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Original article

Tick (*Ixodes ricinus*) abundance and seasonality at recreational sites in the UK: Hazards in relation to fine-scale habitat types revealed by complementary sampling methods

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ABSTRACT

The seasonal risk to humans of picking up *Ixodes ricinus* ticks in different habitats at 3 recreational sites in the UK was assessed. A comprehensive range of vegetation types was sampled at 3-weekly intervals for 2 years, using standard blanket-dragging complemented by woollen leggings and square 'heel flags'. Ticks were found in all vegetation types sampled, including short grass close to car parks, but highest densities were consistently found in plots with trees present. Blankets picked up the greatest number of ticks, but heel flags provided important complementary counts of the immature stages in bracken plots; they showed clearly that the decline in tick numbers on blankets in early summer was due to the seasonal growth of vegetation that lifted the blanket clear of the typical questing height, but in reality ticks remained abundant through the summer. Leggings picked up only 11% of the total nymphs and 22% of total adults counted, but this still represented a significant hazard to humans. These results should prompt a greater awareness of the fine-scale distribution of this species in relation to human activities that determines the most likely zones of contact between humans and ticks. Risk communication may then be designed accordingly.

Introduction

The fundamental importance of sample size in the statistical analysis of ecological data dictates that environmental scientists tend to try to maximise the former in order to optimise the latter. Where acarology is concerned, this promotes a focus on sampling for ticks where they are most abundant and available – the tick-infested habitats within any given ecotype. Ticks, however, do not limit themselves to optimum conditions; indeed, optimum conditions for the tick collector may at least partly reflect the preferences of tick hosts at the time of drop-off, and not merely the environmental conditions most conducive to tick survival. Furthermore, in the context of human disease risk, it is more pertinent to consider areas where humans and ticks most often come into contact; given increasing awareness (and therefore attempted avoidance) of ticks and tick-borne disease, the obviously tick-infested areas may not be the most risky areas, despite being the most hazardous. Here we define 'hazard' as the level of the potential danger posed, and 'risk' as the combination of the level of danger and the degree of its likely impact on humans. A half-hectare patch of bracken (*Pteridium aquilinum* L., Dennstaedtiaceae) might harbour 10 times more questing ticks than a half-hectare patch of grass adjacent to it, but if humans are 50 times more likely to brush the grass than the bracken with their bare skin (e.g. for a picnic), then the bracken is more hazardous, the grass more risky.

The habitat in which ticks are found also determines the efficacy of any given sampling method (Ginsberg and Ewing, 1989a,b). Blanket dragging becomes decreasingly efficient as vegetation height increases, since the blanket is in contact with a diminishing proportion of the surface area of the substrate. The tick hazard for humans is best measured by collecting ticks on the investigator's clothing (Carey et al., 1980; Ginsberg and Ewing, 1989a,b), though using actual clothing such as cotton trousers (Ginsberg and Ewing, 1989b) may return smaller samples than custom-made garments of a fluffier material, such as wool (Gigon, 1985).

In this paper, we present results of a survey regime in which distinct habitats within each of 3 recreational sites in the UK were sampled for all stages of the sheep tick (*Ixodes ricinus* L., Ixodidae). *Borrelia burgdorferi* s.l., the causative agent of Lyme borreliosis, circulates to variable degrees at all sites, consistent with the general European pattern that these spirochaetes are present more or less wherever there are ticks. The purpose was not to focus on areas considered to harbour high densities of ticks, but rather to sample ticks from a selection of vegetation types representative of the whole site, using a variety of woollen collection devices that

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Table 1
Mean abundance of nymphal ticks counted on blankets and heel flags in each vegetation plot at each site over the highest 30 days encompassing the peak date.

Sites and vegetation plots	Blanket		Heel flags	
	Date of peak	Ticks per m^2	Date of peak	Ticks per m^2
Exmoor				
Mixed *Vaccinium*/heather in woodland	17. March	2.97	19. May	1.22
Vaccinium spp. in *Pinus* woodland	30. April	1.55	30. April	0.53
Vegetated woodland floor	30. April	1.39	19. May	0.90
Bracken on path edge bordering wood	10. April	1.99	1. July	2.68
Short grass by car park, bordering scrub	2. June	0.44	30. April	0.31
Heather in open near woodland	30. April	0.31	30. April	0.85
New Forest				
Bracken in mixed woodland	12. March	3.09	20. June	2.42
Grassy path edge in mixed woodland	9. May	1.09	20. June	0.22
Leaf litter on beech and oak woodland floor	30. May	0.34	1. May	0.22
Bracken in open	12. March	0.44	12. March	0.19
Short grass next to car park and woods	30. May	0.22	14. April	0.09
Heather in open	1. May	0.03	8. September	0.05
Richmond Park				
Bracken bordering woodland	18. May	1.36	18. May	1.35
Bracken in open woodland	2. April	0.86	18. May	0.44
Vegetated wood floor with long grass	6. May	0.49	6. May	0.19
Short grass within woodland	18. May	0.31	18. May	0.13
Short grass, path edge near bracken/wood	18. May	0.09	–	0
Rhododendron stand	6. May	0.02	6. May	0.19
Long rough grass in open	–	0	–	0

represent the full range of human contact surfaces better than does standard blanket dragging alone. The 3 sites represent a range of 'visitor awareness' with respect to ticks and Lyme disease (Jennifer Taylor, unpubl. observations), and the present observations of ticks will later be combined with independently collected contemporary data on the movement habits of human visitors in order to establish spatial and temporal patterns of disease risk and so direct appropriate risk communication strategies (Quine et al., in press).

Methods

The 3 fieldwork sites in southern England contrasted in both natural characteristics and recreational visitor use. In ascending order of the latter: (1) Webber's Post, near Luccombe, Exmoor National Park, a remote upland setting (3°35′W, 51°10′N), (2) Wilverley Plain, near Brockenhurst, New Forest, an accessible lowland woodland (1°34′W, 50°49′N), and (3) Richmond Park, Greater London, a peri-urban park (0°16′W, 51°26′N). Data were collected from March 2008 to December 2009 at 3-weekly intervals. Six to seven plots at each site were selected for sampling on the basis of their distinct vegetation types, as listed in Table 1.

Ticks were counted by dragging a white woollen blanket measuring 100 cm long × 75 cm wide across the vegetation surface and were also collected simultaneously from woollen leggings worn by the investigator. To the hem of each heel of the leggings was attached by Velcro a 25 cm × 25 cm square of wool for sampling the vegetation at ground level (Fig. 1). In tall but sparse vegetation, such as bracken, these square flags sampled a different level of the substrate from the blanket; in shorter and denser vegetation the 2 methods sampled similar parts of the tick's habitat, but the smaller heel flags had a lower probability of contacting the relatively sparsely distributed ticks. The blanket was held to the side of the investigator using a stiff, wooden rod, rather than dragged behind, so as to avoid competition with the heel flags or leggings for the same ticks. The sampling methods were thus simultaneous, but in parallel. Ticks were removed and counted at the end of each of 10 replicates of 5-m transects per plot on each visit (i.e. a total of 50 m of transects per plot). Larvae, however, were not counted on the leggings because of the difficulty of quick but reliable inspection in the field. At each plot visit, vegetation height was measured with a metre rule at the start of each transect. Soil moisture was recorded at 5 points using a Theta Probe (Delta-T Devices, Cambridge, UK); relative humidity and temperature at ground level and 50 cm above ground were measured using Tinytag TH-2500 thermohygrometer (www.tinytag.info), and weather conditions were noted. Such snapshots of moisture and temperature conditions are useful only to give a very general impression of the overall seasonal progression and to flag up any unusual weather.

Within each plot, the data were combined into 2-year means. To overcome the fact that ticks were not sampled at each site on the same days in each year, the data series were converted to daily values using a simple linear interpolation. Indices of mean abundance were based on these 2-year mean daily values throughout the full calendar year to accommodate the variable seasonal patterns (see below). Within-site, between-plot comparisons were made using

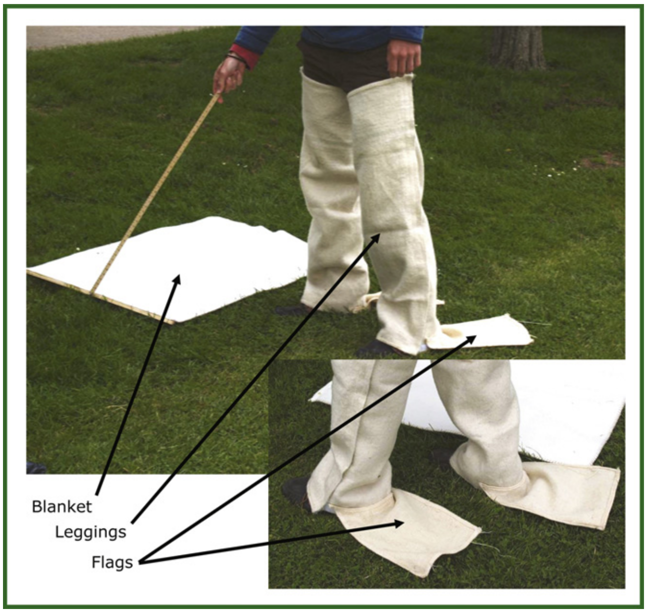

Fig. 1. The three sampling methods shown as used, with the blanket dragged in parallel with the leggings and heel flags.

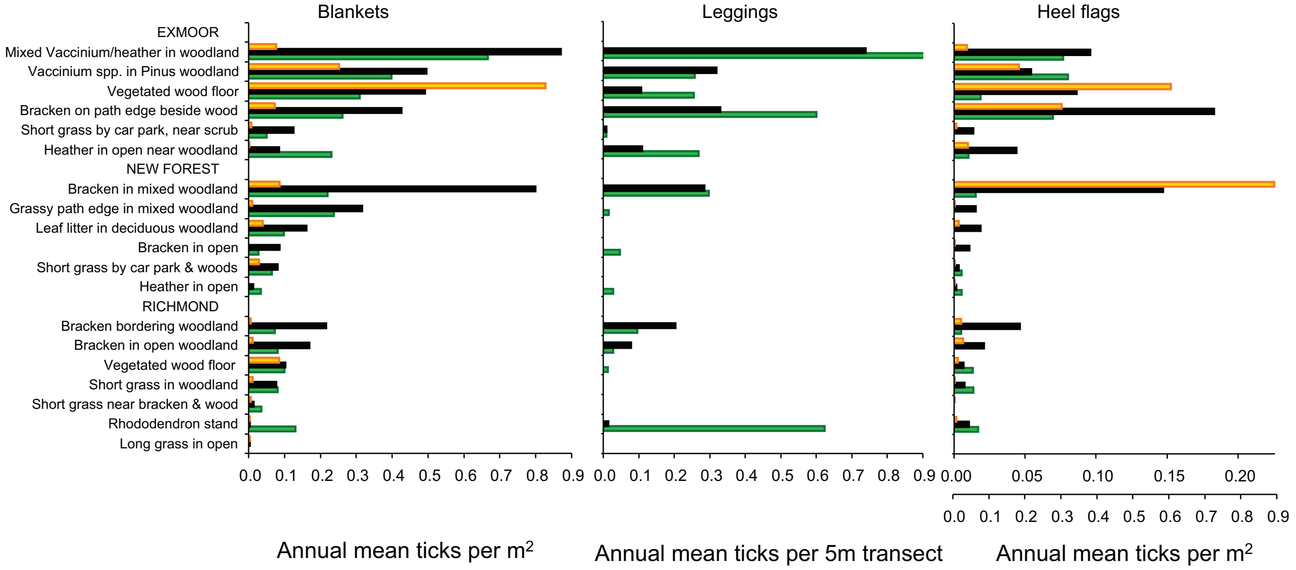

Fig. 2. Mean abundance of *Ixodes ricinus* larvae (gold), nymphs (black), and adults (green) in each vegetation plot over both survey years from each sampling method. For comparability, larvae are rescaled at 1/10 and adults at 5×. Two *x*-axes are shown for the heel flags, representing the 2 extremes of estimates of the relative sampling intensity for flags vs. blanket (see 'Methods').

Wilcoxon signed-rank tests on the raw data, as they were collected simultaneously within each site. The apparent mean densities of ticks measured by each of the 3 sampling methods (blanket, leggings, and heel flags) in each vegetation type were calculated to assess the relative likelihood of humans picking up ticks on different parts of their clothing while walking in different habitats. While numbers of ticks counted on the blanket and heel flags can be translated into densities according to the area swept by each piece of cloth per 5-m transect, those on the leggings cannot and are presented simply as numbers per 5-m transects. It is a moot point, however, whether to adjust the area sampled by the 2 flags relative to the blanket according to their leading edges to give relative measures of the area swept or according to their total areas to account for the much briefer contact time as the small flags pass over the vegetation. The former gives a ratio of 1.5 (0.25 m per flag vs. 0.75 m) and the latter a ratio of 6.0 (0.25 m × 0.25 m per flag vs. 0.75 m × 1 m). As the true ratio probably lies somewhere in between, both measures are presented in Fig. 2.

Results

The ratio of total numbers of ticks of each instar counted (24,507 larvae, 6827 nymphs, and 1037 adults) was broadly in line with biological expectations (100:10:2), given that larvae were not counted on the leggings. Likewise, the overall ratio of adult males to females was 1:0.87 (males persist on vegetation for longer, looking for repeat matings). Nymphs will therefore be used to illustrate some of the results, as these pose the most significant health risk to humans (Robertson et al., 2000), except where stage-specific biology raises additional points.

Comparisons between sites

Overall, tick abundance was highest at the Exmoor site, followed by the New Forest, then Richmond Park (Fig. 2). Given the similarity of the temperature and relative humidity recorded in the field (Fig. 3), differential host density is likely to be the major contributing factor to inter-site differences. Although not measured during this study, deer density is known to be unusually high on Exmoor and lowest in Richmond Park despite the managed herds of fallow deer (*Dama dama* L., Cervidae) there. Curiously, of the sampled plots, the least tick-infested was an area of long grass commonly occupied by deer in Richmond Park, where only a single nymph was found in 2008 (sampling was abandoned for 2009).

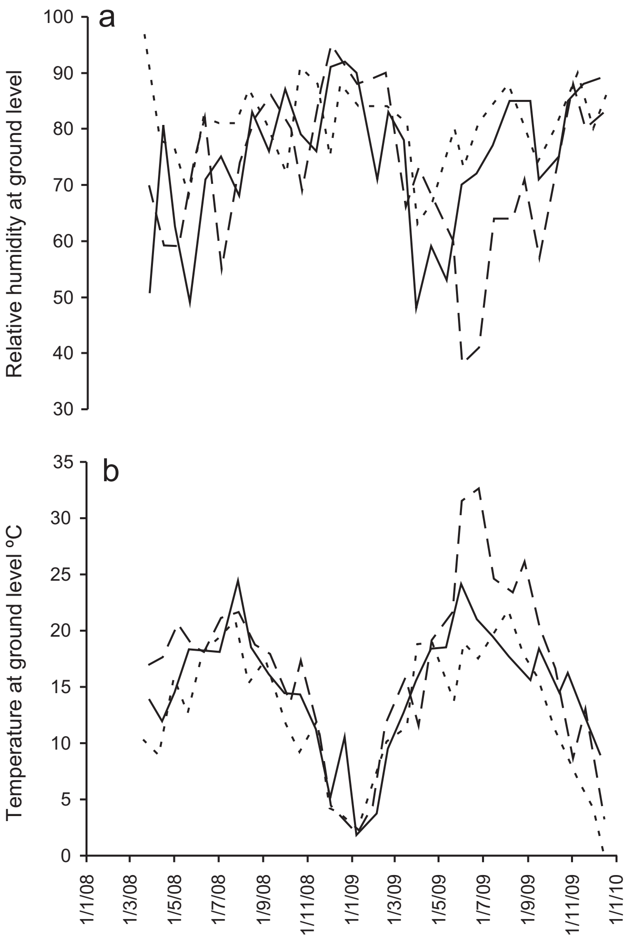

Fig. 3. Relative humidity (a) and temperature (b) measured during tick sampling at equivalent vegetation plots (relatively sheltered short grass, close to woodland) at Exmoor (dotted line), New Forest (solid line), and Richmond (dashed line).

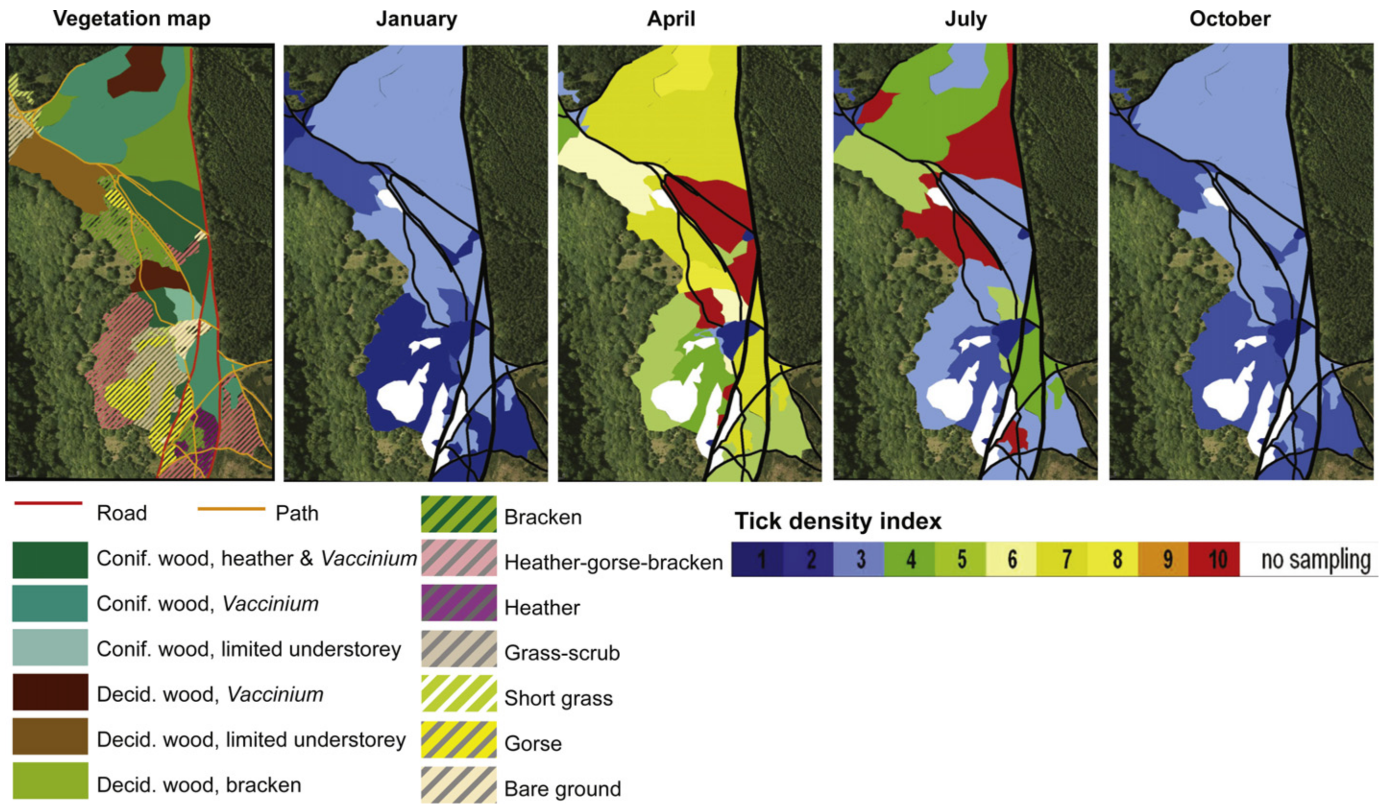

Fig. 4. Maps to illustrate the potential use of knowledge of land cover and seasonal tick hazards according to vegetation type on Exmoor. Taking the average for the 2 sample years, mean monthly counts of nymphs in each plot were rescaled to give values of 1–10 separately for blanket, heel flags, and legging samples. For each plot-month, the 3 values for these sampling methods (equal weighting in this case, but easily adjustable) were averaged to produce a combined relative risk value.

Comparisons between plots/habitats

Across sites, the presence of trees typically increased tick abundance for any given ground vegetation; of the 2 bracken plots in the New Forest, that in the woodland had higher tick density (nymphs on blankets: 0.846 m^{-2}) than that in the open (0.086 m^{-2}; Wilcoxon signed-rank test, $P < 0.001$), and the same applied to heather plots at Exmoor (wooded: 0.874 m^{-2}; open: 0.089 m^{-2}; $P < 0.001$) (Fig. 2). Taking the results from the blankets (vegetation surface) and heel flags (lower in the vegetation) together (Fig. 2), it is clear that short grass, even when bordering woodland, is generally less favourable than shrub-level vegetation as a habitat for ticks, as is well known due to the drier microclimate there, but it is not safe to assume an absence of ticks in such places where people often sit. Areas of heather in the open, which tend to be very dry at ground level and through which people commonly walk, also have low tick densities, especially of immature stages.

The numbers of nymphal ticks picked up by blankets and heel flags at times of peak seasonal abundance (Table 1) give a better measure of the highest levels of hazard for humans than do overall annual means. Thus, although short grass is clearly not a favourable habitat for ticks, nevertheless at certain times of the year ticks may be sufficiently abundant to constitute a risk to humans (see below).

Using a simple Geographical Information System (GIS), these sorts of results may be extended to adjacent local areas of similar habitat types to produce maps of relative hazard in different parts of recreational sites in relation to seasonal visitor activities (Fig. 4 for an example for the area around Webber's Post in Exmoor), although we would caution against extrapolating to larger spatial scales, where host density and macroclimate may be different.

At all 3 sites, there was a general tendency for tick activity to start earlier in the year in shrub and woodland plots than in nearby plots with short grass or heather, although vegetated wood floor was similar to heather (Fig. 5). The abundance of nymphs declined sharply in each vegetation plot approximately 4 months after the onset of questing, possibly due to exhaustion of fat (energy) reserves. This decline started earlier (after 3 months) in bracken, however, perhaps reflecting the decline in sampling efficiency as bracken grows (see below). In contrast, nymphs in short grass per-

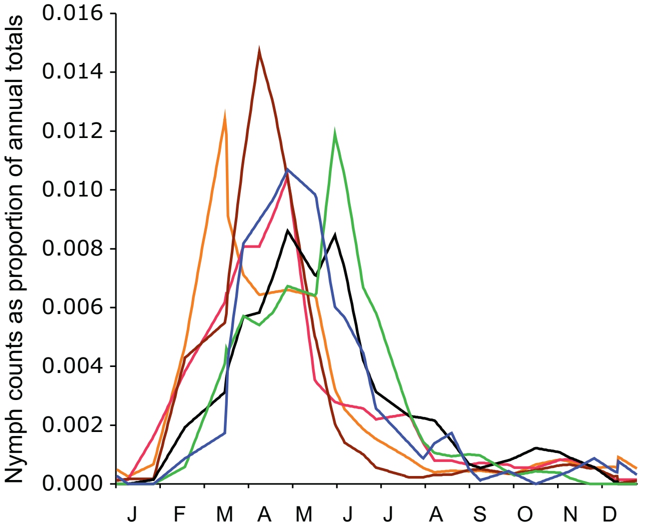

Fig. 5. Mean seasonal profile of the abundance of *Ixodes ricinus* nymphs counted on blankets in each vegetation plot at Exmoor. The 2-year mean count for each day of the year is expressed as the proportion of the annual mean total per plot. Mixed *Vaccinium*/heather woodland shrubs (orange), *Vaccinium* in *Pinus* woods (red), bracken in woods (brown), vegetated woodland floor (black), short grass (green), heather in the open (blue).

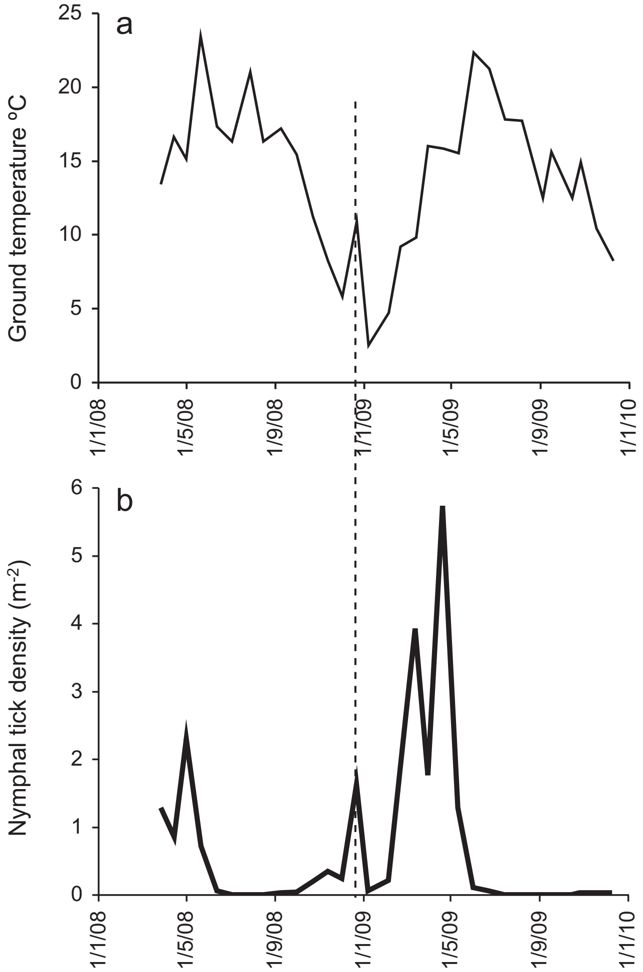

Fig. 6. Ground temperature (a) measured at field visits to the woodland bracken plot in the New Forest and densities of *Ixodes ricinus* nymphs (b) at the same plot. The dashed vertical line identifies the anomalous warm day and coincident spike of tick activity in December 2008.

sisted for rather longer. A spike in nymph and adult density in the New Forest seen on 22 December 2008 (in all plots but most obviously in the wooded bracken plot, Fig. 6 for nymphs) coincided with an anomalous rise in temperature, indicating that a period of warm temperature in winter could cause temporary activation of quiescent ticks (see ‘Discussion’).

Comparisons between sampling methods for different tick stages

The different sampling methods yielded complementary information on the presence of ticks in different parts of the vegetation (Fig. 2) and at different times of the year, reflecting the combination of vegetation structure and tick biology. Despite uncertainty in the estimated absolute apparent densities applicable to heel flags (see ‘Methods’), certain clear patterns emerge. Obviously the leggings were not appropriate for sampling ticks in the short grass/leaf litter plots (NB larvae not counted). Predictably, heel flags were much worse than the blanket at picking up adult ticks in tall vegetation (e.g. bracken in woodland in the New Forest, flags 0.002 ticks m^{-2} vs. blanket 0.047 ticks m^{-2}; Wilcoxon rank-sum test, $P = 0.0031$), reflecting the greater time adult ticks spend questing high up in the vegetation where possible. For the immature stages, the flags also picked up rather fewer ticks than did the blankets in most habitats, perhaps due to the ticks’ precise questing heights or the speed with which flags passed over the vegetation even during slow walking; this was particularly marked in short grass for all tick stages (Wilcoxon rank-sum test, $P < 0.05$), perhaps due to the small area of the flags relative to the low density of ticks. They were, however, especially useful for both immature stages along the bracken-edged path and in the open heather at Exmoor, and also for larvae in bracken in woodlands in the New Forest (see below).

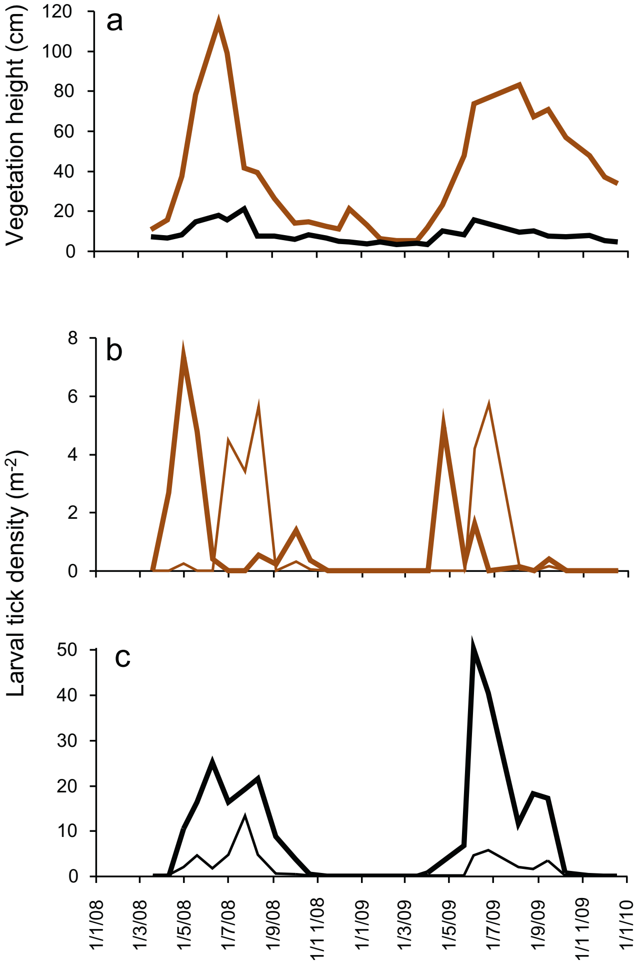

Fig. 7. Effect of vegetation height (a) in bracken (brown) or on a vegetated woodland floor (black) in Exmoor on the differential seasonal patterns of the abundance of *Ixodes ricinus* larvae recorded by blanket (thick line) and heel flags (thin line) in woodland bracken (b) or vegetated woodland floor (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

Seasonal patterns detected by the 3 sampling methods were generally similar, apart from in the woodland bracken plots at the New Forest and Exmoor, where larval counts from blanket and heel flags demonstrated strongly contrasting patterns. When the bracken grew up from May onwards (Fig. 7a), larvae were no longer accessible to blankets skimming the top of the vegetation, but were still picked up by heel flags (Fig. 7b). In contrast, where vegetation on the woodland floor did not change height so dramatically, larvae were picked up by both the blanket and heel flags throughout the summer and early autumn (Fig. 7c). Nymphs were also affected in this way but to a lesser degree, and leggings continued to sample this stage relatively better than did the blanket through June and July (i.e. counts on leggings did not show the same decline).

Discussion

Complementary information from different sampling methods

Dragging a blanket across the perceived most favourable vegetation type is the standard method for collecting data on *I. ricinus* population ecology. The results of this study show clearly how the quality of such data and their usefulness in assessing tick hazards for humans may be diminished by missing ticks in other types of vegetation and in different parts of the vegetation as its structure changes seasonally. While blankets are almost always more 'efficient' in crude numerical terms, the data they return are not always accurately representational. By augmenting blanket dragging with heel flags and leggings, we were able to assess more thoroughly and realistically the risk of humans coming into contact with ticks. The most appropriate method of sampling varies with the physical nature of a tick's habitat and the tick stage of most interest, given the vertical separation of their questing positions (Gigon, 1985; Ginsberg and Ewing, 1989b; Mejlon and Jaenson, 1997). It also depends upon the exact purpose of the study, in this case to determine more precisely than usual whether some parts of recreational woodlands are free of tick hazard during the main visitor season.

The leggings were almost as good as blankets at picking up nymphs and adults from the higher vegetation, although predictably useless in low vegetation (Fig. 2), but added little extra information on tick presence and abundance. Nevertheless, as a measure of how many ticks might be picked up on legs while people walk through moderately high vegetation (as opposed to purposefully seeking out ticks with a blanket), the leggings give some indication of the proportion of such ticks that may attach to humans. On average over the 2 years during May–July, 4.4 nymphs and 0.9 adults would have been removed daily from leggings per 50-m transect in bracken in the New Forest woodland (with a further 5.4 nymphs and 0.7 adults in February–April), compared with a mean of 1.26 ticks (nymphs and adults) per person removed at a clinic in the same location during April–October (the vast majority during May–July) in 1996 and 1997 (Robertson et al., 2000). Presuming that tick abundance has not increased hugely over the intervening decade, this suggests either that only a small fraction of ticks that climb onto trouser legs during a full-length walk in such a habitat at this site go on to attach to humans, or that most people pick up ticks from habitats with far lower tick densities. Observations of visitor habits support the latter explanation, as visitors favour areas of accessible short vegetation, in particular open grassy areas, over tall or prickly vegetation (Picozzi, 1971) and remain on paths for the majority, if not all of their visit (Jennifer Taylor, unpubl. observations). It is presumed, but never tested, that wearing long trousers is protective, but ticks may not be able to cling on to bare skin, hairy or not, as well as to cloth, depending on its texture.

It was equally predictable that heel flags would be better at picking up larvae that quest close to the ground, but less good for nymphs and adults in any vegetation that allows these stages to quest at levels of above c. 10 cm. Curiously, on the very substrates – short grass and leaf litter – that we might predict to be sampled at least as well by heel flags as by blankets, the apparent mean density for all stages was much higher from blanket counts than heel flag counts (Fig. 2) (e.g. New Forest, mean for both substrates: larvae: blanket 0.336 ticks m^{-2} vs. flag 0.017–0.068 ticks m^{-2}; nymphs: blanket 0.120 ticks m^{-2} vs. flag 0.011–0.044 m^{-2}; adults: blanket 0.016 ticks m^{-2} vs. flag 0.001–0.004 ticks m^{-2}, depending on the relative sampling intensity–see 'Methods'). Given the very low density of ticks in these habitats and also their typically aggregated distribution, heel flags are clearly too small to sample ticks adequately. In addition, while heel flags pass through the vegetation relatively rapidly, the greater weight of the dragged blanket may flatten the vegetation in places, hence ensuring contact with more than just the very tips of the vegetation. The advantage of the heel flags, however, is demonstrated in Fig. 7; as vegetation height increases, the blanket can no longer remain in contact with areas where ticks are questing, whereas the heel flags sample the same area regardless of vegetation height. This affected both immature stages, but was less marked for nymphs, presumably because they quest at higher levels and also their major spring activity season occurs earlier before the bracken has grown so high. Interestingly, larvae were scarce on heel flags in bracken in April–May when they were most abundant on blankets (Fig. 7b), suggesting that even larvae may quest above heel level when conditions are sufficiently moist. Given the preponderance of studies based on blanket dragging in bracken, a well-recognised prime habitat for ticks, supplementing information on the seasonal abundance of ticks with samples from heel flags would be valuable for answering questions in both science and public health. This comparative study clearly relates the earlier disappearance of ticks collected by blankets from bracken to seasonal vegetation structure rather than to desiccation or energy depletion in drier, warmer conditions (Randolph and Steele, 1985).

Tick traps baited with carbon dioxide may be the most unbiased method for making between-habitat comparisons. Although Ginsberg and Ewing (1989a) reported that *I. dammini* (*I. scapularis* Say, Ixodidae) ticks did not respond to the traps as well as individuals of *Amblyomma americanum* L. (Ixodidae), such a trap compared favourably with blanket dragging for all stages of *I. ricinus* (Gray, 1985).

Tick hazard across plots and sites

The relatively small-scale, intensive data presented here for each habitat are strictly comparable because they were collected by the same person over the same short period, unlike a previous large-scale, extensive tick and Lyme borreliosis habitat assessment based on a retrospective gathering of data from 105 habitats in 16 countries across Europe (Gray et al., 1998). The finding that the wooded plots tended to contain more ticks than their non-wooded counterparts is consistent with many previous observations spanning many decades in both the Old and the New World (inter alia Daniel et al., 1977; Eisen et al., 2010) and is unsurprising. The presence of trees inhibits wind, therefore reducing saturation deficit (Gray, 1991), which enables ticks to quest for longer periods (Perret et al., 2000) and at higher levels in the vegetation while using less energy (Randolph and Storey, 1999). Furthermore, trees and their attendant seed crops may attract a wider diversity and higher abundance of host species upon which ticks can feed (Jones et al., 1998). More noteworthy than the specific location of the most tick-infested habitats was the range of vegetation types across which ticks were found in significant numbers. The short grass plots close to the car parks at Exmoor and the New Forest, for example, offer a much more exposed substrate than the rough unimproved hill grazings long associated with ticks (Milne, 1946), but during the shoulder and peak recreation demand season (March–August), the density of nymphs there (on the blanket, Exmoor, 0.232 m^{-2} and New Forest, 0.113 m^{-2}) was comparable with that in the woodland under-storey vegetation at Richmond Park (0.181 m^{-2}). This is non-trivial, given that humans are far more likely to spend longer periods in, and make closer skin contact with, the ostensibly innocuous short grass next to a quiet car park (for resting, sun-bathing, picnics, etc.) than with the rough vegetation in a public park studded with signs warning of ticks and Lyme disease, particularly during seasons that coincide with high tick activity. In combination with land cover maps and knowledge of visitor pressure, more extensive maps derived here from intensive field sampling (Fig. 4) allow a better assessment of the relative overall risks within each recreational site. Indeed, even were any given woodland to harbour tick densities 5 times greater than those in a nearby patch of short grass, management attention (be it active tick control measures or simply signage) would be better focussed on the short grass, where the preference and concentration of visitor activities is greatest and people's expectation of tick hazard is low.

Ticks are limited by both abiotic (climatic, land cover) and biotic (host) factors; in the UK, there are many areas of abiotically suitable habitats that do not house *I. ricinus* evidently related to their small patch size, thought to be too small to house resident populations of deer or other large hosts for adult *I. ricinus* (S.E. Randolph, unpubl. observations). In this study, we showed that ticks spill out of ideal woodland habitats into a broad range of vegetation types nearby. They must be deposited there by dropping engorged from hosts and then survive through their long development period to quest again as hungry ticks. The seasonal patterns (Fig. 5) indicate that questing ticks survive in short grass and heather through the summer no less well than in more wooded habitats. It is not known, however, whether such sub-populations are self-sustaining or depend on repeated input from woodland tick populations carried by hosts moving between the two (Boyard et al., 2008). A study in France showed that the greater the distance from woodlands and the less the sheltering vegetation such as hedgerows, however, the fewer the ticks there are (Boyard et al., 2007, 2008). The popular misconception of a handful of tick hotspots in the UK is no longer tenable at either the large or small scale; ticks are known to be widely distributed across much of the UK (Scharlemann et al., 2008), while the present intensive sampling has revealed the ubiquity of *I. ricinus* for much of the year, albeit at different densities, in the broad range of vegetation types present in the 3 study areas.

Human visitor pressure in accessible recreational areas and popular visitor attractions such as the New Forest is high relative to other rural locations; the New Forest is the most densely visited of all the National Parks (estimated at 13.5 million visitor days annually, equal to 7.5 visits/km^2/year for the whole area, but unevenly distributed – http://www.newforestnpa.gov.uk/tourism-1-factsandfiguresweb.pdf), while that of peri-urban Richmond Park is very much higher (estimated at about 4–4.5 million visits equal to >419,000 visits/km^2/year–Simon Richards, park manager, pers. communication). This raises one part of the basic 2-part equation for tick-borne disease risk (risk = infected tick density × human exposure). Ticks are relatively scarce in Richmond Park, but human exposure is exceptionally high, while ticks in the New Forest are no more abundant than in other prime deer habitats in the UK (Randolph et al., 2002). The infection prevalence of *B. burgdorferi* s.l. in nymphal ticks (with adults in parenthesis) collected during this study was 2.8% (5.9%) in Richmond Park, 6.0% (7.0%) on Exmoor, and 7.8% (33.0%) in the New Forest, within the range observed elsewhere in the UK (Vollmer et al., 2011) and in mainland Europe (Hubálek and Halouzka, 1998). We see no biological reason to suppose, nor epidemiological data to suggest, that the New Forest, for example, is any more hazardous than large patches of similar woodland elsewhere in the UK, despite its reputation as a hotspot for ticks and Lyme disease. Any excess in the numbers of cases identified in this area (and in Thetford Forest with a similar reputation), which is in any case not apparent from the available epidemiological data, appears to be due to the frequency of human visits rather than infected ticks. The risk per person is not higher. It should also be noted that raising the awareness of tick-borne disease is liable to turn into a self-fulfilling prophecy, since positive diagnosis will result from greater awareness of disease aetiology and symptoms.

Seasonal patterns

The results for January and February were drawn from 2009 only as sampling did not start until March 2008, but daily maximum and minimum temperatures during the spring (from second week of February) were very similar in 2008 and 2009 in SW England. Patterns of seasonal activity (Fig. 5) followed those previously recorded for southern England (Randolph et al., 2002), but did not conform to the suggestion (based on a review of 15 different unspecified locations) that nymphs and adults become active first in the most exposed habitats (Gray, 1991). On the contrary, at all 3 sites, tick activity started earlier in shrub and woodland plots than nearby plots with short grass. Unless this is an artefact of low tick density making the spring rise less detectable, it may reflect the tick's responses to the more buffered (i.e. generally warmer) temperatures of early spring in sheltering woody cover. At the other end of the season, however, nymphs persisted for rather longer in short grass than in other habitats, perhaps because they used less energy in ascending the shorter vegetation, and/or because lower host density there leaves ticks questing for longer.

The data shown in Fig. 6 provide evidence of the opportunistic nature of tick quiescence once behavioural diapause is terminated (Belozerov, 1982); a brief spike of tick activity in late December 2008 (after the winter solstice) coincided with an obvious warm period. Questing by nymphs in winter as long as daily maximum temperatures exceed the threshold (c. 7 °C) is well recorded (Randolph et al., 2002; Dautel et al., 2008) and should not be viewed as an anomalous finding. More experimental investigations are needed to define the precise interactions of natural day length, thought to be the cue for both onset and cessation of behavioural diapause (Belozerov, 1982), and natural diurnal temperatures that permit such apparently opportunistic questing. Empirically, the present observation fits the current suggestion that activity may be resumed if temperature is high enough, and day length is no longer shortening (Randolph, 2004). Such ticks may, however, pay the penalty of using up their non-renewable energy supplies earlier in the main questing season, as these are thought to be sufficient for only 4 months of activity by nymphs (Steele and Randolph, 1985; Randolph and Storey, 1999).

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