Published in International Journal of Medical Microbiology 298, supplement 1, 55-59, 2008
which should be used for any reference to this work

Influence of some climatic factors on *Ixodes ricinus* ticks studied along altitudinal gradients in two geographic regions in Switzerland

Lise Gern*, Francisca Morán Cadenas, Caroline Burri

Institut de Biologie, Emile-Argand 11, CH-2009 Neuchâtel, Switzerland

Abstract

In the context of climate change, the seasonal activity of questing *Ixodes ricinus* and their infection with *Borrelia burgdorferi* sensu lato (s.l.) were examined in relation to some climatic data along altitudinal gradients in Switzerland. The first study took place in an Alpine area (Valais) from 750 to 1020 m above sea level. The other gradient was located on a mountain in the foothills of the Jura chain (Neuchâtel) from 620 to 1070 m above sea level. In the Alpine area, the highest questing tick density was observed at the highest altitude. At the lowest altitudes (750 and 880 m), very high saturation deficits, >10 mmHg, were present during most of the tick activity season and they seem to have impaired the thriving of tick populations. The second study in Neuchâtel (2003–2005) was a follow-up of a previous study (1999–2001) in which it was observed that tick density decreased with increasing altitude. During the follow-up study, substantial differences in questing tick density and phenology of ticks were observed: At high elevations, questing tick densities were 2.25 and 3.5 times higher for nymphs and adults, respectively, than during 1999–2001. As observed during 1999–2001, questing tick density decreased with increasing altitude in this site in 2003–2005. Tick questing density remained higher at the lowest altitude. Increased temperatures during summer months, more favorable for ticks, reaching values similar to those registered in the first study at the lowest elevations are probably responsible for the higher tick questing density at high altitudes. *B. burgdorferi* s.l. infection prevalence in ticks decreased with increasing altitudes along both altitudinal gradients. Long-lasting high saturation deficit values may limit the development of tick populations as too high a moisture stress has a negative effect on tick survival. This factor may have a permanent impact, as it is probably the case at the lowest altitudes in the Alpine area or a more transient effect like in the Neuchâtel gradient.

Keywords: *Ixodes ricinus*; Climate; Questing ticks; Seasonal activity; *Borrelia burgdorferi*; Altitude

Introduction

The tick *Ixodes ricinus* is widely distributed in Europe and is also present in the mountains of North Africa (Gern and Humair, 2002). This tick species is known as the most important vector in Europe of the spirochetes that cause Lyme borreliosis. Lyme borreliosis spirochetes belong to the complex *Borrelia burgdorferi* sensu lato (s.l.), which includes 12 different genospecies. In Europe, at least 7 of them are transmitted through the bite of *I. ricinus* (Rauter and Hartung, 2005; Richter et al., 2006).

*Corresponding author. Tel.: +41 32 718 3000; fax: +41 32 718 3001.
E-mail address: lise.gern@unine.ch (L. Gern).

To find a host, *I. ricinus* climbs onto low vegetation to quest for a passing vertebrate. Host questing activity can be influenced by exogenous factors including temperature, humidity, light, and endogenous factors. Questing tick density in an area can be evaluated by flagging low vegetation. The seasonal evolution of questing tick density over time has been defined as tick phenology (Jouda et al., 2004a, b; Perret et al., 2004). *I. ricinus* phenology varies considerably throughout its wide distribution (Gray, 1991). *I. ricinus* questing activity may show a unimodal pattern or a bimodal pattern reaching its maximum density either in spring (Gray, 1984) or in autumn (Korenberg, 2000). There might also be variations in tick phenology from year to year at a given site (Tälleklint and Jaenson, 1996; Perret et al., 2000; Randolph et al., 2002; Jouda et al., 2004a, b). Variations in the seasonal questing activity of *I. ricinus* may be associated with major variations in biotic (host species, host abundance and behavior, and vegetation structure) as well as abiotic factors (climate). Previous observations on the phenology of *I. ricinus* in Neuchâtel (Switzerland) showed that the onset of tick activity in spring and the presence of an autumnal peak of ticks were related to temperature (Perret et al., 2000, 2004; Jouda et al., 2004a). Randolph et al. (2002) observed a correlation between the cumulated summer temperature and the time of emergence of ticks in autumn. They showed that in *I. ricinus* the duration of development from one stage to the other one is inversely proportional to temperature (Campbell, 1948; cited in Randolph et al., 2002). According to these authors, temperature might allow fast development of spring fed ticks allowing these ticks to quest again the same year. Under such a scenario, an autumnal peak would be expected when temperatures are high in summer and no autumn peak otherwise. These relations between seasonal questing tick activity and temperature were observed along an altitudinal gradient (Jouda et al., 2004a). In fact, at the highest altitude, where annual mean temperature was lowest, the onset of tick activity in spring was delayed and no autumn peak was observed compared to the lowest altitude. Jouda et al. (2004a) reported variable phenologies and variable *Borrelia* infection rates of ticks at different altitudes, under different temperature conditions, within the same forest at a short distance. This suggested that such altitudinal gradients offered the opportunity to follow the impact of different climatic scenarios on the seasonal activity of questing tick populations.

Therefore, in the context of global climate warming, the seasonal activity of questing *I. ricinus* ticks as well as their infection rate with *B. burgdorferi* s.l. were monthly investigated and examined in relation to climatic data (temperature, relative humidity, and saturation deficit) along two altitudinal gradients in two studies in Switzerland (Burri et al., 2007; Morán Cadenas et al., 2007). The first altitudinal gradient from 750 to 1020 m above sea level was located on the north-facing slope of a mountain chain in an Alpine area (Rhône Valley) (Burri et al., 2007). This study was conducted from March 2004 to February 2005. The other gradient, from 620 to 1070 m above sea level, was located on the south-facing slope of a mountain in the foothills of the Jura chain (Chaumont, Neuchâtel) (Morán Cadenas et al., 2007). That latter study was a follow-up over 3 years (2003–2005) of Jouda et al. (2004a) that had similarly been conducted over 3 years (1999–2001).

Ticks and desiccation

The survival of ticks is limited by their ability to maintain their water content in a desiccating atmosphere. Indeed the atmosphere is often unsaturated, resulting in a water loss for ticks. To maintain their water balance, ticks actively absorb water from subsaturated atmosphere through specialized tissues in their hypostome, if the relative humidity surpasses a certain critical value (Gaede and Knülle, 1997). To do so, ticks may leave their questing site and move down to the leaf litter where active water vapor sorption may take place. If saturation deficit is high (saturation deficit integrates temperature and relative humidity to give a measure of the drying power of the atmosphere; it was calculated according to Randolph and Storey, 1999), questing periods will be significantly shortened (Perret et al., 2003). High saturation deficit also has an effect on tick survival, more particularly on nymphs than on adults (Perret et al., 2004). If ticks frequently have to leave their questing places to move to the ground for rehydration, they will rapidly exhaust their energy reserves before they may find a host and die. Influence of high saturation deficits on tick questing activity has been shown in nature, in quasi-natural arenas, in arena placed in natural settlements and in the laboratory (Randolph and Storey, 1999; Perret et al., 2000, 2003, 2004).

Influence of saturation deficit

In nature, the density of questing ticks is usually estimated by dragging a white flag over low vegetation. It is important to note that this method does not allow sampling ticks in quiescence in the leaf litter. Flagging is therefore not a means to estimate the whole tick population density, but only a means to estimate the density of those ticks that are questing. What was measured by Burri et al. (2007) and Morán Cadenas et al. (2007) was the questing tick density. To do so, in each site, ticks were monthly collected over a distance of 150 m. The questing tick density over one year was expressed as a single number (cumulative tick density, CTD) as described by Eisen et al. (2003) and Jouda et al. (2004a, 2004b). Environmental data such as air temperature at 60 cm height and relative humidity were recorded monthly at each sampling site, and air temperature data were obtained from automatic meteorological stations (Meteosuisse) as described by Burri et al. (2007) and Morán Cadenas et al. (2007).

When tick phenology was studied along an altitudinal gradient (at 750, 880, and 1020 m above sea level) in a very dry area in Switzerland (Valais), it was observed that questing tick density was the highest at the highest altitude where CTD for nymphs reached 2616, whereas CTDs were around 500 at the two lower altitudes (Burri et al., 2007). At the two lower altitudes, high to very high saturation deficits were present during most of the tick activity season, reaching saturation deficit values >10 mmHg from April/May to October impairing the tick population with mean annual temperatures of 14.2 and 14 °C and maximum temperatures reaching 32.6 and 28.9 °C at 750 and 880 m above sea level, respectively (Burri et al., 2007). In contrast, at the highest altitude, mean annual temperature value was 9.2 °C, maximum temperature was below 20 °C and saturation deficit never reached values >5 mmHg. It is known from literature that saturation deficit values <5 mmHg are favorable for tick behavior and tick development (MacLeod, 1935; Perret et al., 2003). At all elevations, most questing tick activity was observed at 2–7 mmHg (Burri et al., 2007). As mentioned before, high saturation deficits force ticks to often leave their questing places and to move to the ground to rehydrate. By doing so, they rapidly exhaust all their energy resource and may die before finding a host, which diminishes tick questing density. Moisture stress due to high and long-lasting saturation deficit values (>10 mmHg) as measured at the lowest elevations may explain why at the lowest altitudes a lower questing tick density was recorded than at the highest altitude (Burri et al., 2007).

Similarly, the influence of saturation deficit was observed along an altitudinal gradient on Chaumont (Neuchâtel) in a follow-up (2003–2005) of a previous study (1999–2001) on the phenology of *I. ricinus* ticks (Jouda et al., 2004a). The altitudinal gradients included stations at 620, 740, 900, and 1070 m above sea level (Fig. 1) (Jouda et al., 2004a; Morán Cadenas et al., 2007). During the first study period, it was observed that tick density decreased with increasing altitude and that at 900 m the seasonal questing tick activity was very stable (Jouda et al., 2004a). During the follow-up study, similarly questing tick density decreased with increasing altitude. However, substantial differences in questing tick density and phenology of ticks were observed

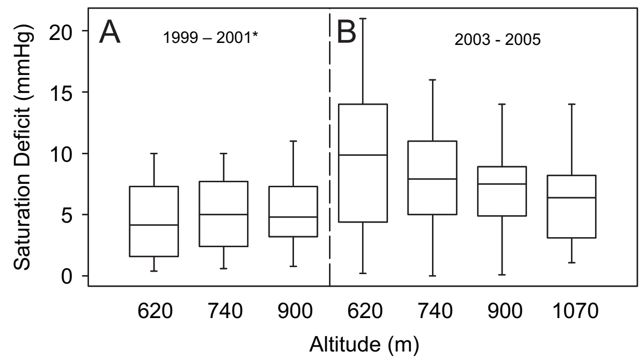

Fig. 1. Saturation deficit (SD) values in two study periods (1999–2001 and 2003–2005) at different altitudes (ranging from 620 to 1070 m above sea level) on the south-facing gradient in Chaumont. (A) 1999–2001 study. (B) 2003–2005 study. *SD values calculated from unpublished data recorded using a squirrel 1200 logger manufactured by Grant Instrument (Shepreth, UK) with the use of temperature and RH humidity probes at 10 cm above ground.

(Morán Cadenas et al., 2007). The seasonal questing activity of ticks living at 900 m above sea level was much less stable than during the first study period and autumn peaks occurred. At high elevations, particularly at 900 m, ticks were significantly more abundant during the follow-up study. In fact, questing tick densities there were 2.25 and 3.5 times higher for nymphs and adults, respectively, during 2003–2005 than during 1999–2001. CTDs during the first study period at 900 m above sea level showed values of 26,177 and 3477 for nymphs and adults, respectively, whereas these values reached 58,896 for nymphs and 12,264 for adults during the second study period. One explanation for this is the increased temperatures recorded during summer months at the highest altitude, reaching values similar to those registered in the first study at 620 m (Morán Cadenas et al., 2007). Increased temperatures during summer months (increase of 1.6 °C between the two study periods) were probably more favorable for ticks to develop from one stage to the other one. Between the two study periods, at the lowest altitude, no difference was observed for nymphs, whereas adults were significantly less abundant during 2003–2005. At that low altitude, adults were significantly less abundant, probably due to long-lasting high saturation deficits (>10 mmHg from March/April to August/September 2004 and 2005) that impaired nymph survival or due to biotic factors like abundance of hosts on which nymphs usually feed. Important differences were noticed in saturation deficit values at the various altitudes between the two study periods. Saturation median values never reached 5 mmHg during the 1999–2001 period, whereas they varied between 5 and 10 mmHg according to elevation during the second study period (Fig. 1).

Borrelia burgdorferi s.l. prevalences in questing ticks

In these studies undertaken in two different geographic areas in Switzerland, not only the seasonal activity of questing ticks and tick density were related to altitude, but also prevalence of *B. burgdorferi* infection in questing ticks. In fact, *B. burgdorferi* infection prevalence in ticks decreased with increasing altitude along both altitudinal gradients (Burri et al., 2007; Morán Cadenas et al., 2007). Prevalences of infection in nymphs, for example, varied from 46% at the lowest altitudes to 20% at the highest altitude in Valais (Burri et al., 2007), whereas they varied from 28.8% to 26.5% in Chaumont (Morán Cadenas et al., 2007). These results confirmed previous reports showing a reduction in tick infection prevalence at higher elevations (e.g., Jouda et al., 2004a). The lower infection rate observed at the highest altitudes may partly be explained by the presence of some Cervidae species that are used to moving to higher altitude in spring and remain there until autumn. Their presence in these sites, when tick questing density is important, may dilute *B. burgdorferi* infection prevalence in ticks since these hosts appear as incompetent hosts for *Borrelia* spp. Four *Borrelia* species were identified by Reverse Line Blot (Poupon et al., 2006) in ticks collected in the two sites: *B. afzelii, B. garinii, B. burgdorferi* s.s., and *B. valaisiana* (Burri et al., 2007; Morán Cadenas et al., 2007). *B. afzelii* and *B. garinii* were the two most frequent species, which corroborates previous findings in Switzerland (Jouda et al., 2004a).

Conclusions

Two studies undertaken along two altitudinal gradients demonstrated how saturation deficit might interfere with tick questing activity in nature. Long-lasting high saturation deficit values may limit the development of tick populations as too high a moisture stress has a negative effect on tick survival. This factor may have a permanent impact as it is probably the case in the Rhône Valley in an Alpine area where ticks living at the lowest altitudes have to face high saturation deficits that may limit their geographical distribution (Burri et al., 2007). This area is known as dry with an annual mean rainfall of 409 mm (Meteosuisse). In another site in the same area in Valais (643 m above sea level) characterized by a very high saturation deficit (annual mean 11.4 and >10 mmHg from March to October), monthly collection of ticks over 1 year showed that establishment of ticks in this site was not possible (unpublished data). Therefore, it is suggested that, at the two lowest altitudes in that part of Switzerland, ticks were possibly at the limit of their maintenance due to continuous moisture stress lasting for many months. In Neuchâtel (Chaumont), where the other altitudinal gradient was located, the area is less dry than the Rhône Valley with an annual mean rainfall of 949 mm. However, saturation deficit values may vary over time as observed in two study periods in another site (Morán Cadenas et al., 2007). Currently, it is unclear if that increase in saturation deficit in that second site is part of a general trend or if it is only a transient event. However, these climate changes allow confirmation of observations made by Perret et al. (2004) showing that some climatic factors may influence tick populations over a 6-year study of seasonal questing tick evolution.

Acknowledgements

These studies were financially supported by the Swiss National Science Foundation (no. 3200B0-100657 and no. 320000-113936).

References

Burri, C., Morán Cadenas, F., Douet, V., Moret, J., Gern, L., 2007. *Ixodes ricinus* density and infection prevalence of *Borrelia burgdorferi* sensu lato along a north-facing altitudinal gradient in the Rhône Valley (Switzerland). Vector Borne Zoonotic Dis. 7, 50–58.

Campbell, J.A., 1948. The life history and development of the sheep tick *Ixodes ricinus* Linnaeus in Scotland, under natural and controlled conditions. Ph.D. Thesis (cited after Randolph et al., 2002).

Eisen, R.J., Eisen, L., Castro, M.B., Lane, R.S., 2003. Environmentally related variability in risk of exposure to Lyme disease spirochetes in northern California: effect of climatic conditions and habitat type. Environ. Entomol. 32, 1010–1018.

Gaede, K., Knülle, W., 1997. On the mechanism of water vapour sorption from unsaturated atmospheres by ticks. J. Exp. Biol. 200, 1491–1498.

Gern, L., Humair, P.-F., 2002. Ecology of *Borrelia burgdorferi* sensu lato in Europe. In: Gray, J.S., Kahl, O., Lane, R.S., Stanek, G. (Eds.), Lyme borreliosis: biology, epidemiology and control. CAB International, Wallingford, Oxon, UK, pp. 149–174.

Gray, J.S., 1984. Studies on the dynamics of active populations of the sheep tick, *Ixodes ricinus* L. in Co. Wicklow, Ireland. Acarologia 25, 167–178.

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.

Jouda, F., Perret, J.-L., Gern, L., 2004a. *Ixodes ricinus* density, and distribution and prevalence of *Borrelia burgdorferi* sensu lato infection along an altitudinal gradient. J. Med. Entomol. 41, 162–169.

Jouda, F., Perret, J.-L., Gern, L., 2004b. Density of questing *Ixodes ricinus* nymphs and adults infected by *Borrelia* *burgdorferi* sensu lato in Switzerland: spatio-temporal pattern at a regional scale. Vector Borne Zoonotic Dis. 4, 23–32.

Korenberg, E.I., 2000. Seasonal population dynamics of *Ixodes* ticks and tick-borne encephalitis virus. Exp. Appl. Acarol. 24, 665–681.

MacLeod, J., 1935. *Ixodes ricinus* in relation to its physical environment. II. The factors governing survival and activity. Parasitology 27, 123–144.

Morán Cadenas, F., Rais, O., Jouda, F., Douet, V., Humair, P.-F., Moret, J., Gern, L., 2007. Phenology of *Ixodes ricinus* and infection with *Borrelia burgdorferi* sensu lato along a north- and south-facing altitudinal gradient on Chaumont mountain, Switzerland. J. Med. Entomol. 44, 683–693.

Perret, J.-L., Guigoz, E., Rais, O., Gern, L., 2000. Influence of saturation deficit and temperature on *Ixodes ricinus* tick questing activity in a Lyme borreliosis-endemic area (Switzerland). Parasitol. Res. 86, 554–557.

Perret, J.-L., Guerin, P.M., Diehl, P.-A., Vlimant, M., Gern, L., 2003. Darkness induces mobility, and saturation deficit limits questing duration, in the tick *Ixodes ricinus*. J. Exp. Biol. 206, 1809–1815.

Perret, J.-L., Rais, O., Gern, L., 2004. Influence of climate on the proportion of *Ixodes ricinus* nymphs and adults questing in a tick population. J. Med. Entomol. 41, 361–365.

Poupon, M.-A., Lommano, E., Humair, P.-F., Douet, V., Rais, O., Schaad, M., Jenni, L., Gern, L., 2006. Prevalence of *Borrelia burgdorferi* sensu lato in ticks collected from migratory birds in Switzerland. Appl. Environ. Microbiol. 72, 976–979.

Randolph, S.E., Storey, K., 1999. Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. J. Med. Entomol. 36, 741–748.

Randolph, S.E., Green, R.M., Hoodless, A.N., Peacey, M.F., 2002. An empirical quantitative framework for the seasonal population dynamics of the tick *Ixodes ricinus*. Int. J. Parasitol. 32, 979–989.

Rauter, C., Hartung, T., 2005. Prevalence of *Borrelia burgdorferi* sensu lato genospecies in *Ixodes ricinus* ticks in Europe: a metaanalysis. Appl. Environ. Microbiol. 71, 7203–7216.

Richter, D., Postic, D., Sertour, N., Livey, I., Matuschka, F.R., Baranton, G., 2006. Delineation of *Borrelia burgdorferi* sensu lato species by multilocus sequence analysis and confirmation of the delineation of *Borrelia spielmanii* sp. nov. Int. J. Syst. Evol. Microbiol. 56, 873–881.

Tälleklint, L., Jaenson, T.G., 1996. Seasonal variations in density of questing *Ixodes ricinus* (Acari: Ixodidae) nymphs and prevalence of infection with *B. burgdorferi* s.l. in south central Sweden. J. Med. Entomol. 33, 592–597.