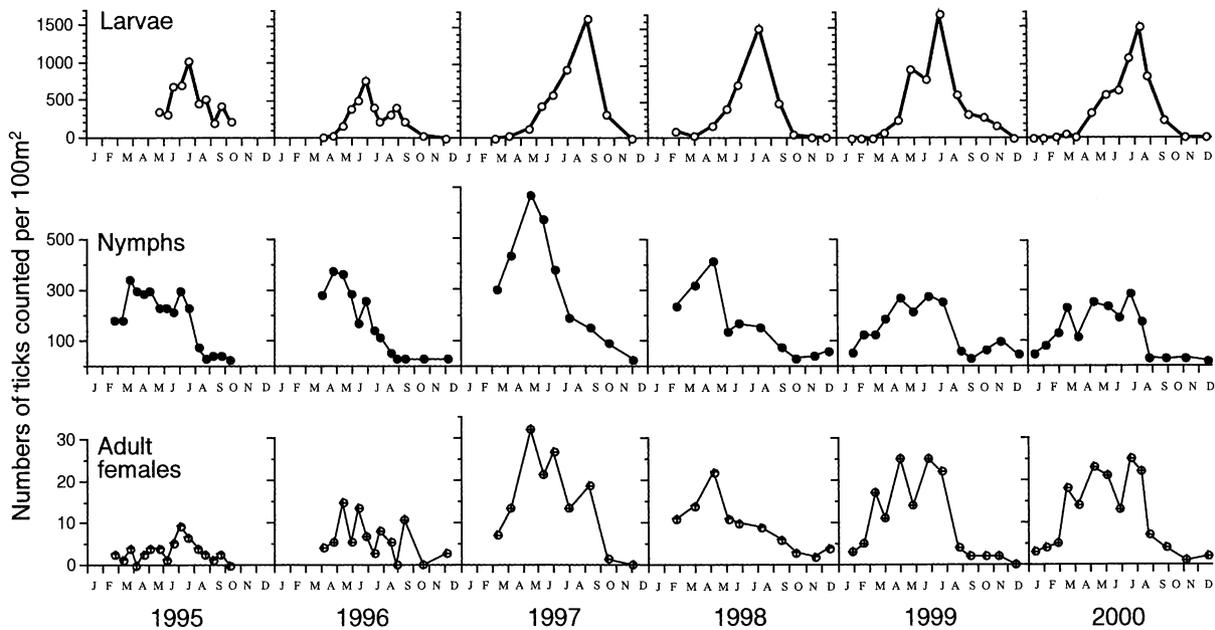
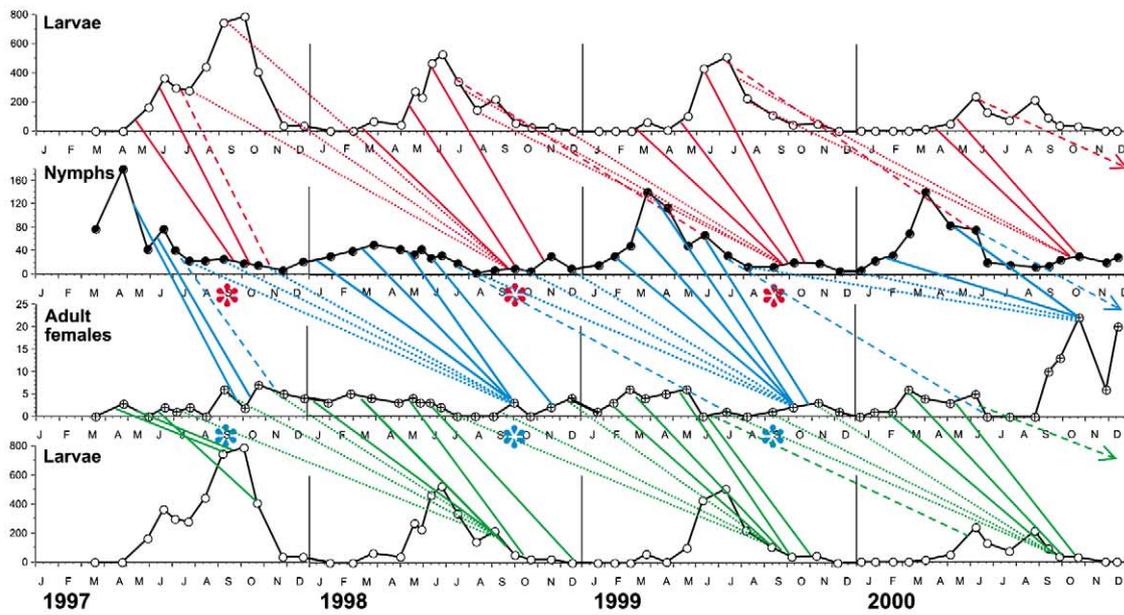


Fig. 3. Annual variation in the seasonal patterns of abundance of questing *Ixodes ricinus* counted at Wimborne St. Giles, Dorset.

a) Ticks counted per 100m²



b) Ticks counted per 100m²

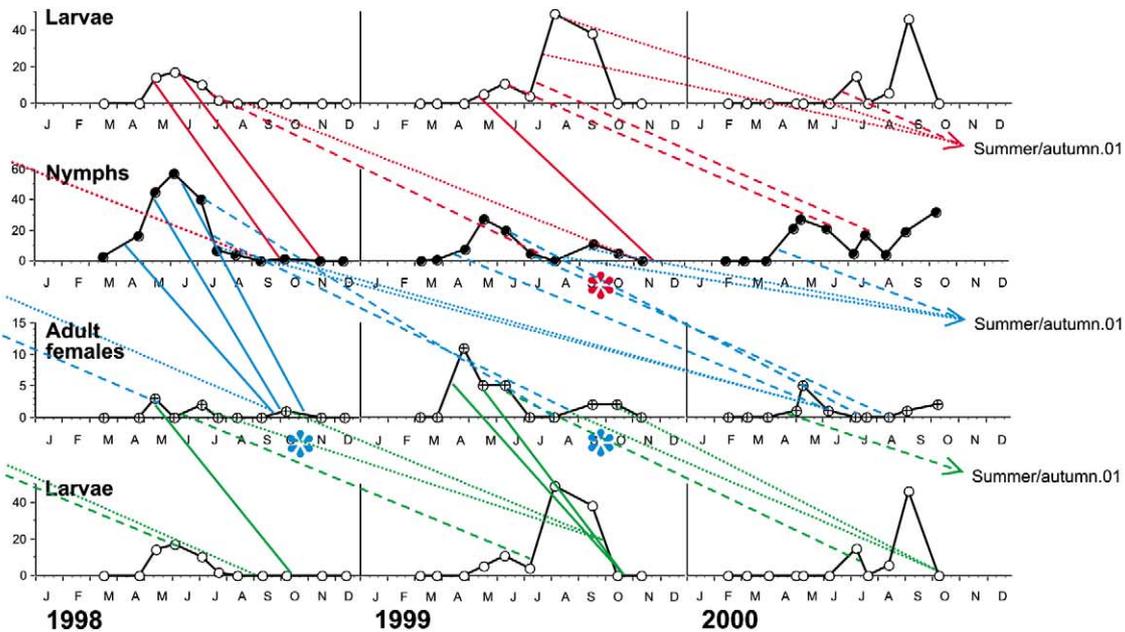


Fig. 4. Inter-stadial periods (coloured lines – see text for more details and the meanings of line symbols) between questing stages of the tick *Ixodes ricinus* counted on the vegetation (black lines), predicted by an hour-summation development model according to the recorded hourly soil temperature and the mean temperature-dependent development rates shown in Fig. 1. Asterisks show dates of first appearance of high-fat (newly recruited) nymphs (red) and adults (blue). (a) Exmoor and (b) Wales.

tick stages (Fig. 4: for each stage, the coloured lines link the date of questing by one stage to the predicted date of questing by the following stage; red for larvae to nymphs; blue for nymphs to adults; green for adult females to larvae). Irrespective of the time of questing by the previous stage, the vast majority of unfed ticks first become available to quest in the autumn, after the middle of August at the earliest and more often in September/October. Seasonal

changes in the soil temperature, and therefore tick development rates, act to compress all emergence dates into the autumn for ticks that undergo direct development after feeding any time before mid-July (solid lines, Fig. 4). Uncertainty about the precise date of the onset of developmental diapause does not affect this result: if those ticks which feed during the latter part of July develop directly, they may emerge as the next stage in late autumn of the same year

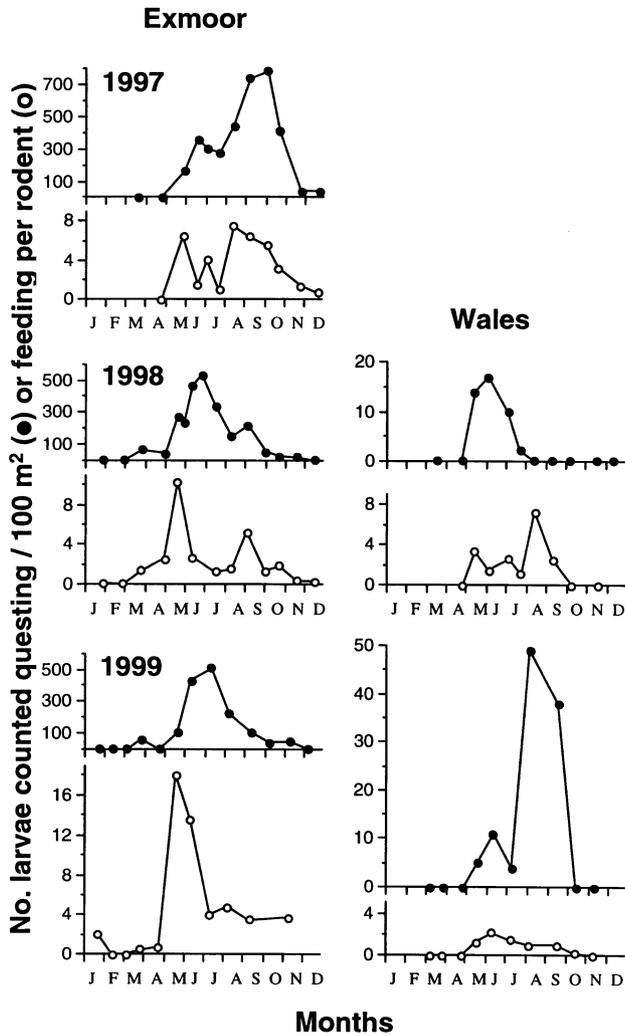


Fig. 5. Comparisons of the numbers of larval *Ixodes ricinus* counted questing on the vegetation and feeding on rodents on Exmoor and in Wales.

if it is warm enough, or in June/July the following year (dashed lines, Fig. 4); if they delay their development, they join all other ticks that feed in the second half of the year and emerge the following autumn (dotted lines, Fig. 4). At the warmest site, in Dorset (data not shown), the pattern is almost identical to that on Exmoor (Fig. 4a), except that ticks are predicted to emerge a few weeks earlier. At the coolest site, in Wales (Fig. 4b), in some years ticks may take nearly 2 years to complete a single inter-stadial period, and a few ticks may possibly emerge in June or July. Even in Wales, however, the common prediction is for developmental recruitment to occur after the period of major increase in numbers of questing ticks each year.

3.3. Seasonal changes in tick fat contents

The fat contents of questing ticks act as a completely independent check on the above predictions, and proved to be entirely consistent with them. Comparisons of monthly fat content were confounded by the significant

($0.05 > P < 0.001$) positive relationship between fat and RDW (in 80% of the samples) (see Fig. 6a for an example) and seasonal shifts in the frequency distribution of RDW (see below). This positive relationship was not satisfactorily corrected for by expressing fat as a proportion of RDW (35% of samples retained a significantly positive relationship), but was largely eliminated (in all but 8% of samples) by using $\text{fat}^{0.5}/\text{RDW}$ as an index of fat content (Fig. 6b).

This transformation normalised the data to allow comparisons of the changing frequency distributions of ticks with different fat contents through the year. The same pattern was repeated each year and was similar for nymphs (Fig. 7) and adults (Fig. 8) at each site (shown only for Exmoor, but data for the other sites are available on request from the author). At the end of the summer all nymphs had very low fat contents (c. 0.2–5 μg) until, in September or October, a large proportion of the sampled ticks had distinctly higher fat contents, commonly up to 15 μg , but sometimes even more. At this point two overlapping cohorts of ticks were clearly present, and ticks were assigned to the new cohort if their fat index exceeded the 95% confidence limits (mean + 2 SD) of the samples taken in July and August (see Fig. 6 for an example). From November onwards

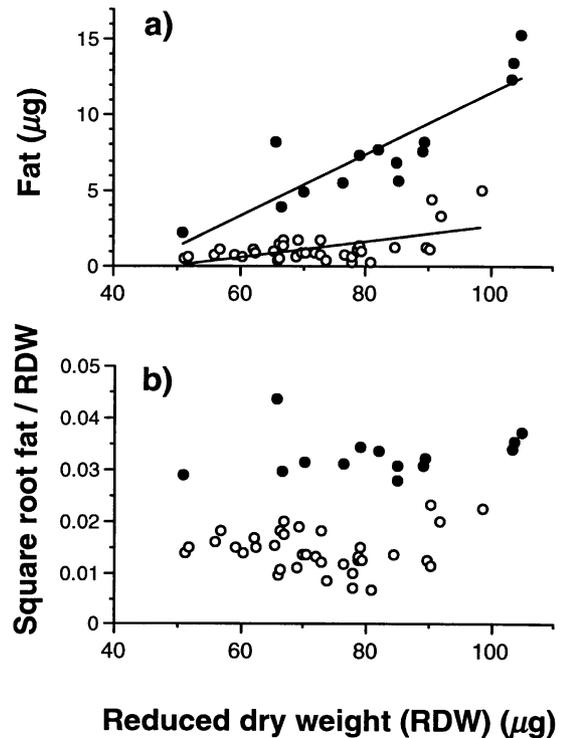


Fig. 6. The effect of size on the fat contents of old (\circ , $n = 36$) and newly recruited (\bullet , $n = 15$) (see text for the basis of designating ticks as old or new) nymphal *Ixodes ricinus*, e.g. those collected on 16 September 1998 in Dorset. (a) Fat content increases with size (reduced dry weight – RDW); old ticks, slope = 0.051, $r^2 = 0.328$, $P < 0.001$; new ticks, slope = 0.205, $r^2 = 0.774$, $P < 0.001$. (b) The square root transformation of fat satisfactorily corrects fat content for tick size; old ticks, slope = 0.0000143, $r^2 = 0.002$, NS; new ticks, slope = 0.0000474, $r^2 = 0.035$, NS.

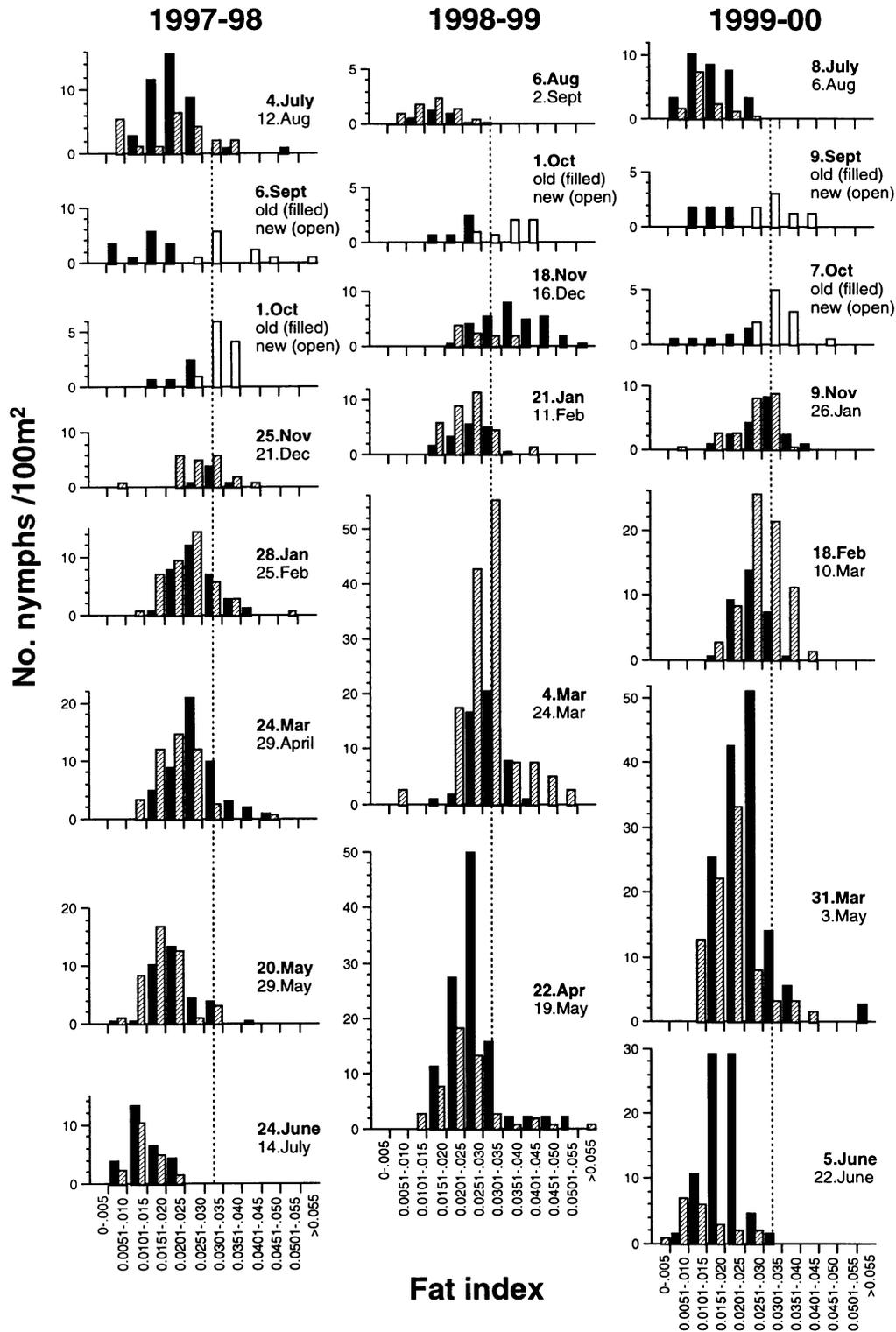


Fig. 7. Seasonal changes in absolute frequency distributions of questing nymphal *Ixodes ricinus* with different fat content indices counted per 100 m² on Exmoor, starting with late summer at the top in each of the 3 years. For reasons of space, data for 2 monthly samples are presented in each histogram, showing the earlier date of each pair as filled bars and the later date hatched. In September/October when old and new recruits occurred within the same sample, new recruits are shown by open bars. The vertical dotted line is purely to guide the eye. Note the variable y-axis scale when nymphs are scarce in the autumn.

there were relatively fewer high-fat ticks and the mode of the distributions shifted to the left. This trend persisted through the following spring. From January through to

April/May, the marked increase in the absolute numbers of moderate-fat ticks was unmatched by any prior increase in high-fat ticks, and this spring population included a much

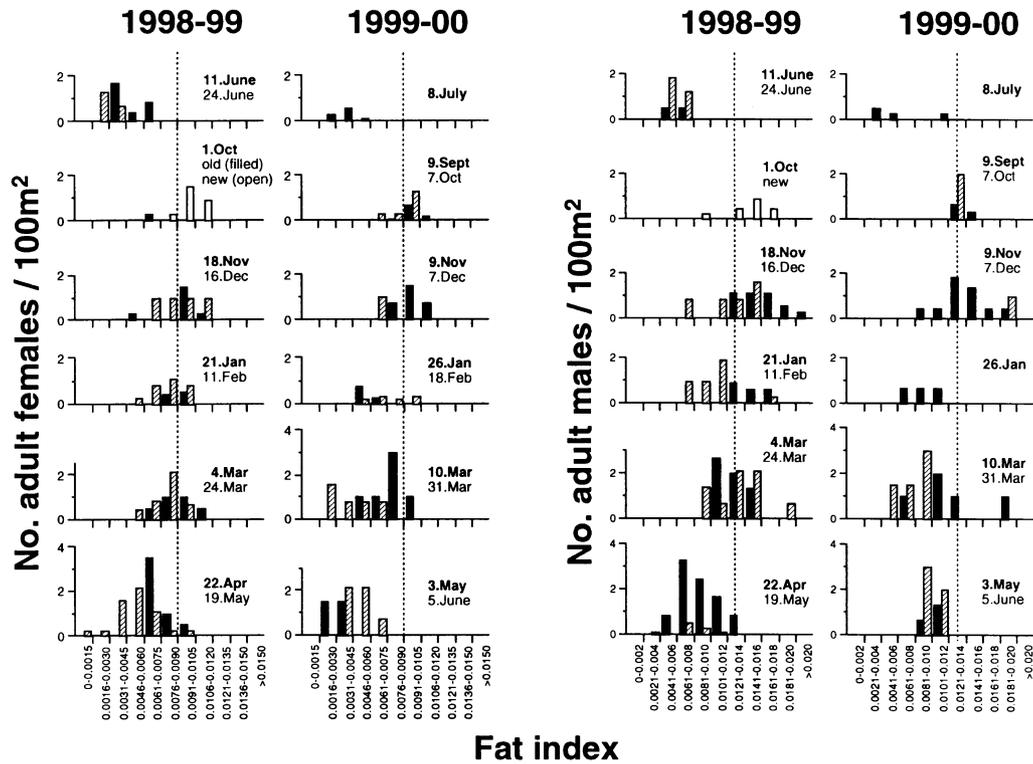


Fig. 8. Seasonal changes in absolute frequency distributions of questing female (left) and male (right) *Ixodes ricinus* with different fat content indices counted per 100 m² on Exmoor, starting with late summer at the top in each of the 2 years. For reasons of space, data for 2 monthly samples are presented in each histogram, showing the earlier date of each pair as filled bars and the later date hatched. In September/October when old and new recruits occurred within the same sample, new recruits are shown by open bars. The vertical dotted line is purely to guide the eye.

smaller proportion of high-fat ticks than seen in the previous autumn. Instead, most of the ticks that became newly active in the spring had lower fat indices, indicating that they had endured a longer interval between emergence from the previous stage and questing than had the new recruits in the autumn. This suggests a single burst of developmental recruitment in the autumn, followed by behavioural quiescence over winter. Only a few ticks with high fat content characteristic of new recruits appeared sporadically at times other than the autumn. Once activation of ticks had ceased by May, ticks with moderate fat indices disappeared through June–September as fat was used up by those ticks which had not yet found a host, so that virtually no very low-fat ticks persisted beyond October.

Very few newly recruited adult female ticks started questing in the autumn (Fig. 8), especially in Dorset and Wales (data not shown), but adults of both sexes appeared in sufficient numbers to reveal developmental recruitment confined to the autumn as for nymphs (apart from an unusually large proportion of high-fat males on Exmoor on 24 March 1999; Fig. 8).

3.4. Seasonal changes in the size of questing ticks

Each new cohort of nymphs that appeared on the vegetation in the autumn showed a normal size (RDW) distribution, virtually symmetrical about a median of 75–85 μg ,

which then changed seasonally in the same way in each year at each site (examples shown in Fig. 9). A sub-set of larger nymphs started questing in February, with only 15–30% having RDW <80 μg and almost none <60 μg . As the year progressed, the questing population was composed increasingly of smaller nymphs, as small ticks appeared from March onwards while the largest ticks (>100 μg) had disappeared by June. By September, 80–100% of persisting old ticks had RDW <80 μg . A similar pattern appeared even over the limited questing season in Wales (Fig. 9c). Where sample sizes were sufficient in Dorset and Exmoor, a similar pattern of changing population size structure through the year was evident for adult female ticks (data not shown).

4. Discussion

All the empirical evidence from these study sites points to the recruitment (i.e. emergence from the previous stage) of a single cohort of each stage of ticks each year in the autumn. The striking coincidence in the timing of the first observed nymphs and adult ticks with high fat content each autumn and the mean emergence predicted from the temperature-dependent development model (Fig. 4) strengthens this conclusion. Usually very few of these newly emerged ticks were counted on the vegetation in the autumn (apart

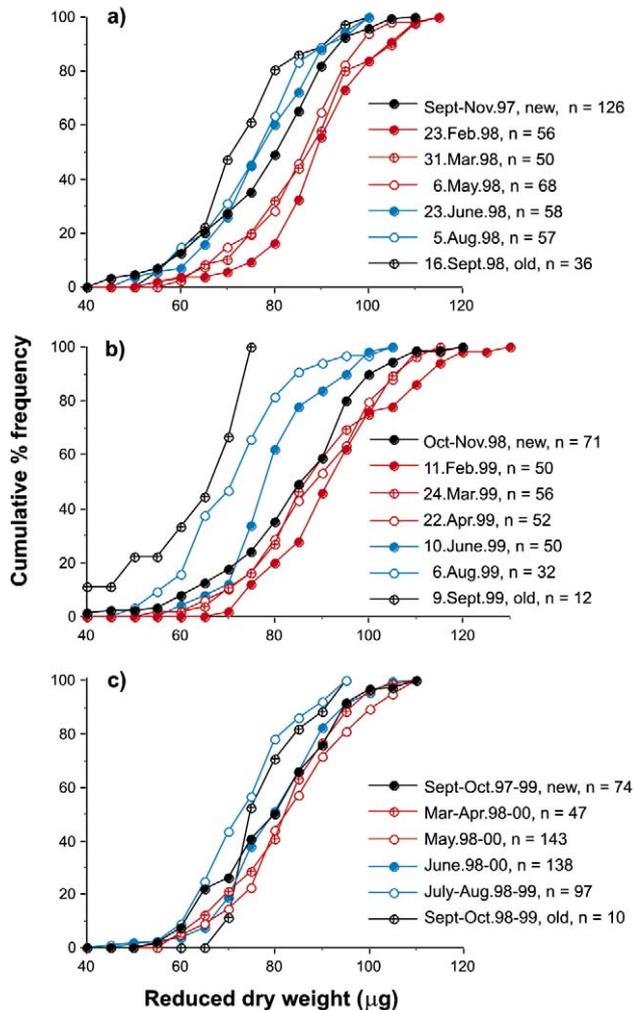


Fig. 9. Seasonal changes in the size (reduced dry weight) composition of populations of questing nymphal *Ixodes ricinus* during the life-span of a single cohort in (a) Dorset 1997–1998, (b) Exmoor 1998–1999 and (c) Wales 1997–2000, three cohorts combined. Sample dates and sizes are shown in the legends.

from larvae in September 1997 and adults on Exmoor in late 2000), but they appeared in increasing numbers through the following spring. Those nymphs and adults which became active early in the spring were large, but had lower fat contents (both absolute and size-corrected) than those which had emerged the previous autumn. By the end of the summer, unfed nymphs and adults had almost exhausted their energy reserves and these old ticks disappeared from the questing population within about 1 year from their recruitment.

These data and model predictions are entirely consistent with earlier studies on tick development, activity, seasonal abundance (Lees and Milne, 1951; Cerny, 1957, 1958; Chmela, 1969; Cerny et al., 1974; Daniel et al., 1976; Gray, 1982, 1985; Steele and Randolph, 1985) and age-grading in Russia (reviewed in Uspensky, 1995), but suggest

a life cycle for *I. ricinus* that is very much simpler than is usually portrayed. A single annual cohort of each stage starts in the autumn; ticks either become active and feed immediately in early autumn or not until the following spring, as observed by Lees and Milne (1951). Those which feed in the autumn suffer delayed development (diapause) and moult to the next stage in the following autumn; those which feed in the spring/summer develop directly and also moult in the following autumn. There is no need to invoke two separate cohorts, with or without interchange (Lees and Milne, 1951; Donnelly, 1976; Gray, 1982, 1985, 1991; Walker, 2001), to explain the common bi-modal pattern of seasonal activity. Walker's (2001) conclusion that nymphs and adults questing in the spring had fat contents as high as those in the autumn, and therefore represented a second separate cohort, may be due to his coarser method of measuring fat. He ranked fat content subjectively according to the proportional volume of the gut stained for lipid; his class 1 ('major proportion') could have included both the highest quantitative fat index of the present study, seen in new autumn recruits, and the lower fat index seen in spring-questing ticks. As in our study, 90% of the very large number of newly active nymphs in April and May in Walker's study had fat scores indicative of 6 months of inactivity post-moult.

Nor is there any need for seasonally variable temperature-dependent development rates (Gardiner and Gettinby, 1981). The combination of seasonal temperatures and a period of delay until after the winter in the onset of development by ticks that feed sometime after mid-July is sufficient to synchronise the emergence of unfed ticks to within a couple of months every autumn. This developmental ('morphogenetic'; Belozero, 1982) diapause occurs in ticks that feed slightly earlier in Scotland (c. 56°N) (end of July) than in Ireland (c. 53°N) (mid-August) or the Czech Republic (c. 49°N) (end of August) (Campbell, 1948; Kemp, 1968; Chmela, 1969; Cerny et al., 1974; Daniel et al., 1976; Gray, 1982). At this time of year, day-length is longer but declines faster with increasing latitude, indicating that the rate of change in day-length to which ticks are exposed may be the trigger for diapause induction (Belozero, 1982). Temperature may also play a part, but would offer a less reliable signal to ticks.

We now need to define quantitatively the precise determinants of tick behaviour and mortality in the field that are superimposed on this simple pattern of developmental recruitment, if we are to explain and predict the dynamics of the questing tick population. Unfortunately, we are not even entirely sure what this behaviour is, as standard sampling methods that measure the standing crop of questing ticks do not detect the underlying processes. Typically, during the autumn relatively more ticks are counted on their hosts than on the vegetation (Steele and Randolph, 1985; Craine et al., 1995; Ogden, N.H., 1995). The epizootiology of Lyme disease in upland habitats of north west England. DPhil thesis, University of Oxford, Oxford; Walker et al.,

2001; this study). This suggests that the apparently low questing activity by newly emergent ticks in the autumn may in fact reflect a low rate of accumulation of ticks on the vegetation, with high input to, but equally high output from, the questing population. The rate of host-finding may be maximal in the autumn, when the saturation deficit is low enough to allow long periods of questing and many host species are at their peak seasonal densities (Corbet and Harris, 1991; Mallorie and Flowerdew, 1994; Craine et al., 1995), especially in woods where pheasants are released in late summer (Hoodless et al., 1998).

Nevertheless, Lees and Milne (1951) observed a high degree of inactivity through the winter in undisturbed ticks laid down in field experiments after August. It remains to be confirmed whether this is a real 'behavioural' diapause (Belozerov, 1982) or facultative quiescence, either of which could be triggered by autumnal conditions (declining temperature and/or day-length). At our field sites, questing nymphs and adults were scarce in September and October even though it was warmer than in February and March when they were more abundant.

The appearance of so many questing ticks in the field through the spring also suggests that a large proportion of newly emergent ticks enter over-winter quiescence, are reactivated by rising spring temperatures (Macleod, 1936; Perret et al., 2000) and accumulate on the vegetation while the rate of reactivation exceeds the rate of loss from the questing population. It appears that the temperature threshold for the onset of activity varies with the size of the tick (details to be the subject of a separate paper), with nymphs and adults appearing before larvae, and larger nymphs and adults appearing before smaller ones. Once recruitment ceases, tick numbers fall, with the largest nymphs and adults disappearing first. This probably reflects not only their earlier arrival, but also their relatively higher energy levels (Fig. 6) permitting them to quest more continuously and so find hosts more rapidly. Smaller ticks (larvae and small nymphs and adults) persist longer through the summer, partly because they become active later, and also because if they are forced into temporary inactivity by high moisture stress during the summer (Randolph and Storey, 1999) they will take longer to find hosts. As Perret et al. (2000) also observed, most of the abrupt, sometimes temporary, declines in questing ticks of all stages at our UK field sites coincided with abrupt increases in saturation deficit above c. 4 mmHg (data not shown), the level at which ticks show positive geotropism (Macleod, 1935). At the same time, any tick that runs out of fat before finding a host will die. Estimates from observations in the field (Steele and Randolph, 1985) and quasi-natural arenas (Randolph and Storey, 1999) indicate a maximum questing period of about 4 months for nymphs. This effectively sets a limit on the longevity of unfed ticks in nature, with the last survivors being replaced each autumn by the succeeding cohort (Lees and Milne, 1951; Uspensky, 1995; Korenberg, 2000; this study).

Geographical variation in the seasonal activity by each tick stage can be accommodated within this framework, with the precise timing of emergence of unfed ticks depending on local temperatures, as predictable from the development model. Only in places with exceptionally warm temperatures throughout the spring and summer might ticks be expected to emerge sufficiently early to avoid diapause induction, develop directly to the next stage within the same calendar year (e.g. feed July, moult September) (as recorded by Chmela, 1969) and so complete a full life cycle in less than 3 years. In the cool conditions of Wales, on the other hand, development rates were so slow (Fig. 2) that some summer-fed ticks were not predicted to emerge until the following June/July (Fig. 4b) (when a few high-fat nymphs did indeed appear in 1999), thereby prolonging the life cycle. Considerable variability can thus arise from the same rules operating under different temperature regimes. Any influence of autumnal temperatures on the onset of over-winter quiescence in unfed ticks could be critical in determining the availability of questing ticks of each stage the following spring. This factor has been identified as a significant correlate of the presence of endemic cycles of tick-borne encephalitis virus (Randolph et al., 2000).

Long series of continuous data such as are reported here, that can yield precise quantitative explanations of the spatially and temporally variable rates of tick demographic processes, are the essential raw material for predictive tick population and disease transmission models. They could be subjected to a variety of analytical techniques to answer a range of questions. In contrast to demographic analyses for the African tick *R. appendiculatus* (Randolph, 1997), only annual, rather than seasonal, estimates of inter-stadial mortality for *I. ricinus* can be derived from these purely observational records; because all the ticks which feed from July of year n to July of year $(n + 1)$ yield ticks of the next stage in the autumn of year $(n + 1)$ (and/or year $n + 2$ at very cool sites), numbers of seasonally distinct groups of ticks cannot be compared before and after the intervening period of development. Daily recruitment and mortality rates of questing ticks should, however, be more easily estimated.

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