

ORIGINAL PAPER

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Influence of saturation deficit and temperature on *Ixodes ricinus* tick questing activity in a Lyme borreliosis-endemic area (Switzerland)

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Abstract Questing *Ixodes ricinus* ticks were sampled monthly in a periurban mixed forest at Neuchâtel, Switzerland, in 1996, 1997, and 1998. A total of 5530 *I. ricinus* nymphs and 1385 adults were collected. The emergence of questing tick populations in spring varied among years in relation to the air temperature. The monthly variation in questing nymph density was negatively correlated with the saturation deficit; there was a strong decrease in tick numbers in late spring and summer as soon as the saturation deficit increased. A variation in tick density in relation to the saturation deficit was also observed between years; the tick density was high when the saturation deficit was low during spring and summer (1997) and was low when the saturation deficit was high (1998). During the 3-year study period, marked climatic differences among years highlighted the influence of temperature and saturation deficit on the phenology of ticks.

Introduction

The tick *Ixodes ricinus* is widespread in Europe, where it has been recognized as an important vector of numerous human and/or animal pathogens, including viruses (e.g., tick-borne encephalitis virus), bacteria (e.g., *Borrelia burgdorferi* sl., *Rickettsia* spp.), and protozoans (e.g., *Babesia* sp., *Trypanosoma* sp.; Aeschlimann et al. 1979, 1986).

Since the 1930s the behavior of free-living stages of *I. ricinus* has been studied at both the population level and the individual level using experimental designs

either in the field (Milne 1950; Mermod et al. 1973; Gigon 1985; Gray 1987) or in controlled environments (MacLeod 1935, 1936; Lees and Milne 1951; Gigon 1985). In most of these papers, temperature and relative humidity were considered to be explanatory variables for tick survival and behavior. However, Randolph and Storey (1999) recently showed that saturation deficit influences questing behavior. As questing behavior determines tick density as well as population size, we investigated the influence of saturation deficit on tick density in a field study. Tick data were obtained from an ongoing survey (Perret et al., manuscript in preparation) on the ecoepidemiology of *B. burgdorferi* in a natural focus in Neuchâtel, Switzerland.

Materials and methods

Sampling of questing ticks

The study site is a mixed forest (deciduous-dominant) situated at 47°01'N and 06°56'E on the slope of a mountain reaching 1000 m in altitude and exposed to the south in the periurban area of Neuchâtel, Switzerland. Its elevation is 550 m above sea level. Questing ticks were sampled by dragging of a white flannel flag (contact surface 1 m²) over the low vegetation. Every 25 m (10 m in 1996) the flag was examined for ticks. Host-seeking nymphs and adults were collected once a month from January 1996 to December 1997 and from April 1998 to December 1998. Rainy and windy days were excluded from sampling. Sampling was conducted between 1:00 and 4:00 p.m.. In 1996 and 1997, ticks were sampled on one side of a 375-m-long circular footpath. In 1998 the sampling area was extended to a 1049-m-long circular footpath that included 250 m of the footpath examined in 1996 and 1997. Ticks were identified according to species, stage, and sex. Tick density was expressed in numbers of ticks per 100 m².

Climatic data

Climatic data were recorded in the city of Neuchâtel, approximately 500 m from the study site, by an automatic station at the Observatoire Cantonal de Neuchâtel. Data were kindly provided by Mr. G. Jornod and Dr. G. Miletì. The average daily saturation deficit was calculated using the following formula:

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$$SD = (1 - RH/100) \times 4.9463 \times e^{(0.0621 \times T)}$$

where SD represents the saturation deficit in millimeters of mercury, RH represents the daily average relative humidity in percent, and T represents the daily average temperature in degrees Celsius. The saturation deficit and the daily maximal and average temperatures were recorded for each day as a 30-day moving average. This was calculated using the values noted for the day of measurement and those recorded for the preceding 29 days. To compare our data with those obtained by MacLeod (1936) we also calculated the 5-day moving average for the daily maximal temperature.

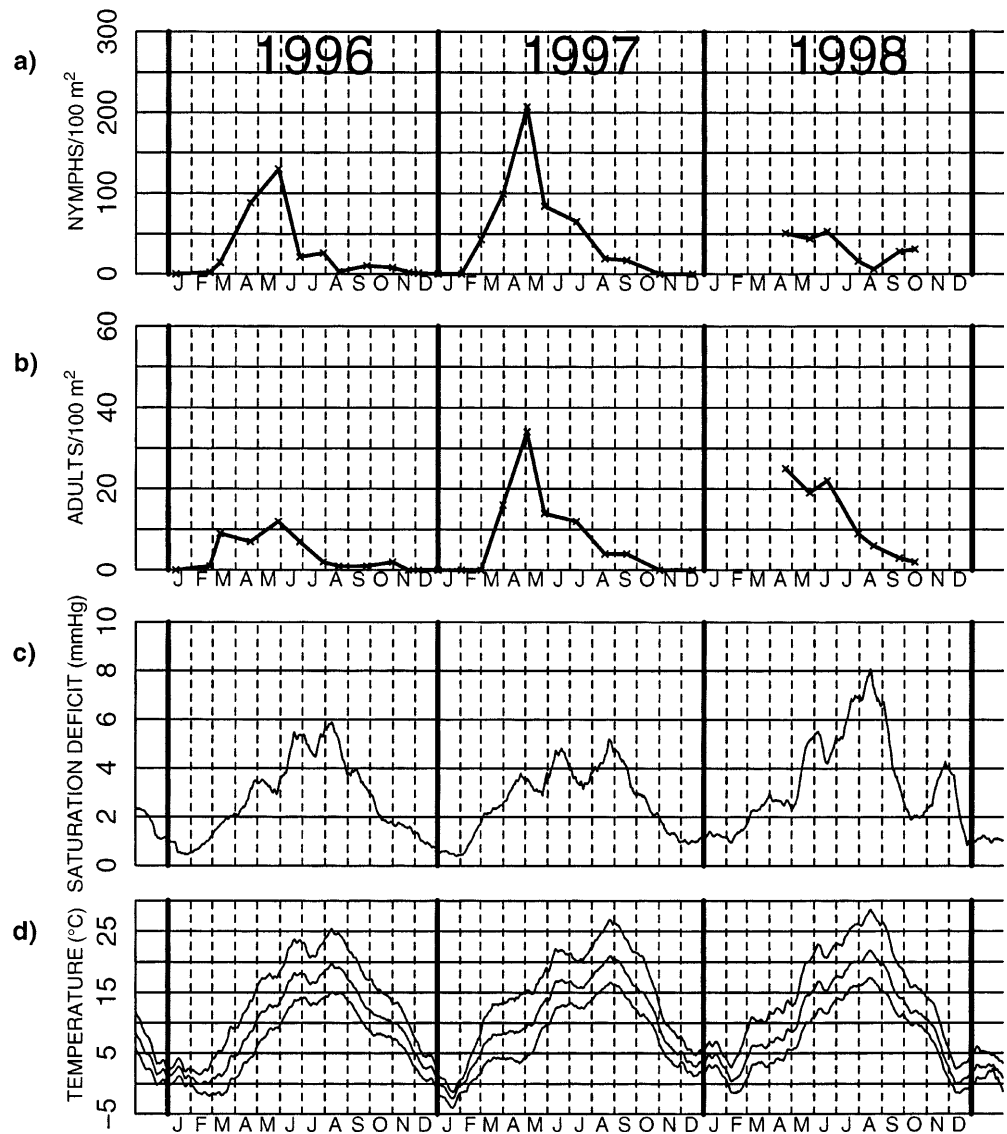
Pearson's correlation (r) between questing nymph density and saturation deficit was calculated using the statistical package R for Linux (version 0.64.2). The questing nymph density was log-transformed to reduce variance heterogeneity. The saturation deficit was calculated by averaging of the values noted for the sampling day and those recorded for the preceding 29, 16, 9, and 4 days. Pearson's correlation between the questing nymph density and the saturation deficit for the sampling day alone was also calculated. Pearson's correlation was also determined between the log-transformed questing nymph density and the 30-day average relative humidity.

Results

Questing ticks

During 1996–1998 a total of 5530 *Ixodes ricinus* nymphs and 1385 adults were collected. Ticks could be collected from the end of February to the beginning of December. The density of questing ticks varied considerably among years, reaching maxima of 130, 207, and 53 nymphs/100 m² and 12, 34, and 25 adults/100 m² in 1996, 1997, and 1998, respectively (Fig. 1a, b). The questing population showed a major spring peak at the end of May 1996 and at the beginning of May 1997. In 1998 the pattern was different for nymphs, with a low population persisting from April to June, decreasing in July, and increasing again in September. In 1997 the onset (early March) and the peak (early May) of tick activity were advanced by nearly 1 month as compared with the onset

Fig. 1a–d Questing tick density and average climatic conditions as recorded in 1996, 1997, and 1998, including **a** numbers of questing nymphs, **b** numbers of questing adults, **c** 30-day moving average values noted for saturation deficit, and **d** 30-day moving average values recorded for the daily minimal, average, and maximal temperature



and peak of tick activity in 1996 (middle of March and end of May, respectively).

Climatic data

The saturation deficit and the daily temperatures were calculated as 30-day moving averages (Fig. 1c, d). Significant climatic differences between years were observed; 1998 was the warmest and driest year, especially in May and July through August, whereas 1997 was the wettest year, particularly during summer. The spring seasons of 1997 (March) and 1998 (March) were warmer than that of 1996 (March; Fig. 1d).

Relationships between climatic data and questing tick activity

Questing ticks could not be collected when the daily maximal temperature was at or below 1.9 °C, and ticks were always collected when the temperature reached or exceeded 10.5 °C. At temperatures ranging between 6.6° and 8 °C, ticks were only occasionally collected (data not shown). Questing ticks could not be collected when daily average temperatures were at or below -1.2 °C, and ticks were always collected when the temperature reached or exceeded 5.2 °C. At temperatures ranging between 1.9° and 3.8 °C, ticks were only occasionally collected (data not shown). A 5-day average of the daily maximal temperature allowed us to discriminate between days with and days without tick activity. Indeed, when the 5-day average of the daily maximal temperature was over 7 °C, questing tick activity was observed (Fig. 2).

The saturation deficit reached high values during the summer in 1996 and 1997 (Fig. 1c), after the peak of questing ticks (April through May), whereas in 1998 it reached a high level by May, and no peak of questing nymphs was observed during this period, but an increase

in nymphal density was observed in the autumn of 1998, when the saturation deficit decreased. In 1998 the number of questing adults was not reduced in spring, and no increase in the questing adult population was observed in autumn.

Pearson's correlation between saturation deficit and questing nymph density was calculated for the pooled data recorded from April to September of the years 1996–1998 ($r = -0.64$). Further statistical analysis was not possible due to the time dependence of the data and the brevity of the study period. Pearson's correlation as calculated for the 17-, 10-, and 5-day average saturation deficit was $r = -0.38$, $r = -0.38$, and $r = -0.33$, respectively. The saturation deficit during the day of sampling was not correlated with the number of questing nymphs ($r = -0.008$).

Unlike the correlation found between the saturation deficit and the nymph density, no correlation was observed between the 30-day average values recorded for relative humidity and nymph density ($r = -0.04$).

Discussion

In the area studied (Neuchâtel, Switzerland) the springtime maximal questing densities recorded for *Ixodes ricinus* were among the highest values recently measured in Europe (usually fewer than 100 nymphs/100 m² and fewer than 15 adults/100 m²; Gray et al. 1998). The impact of intensive sampling on the tick population itself is difficult to assess. However, the flag impact is spread over a surface greater than that actually sampled due to the transport of ticks by hosts over the whole forest. For this reason we consider the impact of sampling among the 3 years examined to be negligible.

During the period ranging from 1996 to 1998 we experienced very strong climatic differences among years. At the same time the density of questing ticks was highly variable among years (maximal density and monthly questing activity). The beginning of tick activity and the highest density of questing ticks occurred approximately 1 month earlier in 1997 as compared with 1996. This was associated with higher temperatures in the spring of 1997 than in the spring of 1996. The difference in temperatures corresponded to a 1-month shift. A shift on the same order of magnitude has also been described by Gilot et al. (1975). This shows that photoperiodicity does not play an important role in the onset of *I. ricinus* activity in a continental area.

MacLeod (1936) observed that sheep infestation in the United Kingdom began at a weekly averaged daily maximal temperature of 7 °C. The same threshold for questing tick activity was observed in Neuchâtel by flagging of vegetation. Interestingly, this threshold seems to be independent of heat factors from the host and instead reflects questing tick activity. Thus, a temperature threshold of 7 °C may be used to predict the emergence of ticks in spring in the United Kingdom, in Switzerland, and, possibly, in other areas.

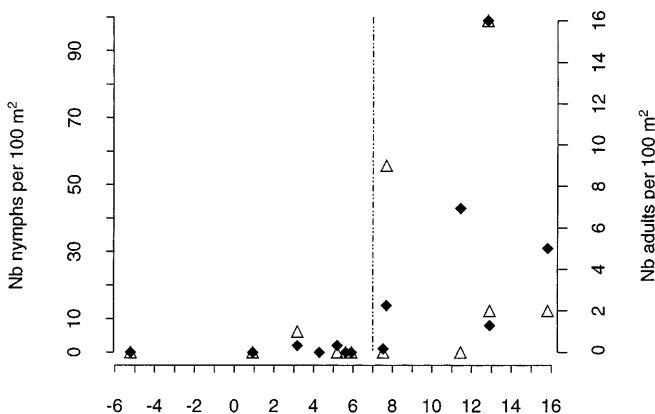


Fig. 2 Questing tick density as recorded from October to March of 1996–1998 in relation to the 5-day average of daily maximal temperature (Black diamonds nymphs, white triangles adults)

It is known that the behavior of free-living stages of *I. ricinus* alternates between questing and resting (MacLeod 1935; Milne 1950; Lees and Milne 1951; Gigon 1985). It has also been reported that questing is interrupted when ticks have lost too much water (Lees and Milne 1951) and that immature ticks demonstrate a positive geotropism when the temperature reaches 24 °C (MacLeod 1935). More recently, Randolph and Storey (1999) showed that high-saturation-deficit events induced tick movements and increased energy loss. This energy loss is due not only to tick movements but also to active water sorption (Lees 1946; Gaede and Knülle 1997), which means that high-saturation-deficit events shorten both the life span of ticks, as they have limited amounts of energy, and their questing periods, since ticks do not display questing behavior during water sorption. Increased tick mortality and shorter questing periods may partly explain why the questing tick density observed in our study was lower in 1998, when the saturation deficit was high, as compared with 1996 and 1997. Indeed, when the saturation deficit increased during the summer, the tick density decreased. Moreover, the peak of nymphal density was dramatically reduced in May 1998, when the saturation deficit was exceptionally high in the spring (Pearson's $r = -0.64$). In the autumn of 1998, when the saturation deficit was lower, the nymphal population quested again, resulting in a peak of questing nymphs in autumn that did not occur in 1996 and 1997. We suggest that this autumnal peak is the result of two components: a demographic component represented by the onset of spring-fed larvae and mostly a behavioral component represented by the reappearance of nymphal questing activity. In contrast to 1998, 1997 was rather wet and the tick density reached an extremely high level, which means that the low saturation deficit positively influenced the questing behavior of ticks. Demographic variations in the larval population alone can hardly explain the variations in phenology observed in 1997 and 1998, as the estimated number of larvae fed by the rodent population in the area studied was higher in 1997 than in 1996 (Perret et al., manuscript in preparation).

In MacLeod's (1935) experiment on geotropism, ticks demonstrated a quickly positive geotropism when the temperature reached 24 °C and when the saturation deficit reached 4.4 mmHg (calculated with 80% relative humidity). The same threshold can be noted in our data under natural conditions, since the tick density decreased when the saturation deficit exceeded 4.4 mmHg. These observations suggest that the behavior of unfed ticks is strongly influenced by tick water loss, which is influenced by saturation deficit. On the other hand, saturation deficit seems to have less impact on the density of *I. ricinus* adults than on that of nymphs.

In summary, in Neuchâtel during 1996, 1997, and 1998 the density of questing ticks was constrained

between low temperatures in the winter and high saturation deficits in the summer. Further studies investigating the influence of saturation deficit on the density and behavior of questing ticks should be encouraged in other geographic areas in which climatic conditions are very different, e.g., northern Africa or northern Europe, and under controlled experimental conditions. In the long run, long-term series of tick-density data should contribute to the elaboration of a model to forecast tick density.

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