Climate and the seasonal abundance of the tick
Dermacentor reticulatus

B. O. SANDS, K. E. BRYER and R. WALL
School of Biological Sciences, University of Bristol, Bristol, U.K.

Abstract. Dermacentor reticulatus (Ixodida: Ixodidae, Fabricius 1794) is one of the most widely distributed and abundant tick species in central Europe and is a vector for a range of pathogens. Nevertheless, many aspects of its ecology and distribution remain poorly understood. To quantify the seasonal abundance of this species in the U.K. and the environmental factors that determine this, weekly sampling at sites throughout Wales and southern England was undertaken for 12 months. This showed that the activity of adult D. reticulatus peaked February and March and that no individuals were collected between May and mid-October; no questing tick activity was observed when the 5-day average temperature was greater than 15 °C. A single nymph was collected by dragging, confirming speculation over the nidicolous status of larval and nymphal stadia. Laboratory analysis found that D. reticulatus were able survive cold shock and the lower lethal temperature was estimated to be between −18 and −20 °C. Habitat was significantly associated with tick activity, with higher numbers of ticks collected from low lying vegetation in marsh environments than from exposed grassland or woodland. A strong association was observed between activity and saturation deficit suggesting that the seasonal pattern of activity seen in the field, within the sites where it was abundant, is more strongly determined by temperature than humidity. Range expansion within the U.K. should be expected, bringing with it an elevated disease risk for animal and human hosts.

Key words. Babesiosis, humidity, phenology, piroplasmosis, range expansion, saturation deficit, temperature.

Introduction

Dermacentor reticulatus is one of the most widely distributed and abundant tick species in central Europe (Rubel et al., 2014, 2016; Mierzejewska et al., 2015a). Adult D. reticulatus feed on a wide range of wild hosts plus dogs, horses, cattle and occasionally, humans (Biernat et al., 2014; Medlock et al., 2017). It is of particular interest due to its importance as a vector; over 40 different pathogens, known to infect both animals and humans, have been detected in D. reticulatus (Földvári et al., 2016). Pathogens transmitted by D. reticulatus in Eurasia include tick-borne encephalitis virus, Rickettsia spp., Anaplasma spp., Babesia spp., Kemerovo virus, Borrelia spp., Francisella spp., Babesia canis and Theilaria equi (Zivkovic et al., 2007; Špitalská et al., 2012; Földvári et al., 2013, 2016; Rubel et al., 2016; Gray et al., 2019). However, despite this, the ecology of D. reticulatus is less well known than other common species, such as Ixodes ricinus, partly because data relating to the immature instars are lacking. They are almost never collected in blanket-drags and are thought to exhibit nidicolous behaviour, remaining in the burrows or nests of their small mammal hosts (Pfafflé et al., 2015). As a result, the role of many of the key ecological and epidemiological drivers that effect D. reticulatus population and disease transmission dynamics remain relatively poorly studied, particularly in relation to climate and habitat.

The distribution of D. reticulatus appears to be expanding north through Europe (Rubel et al., 2016), for example, in north-
ern Germany *D. reticulatus* has significantly expanded its range over the past 50 years (Drehmann et al., 2020). These changes are likely to be the result of a range of factors including climate change, increasing wild host abundance and changing patterns of land use, particularly the abandonment of agricultural land (Karbowiak, 2014; Mierzejewska et al., 2015a; Paulauskas et al., 2018). Newly established populations have been observed in Poland (Zygnier et al., 2009), Germany (Dautel et al., 2006) and the Netherlands (Matjila et al., 2005). Movement of animal hosts between sites using wildlife corridors such as river valleys, more regular travel to the countryside with domestic dogs, and an increase in livestock trading routes have all been implicated in the increase in the rate of spread (Mierzejewska et al., 2015b; Rubel et al., 2016; Medlock et al., 2018). Oviposition by *D. reticulatus* is presumed to occur in spring and, given appropriate conditions, the life-cycle may be completed in only one or two years (Gray et al., 2009; Pfäffle et al., 2015) giving *D. reticulatus* a relatively rapid rate of population increase.

Known as the ornate cow tick, marsh tick or winter tick in the U.K., (Medlock et al., 2018), *D. reticulatus*, is probably at the edge of its current geographic range. Small, isolated U.K. populations are known to have been present for at least 100 years (Medlock et al., 2011) and questing *D. reticulatus* have been recorded in every month of the year with an activity peak in March and April (Medlock et al., 2017). However, it remains a relatively rare species; a recent national survey found only two *D. reticulatus* samples on non-travelled animals from clinical examination of over 8000 dogs (Abdullah et al., 2016). In the U.K., *D. reticulatus* is thought to be associated primarily with maritime grassland and sand dune habitats, including grazing marsh, at coastal sites in Devon, west Wales and East Anglia (Jamsen & Medlock, 2011; Medlock et al., 2017). Historical and current records suggest that many of the sites in the U.K. where this species is found are old rabbit warrens (Medlock et al., 2017). Other U.K. populations may as yet be undiscovered.

Prior to 2016, babesiosis (piroplasmosis) resulting from infection by *B. canis* was unknown in the U.K. However, in March 2016, a cluster of cases of canine babesiosis was reported in the county of Essex in non-travelled dogs indicating that for the first time this pathogen had become established (Hansford et al., 2016; Medlock et al., 2017). A previously unknown population of *D. reticulatus* was then found in an area of grassland; it has been suggested that this population may be linked to the movement of livestock and dogs in the area. Given that *D. reticulatus* has previously been considered a coastal tick species in the U.K., associated with sand dunes and coastal grassland, the presence of the Essex population was unexpected (Medlock et al., 2017). The outbreak of *B. canis* highlights the urgent need for an improved understanding of the ecology and behaviour of this tick in the U.K. to be able to predict the potential for changes in range expansion. The aim of the present study therefore was to quantify the seasonal abundance of *D. reticulatus* in the field, investigate its associations with climate and habitat, and to quantify the effects of temperature and relative humidity on its survival in the laboratory.

### Materials and methods

#### Seasonal abundance

Weekly sampling of *D. reticulatus* was carried out over six sites to allow associations between climate, habitat and patterns of tick questing activity to be determined. Ticks were collected at two coastal dune systems in Gwynedd, Wales; Morfa Harlech (52.8731°N, 4.1294°W) and 8 miles south, Morfa Dwyfryn (52.7813°N, 4.1182°W). The sites contained some small bodies of water and were grazed by cattle. Collection sites on the north coast of Devon were at Braunton Burrows (51.0928°N, 4.207895°W), a dune area of approximately 1400 hectares grazed by cattle, and Northam Burrows Country Park (51.0545°N, 4.2245°W), a saltmarsh and dune system grazed by horses and sheep. On the south coast of Devon, Bolt Tail headland immediately to the southwest of Hope Cove (50.2427°N, 3.8660°W) was sampled, and was grazed by sheep. The site in Essex was at Old Hall Marshes (51.7747°N, 0.8407°E), an RSPB nature reserve containing many bodies of water, extensive saltmarsh, reedbeds and marshes grazed by cattle and horses.

Ticks were collected by blanket dragging and identified based on morphological characteristics including an ornate scutum with eyes, anal grooves circle anus posteriorly, presence of festoons and short wide palps (Estrada-Peña et al., 2017). The presence of a rear-pointing spur on the palp of both males and females was used to distinguish *D. reticulatus* from *D. marginatus* which is widespread in Europe but very rare in the U.K. To achieve a randomized survey of the sites, maps showing the layout of each site were generated with a 200 m grid overlaid, and five grid coordinates were randomly selected for sampling each visit. At each grid coordinate, 5 × 25 m blanket drags were performed, with every sub-group of 5 drags at least 20 m apart, giving a total of 625 m sampled per site visit. For this, white cloth sheets (1 m × 1 m) were dragged slowly across the vegetation and turned over every 5 m, ticks were then removed and collected. Vegetation data and livestock grazing patterns were also recorded at each collection site.

Climatic data were collected from weather stations in North (IDEVONWE1) and South Devon (IEASTPRA2), NW Wales (ITREMA2) and Essex (IMALDON14), all of which were less than 30 km from the tick sampling sites. The maximum daily saturation deficit was calculated using the formula: SD = (1 − RH_{min}/100) × 4.9463 × e^{−0.0621 × T_{max}}), where SD represents the saturation deficit in mm of mercury, RH_{min} represents the daily minimum relative humidity (%), and T_{max} represents the daily maximum temperature (°C). Maximum daily wind speed and hours of daylight were also recorded.

#### Effects of temperature and humidity on mortality

Glass desiccator jars (2.4 L, VWR International, Radnor, PA, U.S.A.) were used to maintain different humidity environments. Five different relative humidities: 20, 40, 60, 80 and 95% RH, were created by adding 100 mL of different concentrations of potassium hydroxide (KOH) (Solomon, 1951), to the bottom of each desiccator jar. Desiccators were placed in incubators (MLR-351H; Sanyo, Panasonic, Loughborough, U.K.) at 4, 15

© 2021 The Authors. *Medical and Veterinary Entomology* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society. *Medical and Veterinary Entomology*, **35**, 434–441
and 30 °C. An EasyLog USB Data Logger (Lascar Electronics, Whiteparish, U.K.) was used to check the humidity in each desiccator jar and the KOH solution was changed every 2 weeks. Three 50 mL plastic tubes (Sarstedt Inc., Nümbrecht, Germany) were placed into each desiccator on a wire gauze. Ticks were collected via blanket dragging, as described above. Each tube contained five *D. reticulatus* (mixed sex) and several strips of filter paper (Whatman No. 1) to allow ticks to climb. The lid of each tube was covered with fine nylon mesh, secured with a rubber band, to allow equilibration with the desiccator atmospheric relative humidity. Ticks were removed every 2 or 3 days and mortality recorded. Mortality was determined as a persistent lack of movement over a period of 5 min when ticks were placed on the investigator’s hand and gently stimulated with forceps. Mortality assessment was continued for a maximum of 9 weeks or until all the ticks were dead. Overall, 225 adult *D. reticulatus* ticks were used in these assays.

To investigate the activity of *D. reticulatus* to withstand low temperatures in cold shock experiments, replicates of three tubes containing 5 ticks were placed in a freezer at −9, −15, −18 and −20 °C for 24 h. Ticks were then removed and left at room temperature for 24 h before being assessed for mortality, as described above. In addition, four desiccator jars were set up as above (40, 60, 80 and 95% RH) and placed in a freezer at −4 °C for 13 weeks, before being removed and mortality recorded.

**Statistical analysis**

All analyses were undertaken using the R statistical package (R Core Team, 2019). The number of *D. reticulatus* caught at each sample was used to assess activity. For analysis of the effects of climate, the data were detrended to remove the seasonal pattern by fitting a second-order polynomial regression and calculating the residuals (Iler et al., 2016). The detrended data were over-dispersed, so a negative binomial probability distribution was used to examine seasonal activity in a generalized linear model in which month was the independent variable, with Tukey multiple comparisons. Subsequently, a Pearson correlation matrix between climatic predictors was constructed to minimize the problem of multicollinearity. When a variable was correlated ≥70% to another, only one was included in subsequent analysis. The Pearson correlation coefficient, *r*, for hours of daylight was 0.67 with average daily temperature and 0.7 with saturation deficit, so hours of daylight was removed from the analysis. Non-parametric rank correlations of detrended tick abundance with climatic parameters were calculated using Kendall’s Tau (*T*) correlation coefficient. The data satisfied the assumption of a monotonic distribution.

For each sampling site, the vegetation and terrain were recorded. Vegetation included woodland, fern, bramble, meadow (short, rough or long), creeping willow, rush, marram grass and sea buckthorn. Terrain was flat, sand dune, marsh, golf course, path edges, water edge, bank, sea wall, cliff and exposed. The data were not an appropriate fit for Poisson or negative binomial distributions, showing overdispersion despite attempts at transformation. A conditional inference tree (package part; Therneau & Atkinson, 2019) including the categorical independent variables ‘vegetation’ and ‘terrain’ was therefore constructed for the number of ticks per 100 m² between October and July when ticks were present, which provided an alternative form of nonparametric analysis.

For the laboratory investigation, a generalized linear mixed model with a Poisson distribution for count data was performed with temperature (4, 15, 30 °C), humidity (20, 40, 60, 80, 90% RH) and time (day 10, 30, 50, 63) as covariates and the number of ticks alive as the dependent variable. Experimental unit (each individual desiccator) nested within time was included as a random effect to control for correlation due to repeated measures. Residuals were checked for normality, deviance and plotted against the number of ticks alive to visualize dispersion. Finally, saturation deficit was calculated for each temperature and humidity treatment and used as a continuous independent variable in a Poisson regression with number of ticks alive as the response variable.

**Results**

**Seasonal activity and environmental predictors**

No questing ticks were collected between July and October (Fig. 1). Tick activity increased significantly between October and November (*Z* = 4.3, *P* < 0.001), and between January and February (*Z* = −5.6, *P* < 0.001) and abundance decreased significantly between April and May (*Z* = −4.1, *P* < 0.001).

There was a significant negative correlation between saturation deficit and tick activity (*T* = 0.264, *P* < 0.001; Fig. 1). There were also significant correlations between average temperature (*T* = 0.386, *P* < 0.001) and wind speed (*T* = 0.150, *P* < 0.001) and tick activity. The strength of the correlations for saturation deficit and temperature can be considered moderate, while that for wind speed was weaker, based on Kendall’s formula where Pearson’s *r* = sin(0.5π*T*). No questing tick activity was observed when the 5-day average temperature exceeded 15 °C.

Vegetation type was significantly associated with tick activity (*P* = 0.021), with a greater abundance of ticks collected from creeping willow (*Salix repens*) than bramble (*Rubus fruticosus*), marram grass (*Ammophila* spp.), grass meadow (rough and short), sharp rush (*Juncus articulatus*) or deciduous woodland (Fig. 2). Terrain was also significantly associated with tick activity (*P* = 0.012), with a greater abundance of ticks being collected from marsh, seawall, bank and path edge habitats than exposed, cliff, sand dune or golf course habitats (Fig. 2).

**Effects of temperature and humidity on mortality**

There were significant interactions between temperature, humidity and time (*Z* = 3.8, *P* < 0.001), so the mortality at each time point was analysed separately. At day 10, there was no significant relationship between humidity and tick survival at any of the temperatures. At day 30, there was a significant interaction between humidity and temperature (*Z* = 4.74, *P* < 0.001). At both 30 °C (*Z* = 4.22, *P* < 0.001) and 15 °C (*Z* = 3.71, *P* < 0.001), there was a significant relationship between humidity and tick survival with fewer ticks surviving.
at low humidities. At 4°C, there was no significant relationship between humidity and tick survival. At day 63, there was a significant relationship between humidity and tick survival at all three temperatures: 30°C ($Z_{14} = 3.15$, $P = 0.0017$), 15°C ($Z_{14} = 3.63$, $P < 0.001$), and 4°C ($Z_{14} = 3.86$, $P < 0.001$) with fewer ticks surviving at low humidities. At day 30, predicted humidity thresholds were extrapolated using regression coefficients and found to be 35% RH at 30°C and 24% RH at 15°C. At 63 days, extrapolation gave humidity thresholds for survival of 36% at 30°C, 28% at 15°C and 19% at 4°C.

To examine the interaction between humidity and temperature, the regression coefficients for each significant generalized linear model, from day 30 onwards, were plotted against temperature and analysed by linear regression. There was a significant positive relationship between temperature and the regression coefficients ($F_r = 82.63$, $P < 0.001$) indicating that as increasing temperatures, humidity had a greater impact on tick survival, with higher humidities required for survival (Fig. 3).

Analysis of saturation deficit showed that on day 10 there was no significant relationship with tick survival ($Z_{44} = −1.88$, $P = 0.06$; Fig. 4). On day 30, there was a significant relationship between saturation deficit and tick survival ($Z_{44} = −6.096$, $P < 0.001$); fewer ticks survived at higher saturation deficit (Fig. 4). Using the predict() function, a threshold saturation deficit of 1.2 was identified, at or above which tick survival was <1 (0.87 ± 0.22SE). On day 63, there was a significant relationship between saturation deficit and tick survival ($Z_{44} = −5.364$, $P < 0.001$); fewer ticks survived at higher saturation deficit (Fig. 4). Using the predict() function, a threshold saturation deficit of 0.7 was identified, at or above which tick survival was <1 (0.81 ± S.E. 0.19).

Ticks were able to withstand exposure to temperatures down to −18°C for 24 h (Fig. 5). At −9, −15, −18 and −20°C, mean percentage survival (±SD) was 100 ± 0, 53 ± 12, 20 ± 20 and 0 ± 0, respectively. After 93 days exposure to −4°C, there was

© 2021 The Authors. Medical and Veterinary Entomology published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.
no significant relationship between humidity and tick survival ($t_{10} = -2.03, P = 0.07$; Fig. 5), and mean percentage survival ($±SD$) was $20 ± 20, 27 ± 23, 40 ± 20$ and $53 ± 31$ at $40, 60, 80$ and $95\%$ RH, respectively.

Discussion

Despite the fact that it is a widespread and an important vector of disease pathogens, many aspects of the ecology of *D. reticulatus* remain poorly understood, with studies providing conflicting results. Temperature has been shown to have an important effect on questing activity and mortality of adult *D. reticulatus* and it has been suggested that *D. reticulatus* is more cold-tolerant than other tick species, such as *I. ricinus* (Martinod & Gilot, 1991; Bartosik et al., 2011). This allows it to initiate questing activity earlier in the year and show activity during winter months when temperatures are too low for *I. ricinus* (Tharme, 1993; Tokhov et al., 2014). Active questing of *D. reticulatus* ticks has been observed at temperatures as low as $1\, ^\circ C$ and a soil temperature of $−0.1\, ^\circ C$ in mainland and Eastern Europe (Nosek, 1972; Hubálek et al., 2003). A study in the U.K. found *D. reticulatus* still questing at $3.3\, ^\circ C$ when the overnight temperature was $−5.4\, ^\circ C$ and the collection site was frozen (Tharme, 1993). In contrast, the threshold temperature for *I. ricinus* questing activity is considered to be around $6−7\, ^\circ C$ (MacLeod, 1935; Perret et al., 2000). In the current study, the influence of temperature on survival was also demonstrated with no questing tick activity observed when the 5-day average temperature exceeded $15\, ^\circ C$ and *D. reticulatus* was shown to be able survive cold shock. The lower lethal temperature for this species was estimated to be between $−18$ and $−20\, ^\circ C$. In contrast, the lower lethal temperature of *I. ricinus* has been shown to be around $−10$ to $−5\, ^\circ C$ (Alasmari & Wall, 2021).

As a result, of their cold tolerance, the activity of adult *D. reticulatus* generally begins in late August/September and continues through to April/May (Rubel et al., 2016). Here, the winter activity of this tick was confirmed, and a strong seasonal pattern was recorded in populations derived from locations across southern England and Wales, with adult *D. reticulatus*, collected by blanket drags throughout winter, peaking in February and March and no individuals collected between May and mid-October. A single nymph was collected by dragging, confirming speculation over the nidicolous status of larval and nymphal stadia and suggesting that future studies must include small mammal surveys to target the immature stages (Tharme, 1993). The winter activity pattern, however, does vary with latitude; in western Siberia, the most easterly part of the known range of *D. reticulatus*, adults were observed questing for only 3 months during spring and 3 months during the summer, and ticks were not found between September and April because of the extreme low temperatures (Rubel et al., 2020).

© 2021 The Authors. Medical and Veterinary Entomology published by John Wiley & Sons Ltd on behalf of Royal Entomological Society, Medical and Veterinary Entomology, 35, 434–441
In central Europe, *D. reticulatus* appears to be largely associated with open agricultural and swamp habitats, and the species has been reported to be able to survive submergence for extended periods of time (Rubel et al., 2016). However, established populations have also been reported to survive in dry conditions, such as on heathland and grassland, but are rarely observed in dark or coniferous forests (Cerny et al., 2001, 2003). Here, habitat was significantly associated with tick activity, with higher numbers of ticks collected from low lying vegetation in marsh environments than from exposed grassland or woodland.

The relationship between relative humidity and activity and survival is less clear than with temperature. For example, it has been suggested that *D. reticulatus* may be more sensitive to desiccation than *Ixodes* species because of its strong association with damp environments (Nosek, 1972; Hubálek et al., 2003). Greater than average annual rainfall has been associated with higher survival and increased activity of *D. reticulatus* (Süss et al., 2008; Olivieri et al., 2017). Similarly, the mortality of *D. reticulatus* was found to increase with higher saturation deficit in studies in eastern Europe, (Meyer-König et al., 2001a) and activity was highest when the relative humidity was at its highest, between 55 and 65% (Buczko et al., 2017). In contrast, other studies have found no correlation between rainfall and *D. reticulatus* activity (Martinod & Gilot, 1991; Hubálek et al., 2003) and no correlation between activity and humidity (Bartosik et al., 2011). Indeed, it has been suggested that *D. reticulatus* may even be more resistant to desiccation (Lees, 1946). Here, a strong association was observed between activity and saturation deficit in the field, with no questing tick activity observed at a saturation deficit of higher than 0.7. Laboratory investigations similarly identified a threshold saturation deficit of 0.7, above which <1 ticks survived over 63 days. Hence, these data suggest that the seasonal pattern of activity seen in the field, within the sites where it is abundant, is more strongly dictated by temperature than humidity and that humidity is unlikely to be limiting in the periods when *D. reticulatus* is active since the saturation deficit was only above 0.7 for short periods during mid-summer.

The results from this study, therefore, confirm that *D. reticulatus* is a relatively cold-adapted species with patterns of seasonal activity driven more strongly by temperature than by low humidity. It is clearly highly sensitive to climatic conditions, with a specific and distinct environmental niche. It is a species that might be expected to be strongly affected by climate change and less severe winter temperatures in central Europe may, at least in part, account for the observed rapid range expansion to more northerly latitudes (Dautel et al., 2006; Gray et al., 2009). Over the past 50 years, *D. reticulatus* in Germany has expanded its range from only two known populations to being present in all but two federal states (Drehmann et al., 2020). Nevertheless, the spatial distribution of this species within the U.K. remains something of an enigma, since it is largely confined to coastal habitats (Medlock et al., 2011), whereas this is not the case in continental Europe. The factors that account for and have maintained this distribution are unknown, but may represent isolated points of introduction with limited scope for dispersal, possibly associated with its nidicolous larval and nymphal stadia. There would appear to be no clear climatic or habitat limitations restricting range expansion within the U.K., as demonstrated by the recent identification of an inland population in Essex, bringing with it an elevated disease risk for animal and human hosts (de Marco et al., 2017).

**Acknowledgements**

We are grateful to the Dogs Trust for funding this study, and Public Health England for advice and practical assistance. This work was carried out with the approval of the University of Bristol ethics committee: UB/18/076. The authors declare no conflicts of interest.

The authors declare no conflicts of interest.

**Data availability statement**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

**References**

Abdullah, S., Helps, C., Tasker, S., Newbury, H. & Wall, R. (2016) Ticks infesting domestic dogs in the UK: a large-scale surveillance programme. *Parasites & Vectors*, 9, 391.

Alasmari, S. & Wall, R. (2021) Metabolic rate and resource depletion in the tick *Ixodes ricinus* in response to temperature. *Experimental and Applied Acarology*, (In Press), 83, 81–93.
Bartosik, K., Węsiowski, Ł. & Buczek, A. (2011) Abundance and seasonal activity of adult Dermacentor reticulatus (Acar.: Ixodidae) in eastern Poland in relation to meteorological conditions and the photoperiod. *Annals of Agricultural and Environmental Medicine*, **18**, 340–344.

Biernat, B., Karbowiak, G., Werszko, J. & Stańczak, J. (2014) Prevalence of tick-borne encephalitis virus (TBEV) RNA in *Dermacentor reticulatus* ticks from natural and urban environment, Poland. *Experimental and Applied Acarology*, **64**, 543–551.

Buczek, A., Zając, Z., Wojniak, A., Kulina, D. & Bartosik, K. (2017) Locomotor activity of adult *Dermacentor reticulatus* ticks (Ixodida: Ixodidae) in natural conditions. *Annals of Agricultural and Environmental Medicine*, **24**, 271–275.

Cerný, V., Szymanski, S., Dusbabek, F., Daniel, M. & Honzakova, E. (1982) Survival of unfed *Dermacentor reticulatus* (Fabr.) adults under natural conditions. *Wiadomości Parazytologiczne*, **28**, 27–31.

Dautel, H., Dippel, C., Oehme, R., Hartelt, K. & Schettler, E. (2006) Evidence for an increase in geographical distribution of *Dermacentor reticulatus* in Germany and detection of Rickettsia sp. Rpa4. *International Journal of Microbiology*, **296**, 149–156.

Drehmann, M., Springer, A., Lindau, A. et al. (2020) The spatial distribution of *Dermacentor* ticks (Ixodidae) in Germany—evidence of a continuing spread of *Dermacentor reticulatus*. *Frontiers in Veterinary Science*, **7**, 578220.

Estrada-Peña, A., Mihalca, A.D. & Petney, T.N. (2017) Ticks of Europe and North Africa: A Guide to Species Identification, p. 404. Springer, Cham.

Földvári, G., Rigó, K. & Lakos, A. (2013) Transmission of *Rickettsia slovaca* and *Rickettsia raoillii* by male *Dermacentor marginatus* and *Dermacentor reticulatus* ticks to humans. *Diagnostic Microbiology and Infectious Disease*, **76**, 387–389.

Földvári, G., Široký, P., Szerkeres, S., Majoros, G. & Srong, H. (2016) *Dermacentor reticulatus*: a vector on the rise. *Parasites & Vectors*, **9**, 314.

Gray, J.S., Dautel, H., Estrada-Peña, A., Kahl, O. & Lindgren, E. (2009) Effects of climate change on ticks and tick-borne diseases in Europe. *Vector Ecology: Journal of the Society for Vector Ecology*, **6**, 19–45.

Gray, J.S., Estrada-Peña, A. & Ziml, A. (2019) Vectors of Babesiosis. *Annual Review of Entomology*, **64**, 149–165.

Hansford, J.M., Hansford, K.M., Vaux, A.G.C. et al. (2017) Distribution of the tick *Dermacentor reticulatus* in the United Kingdom. *Medical and Veterinary Entomology*, **31**, 281–288.

Meyer-König, A., Zahler, M. & Gothe, R. (2001a) Studies on survival of *D. reticulatus* (Acari: Ixodidae). *Experimental and Applied Acarology*, **25**, 993–1004.

Mierzejewska, E.J., Welc-Faleciak, R., Karbowiak, G., Kowalec, M., Behnke, J.M. & Bajer, A. (2015a) Dominance of *Dermacentor reticulatus* over *Ixodes ricinus* (Ixodidae) on livestock, companion animals and wild ruminants in eastern and central Poland. *Experimental and Applied Acarology*, **66**, 83–101.

Mierzejewska, E.J., Alsarraf, M., Behnke, J.M. & Bajer, A. (2015b) The effect of changes in agricultural practices on the density of *Dermacentor reticulatus* ticks. *Veterinary Parasitology*, **211**, 259–265.

Nosek, J. (1972) The ecology and public health importance of *Dermacentor marginatus* and *D. reticulatus* ticks (Acar: Ixodidae). *Journal of Medical and Veterinary Entomology*, **19**, 93–102.

Olivieri, E., Garzoni, A.L., Zanzani, S.A., Veronesi, F. & Manfredi, M.T. (2017) Seasonal dynamics of adult *Dermacentor reticulatus* in a peri-urban park in southern Europe. *Ticks and Tick-Borne Diseases*, **8**, 772–779.

Paulauskas, A., Galdikas, M., Galdikaitė-Brazienė, E., Stanko, M., Kahl, O., Karbowiak, G. & Radziejewska, J. (2018) Microsatellite-based genetic diversity of *Dermacentor reticulatus* in Europe. *Infection, genetics and evolution*, **66**, 200–209.

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). *Parasitology Research*, **86**, 554–557.

Rubel, F., Brugger, K., Monazahian, M. et al. (2014) The first German map of georeferenced ixodid tick locations. *Parasites & Vectors*, **7**, 477.

Rubel, F., Brugger, K., Pfeffer, M. et al. (2016) Geographical distribution of *Dermacentor marginatus* and *Dermacentor reticulatus* in Europe. *Ticks and Tick-Borne Diseases*, **7**, 224–237.

Rubel, F., Brugger, K., Belova, O.A. et al. (2020) Vectors of disease at the northern distribution limit of the genus *Dermacentor* in Eurasia: *D. reticulatus* and *D. silvarum*. *Experimental and Applied Acarology*, **82**, 95–123.
Solomon, M.E. (1951) Control of humidity with potassium hydroxide, sulphuric acid or other solutions. Bulletin of Entomological Research, 42, 543–554.

Špitalská, E., Štefanidesová, K., Kocianová, E. & Boldič, V. (2012) Rickettsia slovaca and Rickettsia raoultii in Dermacentor marginatus and Dermacentor reticulatus ticks from Slovak Republic. Experimental and Applied Acarology, 57, 189–197.

Süss, J., Klaus, C., Gerstengarbe, F.W. & Werner, P.C. (2008) What makes ticks tick? Climate change, ticks, and tick-borne diseases. Journal of Travel Medicine, 15, 39–45.

Tharme, A.P. (1993) Ecological studies on the tick Dermacentor reticulatus. PhD Thesis, University of Wales.

Therneau, T. & Atkinson, B. (2019) rpart: Recursive Partitioning and Regression Trees. R package version 4.1-15. https://CRAN.R-project.org/package=rpart [accessed on 28 December 2020].

Tokhov, Y.M., Lutsuk, S.N. & Dyachenko, Y.V. (2014) Phenology of ixodid ticks of the genus Dermacentor in the Central Ciscaucasia. Entomological Review, 94, 426–433.

Zivkovic, Z., Nijhof, A.M., De La Fuente, J., Kocan, K.M. & Jongejan, F. (2007) Experimental transmission of Anaplasma marginale by male Dermacentor reticulatus. BMC Veterinary Research, 3, 32.

Zygner, W., Górski, P. & Wędrychowicz, H. (2009) New localities of Dermacentor reticulatus tick (vector of Babesia canis canis) in central and eastern Poland. Polish Journal of Veterinary Sciences, 12, 549–555.

Accepted 26 March 2021
First published online 4 May 2021

© 2021 The Authors. Medical and Veterinary Entomology published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.

Medical and Veterinary Entomology, 35, 434–441