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Analysis of the environmental and host-related factors affecting the distribution of the tick *Dermacentor marginatus*

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Introduction

Investigating environmental and host-related factors affecting the distribution of tick vectors is central to explore the ecology and the epidemiology of tick borne zoonoses. *Rickettsia slovaca* and *Rickettsia raoultii* are associated with tick-borne lymphadenopathy (TIBOLA), also called *Dermacentor*-borne necrosis erythema and lymphadenopathy (DEBONEL), which is an emerging infection in several European countries (Oteo et al. 2004; Lakos 2007; Selmi et al. 2008; Parola et al. 2009; Rieg et al. 2011). Although these agents are found both in *Dermacentor marginatus* and in *Dermacentor reticulatus* ticks, most studies on factors associated with changes in the geographical distribution of the infection focus on *D. reticulatus* (Sréter et al. 2005; Karbowiak 2014; Mierzejewska et al. 2015; Földvári et al. 2016). In this aspect *D. marginatus* is at the moment poorly studied, although it represents so far the only species of the genus *Dermacentor* that can act as vector for TIBOLA southward of the Alps.

Dermacentor marginatus has been reported in steppes, Alpine steppes, semi-desert areas, oak forests and neighbouring margins, dry meadows, biotopes characterized by xerophilic plant communities, salt meadows and near villages (Nosek 1972; Gilot and Pautou 1983; Hornok and Farkas 2009; Akimov and Nebogatkin 2011; Walter et al. 2016), indicating the plasticity of this tick species.

A recent study, conducted in a northern Mediterranean area (Selmi et al. 2017), applied a host–vector–pathogen approach to unravel the interactions between those key components of TIBOLA transmission. A strong host–parasite association was observed between wild boar and adult *D. marginatus*, confirming results of surveys in Sardinia (Satta et al. 2011) and Corsica (Grech-Angelini et al. 2016). In Europe, an increased density of wild boar has been reported during the past few decades (Boitani et al. 1995; Neet 1995; Apollonio et al. 2010), creating conflict situations between humans and wildlife for the damage to agricultural crops (Geisser and Reyer 2004). More recently, the presence of the wild boar was reported in (peri-)urban areas, as demonstrated by a survey, which was carried out in 25 countries (http://wildl ifean dman.be/docs/urban -wild-boar-inter natio nal-surve y.pdf).

We used data on surveillance of tick bites on humans, to investigate the association between habitat and the risk of exposure to D. marginatus in three regions. Moreover, in the same area, we analysed data on the collection of questing ticks, with specific interest in the association between presence of *D. marginatus* and environmental variables, including the effects of wild boar abundance and distribution (Trout Fryxell et al. 2015). By comparing results of the analysis of data on human surveillance and on host-seeking ticks, we formulated hypotheses on factors affecting TIBOLA incidence patterns such as, for example, increased risk for women and children (Lakos et al. 2012).

Materials and methods

Study area

The study was carried out in three regions of the Italian and French territory: Liguria, Tuscany and Corsica, covering an area ranging from 7.8° to 10.9°E longitude and 41.7° to 44.5°N latitude. The area is characterized by a typical Mediterranean climate (Peel et al. 2007), with warm to hot, dry summers and mild to cool, wet winters. The rainfall level fluctuates considerably in the area and affects the natural environment and the balance of ecosystems. Most areas of southern Tuscany have less than 600 mm of rainfall, spread throughout the year with a dry period during the summer, while the mountainous areas of Liguria and northern Tuscany have abundant rainfall in summer and cumulate up to 2000 mm per year. In Corsica, we can differentiate the level of rainfall between the coastal part, with dry summers and in some parts less than 600 mm of rain a year, and the mountainous part of the island, with higher rainfall and abundant snowfall on the highest peaks. As an adaptation to climatic conditions of these regions, there is a strong diversity of vegetation types in the study area. The arid area of southern Tuscany and Corsica favours the development of shrublands, i.e. dense thickets of evergreen sclerophyllous plants. On the coastline, maritime pine (*Pinus pinaster*) and eucalyptus (Eucalyptus globulus) are also widespread. The relatively humid habitat of Liguria and northern Tuscany is dominated by deciduous trees: pedunculate oak (*Quercus robur*), sessile oak (*Quercus petraea*), turkey oak (*Quercus cerris*), European hornbeam (*Carpinus betulus*), acacia (*Robinia pseudoacacia*) and poplar (*Populus* spp.). The vegetational belt between 500 and 1000 m is characterized by the presence of hop hornbeam (*Ostrya carpinifolia*), downy oak (*Quercus pubescens*), maple tree (*Acer campestre*), chestnut tree (*Castanea sativa*) and conifers as black pine (*Pinus nigra*) and pine larch (*Pinus nigra laricio*) in Corsica. The vegetational belt above 1000 m is dominated by beech woods (*Fagus sylvatica*). Wild ungulates, which are important maintenance hosts for adult tick populations, are differently distributed in the three regions. Roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and red deer (*Cervus elaphus*) are widespread in Tuscany and Liguria, but not in Corsica, that harbours only a low number of the indigenous swarthy Sardinian deer (*Cervus elaphus corsicanus*), while the mouflon (*Ovis aries musimon*) is present, but with significant differences in density. Finally wild boar (*Sus scrofa*) is very common and widespread in the three regions, and has become invasive and requires a management strategy.

Data of human exposure to ticks

The surveillance data was collected at the permanent observatory on vector-borne diseases (OPPV) at the Lucca local health unit (ASL 2) in Tuscany (Selmi et al. 2008), where a surveillance system was developed to estimate TBDs risk in patients exposed to tick bites. The database mainly refers to patients that are resident in Tuscany and, to a lesser extent, to patients resident in the regions of Liguria and Corsica and includes tick data (species, stage, sex), patient data (sex and age) and habitat frequented by patients when they were bitten. Here we use a part of the information collected from 1158 patients admitted to health facilities, for a tick removal, in the period 2006–2016. The report only considers the cases of exposure to the bite from hard tick species sheltering in natural areas. As almost all the ticks extracted from the patients belonged to the species D. marginatus and Ixodes ricinus, for the purpose of this research we used I. ricinus as a ‘surrogate species’, as defined by Wiens et al. (2008) and Caro (2010), namely, ‘a species used to represent other species or aspects of the environment’. In this sense, and strictly limited to the results obtained in this study area, I. ricinus is a good proxy to represent the exposure conditions that the patients experienced when they came into contact with a non-*D. marginatus* tick. Although not chiefly interested in the ecology of I. ricinus, the perspective to use a ‘dissimilarity approach’ (Werle et al. 2007), offers interesting opportunities to improve the ecological knowledge of the *D. marginatus* tick, by comparing the environmental characteristics affecting the distribution of D. marginatus, with those of the undoubtedly ecologically well-known I. ricinus (Gray 1984, 1991; Randolph 2004; Medlock et al. 2008; Dobson et al. 2011; Mannelli et al. 2012).

Entomological data

Entomological data were obtained by merging tick collection data from three different public authorities: OPPV, University of Turin (UNITO) and Experimental Zooprophylactic Institute of Piedmont Liguria and Valle d’Aosta (IZSPLV). The OPPV dataset refers to ticks collected in north western Tuscany, from April 2005 to November 2006 and from March 2007 to April 2009; in Tuscany and Liguria, from March to October 2012; in Corsica from April to October 2014. The UNITO dataset refers to ticks collected in north western Tuscany in August 2006, from March to August 2007, from May to October 2009, from April to October 2010, from April to November 2011 and from May to July 2012. The ISZPLV dataset refers to tick collected in Liguria, from March to August 2011, carried out in collaboration with UNITO.

The protocols used for tick sampling (i.e. dragging) and for entomological and environmental data recording, have been described in previous papers (Ceballos et al. 2014; Ragagli et al. 2016; Selmi et al. 2017). We identified and coded as a ‘site’, a given location where a series of dragging sessions were carried out, as long as they were within a 500 m radius and shared the same environmental variables value. For each dragging session, an area of 3 × 100 m2 was sampled. A site was considered positive when at least a stage of a tick was found, regardless of the quantity (Guerra et al. 2002).

Key variables

We identified seven key variables (Table 1) to test the occurrence of *D. marginatus* and *I.ricinus* in the environment. Site conditions were characterized by three field collected variables: habitat type, dominant plant species and altitude. Remote sensing and geographic information system (GIS)-based method were used to characterize four general site properties: CORINE, nighttime lights and human population density and minimum distance to roads.

From the CORINE Land Cover (CLC) data set (data available at https ://www.eea.europ a.eu/data-and-maps/data/clc-2000-vecto r-6) we derived the classes of interest by using the first three out of the five hierarchical classification levels, that consider (1) artificial surfaces, (2) agricultural areas, (3) forest and semi natural areas, (4) wetlands and (5) water bodies.

Nighttime lights are a class of urban remote sensing products derived from satellite sensors with specialized low-light imaging capabilities. The original instrument is the Operational Linescan System (OLS) flown by the US Air Force Defense Meteorological Satellite Program (DMSP) (data available at https ://ngdc.noaa.gov/eog/dmsp/downl oadV4 compo sites .html). The DMSP nighttime lights provide an annual cloud-free composite of average digital brightness value for the detected lights, that present a panoramic view of humanity from space, in particular how population, commerce, and resource consumption are distributed and provide a proxy for anthropogenic development (Sutton 1997; Small et al. 2011). Each pixel gives the annual average brightness level in units of 6 bit digital numbers (DN) spanning the range 0–63. From DMSP data we derived three classes of radiances, corresponding to 0, 1–10, 11–36, to respectively inform on absence, moderate and high presence in anthropogenic development.

A 100 × 100 m European population grid map, realized by using disaggregation algorithms on the 2000/2001 census estimates, produced by an international statistical institute in Europe (Gallego 2010) (data available at http://datas ervic e.eea.europ a.eu/datas ervic e/), was used to describe the estimated human population density for each monitoring site. We re-classified the original data set to constitute five ordinal levels to describe differences in population density among pixels, corresponding to 0, 1–20, 21–100, 101–200, > 200 inhabitants/ha.

The analysis of the variable minimum distance to a road were performed regardless of road hierarchy, that categorizes roads according to their function and capabilities, except for the requirement to be suitable for vehicles. Hypsographic data available for the study area were downloaded from national data service platforms (http://www.tutti talia .it/comun i/altit udine / and http://www.carte sfran ce.fr/ carte -franc e-depar temen t/carte -depar temen t).

Statistical analysis

We used generalised estimating equations (GEE) with logit-link and binomial error, to study the relationship between environmental variables and tick presence. Using GEE (exchangeable correlation structure, SAS Software, ver. 9.4), we accounted for correlation arising from repeatedly collecting ticks at the same sites across the study period (Diggle et al. 2002). Each analysis was performed by using the environmental factors as predictors and the positive or negative sampling session as outcome variables. To examine the effect of each categorical variable in the models, the odds ratio was interpreted relative to the reference baseline category. From the viewpoint of overall statistical quality of prediction by a model that compares more than two exposure levels, the choice of the baseline category is arbitrary and only the values and interpretation of the coefficients will change. In case of categorical variables, we chose baseline levels useful to enhance the differences between *D. marginatus* and *I. ricinus* risk presence.

We tested the associations for statistical significance using a standard χ2 test in R statistical software (R Development Core Team 2017) and the level of significance was set at 0.05.

Geographic information system (GIS)-based method for determining the road distance measurements were performed using GRASS GIS software (Grass Development Team 2010).

Results

Human surveillance

A total of 1158 cases of tick bite were reported at the OPPV during 2006–2016 (Table 2). In 48.8% of the cases (n = 565), the patients provided a tick sample for identification. The vast majority of the examined ticks were identified as I. ricinus (88.5%, n = 500). *D. marginatus* resulted in being the second most important anthropophagic tick in our study (9.1%, n = 51). Thus, *I. ricinus* and *D. marginatus* are the predominant human-biting tick species in the area, accounting for 97.6% of all those submitted to OPPV. Only adult *D. marginatus* were found on the patients and 76.5% of them were female. For all *I. ricinus* submitted, 58.7% were female, 40.7% immature and 0.6% male.

Three further tick species were identified through tick surveillance; in order of frequency: *Hyalomma marginatum, Haemaphysalis punctata, Ixodes hexagonus* and they summed a total of 2.4%.

The interpretation of the bivariate analysis of the surveillance data is summarized in Table 3.

Collection of ticks

The research data set includes 2542 sampling sessions for a total of 435 investigated sites and details of sampling is summarized in Table 4. *D. marginatus* occurrence was confirmed in 117 out 435 sites (26.8%) and in 222 out 2542 sampling sessions (8.7%), while I. ricinus was confirmed in 230 sites (52.8%) and in 782 sampling sessions (30.7%). We observed a significant difference in the number of the positive sites among Corsica, Liguria and Tuscany, both for *D. marginatus* presence (respectively 41.3, 13.9 and 30.6%) ($\chi 2 = 154$, df = 2, $P < 0.0001$) and *I. ricinus* presence (respectively 30.4, 46.9 and 59.1%) ($\chi 2 = 31$, df = 2, $P < 0.0001$). In particular, we noted that Corsica was the only region in which the number of positive sites was higher for *D. marginatus* than for *I. ricinus.*

The results of the logistic regression analysis of the association between each variable, and the collection of host seeking *D. marginatus* and *I. ricinus* are shown in Table 5. A complete list of D. marginatus positive sites, with the relative coordinates, is summarized in Table SM_1 (Online Resource).

Analysis of the environmental variables

The habitat showed itself to be an interesting environmental factor to highlight dissimilarity between *D. marginatus* and *I. ricinus* preference. There were proportionately more *D. marginatus* positive dragging sessions in the level ‘meadow’ than in the baseline level ‘forest’. Conversely, *I. ricinus* decreased significantly in the levels ‘scrubland’, ‘cropland’ and ‘meadow’.

The association between tick’s presence and plant typologies revealed the preference of *D. marginatus* for the levels ‘grass’ and ‘poplar’ and highlight the preference of *I. ricinus* for broad-leaved forests, whereas its presence was scarce when the plant typology was adapted to dry terrains, i.e. ‘sclerophyll’ and ‘holly oak’, or in absence of arboreal coverage.

The altitude in the study area ranges from 3 to 1660 m above sea level. To estimate the association with tick presence, we divided the measurements into four ordinal classes. Using the altitudinal belt 0–100 m as baseline category, we observed a small difference in the increase of *D. marginatus* risk presence in the altitudinal belt below 800 m, while the odds ratio is reduced by more than half above 800 m. On the contrary, increasing the elevation I. ricinus presence increased up to three times. The analysis of the hypsographic demography of our study area shows that from the lower to the upper altitudinal belt, there live respectively 87.9, 8.8, 3.2 and 0.1% of the human population. This data indicate that the altitudinal belt 0–100 m is both the most inhabited by the resident population and the one in which we found a greater presence of *D. marginatus* (13%) compared to that of I. ricinus (4.8%).

We used the first three classes of the CORINE, since the totality of our sampling results fall within these categories, and we used the ‘artificial surface’ category as a baseline. The related logistic regression model did not meet the $P < 0.05$ statistical significance level in the analyses, as a consequence, the CORINE variable was not taken into consideration in the discussion.

The analysis of the minimum distance to roads with respect to *D. marginatus* and *I. ricinus* positive dragging sites, gave different results in the three region. In Tuscany and Liguria the mean distance value for *D. marginatus* was lower than for *I. ricinus*, respectively 431 versus 1040 m and 44 versus 71 m, while in Corsica the mean distance value was higher for *D. marginatus* than for *I. ricinus*, respectively 132 versus

117 m. The odds of *D. marginatus* presence progressively increases with the decrease in the distance between dragging sites and roads. The effect of the distance calculated by the odds ratios for *I. ricinus* showed an exactly antithetical behaviour.

Statistically significant difference between levels of the variable night time lights was observed for the odds of *D. marginatus* presence, that increased markedly in the level ‘11–36’, the class of radiance that characterizes areas with a high anthropogenic development, and for the odds of *I. ricinus* presence that decreased in the level ‘1–10’.

We observed that increasing the population density also increased the frequency of *D. marginatus* positive dragging sessions and the level ‘> 200’, which expresses the highest density of human population in the study area, showed an odds ratio of 7.03. On the contrary, *I. ricinus* was sensitive to population density in the sense that increasing the density caused a decrease in the probability of the presence of this tick species.

Discussion

The surveillance system activated at the OPPV integrated the mandatory surveillance with the report of the tick bites, an investigation of the cases and the identification of the tick species.

Our data indicates that I. ricinus is the most widespread human biting tick in our area and *D. marginatus* is the second most important species. Other species have a negligible incidence in the statistic of the tick bites in local population. The results of the surveillance indicate that *D. marginatus* is more easily contacted in the peridomestic habitat rather than in forests or meadow.

There are detectable age and sex differences in tick species and habitat types preferences. In particular, morbidity is heavily biased towards female both in regard to habitat types and to tick species. Children (< 11 years old) are also more exposed to a tick bite in home proximity, but a statistically significant predominance for a tick species was not evident.

The results of the tick collection indicate that *D. marginatus* and *I. ricinus’s* positive dragging sessions segregate along habitat, altitude and vegetation typology axes. The analysis of the variable ‘habitat’ confirms the well known association between I. ricinus and forested rather than unforested areas and provides information on the ideal biotope for I. ricinus, as reported by Aeschlimann (1981). *D. marginatus* exhibits preference for the level ‘meadow’, confirming the literature data (Nosek 1972; Rubel et al. 2016), but it shows no preferences for the levels ‘forest’, ‘scrubland’ and ‘cropland’.

In regard to vegetation typology, I. ricinus shows preference for broad-leaved woods that provide favourable soil conditions (Gray 1991), while its presence decreases when the tree species is adapted to low moisture terrains. Our analysis failed to show similar dependencies for *D. marginatus* and to more directly explore the sensitivity of the tick species to surrounding environmental conditions. However a peculiar preference was noted for the class ‘poplar’. Poplar has been already reported as a plant favouring the presence of this species by Gilot and Pautou (1983). Actually *Populus* spp. are managed in short rotation under intensive culture and have become a highly promising crop option, especially for marginal agricultural land. From this point of view, the presence of the poplar can be interpreted as a proxy variable for proximity to anthropic environments as well as for lowland habitat, because the cultivation is usually carried out at a limited altitude.

The variable 'altitude' indicates that *D. marginatus* is more or less well represented in all the altitudinal belts and shows the greatest divergence in probability presences compared to *I. ricinus*, in the very extreme variable levels. We also analysed the joint difference in response to altitude for tick presence and the distribution of the local human population by elevation. This data indicates that the majority of the human population of the study area lives at an altitudinal belt characterized by a much higher presence of *D. marginatus* than *I. ricinus*.

In a nutshell, the presence of *D. marginatus* does not seem to be precluded by any particular habitat type. In terms of ecological opportunities *D. marginatus* is more tolerant to a wider range of environmental conditions and less influenced by habitat structure in respect to *I. ricinus*. Consequently, we believe that defining an ecological niche for *D. marginatus* is unrealistic. This consideration also supports the limited results obtained by habitat models used to link *D. marginatus* distribution with environmental variables in Germany (Rubel et al. 2014), Portugal (Santos-Silva et al. 2011) and Romania (Mihalca et al. 2012).

The result of the analysis of three anthropogenic and demographic site properties, the variables distance to roads, human population density and night-time lights, gives evidence that *D. marginatus* and *I. ricinus* positive dragging sessions also segregate for factors closely related to human presence and activity, in particular we observed that D. marginatus has a spatial preference for proximity to human settlements. This result, in lack of a significant association between *D. marginatus* presence and environmental variables, may encourage speculation on the use of hosts for dispersal (McCoy et al. 2013).

In Europe, adult *D. marginatus* is associated to domestic and wild herbivores and the quantitative importance of different hosts differs according to the regions. The main hosts for this tick species are sheep in Germany (Liebisch and Rahman 1976), cattle in Ukraina (Akimov and Nebogatkin 2011), several domestic herbivores (horse, cattle, goat, sheep) and pigs in France (Gilot and Pautou 1983) and wild and domestic Artiodactyla in Central Europe (Nosek 1972). However, in the southernmost regions of Europe, the association between *D. marginatus* and wild boar is consolidated, as reported in Spain (Ortuño et al. 2006), Corsica (Grech-Angelini et al. 2016), and Italy (Selmi et al. 2009; Masala et al. 2012; Selmi et al. 2017).

I. ricinus is a generalist species, but infestation of roe deer by *I. ricinus* in its adult stages, is considered very specific (Carpi et al. 2008; Gray et al. 1992; Rizzoli et al. 2009). To define to what extent the use of wild boar for dispersal contributed to disseminate *D. marginatus* in close proximity to humans dwellings, we examined the differences in results obtained in Tuscany and Liguria, with those obtained in Corsica. In Corsica, unlike Tuscany and Liguria, both the number of positive sites and the mean distance among positive dragging sessions and roads were greater for *D. marginatus* than for *I. ricinus*. It is worth noting that in this region, while wild boar remains the primary host for *D. marginatus, I. ricinus*, in the absence of the roe deer, is mainly collected from cattle (usually reared over all the territory and kept outside all year) (Grech-Angelini et al. 2016). The domesticated ungulates have a more relaxed response to anthropogenic disturbance and they do not perceive human activities as a threat (Nieminen 2013), therefore they are most likely to be found in close proximity to human settlements, where they can disseminate their host associated ticks.

At least in the tick system we examined in this study area, the effects of hosts abundance and distribution seem to significantly influence the presence of the tick species. Moreover, where a tick species forms different host-associated populations within local communities, these different populations show differences in performance, such as the difference in the distance to the roads we noted between *D. marginatus* and I. *ricinus* presence, when the latter is associated with the roe deer in Tuscany and Liguria, rather than the cattle in Corsica. We are aware that the tick–host–environment interplay that we observed in this area, can change over time. A political-administrative redefinition of the ‘optimal population size’ for the wild boar might be introduced any moment now, to prevent agricultural damage or ungulate-traffic collisions. It would be reasonable to follow how the patterns of host use evolve over time, to advance our understanding of the wildlife origin of TBDs.

When a *D. marginatus* engorged female infected by *Rickettsia* spp. detaches from the wild boar and falls to the ground in proximity to human dwellings, it will give rise to a number of transovarially infected larvae. The female descendents will have a great possibility to remain confined to the same area because of the limited displacement of the immature stages. Therefore, a relevant amount of questing adult *D. marginatus* is expected to emerge in locations with high human population density: this could modify the transmission dynamics of *D. marginatus*-borne diseases by increasing the contact rates between ticks and their pathogens and humans. In these conditions, potential interactions between *D. marginatus* and humans can be realised simply by carrying out trivial outdoor activities, not being necessary the existence of sub-population classes engaged in particular out-door recreational activity or prone to visit heavily infested areas, which instead is the context that characterizes the increase of I. ricinus-human contact in several countries of Europe (Linard et al. 2007; Randolph 2008). It is worth noting that people who are exposed to tick contact in peridomestic settings often exhibit lack of awareness and tend not to consider proper protective measures against tick bites, such as performing tick checks, wearing protective clothing or application of insect repellents (Connally et al. 2009). In these circumstances, it is more likely that the tick will succeed in biting.

The underlying causes that determine age and sex differences in TIBOLA morbidity, which govern the demographic impacts of the disease in human populations have long been debated (Lakos 2002; Raoult et al. 2002). Most of the studies tend to associate the phenomenon with physiological factors that increase the susceptibility in children and women, explaining that the higher probability of the tick bite in head–neck region reflects a possible *D. marginatus* attraction to the often longer hair of women and girls (Parola et al. 2009; Lakos et al. 2012). Based on the results of our study, we hypothesize that the sex bias may be due to the fact that the majority of tick contacts in females are in home proximity, where they experience a tick contact in conditions of increased vulnerability towards the species most commonly found in proximity to human dwellings that, according to our data, is the *D. marginatus*.

In conclusion, linking tick ecology and public health data is highly recommended. This unified method offered us the opportunity to clarify which mechanisms and environmental conditions affect human—*D. marginatus* contacts in this area. The result of our study suggests that the distribution of *D. marginatus* borne diseases follows different drivers on respect to those considered for archetypal emerging TBDs, such as the climatic changes or the modification of land use, that are indicated for the Lyme borreliosis emergence in both Europe and North America. Rather, host-mediated dispersal is a key factor affecting *D. marginatus* distribution, due to the adaptive behaviour of the wild boar and to its capability to live in close proximity to humans. Future studies should investigate how changes in anthropogenic pressure on wild boar may influence a local tick-host system and affect the dynamic of *D. marginatus*-borne diseases.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

References

Aeschlimann A (1981) The role of hosts and environment in the natural dissemination of ticks. Studies on a Swiss population of *Ixodes ricinus* L., 1758. Rev Adv Parasitol Warszawa 4:859–869

Akimov IA, Nebogatkin IV (2011) Distribution of ticks from of the genus dermacentor (Acari, Ixodidae) in Ukraine. Vestn Zool 45(1):35–40

Apollonio M, Andersen R, Putman R (eds) (2010) European ungulates and their management in the 21st century. Cambridge University Press, Cambridge

Boitani L, Trapanese P, Mattei L (1995) Demographic patterns of wild boar (*Sus scrofa* L.) population in Tuscany, Italy. J Mount Ecol 3:197–201

Caro T (2010) Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press, Washington, DC

Carpi G, Cagnacci F, Neteler M, Rizzoli A (2008) Tick infestation on roe deer in relation to geographic and remotely sensed climatic variables in a tick-borne encephalitis endemic area. Epidemiol Infect 136:1416–1424

Ceballos AL, Pintore MD, Tomassone L, Pautasso A, Bisanzio D, Mignone W, Casalone C, Mannelli A (2014) Habitat and occurrence of ixodid ticks in the Liguria region, northwest Italy. Exp Appl Acarol 64:121–135

Connally NP, Durante AJ, Yousey-Hindes KM, Meek JI, Nelson RS, Heimer R (2009) Peridomestic Lyme disease prevention results of a population-based case-control study. Am J Prev Med 37:201–206

Diggle P, Heagerty P, Liang KY, Zeger S (2002) Analysis of longitudinal data. Oxford University Press, Oxford

Dobson ADM, Finnie TJR, Randolph SE (2011) A modified matrix model to describe the seasonal population ecology of the European tick, Ixodes ricinus. J Appl Ecol 48:1017–1028

Földvári G, Široký P, Szekeres S, Majoros G, Sprong H (2016) Dermacentor reticulatus: a vector on the rise. Parasit Vectors 9:314

Gallego FJ (2010) A population density grid of the European Union. Popul Environ 31:460–473. http://www.jstor .org/stabl e/40666 610

Geisser H, Reyer HU (2004) Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. J Wildl Manage 68:939–946

Gilot B, Pautou G (1983) Distribution and ecology of Dermacentor marginatus (Sulzer, 1776) (Ixodoidea) in the French Alps and their foothills. Acarol 24:261–273

GRASS Development Team (2015) Geographic resources analysis support system (GRASS) software, version 6.4. Open source geospatial foundation. Electronic document. http://grass .osgeo .org

Gray J (1984) Studies on the dynamics of active populations of the sheep tick, Ixodes ricinus L. in co. Wicklow, Ireland. Acarol 25:167–178

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

Gray JS, Kahl O, Janetzki C, Stein J (1992) Studies on the ecology of Lyme disease in a deer forest in County Galway, Ireland. J Med Entomol 29:915–920

Grech-Angelini S, Stachurski F, Lancelot R, Boissier J, Allienne J-F, Marco S, Maestrini O, Uilenberg G (2016) Ticks (Acari: Ixodidae) infesting cattle and some other domestic and wild hosts on the French Mediterranean island of Corsica. Parasit Vectors 9:582. https ://doi.org/10.1186/s13071-016-1876

Guerra M, Walker E, Jones C et al (2002) Predicting the risk of Lyme disease: habitat suitability for Ixodes scapularis in the north central United States. Emerg Infect Dis 8:289–297. https ://doi. org/10.3201/eid08 03.01016 6

Hornok S, Farkas R (2009) Influence of biotope on the distribution and peak activity of questing Ixodid ticks in Hungary. Med Vet Entomol 23:41–46

Karbowiak G (2014) The occurrence of the Dermacentor reticulatus tick—its expansion to new areas and possible causes. Ann Parasitol 60:37–47

Lakos A (2002) Tick-borne lymphadenopathy (TIBOLA). Wien Klin Wochenschr 114:648–654

Lakos A (2007) Tick-borne lymphadenopathy—a new rickettsial disease? Lancet 350:1006

Lakos A, Kőrösi A, Földvari G (2012) Contact with horses is a risk factor for tick-borne lymphadenopathy (TIBOLA): a case control study. Wien Klin Wochenschrt 124:611–617

Liebisch A, Rahman MS (1976) Prevalence of the ticks Dermacentor marginatus (Sulzer, 1776) and Dermacentor reticulatus (Fabricius, 1794) and their importance as vectors of diseases in Germany (in German). Trop Med Parasitol 27:393–404

Linard C, Lamarque P, Heyman P, Ducoffre G, Luyasu V, Tersago K, Vanwanbeke SO, Lamb EF (2007) Determinants of the geographic distribution of Puumala virus and Lyme borreliosis infections in Belgium. Int J Health Geogr 6:15. https ://doi.org/10.1186/1476-072X-6-15

Mannelli A, Bertolotti L, Gern L, Gray J (2012) Ecology of Borrelia burgdorferi sensu lato in Europe: transmission dynamics in multi-host systems, influence of molecular processes and effects of climate change. FEMS Microb Rev 36:837–861

Masala G, Chisu V, Satta G, Socolovschi C, Raoult D, Parola P (2012) Rickettsia slovaca from Dermacentor marginatus ticks in Sardinia, Italy. Ticks Tick Borne Dis 3:393–395

McCoy KD, Leger E, Dietrich M (2013) Host specialization in ticks and transmission of tick-borne diseases: a review. Front Cell Infect Microbiol 3:57. https ://doi.org/10.3389/fcimb .2013.00057

Medlock JM, Pietzsch ME, Rice NVP, Jones L, Kerrod E et al (2008) Investigation of Ecological and Environmental Determinants for the Presence of Questing Ixodes ricinus (Acari: Ixodidae) on Gower, South Wales. J Med Entomol 45:314–325

Mierzejewska EJ, Pawełczyk A, Radkowski M, Welc-Falęciak R, Bajer A (2015) Pathogens vectored by the tick, Dermacentor reticulatus, in endemic regions and zones of expansion in Poland. Parasit Vectors 8:490

Mihalca AD, Dumitrache MO, Magdas C, Gherman CM, Domsa C, Mircean V, Ghira IV, Pocora V, Ionescu DT, Barabási SS, Cozma V, Sándor AD (2012) Synopsis of the hard ticks (Acari: Ixodidae) of Romania with update on host associations and geographical distribution. Exp Appl Acarol 58:183–206

Neet CR (1995) Population dynamics and management of Sus scrofa in western Switzerland: a statistical modelling approach. J Mount Ecol 3:188–191

Nieminen M (2013) Response distances of wild forest reindeer (Rangifer tarandus fennicus Lönnb.) and semi-domestic reindeer (R. t. tarandus L.) to direct provocation by a human on foot/snowshoes. Rangifer 33:1–15

Nosek J (1972) The ecology and public health importance of Dermacentor marginatus and D. reticulatus ticks in Central Europe. Folia Parasitol (Praha) 19:93–102

Ortuño A, Quesada M, López S, Miret J et al (2006) Prevalence of Rickettsia slovaca in Dermacentor marginatus ticks removed from wild boar (Sus scrofa) in northeastern Spain. Ann NY Acad Sci 1078:324–327

Oteo JA, Ibarra V, Blanco JR, Martinez AV, Marquez FJ, Portillo A et al (2004) Dermacentor-borne necrosis erythema and lymphadenopathy: clinical and epidemiological features of a new tick-borne disease. Clin Microbiol Infect 10:327–331

Parola P, Rovery C, Rolain JM, Brouqui P, Davoust B, Raoult D (2009) Rickettsia slovaca and R. raoultii in tick-borne rickettsioses. Emerg Infect Dis 15:1105–1108

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol Earth Syst Sci 11:1633–1644

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-proje ct.org/

Ragagli C, Mannelli A, Ambrogi C, Bisanzio D, Ceballos L, Grego E, Elisa Martello, Selmi M, Tomassone L (2016) Presence of host-seeking Ixodes ricinus and their infection with Borrelia burgdorferi sensu lato in the Northern Apennines, Italy. Exp Appl Acarol 69:167–178. https ://doi.org/10.1007/s1049 3-016-0030-9

Randolph SE (2004) Tick ecology: processes and patterns behind the epidemiological risk posed by Ixodid ticks as vectors. Paras 129:37–65

Randolph S (2008) Tick-borne encephalitis incidence in Central and Eastern Europe: consequences of political transition. Microbes Infect/Inst Pasteur 10:209–216. https ://doi.org/10.1016/j.micin f.2007.12.005

Raoult D, Lakos A, Fenollar F, Beytout J, Brouqui P, Fournier PE (2002) Spotless rickettsiosis caused by Rickettsia slovaca and associated with Dermacentor ticks. Clin Infect Dis 34:1331–1336. https://doi.org/10.1086/34010 0

Rieg S, Schmoldt S, Theilacker C, de With K, Wölfel S, Kern WV, Dobler G (2011) Tick-borne lymphadenopathy (TIBOLA) acquired in Southwestern Germany. BMC Infect Dis 11:167

Rizzoli A, Hauffe HC, Tagliapietra V, Neteler M, Rosa R (2009) Forest structure and roe deer abundance

predict tick-borne encephalitis risk in Italy. PLoS ONE 4:e4336. https ://doi.org/10.1371/journ

al.pone.00043 36

Rubel F, Brugger K, Monazahian M, Habedank B, Dautel H, Leverenz S, Kahl O (2014) The first German

map of georeferenced ixodid tick locations. Parasit Vectors 7:477

Rubel F, Brugger K, Pfeffer M, Chitimia-Dobler L, Didyk YM, Leverenz S, Dautel H, Kahl O (2016) Geographical distribution of Dermacentor marginatus and Dermacentor reticulatus in Europe. Ticks Tick Borne Dis 7:224–233

Santos-Silva MM, Beati L, Santos AS, Sousa RD, Nuncio MS, Melo P, Santos-Reis M, Fonseca C, Formosinho

P, Vilela C, Bacellar F (2011) The hard-tick fauna of mainland Portugal (Acari: Ixodidae): an update on geographical distribution and known associations with hosts and pathogens. Exp Appl Acarol 55:85–121

SAS Institute Inc. (2017) SAS 9.4 help and documentation. SAS Institute Inc., Cary

Satta G, Chisu V, Cabras P, Fois F, Masala G (2011) Pathogens and symbionts in ticks: a survey on tick species distribution and presence of tick-transmitted micro-organisms in Sardinia, Italy. J Med Microbiol 60:63–68

Selmi M, Bertolotti L, Tomassone L, Mannelli A (2008) Rickettsia slovaca in Dermacentor marginatus and tick-borne lymphadenopathy, Tuscany, Italy. Emerg Infect Dis 14:817–820

Selmi M, Martello E, Bertolotti L, Bisanzio D, Tomassone L (2009) Rickettsia slovaca and Rickettsia raoultii in Dermacentor marginatus ticks collected on wild boars in Tuscany, Italy. J Med Entomol 46:1490–1493

Selmi M, Ballardini M, Salvato L, Ricci E (2017) Rickettsia spp. in Dermacentor marginatus ticks: analysis of the host–vector–pathogen interactions in a northern Mediterranean area. Exp Appl Acarol 72:79– 91. https ://doi.org/10.1007/s1049 3-017-0132-z

Small C, Elvidge CD, Balk D, Montgomery M (2011) Spatial scaling of stable night lights. Remote Sens Environ 115:269–280

Sréter T, Széll Z, Varga I (2005) Spatial distribution of Dermacentor reticulatus and Ixodes ricinus in Hungary: evidence for change? Vet Parasitol 128:347–351

Sutton P (1997) Modeling population density with night-time satellite imagery and GIS. Comput Environ Urban Syst 21:227–244

Trout Fryxell RT, Moore JE, Collins MD, Kwon Y, Jean-Philippe SR, Schaeffer SM et al (2015) Habitat and vegetation variables are not enough when predicting tick populations in the Southeastern United States. PLoS ONE 10:e0144092. https ://doi.org/10.1371/journ al.pone.01440 92

Walter M, Brugger K, Rubel F (2016) The ecological niche of Dermacentor marginatus in Germany. Parasitol Res 115:2165–2174. https ://doi.org/10.1007/s0043 6-016-4958-9

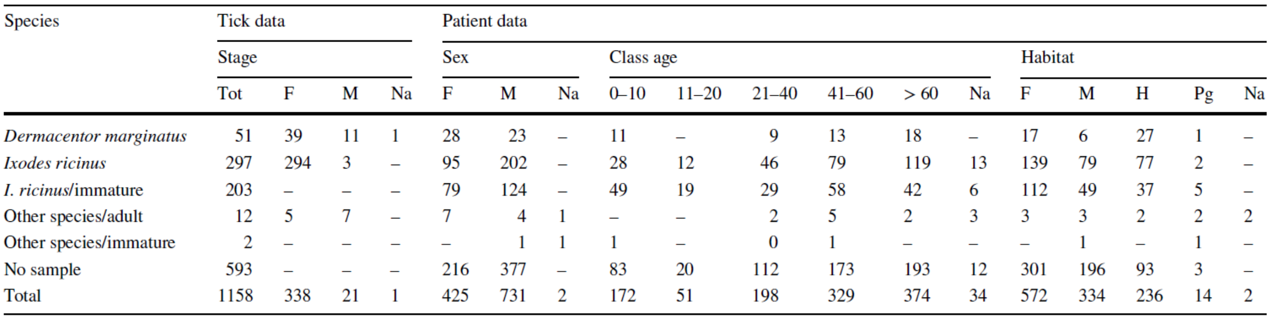
Werle SF, Norman A, Johnson NA, Dumont ER, Parasiewicz P (2007) Ecological dissimilarity analysis: a simple method of demonstrating community-habitat correlations for frequency data. Northeast Nat 14:439–446

Wiens JA, Hayward GD, Holthausen RS, Wisdom MJ (2008) Using surrogate species and groups for conservation planning and management. Bioscience 58:241–252. https ://doi.org/10.1641/B5803 10

Table 1 Variables tested for occurrence of *Dermacentor marginatus* and *Ixodes ricinus* in the study area

Variable	Variable description	Data source	Levels (n)	Levels description
Environmental				
Habitat type	Uniform environmental condition of the area (biotope)	Field-collected	4	Forest; meadow; scrubland; cropland
Dominant plant species	Plant species	Field-collected	14	Ash; beech; birch; chestnut; conifer; grass; grass-field-rocks; hazelnut; holly oak; mixed conifer forest; oak; poplar; sclerophyll; vine-olive tree
Topographic				
Altitude	GPS altitude measurements (m a.s.l.)	Field-collected	4	“0–100”; “101–400”; “401–800”; “> 800”
Land use				
CORINE	Homogeneus landscape of the firsts three hyerarchical classes of the CLC level 1	Remote sensing	3	Artificial surfaces; agricultural areas; forest and semi natural areas
Anthropogenic				
Distance from roads	Minimum distance to roads (m)	Spatial analysis	3	“< 100”; “101–500”; “> 500”
Nighttime lights	Annual average brightness level layer (units/km^2)	Remote sensing	3	“0”; “1–10”; “11–36”
Demographic				
Human population density	Dasymetric population density layer (number inhabitants/ha)	Spatial analysis	4	“0”; “1–20”; 21–200”; “> 200”

Table 2 Results of human tick-bite exposure survey at the OPPV

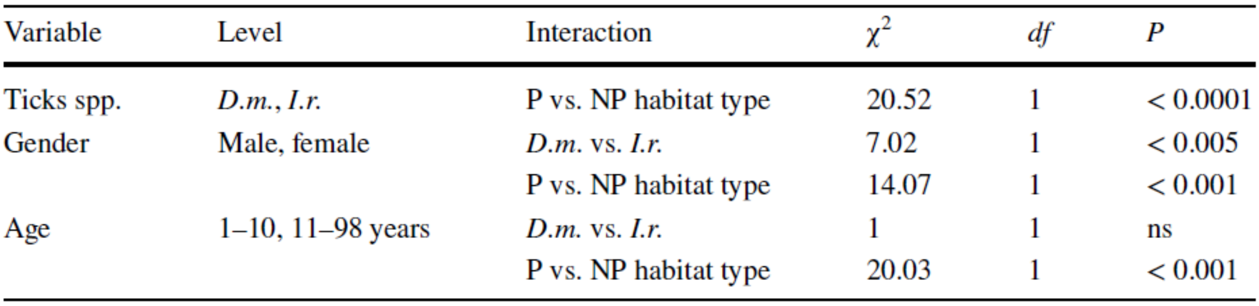


Species	Tick data				Patient data														
	Stage				Sex			Class age						Habitat					
	Tot	F	M	Na	F	M	Na	0–10	11–20	21–40	41–60	> 60	Na	F	M	H	Pg	Na
Dermacentor marginatus	51	39	11	1	28	23	–	11	–	9	13	18	–	17	6	27	1	–
Ixodes ricinus	297	294	3	–	95	202	–	28	12	46	79	119	13	139	79	77	2	–
I. ricinus/immature	203	–	–	–	79	124	–	49	19	29	58	42	6	112	49	37	5	–
Other species/adult	12	5	7	–	7	4	1	–	–	2	5	2	3	3	3	2	2	2
Other species/immature	2	–	–	–	–	1	1	1	–	0	1	–	–	–	1	–	1	–
No sample	593	–	–	–	216	377	–	83	20	112	173	193	12	301	196	93	3	–
Total	1158	338	21	1	425	731	2	172	51	198	329	374	34	572	334	236	14	2

Other species include, in order of frequency, *Hyalomma marginatum, Haemaphysalis punctata, Ixodes hexagonus*. Habitat refer to the typology of habitat attended by patients when they experienced a tick bite: forest (F), meadow (M), home proximity (H) and public garden (Pg). Na is for data not available

The patients were admitted to the healthcare system of the Tuscany, Liguria and Corsica in 2006–2016

Table 3 Bivariate analysis of data from the human surveillance



Variable	Level	Interaction	χ^2	*df*	*P*
Ticks spp.	*D.m.*, *I.r.*	P vs. NP habitat type	20.52	1	< 0.0001
Gender	Male, female	*D.m.* vs. *I.r.*	7.02	1	< 0.005
		P vs. NP habitat type	14.07	1	< 0.001
Age	1–10, 11–98 years	*D.m.* vs. *I.r.*	1	1	ns
		P vs. NP habitat type	20.03	1	< 0.001

‘P’ is for peridomestic habitat (home proximity) and ‘NP’ is for non-peridomestic habitat (forest, meadow and public garden). D.m. = *Dermacentor marginatus*, I.r. = *Ixodes ricinus*

Statistical significance of the association regarding: (1) tick species according to habitat type; (2) gender of the patients according to tick species and habitat type; (3) age of patients according to tick species and habitat type

Table 4 Questing ticks collected by dragging in the study area, from April 2005 to October 2014

Region	Province	Sampling sites (n)	*Dermacentor marginatus* positive site		*Ixodes ricinus* positive site		Dragging sessions (n)	*D.m.* positive dragging sessions		*I.r.* positive dragging sessions	
			%	95% CI	%	95% CI		%	95% CI	%	95% CI
Corsica	CdS	20	0.65	0.43–0.81	0.40	0.21–0.61	240	0.13	0.09–0.17	0.21	0.16–0.26
	HC	26	0.23	0.11–0.42	0.23	0.11–0.42	318	0.05	0.03–0.09	0.06	0.04–0.09
Liguria	Genova	40	0.15	0.07–0.29	0.60	0.44–0.73	195	0.03	0.01–0.06	0.30	0.24–0.37
	Imperia	43	0.07	0.02–0.18	0.23	0.13–0.37	200	0.01	0.01–0.04	0.11	0.07–0.16
	Spezia	32	0.16	0.07–0.31	0.62	0.45–0.77	154	0.04	0.02–0.09	0.35	0.28–0.43
Tuscany	Livorno	16	0.25	0.10–0.49	0.56	0.33–0.76	143	0.03	0.01–0.07	0.11	0.07–0.18
	Lucca	229	0.27	0.21–0.33	0.59	0.51–0.64	1016	0.11	0.10–0.13	0.48	0.45–0.51
	Massa	9	0.66	0.35–0.87	0.88	0.56–0.98	82	0.12	0.07–0.21	0.50	0.39–0.60
	Pisa	20	0.60	0.38–0.78	0.55	0.34–0.74	194	0.11	0.07–0.16	0.15	0.10–0.20
Tot		435	0.27	0.23–0.31	0.52	0.48–0.57	2542	0.09	0.08–0.11	0.30	0.29–0.32

Table 5 Association between environmental variables value and *Dermacentor marginatus* and *Ixodes ricinus* presence, estimates from generalized estimating equations (GEE)

Variable	Level	*D. marginatus*				*I. ricinus*			
		%	OR	95% CI	*P*	%	OR	95% CI	*P*
Habitat					< 0.001				< 0.001
	Forest	0.650	1			0.920	1		
	Scrubland	0.080	0.98	0.51–1.91	ns	0.050	0.33	0.20–0.52	< 0.001
	Cropland	0.030	1.21	0.57–2.57	ns	0.001	0.03	0.01–0.14	< 0.001
	Meadow	0.240	3.70	2.14–6.40	< 0.001	0.029	0.37	0.22–0.61	< 0.001
Dominant plant species					< 0.001				< 0.001
	Chestnut	0.363	1			0.284	1		
	Ash	0.005	0.80	0.56–1.16	ns	0.001	0.18	0.14–0.25	ns
	Beech	0.035	0.10	0.03–0.30	< 0.001	0.244	1.00	0.67–1.49	ns
	Birch	0.010	0.95	0.19–4.67	ns	0.009	1.35	0.72–2.51	ns
	Conifer	0.075	0.48	0.24–0.96	< 0.05	0.059	0.36	0.16–0.79	< 0.001
	Grass	0.190	1.63	0.80–3.29	ns	0.024	0.23	0.12–0.44	< 0.001
	Grass-field-rocks	0.026	0.46	0.15–1.38	ns	0.024	0.21	0.10–0.44	< 0.001
	Hazelnut	0.017	0.70	0.17–2.85	ns	0.027	1.52	0.58–3.97	ns
	Holly oak	0.030	0.27	0.11–0.64	< 0.01	0.019	0.15	0.06–0.37	< 0.001
	Mixed forest	0.045	0.59	0.25–1.37	ns	0.109	1.07	0.77–1.50	ns
	Oak	0.094	0.54	0.28–1.02	< 0.05	0.169	0.93	0.58–1.47	ns
	Poplar	0.035	2.90	0.62–13.41	ns	0.011	0.77	0.33–1.76	ns
	Sclerophyll	0.040	0.82	0.34–1.98	ns	0.015	0.34	0.15–0.74	< 0.001
	Vine-olive tree	0.035	0.89	0.37–2.15	ns	0.004	0.12	0.03–0.16	< 0.001
Altitude					< 0.001				< 0.001
	0–100	0.130	1			0.048	1		
	101–400	0.260	1.37	0.62–2.99	ns	0.127	1.70	0.87–3.29	ns
	401–800	0.420	2.07	1.03–4.17	< 0.05	0.315	3.44	1.93–6.12	< 0.001
	> 800	0.190	0.42	0.20–0.91	< 0.05	0.510	3.03	1.74–5.27	< 0.001
CORINE					ns				ns
	Artificial surface	0.013	1			0.001	1		
	Agricoltural areas	0.242	1.24	0.09–16.15	ns	0.129	0.86	0.29–2.50	ns
	Forest	0.745	1.02	0.07–13.67	ns	0.870	0.90	0.28–2.89	ns
Distance from roads					< 0.001				< 0.001
	> 500	0.197	1			0.340	1		
	101–500	0.243	0.93	0.57–1.51	ns	0.295	0.83	0.60–1.16	ns
	0–100 mt	0.560	1.03	0.65–1.64	ns	0.365	0.55	0.39–0.77	< 0.001
				< 0.001					< 0.001
	0	0.668	1			0.847	1		
	1–10	0.036	0.78	0.34–1.81	ns	0.020	0.30	0.15–0.58	< 0.001
	11–36	0.296	2.59	1.58–4.23	< 0.001	0.133	0.83	0.51–1.32	ns
Population density					< 0.001				< 0.001
	0	0.112	1			0.270	1		
	1–20	0.588	3.14	1.72–5.75	< 0.001	0.585	1.48	1.00–2.20	< 0.05
	21–200	0.238	2.89	1.38–6.07	< 0.005	0.134	0.84	0.51–1.40	ns
	> 200	0.062	4.99	1.54–16.19	< 0.005	0.011	0.54	0.20–1.46	ns