FOLIA PARASITOLOGICA 42: 73–80, 1995

Seasonal variation in the role of grey squirrels as hosts of *Ixodes ricinus*, the tick vector of the Lyme disease spirochaete, in a British woodland

N. G. Craine[1,2], **S. E. Randolph**[1]* and **P. A. Nuttall**[2]

[1]Department of Zoology, University of Oxford, England;
[2]NERC Institute of Virology and Environmental Microbiology, Oxford, England

Key words: *Ixodes ricinus,* squirrels, mice, voles, pheasants, seasonality, *Borrelia burgdorferi*

Abstract. Data are presented on the variable patterns of the seasonal dynamics of *Ixodes ricinus* L. ticks seen questing on the vegetation and feeding on small rodents (mice and voles) and squirrels within a British woodland focus of Lyme borreliosis. Information on tick infestation levels on pheasants is also presented. The results show a prolonged, unimodal pattern of tick activity, with ticks feeding throughout the year in this sheltered habitat. If host density is taken into account, squirrels are quantitatively more important than small mammals as hosts for larval ticks from April until July, and overwhelmingly so for nymphal ticks throughout the year. The observed inter- and intraspecific differences in tick infestation levels are related to the behaviour of both hosts and ticks. Squirrels, as competent hosts for *Borrelia burgdorferi* and frequent occupants of habitats closely associated with man, will contribute significantly to the risk of Lyme disease.

The relationship between the tick *Ixodes ricinus* Linnaeus, principal European vector of *Borrelia burgdorferi* s.l. Johnson, Schmid, Hyde, Steigerwalt et Brenner, and its hosts defines the transmission dynamics of Lyme borreliosis. Despite the well recorded wide host range of *I. ricinus*, researchers on the enzootiology of Lyme disease in Europe have concentrated on small rodents (Gray et al. 1992, Matuschka et al. 1992, DeBoer et al. 1993, Humair et al. 1993) and in one instance on hares (Talleklint and Jaenson 1993). This may be due to the influence of conclusions from studies in the USA that mice are quantitatively the most important reservoir host for *B. burgdorferi* (Mather et al. 1989). In British woodlands, however, this restricted view is likely to underestimate the complexity of the web of transmission pathways. The relative importance of different vertebrate species as potential amplifying hosts for *B. burgdorferi* depends on both their abundance and their quantitative relationship with *I. ricinus,* which may vary seasonally as changes in tick activity and host behaviour influence the tick/host contact rate. Rarely have the seasonal dynamics of tick/host relationships been studied for different host species within the same ecosystem, thereby providing a true comparison. The results presented in this paper come from a larger study on the enzootiology of Lyme disease (Craine 1994, Randolph and Craine 1995), in which the reservoir competence of grey squirrels (*Sciurus carolinensis* Gmelin) for *B. burgdorferi* has been demonstrated for the first time. Also the reservoir competence of pheasants was indicated by the very much higher infection prevalence in nymphs that had engorged on pheasants (16.6%) compared with that in questing nymphs (6.8%) from the same site.

MATERIALS AND METHODS

Field study site

The study was carried out in Thetford Forest, Norfolk, an area of high referral of suspected Lyme disease patients (East Anglia Health Authority). Furthermore, during 1990 a large proportion (17/40) of Forestry Commission workers in the Thetford area, who are often bitten by *I. ricinus* ticks, tested positive for the presence of antibody against *Borrelia burgdorferi* (R. Whittaker, Forestry Commission, Thetford, pers. comm.).

Thetford Forest, covering 20,000 ha of predominantly well drained sandy soil on the Norfolk/Suffolk border, is the largest area of lowland forest in England, where the Forestry Commission operates a twenty year rotation involving Sitka spruce (*Picea sitchensis*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Grand fir (*Abies grandis*), and Corsican pine (*Pinus nigra*). Some stands of conifers are bounded by strips of mixed deciduous woodland comprising sycamore (*Acer pseudoplatanus*), beech (*Fagus sylvaticus*), birch (*Betula verrucosa*) and oak (*Quercus robur*).

Correspondence to: Dr S. E. Randolph, Department of Zoology, South Parks Road, Oxford, OX1 3PS, U.K.

The study was carried out at three sites in the Forest, not as a comparative study but in order to maximise the number of animals trapped. At each site sampling was undertaken across both mixed deciduous woodland strips and mature conifer stands.

Sampling questing ticks

Questing ticks were sampled monthly from February to November in 1992 by dragging a light-coloured 1.5 m × 1.0 m woollen blanket over the vegetation. Drags of 25 m length (area 37.5 m^2) were repeated 8 times per site on each sample occasion, giving a total sample area of 300 m^2 per site per month. Dragging was always carried out at 1100 hrs, unless there were adverse weather conditions such as heavy rain. The ticks collected on the blanket were counted and removed at the end of each 25 m drag.

Sampling feeding ticks

Of the large range of potential host species for *I. ricinus*, not all are quantitatively significant. In this study attention was focused on those species thought by the Thetford Forest head gamekeeper (on the basis of observations over forty years) to feed a significant fraction of the immature tick population. These were wood mice (*Apodemus sylvaticus*), bank voles (*Clethrionomys glareolus*), grey squirrels (*Sciurus carolinensis*) and pheasants (*Phasianus colchicus*). Certain hosts known to feed *I. ricinus* (hares (*Lepus capensis*), foxes (*Vulpes vulpes*) and badgers (*Meles meles*)) were present in the Forest, but at such low densities (<<1/ha) that they were ignored. Rabbits (*Oryctolagus cuniculus*) were not sampled as their distribution in the Forest was very patchy and they were scarce in the particular areas studied. Furthermore, an examination of 15 rabbits shot in Thetford Forest in September 1992 and 20 rabbits shot on the neighbouring Elvedon estate in May 1993 suggested that tick infestation levels were low on this species. Information on the hosts of adult ticks was limited as access to such hosts was difficult and irregular. Although in other studies adult ticks have been reported on European hares (Talleklint and Jaenson 1993), in Thetford Forest adults were only ever found on roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), which were examined for both adult and immature tick stages between February and July, depending on the deer culling programme of the Forestry Commission.

Small rodents were trapped using 100 Longworth Humane traps (Longworth Scientific, Abingdon) set in pairs at 8–10 m intervals along a transect line. The traps were set for four nights every month from May to November in 1991, and February to November in 1992. In order to maximise the number of individuals, the traps were moved between sites on each day. Each trapped animal was anaesthetised with Methoxyfluorane before the attached ticks were counted. The vast majority of ticks were *I. ricinus; I. trianguliceps* larvae, nymphs and adults were recorded on so few occasions that they were not considered further in this study. Animals were weighed and measured (nose tip to tail base) before being released at the point of capture (the entire period of anaesthesia lasted approximately 3–4 minutes).

Grey squirrels were trapped by Mr T. Venning of the Thetford Forestry Commission using a Forestry Commission humane squirrel trap and subsequently killed with carbon dioxide, as part of a red squirrel re-introduction programme.

Detailed examination of a sub-sample of the animals trapped (n = 25) showed that 95% of the ticks were carried on the ears, and only on very heavily infected animals were ticks found on the upper dorsal abdomen. Therefore from September 1992 to July 1993 all the squirrels were examined briefly immediately after being killed to count any ticks present on the body, then the ears were removed, placed individually in sealed plastic bags and stored at –20°C until the ticks were counted in the laboratory. The squirrels were sexed, weighed, assigned to one of four body-fat categories and assessed for reproductive status.

Ticks were monitored on pheasants shot by the Methwold Shoot in the northern sector of Thetford Forest on three occasions in October and November 1991/2. The ticks on each bird were counted for a two minute period immediately after the birds had been shot.

In order to explore the relative importance of different species as hosts to *I. ricinus,* the infestation capacity of each host species was calculated as the product of host density and mean daily numbers of ticks feeding per host (i.e. observed mean infestation levels divided by the average feeding period, four days for larvae and six days for nymphs) for each month, to take account of seasonal changes in both tick and host population. (As long as the distribution of ticks over the whole host population is similar to that observed over the sampled population, mean, rather than median, infestation levels will give a more accurate estimate of total tick numbers on the host population.) The mean monthly infestation levels of ticks on mice and voles were calculated as the means for 1991 and 1992 for those months in which observations were made in both years. As vertebrate densities were not estimated during this study, the monthly population densities for each host species were based on the following sources: *A. sylvaticus* and *C. glareolus,* Mallorie and Flowerdew (1994), interpolating between mean summer and winter estimates for seventeen sites in Britain over six years (1982–1987); *S. carolinensis,* Gurnell (1983) and T. Venning, red squirrel research project, Thetford (pers. comm.).

Statistical analysis

Unequal sample sizes and the skewed distribution of ticks on their hosts required the use of the non-parametric Mann Whitney U test (Sokal and Rohlf 1981) to compare tick infestation levels on different classes of hosts. For this reason, tick infestations are described in terms of the median levels and the numbers of ticks seen on the most heavily infested 25% of the sampled host populations, while figures show the 10, 25, 75 and 90 percentiles. P values of < 0.05 were taken as the limit of statistical significance.

RESULTS

Seasonal pattern of questing ticks collected on blanket drags

The seasonal pattern of larval activity determined from blanket drags showed one peak in July, with questing ticks observed from June to September (Fig. 1a). The large variance in the monthly observations reflects the well known spatial heterogeneity in the distribution of questing larvae, due mostly to their limited dispersal after emergence from egg masses. The recorded numbers of questing nymphs rose steadily from early February to a peak in June, remained more or less constant until October, and then declined abruptly in November (Fig. 1b). Adult ticks collected on blanket drags showed a similar pattern to that of nymphs although their numbers continued to increase through to September, with a minor decrease in August, before declining in the autumn (Fig. 1c). The smaller variances for nymphs and adults indicate a less aggregated distribution of these stages compared with larvae.

Seasonal patterns of immature ticks on hosts

The seasonal pattern of larval infestations on hosts (Figs. 2 and 3a) shows that larvae were in fact active for a much greater part of the year than was detected by blanket dragging. The highest infestation levels on mice were in August and September in both years, when the median number of larvae was 10–30, with 25% of the examined mice carrying over 22 larvae, up to a maximum of 58. This was one month after the blanket-detected peak of questing larvae in July and August (c.f. Fig. 1a). Many fewer larvae were seen on mice during June and July in 1992 (when the most heavily infested 25% carried between 2 and 10 larvae) than in 1991 (when the top 25% carried 12–42 larvae). Many fewer bank voles were trapped, but the seasonal pattern of larval infestations was similar to that on mice, although at very much lower levels; larvae were seen in ones and twos from March to November, with peak infestations seen in August, when up to six larvae were seen per host (and, exceptionally, 22 larvae on one bank vole in June 1991). Nymphs were seen very rarely on small rodents; single nymphs were seen on six mice, two nymphs on one mouse and three nymphs on one vole, all but three between June and September.

From April to July squirrels fed many more larvae (median 8.5–18.5, with the most heavily infested 25% carrying 20–100 larvae), by almost an order of magnitude, than did mice (median 1–3.5) In the late summer and autumn of 1992, however, squirrels and mice fed similar numbers of larvae (Figs. 2 and 3a); at this time of year squirrels forage increasingly in the tree canopy rather than on the ground. In addition, squirrels fed large numbers of nymphs, whose infestation levels again peaked in the spring and early summer (median 3.5–8.5, with the most heavily infested 25% carrying 30–100 nymphs) (Fig. 3b) despite the high numbers of questing nymphs detected throughout the summer and autumn (Fig. 1b).

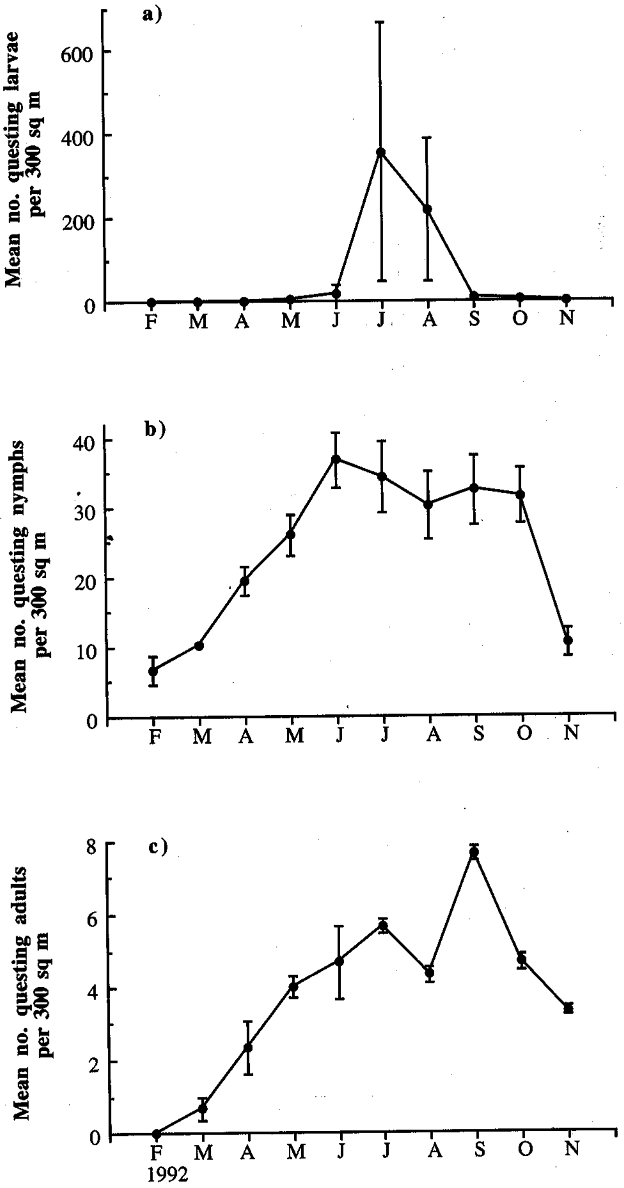

Fig. 1. The mean numbers (± 1 s. e.) of a) larval b) nymphal and c) adult *Ixodes ricinus* picked up by blanket drags during 1992 at Thetford Forest, Norfolk. Each point is the mean for 300 m^2 sampled at each of three separate sites within the forest (see text).

Of the 103 pheasants sampled in October and November, when larval tick activity was low, only six were feeding one or two larvae each, but 50% were feeding at least one nymph, while 25% carried between 2 and 15 nymphs each. In another woodland focus of Lyme disease, Wimborne Forest in Dorset, the median infestation levels on pheasants in July were 9 larvae/host (with 25% feeding 10–30 larvae) and 1 nymph/host with 25% feeding 6–9 nymphs), on average about three times as

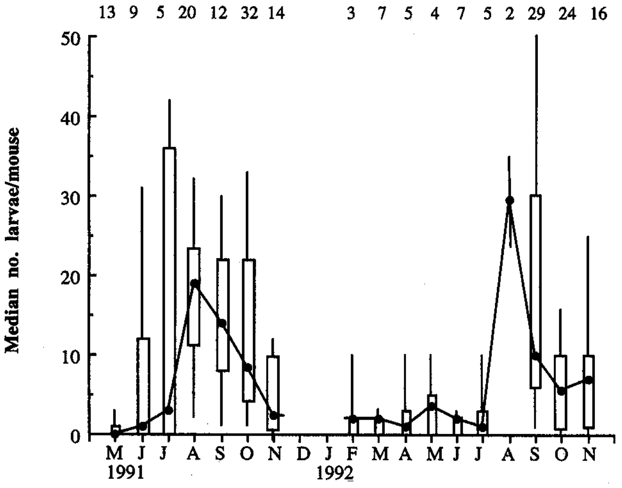

Fig. 2. The median numbers of larval *Ixodes ricinus* (± 1 s. e.) per host feeding on wood mice, *Apodemus sylvaticus*, during 1991–1992 in Thetford Forest; the number of mice trapped are shown along the top. Vertical bars show limits of 25 and 75 percentiles; vertical lines show limits of 10 and 90 percentiles.

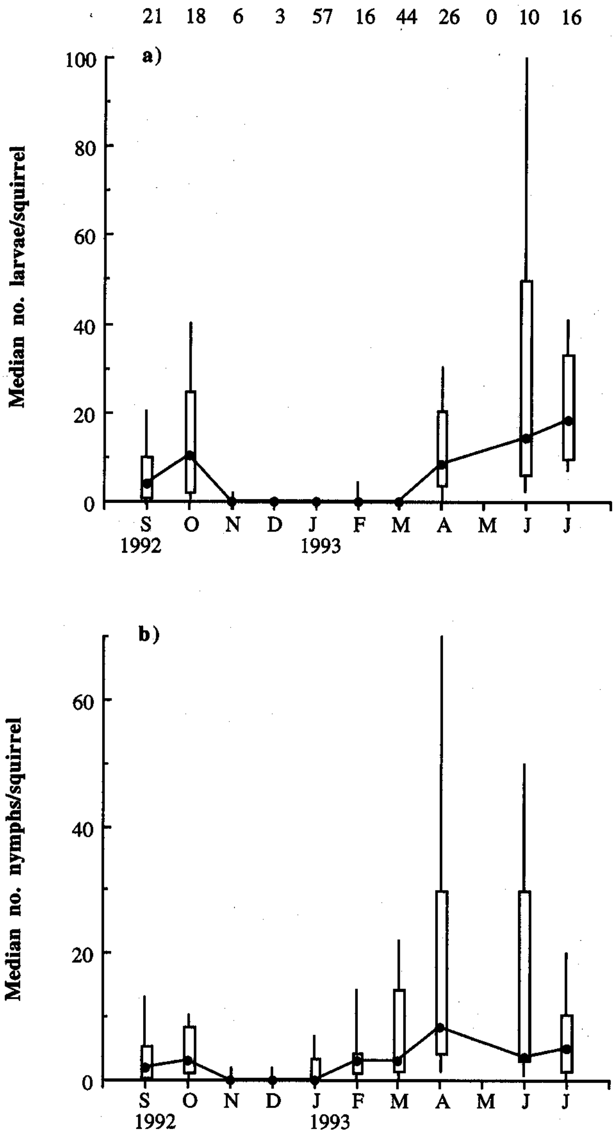

Fig. 3. The median numbers of a) larval and, b) nymphal *I. ricinus* per host (± 1 s.e.) feeding on grey squirrels, *Sciurus carolinensis*, trapped in Thetford Forest between January and December 1993; the numbers of squirrels trapped are shown along the top. Vertical bars show limits of 25 and 75 percentiles; vertical lines show limits of 10 and 90 percentiles.

many larvae as seen on mice and approximately one half to one quarter as many ticks as seen on squirrels in July in Thetford Forest.

Large numbers of ticks of all three stages were seen, but not counted, on both roe and red deer throughout the period from February to July.

Tick carrying capacity of different host species

The monthly population densities for each host species used for these estimations are shown in Fig. 4a. The estimated relative infestation capacities (Figs. 4b and c) show that during the early part of the season (April to June) squirrels feed more larvae *in toto* than do small mammals, but from July onwards mice are much the most important hosts for larvae because of their higher population densities than squirrels. Most larvae are fed in the late summer to autumn, while most nymphs are fed in the spring and early summer and predominantly by squirrels.

Distribution patterns of ticks on hosts

The ticks showed a strongly overdispersed distribution on their hosts. Within any one period of similar average infestation levels, on each host species the distributions of larvae and nymphs approximated to the negative binomial distribution (Table 1). In part these aggregated distributions were generated by the different numbers of ticks carried by different sex and size classes of hosts. There were no consistent differences in the mean larval infestation levels on male and female mice; although from February to July males fed about twice as many larvae (mean 5.15 ± 1.53) as did females (mean 2.88 ± 1.73), from August to November males and females fed similar numbers of larvae (means of 13.59 and 14.32 respectively). Throughout the summer and autumn (June – November), when larvae were most abundant and there was a wide range of size classes within the mouse population, there was a positive correlation between body length and mean larval

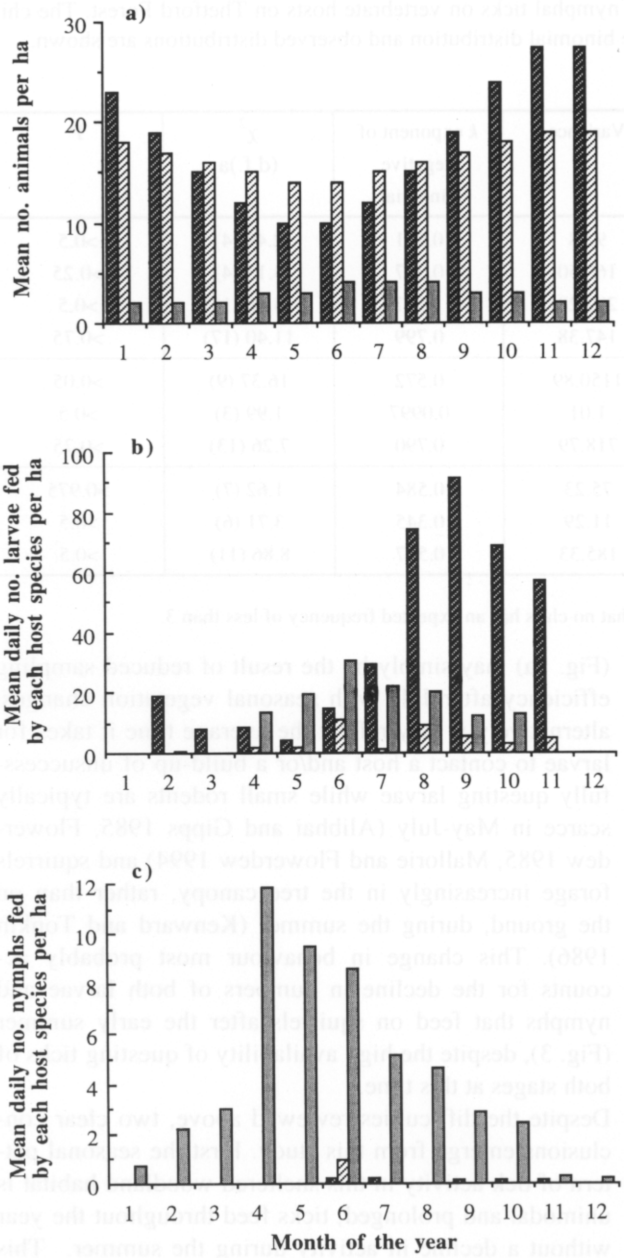

Fig. 4. The seasonal variation in a) approximate host densities of *Apodemus sylvaticus* and *Clethrionomys glareolus* (based on Mallorie and Flowerdew 1994) and *Sciurus carolinensis* (from Gurnell 1983; T. Venning, pers. comm.), and their b) larval and c) nymphal *Ixodes ricinus* infestation capacities (see text)., *A. sylvaticus*, *C. glareolus*; *S. carolinensis.*

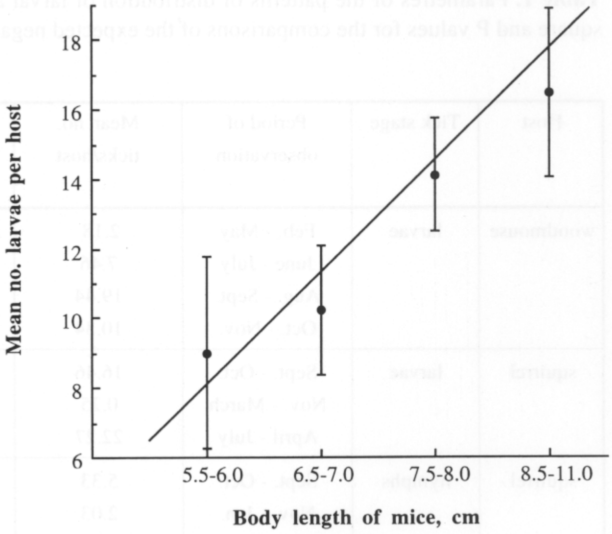

Fig.5. The mean (± 1 s.e.) number of larvae carries by *Apodemus sylvaticus* in four size classes trapped during June to November in 1991 and 1992 in Thetford Forest. The regression line is based on individual data points. Y = - 11.397 + 3.245X, r = 0.212, df = 173, P < 0.01.

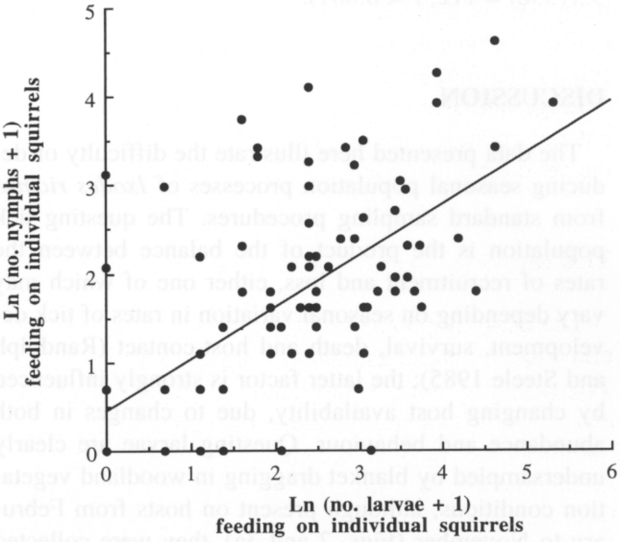

Fig. 6. The correlation of the numbers of larvae and nymphs feeding together on individual squirrels during September and October 1992 and April, June and July 1993 in Thetford Forest. y = 0.438 + 0.584x, r = 0.587, df = 91, P < 0.001.

infestation levels (Fig. 5). Male squirrels consistently fed about twice as many larvae and nymphs as did females, but there was no effect of the weight or fat condition of squirrels on their larval or nymphal infestation levels.

Of particular relevance to disease transmission is the occurrence of high numbers of both larvae and nymphs on the same individual hosts. In the case of the squirrels, during the months when both larvae and nymphs were feeding (September - October 1992 and April - July 1993) there was a significant positive correlation between the numbers of larvae and nymphs feeding together at any one time on individual hosts (Fig. 6). This was true for each of these months, and for each host sex, separately. The low number of nymphs that feed on mice precluded any such relationship for small rodents, nevertheless during June to September, when both

Table 1. Parametres of the patterns of distribution of larval and nymphal ticks on vertebrate hosts on Thetford Forest. The chi-square and P values for the comparisons of the expected negative binomial distribution and observed distributions are shown.

Host	Tick stage	Period of observation	Mean no. ticks/host	Variance	*k* exponent of negative binomial	χ^2 (d.f.)[a]	P
woodmouse	larvae	Feb. - May	2.18	9.58	0.521	2.49 (4)	>0.5
		June - July	7.46	160.50	0.347	4.13 (4)	>0.25
		Aug. - Sept.	19.44	209.28	1.597	13.76 (16)	>0.5
		Oct. - Nov.	10.34	147.38	0.799	11.40 (17)	>0.75
squirrel	larvae	Sept. - Oct.	16.46	1150.89	0.572	16.37 (9)	>0.05
		Nov. - March	0.25	1.01	0.0997	1.99 (3)	>0.5
		April - July	22.27	718.79	0.790	7.26 (13)	>0.75
squirrel	nymphs	Sept. - Oct.	5.33	75.23	0.584	1.62 (7)	>0.975
		Nov. - Jan.	2.03	11.29	0.345	3.71 (6)	>0.5
		Feb. - March	8.40	185.33	0.517	8.86 (11)	>0.5

[a] Degrees of freedom, based on grouping the frequency distributions so that no class has an expected frequency of less than 3.

stages were feeding, the mean larval infestation level on those rodents seen to feed one or more nymphs (30.00 ± 9.07 larvae/host) was two and a half times as high as that on rodents with no nymphs (12.09 ± 1.33) (t = 3.575, df = 112, P < 0.001).

DISCUSSION

The data presented here illustrate the difficulty of deducing seasonal population processes of *Ixodes ricinus* from standard sampling procedures. The questing tick population is the product of the balance between the rates of recruitment and loss, either one of which may vary depending on seasonal variation in rates of tick development, survival, death and host-contact (Randolph and Steele 1985); the latter factor is strongly influenced by changing host availability, due to changes in both abundance and behaviour. Questing larvae are clearly undersampled by blanket dragging in woodland vegetation conditions; although present on hosts from February to November (Figs. 2 and 3a), they were collected on blankets only from June to September (Fig. 1a). Rodents, which are probably a good indicator of the relative abundance of larvae as they forage in the litter layer in a fairly uniform manner throughout the year (apart from an increase in home range size by adult males as the breeding season starts in April - Randolph 1977), reveal peak numbers of feeding larvae in August and September in 1992 (Fig. 2). The high mean infestation levels and increasing population density of small rodents at this time of year show that a large number of questing larvae are available to hosts even though not detected by blanket-dragging. The apparently earlier peak of questing larvae as seen on blankets in 1992 (Fig. 1a) may simply be the result of reduced sampling efficiency after July with seasonal vegetation changes; alternatively it may reflect the average time it takes for larvae to contact a host and/or a build-up of unsuccessfully questing larvae while small rodents are typically scarce in May-July (Alibhai and Gipps 1985, Flowerdew 1985, Mallorie and Flowerdew 1994) and squirrels forage increasingly in the tree canopy, rather than on the ground, during the summer (Kenward and Tonkin 1986). This change in behaviour most probably accounts for the decline in numbers of both larvae and nymphs that feed on squirrels after the early summer (Fig. 3), despite the high availability of questing ticks of both stages at this time.

Despite the difficulties reviewed above, two clear conclusions emerge from this study. First the seasonal pattern of tick activity in this sheltered woodland habitat is unimodal and prolonged; ticks feed throughout the year without a decline in activity during the summer. This contrasts with the classical bimodal pattern usually ascribed to *I. ricinus* (for a review see Gray 1991) and with the unimodal pattern over a much narrower range of the year (April (nymphs) or May (larvae) to August) in the harsh climatic conditions of exposed hillsides (Steele and Randolph 1985). In Thetford Forest the relatively warm, humid conditions, even in winter, apparently allow tick activity throughout the year resulting in much less sharply defined cohorts than recorded in previous studies. Such a pattern implies more or less continuous development, although not at a uniform rate, which significantly increases the potential of the tick to transmit diseases both by decreasing the time between parasite acquisition and transmission by ticks and increasing the availability of ticks to hosts.

Secondly, squirrels are quantitatively more important hosts for both larval and nymphal *I. ricinus* than are small mammals, and, as they are also competent hosts for *B. burgdorferi* (Craine 1994), they are likely to make a significant contribution to the transmission of the Lyme disease spirochaete and to the distribution and abundance of infected ticks that pose a risk to humans (see Randolph and Craine 1995, for a detailed quantitative analysis). Interspecific variation in tick infestation levels has been related to the behaviour of the host as it affects its contact rate with ticks, specifically the ranging activity of hosts (Randolph 1975) in relation to the differential distribution of the tick stages in the habitat (Randolph and Steele 1985). Squirrels pick up more larval ticks than do small mammals probably because they forage over greater areas. The seasonal shift in habitat use by squirrels (see above), together with increasing population densities of small mammals (Fig. 4a), alters the relative importance of squirrels and small mammals as hosts to larvae from July onwards (Fig. 4b), but throughout the year squirrels remain overwhelmingly more important than mice as hosts to nymphs (Fig. 4c). This latter difference may be due more to the behaviour of ticks than of hosts. As nymphs quest higher in the vegetation than do larvae they are likely to miss the small rodents but contact larger hosts. The more humid the climatic conditions the higher ticks will be able to quest without the risk of desiccation (Lees and Milne 1951), which may explain the very much lower (and seasonally restricted) nymphal infestation of rodents in the humid conditions of Britain (mean 0.05 nymphs/host) than in the drier conditions of mainland Europe (mean 0.15–0.6 nymphs/host – Humair et al. 1993, De Boer et al. 1993, Matuschka et al. 1990, Talleklint et al. 1993). The diurnal activity patterns of vertebrates may also contribute to the observed differences. Ticks can only attach during coincident periods of host and tick activity; *I. ricinus* is more active during the day than the night (Lees and Milne 1951) and to some extent at dawn and dusk (R. van Es, pers. comm.), so diurnally active squirrels (Kenward and Tonkin 1986) will coincide with actively questing ticks to a greater extent than will the generally nocturnal, biphasically (dawn and dusk) active mice and voles (Wolton 1983, Montgomery and Gurnell 1985).

The observed intraspecific heterogeneity in tick infestation levels is likely to be the product of intraspecific variation in host behavioural factors, with more wide-ranging adult males picking up more ticks than juveniles or females (Randolph 1975, 1977, Don 1983). This interpretation is supported by the observation that certain hosts are more likely to pick up large numbers of both larvae and nymphs (Fig. 6). Density-dependent resistance to tick feeding, shown by *C. glareolus* but not by *Apodemus* spp. (Randolph 1979, 1994, Dizij and Kurtenbach 1995) and not yet investigated in larger hosts, will reduce the persistence of such heterogeneity beyond the hosts' first encounter with large numbers of ticks. The non-random distribution of ticks amongst their hosts has a significant impact on the transmission dynamics of tick-borne diseases (Randolph and Craine 1995).

Not until we have detailed data on the seasonal pattern of tick infestation levels on all the major hosts within a habitat can the full complexity of *B. burgdorferi* transmission by *I. ricinus* be described and modelled, and so yield reliable predictions of zoonotic risk. Deer and pheasants, for example, are two widespread and increasingly abundant species that are important as hosts to *I. ricinus*, the latter also implicated as a competent amplifying host for *B. burgdorferi* (Craine 1994), for which we have only limited, non-seasonal information as yet. This paper represents a first step towards a more complete quantitative description and understanding of tick-host relationships by highlighting the importance of a hitherto ignored host species, the grey squirrel. The ubiquity of various species of squirrels in Europe and America, frequently in habitats in close association with man, further raises the significance of these results.

Acknowledgements. This work was funded by support from the Natural Environment Research Council of Britain (to NGC and PAN) and the Royal Society, London (to SER). NGC is most grateful for the assistance of the Forestry Commission workers in Thetford Forest, particularly Mr R. Whittaker and Mr T. Venning.

REFERENCES

ALIBHAI S. K., GIPPS, J. H. W . 1985: The population dynamics of bank voles. Symp. zool. Soc. Lond., No. 55: 277–313.

CRAINE N. G. 1994: The epizootiology of Lyme disease. D. Phil. thesis, Oxford University, 145 pp.

DE BOER R., HOVIUS K. E., NOHLMANS M. K. E., GRAY J. S. 1993: The woodmouse (*Apodemus sylvaticus*) as a reservoir of tick-transmitted spirochetes (*Borrelia burgdorferi*) in the Netherlands. Zbl. Bakt. 279: 404–416.

DIZIJ A., KURTENBACH K. 1995: *Clethrionomys glareolus*, but not *Apodemus flavicollis*, acquires resistance to *Ixodes ricinus* L., the main vector of *Borrelia burgdorferi*. Parasite Immunol. 17: 177-183.

DON B. A. C. 1983: Home range characteristics and correlates in tree squirrels. Mammal Rev. 13: 123–132.

FLOWERDEW J. R. 1985: The population dynamics of wood mice and yellow-necked mice. Symp. zool. Soc. Lond., No. 55: 315–333.

GRAY J. S. 1991: The development and seasonal activity of the tick *Ixodes ricinus*: a vector of Lyme borreliosis. Rev. Med. Vet. Entomol. 79: 323–333.

GRAY J., KAHL O., JANETZKI C., STEIN J. 1992: Studies on the ecology of Lyme disease in a deer forest in County Galway, Ireland. J. Med. Entomol. 29: 915–920.

GURNELL J. 1983: Squirrel numbers and the abundance of tree seeds. Mammal Rev. 13: 133–148.

HUMAIR P. F., TURRIAN N., AESCHLIMANN A., GERN L. 1993: *Borrelia burgdorferi* in a focus of Lyme borreliosis: epizootiologic contribution of small mammals. Folia Parasitol. 40: 65–70.

KENWARD R. E., TONKIN M. 1986: Red and grey squirrels; some behavioural and biometric differences. J. Zool. Lond. 209: 279–281.

LEES A. D., MILNE A. 1951: The seasonal and diurnal activities of individual sheep ticks (*Ixodes ricinus* L.). Parasitology 41: 189–208.

MALLORIE H. C., FLOWERDEW J. R. 1994: Woodland small mammal population ecology in Britain: a preliminary reveiw of the Mammal Society survey of wood mice *Apodemus sylvaticus* and bank voles *Clethrionomys glareolus*, 1982–87. Mammal Rev. 24: 1–16.

MATHER T. N., WILSON M. L., MOORE S. I., RIBEIRO J. M. C., SPIELMAN A. 1989: Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete. Am. J. Epidemiol. 130: 143–150.

MATUSCHKA F. R., LANGE R., SPIELMAN S., RICHTER D., FISCHER P. 1990: Subadult *Ixodes ricinus* (Acari: Ixodidae) on rodents in West Germany. J. Med. Entomol. 27: 385–390.

MONTGOMERY W. I., GURNELL J. 1985: The behaviour of *Apodemus*. Symp. zool. Soc. Lond., No. 55: 89–115.

RANDOLPH S. E. 1975: Patterns of distribution of the tick *Ixodes trianguliceps* Burula on its hosts. J. Anim. Ecol. 44: 451–474.

RANDOLPH S. E. 1977: Changing spatial relationships in a population of *Apodemus sylvaticus* with the onset of breeding. J. Anim. Ecol. 46: 653–676.

RANDOLPH S. E. 1979: Population regulation in ticks: the role of acquired resistance in natural and unnatural hosts. Parasitology 79: 141–156.

RANDOLPH S. E. 1994: Density-dependent acquired resistance to ticks in natural hosts, independent of concurrent infection with *Babesia microti*. Parasitology 108: 413–419.

RANDOLPH S. E., CRAINE N. G. 1995: A general framework for comparative quantitative studies on the transmission of tick-borne diseases, using Lyme borreliosis in Europe as an example. J. Med. Entomol. (submitted).

RANDOLPH S. E., STEELE G. M. 1985: An experimental evaluation of conventional control measures against the sheep tick, *Ixodes ricinus* (L) (Acari: Ixodidae). II. The dynamics of the tick-host interaction. Bull. Entomol. Res. 75: 501–518.

SOKAL R., ROHLF F. J. 1981: Biometry. W. H. Freeman, San Francisco, 859 pp.

STEELE G. M., RANDOLPH S. E. 1985: An expererimental evaluation of conventional control measures against the sheep tick, *Ixodes ricinus* (L) (Acari: Ixodidae). I. A. unimodal seasonal activity pattern. Bull. Entomol. Res. 75: 489–499.

TALLEKLINT L., JAENSON T. G. T. 1993: Maintanence by hares of European *Borrelia burgdorferi* in ecosystems without rodents. J. Med. Entomol. 30: 273–276.

TALLEKLINT L., JAENSON T. G. T., MATHER T. N. 1993: Seasonal variation in the capacity of the bank vole to infect larval ticks (Acari: Ixodidae) with the Lyme disease spirochete, *Borrelia burgdorferi*. J. Med. Entomol. 30: 812–815.

WOLTON R. J. 1983: The activity of free ranging wood mice, *Apodemus sylvaticus*. J. Anim. Ecol. 52: 718–794.

Received 9 February 1995

Accepted 17 March 1995