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Parasitized or non-parasitized, why? A study of factors influencing tick burden in roe deer neonates.

Léa Bariod^{1,2,3*}, Sonia Saïd³, Clément Calenge⁴, Stéphane Chabot³, Vincent Badeau⁵, Gilles Bourgoïn^{1,2}

1. Université de Lyon, VetAgro Sup - Campus Vétérinaire de Lyon, Laboratoire de Parasitologie Vétérinaire, Marcy-L'Etoile, France
2. Université de Lyon, Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, Villeurbanne, France
3. Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, Birieux, France
4. Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, Le Perray en Yvelines, France
5. Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement, Champenoux, France

***Corresponding author**

E-mail: bariod.lea@orange.fr

27 **Abstract**

28 *Ixodes ricinus*, the most common species of tick in Europe, is known to transmit major pathogens to animals
29 and humans such as *Babesia* spp. or *Borrelia* spp.. Its abundance and distribution have been steadily
30 increasing in Europe during recent decades, due to global environmental changes. Indeed, as ticks spend
31 most of their life in the environment, their activity and life cycle are highly dependent on environmental
32 conditions, and therefore on climate or habitat changes. Simultaneously, wild ungulates have expanded their
33 range and increased dramatically in abundance worldwide, in particular roe deer (*Capreolus capreolus*),
34 have allowed tick populations to grow and spread. Currently, tick infestation on newborn wild ungulates is
35 poorly documented. However, newborn ungulates are considered more sensitive to tick bites and pathogen
36 transmission because of their immature immune system. Thus, improving knowledge about the factors
37 influencing tick infestation on newborns is essential to better understand their health risks. This study was
38 conducted at Trois-Fontaines forest, Champagne-Ardenne, France (1992-2018). Based on a long-term
39 monitoring of roe deer fawns, we used a novel Bayesian model of the infestation of fawns to identify which
40 biotic or abiotic factors are likely to modify the level of infestation by ticks of 965 fawns over time. We
41 show that tick burden increased faster during the first days of life of the fawns and became constant when
42 fawns were 5 days old and more, which could be explained by the depletion of questing ticks or the turnover
43 of ticks feeding on fawns. Moreover, the humidity, which favors tick activity, was weakly positively related
44 to the tick burden. Our results demonstrate that tick infestation was highly variable among years, particularly
45 between 2000 and 2009. We hypothesize that this results from a modification of habitat caused by hurricane
46 Lothar.

47
48 **Keywords:** *Capreolus capreolus*, newborns, *Ixodes ricinus*, age, climatic variability, habitat, population
49 density

50 **Introduction**

51 Ticks are considered to be one of the most important arthropod vector of diseases in the world [1]. They are
52 of major concern as they can transmit several pathogens to their host during their blood meal, such as viruses,
53 bacteria or protozoans [2,3]. They can also have direct negative effects to their host, such as blood loss
54 (known as spoliation effect [4]) or destruction of host tissue by enzymes present in their saliva [5]. Over the
55 past decades, these ectoparasites have become an increasing worldwide health burden, threatening both
56 humans and animals [6]. The abundance and distribution of ticks can strongly vary among areas and have
57 considerably increased in recent decades [7–9]. In order to understand the population dynamic and the
58 geographic distribution of ticks, and to predict the risks of transmission of tick-borne pathogens, it is of
59 major concern to determine the factors driving abundance and spread of these parasites [10].

60 In Central Europe, *Ixodes ricinus* is the most common hard-tick species. It is of particular concern due to
61 their major role as a vector of many pathogens for both animals and humans, such as *Anaplasma* spp. [11],
62 *Babesia* spp. [12], *Borrelia* spp. [13] and Tick-borne encephalitis virus [14]. This three-host tick species
63 takes one blood meal on their host per life stage (3 life stages: larva, nymph and adult), with blood meals
64 lasting for few days (2-12 days according to their life-stage; [15,16]) before falling in the environment where
65 it moults into the next stage or lay eggs and die [17]. As this tick completes its life cycle in at least 3 years
66 [15], it spends most its life free in the environment. Thereby survival, development and questing activity
67 are highly dependent on the weather conditions and microclimate [18,19].

68 Among the microclimatic requirements, temperature and humidity are the most important factors affecting
69 the development rate, survival and questing activity of ticks [20]. Some studies have estimated that *Ixodes*
70 *ricinus* is looking for a host when the temperature is in average between 7°C and 26°C [21–24] and when
71 the relative humidity is at least 80% to avoid desiccation [7]. When these conditions are met, ticks use the
72 “ambush” technique in climbing up vegetation to quest for a passing host [7]. However, during this activity
73 step, ticks loose moisture, which obliges them to return often to the ground to recover the lost water. The
74 suitability of the ground based-vegetation which retains the moisture and provides shadow is highly

75 important for the tick survival, ticks are abundant in the leaf litter and the low strata vegetation of woodlands
76 and forests [7,25]. *I. ricinus* can survive in deciduous forests or in meadows as long as there is sufficient
77 litter on the ground and the microclimate is moist [26]. However, it has been shown that the abundance of
78 these ticks is higher in deciduous forests, particularly those containing oak and beech, and especially when
79 the shrub cover is important [26,27]. Local microclimate and local vegetation have thus important roles for
80 tick survival and behavior in their seasonal questing activity throughout the year [22,28,29]. In general, a
81 bimodal activity pattern with a dominant peak in spring and a minor peak in autumn is observed for *I. ricinus*
82 in Central Europe when climatic conditions are temperate and wet. In addition, as variations of seasonal
83 weather conditions between years occur, yearly variations of the seasonality of tick activity should also
84 occur [24].

85 The life cycle of *I. ricinus* is also highly dependent on the availability of hosts, because of their questing
86 behavior (i.e., the “ambush” technique; [7]). This ectoparasite species is a ubiquitous tick in Europe, which
87 can parasite a wide range of animal species, including mammals, reptiles and birds [30]. Larvae and nymphs
88 of *I. ricinus* are commonly found on small animals such as rodents [31], although nymphs can also be seen
89 on larger hosts such as sheep [32]. Large vertebrates are the main suitable hosts for blood meals and mating
90 of the adult ticks [26]. The infestation consequences on host will be greater especially if these parasites are
91 found in large quantities [4].

92 Hosts can develop an immune response against ticks to decrease their fixation time and engorgement, and
93 hence, the spoliation effect and the risk of pathogen transmission [33,34]. Resistance to tick infestation
94 implicates both acquired and innate immunity [35]. However, ticks can circumvent host defenses with active
95 components secreted in their saliva which can induce host immunosuppression and facilitate acquisition of
96 blood meals for ticks and the transmission of the tick-borne pathogens [36]. This is why newborns can be
97 considered more sensitive to tick bites. Indeed, they have a naïve and immature immune system even if they
98 are not totally vulnerable thanks to the transmission of acquired immunity by the colostrum of the mother

99 [37,38]. In addition, failure in the transfer of humoral immunity from mothers can happen and increase
100 susceptibility of newborns to tick bites [39,40].

101 The cervids, and particularly the roe deer (*Capreolus capreolus*), are considered as key hosts for the
102 population dynamic of *I. ricinus* [26]. During the last decades, their population have been increasing in the
103 Northern Hemisphere [41,42], which, in turn, has led to the increase and geographical spread of tick
104 populations [10,26,43–45]. Tick activity is the most important in spring and the eggs laying by female ticks
105 takes place at the same time as the birth period of the fawns, *i.e.* around the month of May [24,46].
106 Furthermore, fawns of roe deer have a hider behavior (*i.e.*, they hide in the vegetation cover to limit the
107 probability of detection by a predator; [47]) and have therefore a preference for dense vegetation. Their
108 naïve immune system make also them an easy target for questing ticks even if their movements are limited
109 during the first days of life [48,49]. To our knowledge, no study has yet investigated the factors influencing
110 the level of infestation by ticks on roe deer neonates.

111 Based on previous knowledge on ticks, we predicted a higher tick burden (H1) during warm and wet spring
112 conditions as it favors tick activity. We also predicted (H2) an influence of the habitat on tick infestation,
113 with more parasitized roe deer fawns living in habitats with important shrub cover and ground-based
114 vegetation which retains humidity; and (H3) an influence of the density of roe deer on tick burden, with the
115 highest values of infestation by ticks during the years when roe deer density, calculated the winter preceding
116 the catches of fawns, is the highest. Indeed, as intensity of tick burden on deer increases with high host
117 populations densities, we can assume that ticks will be more abundant in the environment and parasitize
118 fawns more [10,50].

119 Based on a long-term monitoring of the roe deer neonates from 1992 to 2018 in the population of Trois-
120 Fontaines in France, we studied the factors influencing the tick burden of newborn roe deer fawns. This
121 long-term monitoring of the infestation of fawns during their first days of life by the tick *Ixodes ricinus*
122 allowed us to study the effects of factors linked to the host (individual and populational factors) on tick
123 risks, but also of variations in Spring weather conditions (temperature, humidity, extreme events) and habitat

124 characteristics. We used a novel Bayesian model of the infestation of fawns by ticks to identify which biotic
125 or abiotic factors are likely to level of tick infestation of fawns over time.

126 **Materials and methods**

127 **• Ethics statement**

128 In accordance with European and French laws, roe deer captures have been carried out minimizing animal
129 stress and handling time (limited to 10 minutes for a fawn), and ensuring animal welfare, as defined in the
130 guidelines for the ethical use of animals in research. All methods were approved by the authorities (French
131 Ministry of Environment). These experiments were performed in accordance with the conditions detailed in
132 the specific accreditation delivered to the Office National de la Chasse by the Préfecture de Paris. Animal
133 captures and experimental procedures were in line with the French Environmental Code (Art. R421-15 to
134 421-31 and R422-92 to 422-94-1) and duly approved by legislation from the Prefecture of Paris (agreement
135 n°2009-014, n°. 2013-118, n°2019-02-19-003).

136 **• Data collection**

137 **○ Study area**

138 This study was carried out in the Territoire d'Étude et d'Expérimentation (TEE) of Trois-Fontaines, located
139 in north-eastern France (48°38 ' N, 4°54 ' E) (Fig 1). This is an enclosed forest of 1360 ha with an overstory
140 dominated by oak (*Quercus* spp.) and beech (*Fagus sylvatica*), while the coppice is dominated by hornbeam
141 (*Carpinus betulus*) [51]. The climate is continental, characterized by cold winters (mean daily temperature
142 in January-February was 3.2°C between 1992 and 2018, data from Météo France) and hot but not dry
143 summers (mean daily temperature in July is 19.2°C and total rainfall in July and August is 137.63 mm
144 between 1992 and 2018, data from Météo France).

145 **Fig 1. Geographic location in France (on the left) of the study site composed of 172 forest plots (on the**
146 **right).**

172 grid using ground observations and large-scale general circulation model products (Météo France, [56]).
173 This reanalysis is described in Durand et al. [57,58] and several validations have been performed [56,59].
174 In this study, we used the mean values of the temperature (T, in °C) and relative humidity (RH, in %) of the
175 capture day and 4 days before this day. Indeed, nymph and larvae of ticks take a blood meal on their host
176 during in average 3 days, and adult in 7 days, before to detach and fall off [16]. We therefore considered a
177 mean duration of blood meal of 5 days, explaining why we took the weather conditions into account during
178 this time.

179 Our study site contains 172 forest plots measuring in average 7.95 ha, delineated by forest trails. In each
180 forest plot during autumn, the dominant species and its cover proportion were determined for the following
181 years: yearly from 1996 to 2005, in 2009 and in 2012 [51,58]. We used these data to assess the habitat effect
182 on tick infestation. When habitat data was not available for a year: (1) we used habitat data from the closest
183 year (i.e., +/- 2 years max); (2) data after 2014 were not considered, because we did not collect any data on
184 habitat structure after 2012, and we considered that habitat structure had changed too much after 2 years to
185 be ignored in a study of habitat effect on tick infestation.

186 Between 1996 and 1999, forest managers have made openings in the habitat (i.e., pasture area) to improve
187 roe deer habitat. Then, in late December 1999, hurricane Lothar, apparently the strongest hurricane in the
188 region for at least 1000 years, hit the Trois-Fontaines site, disturbing the habitat [59,60]. This event created
189 several openings and modified the microclimatic conditions of the environment.

190 • **Model of the infestation process**

191 We designed a Bayesian model describing the infestation process of the roe deer fawns by ticks during the
192 first 8 days of their life, to test the effect of environmental variables on the infestation rate. All the code and
193 data used for this modelling approach are available in a R package named `tickTF` [63], (Digital Object
194 Identifier: 10.5281/zenodo.5764798), available on Github at the URL:
195 <https://github.com/ClementCalenge/tickTF>. It can be installed in R with the package `devtools` [64], using

196 the function `devtools::install_github("ClementCalenge/tickTF", ref="main")`.
197 The package `tickTF` includes a vignette describing how the user can reproduce easily the model fit (available
198 with the command `vignette("tickTF")`, once the package has been installed). This vignette is also
199 available as the supplementary material of this paper, and describes the complete mathematical development
200 of the model, the implementation of the model using the R package `NIMBLE` [65], the complementary
201 analyses and model checks.

202 In this section, we give a short description of the model, and we refer the reader to the supplementary
203 material for a more complete development.

204 We modelled the infestation process by a Poisson process (e.g. [66]). In other words, the number N_j of ticks
205 present on a given fawn j is supposed to follow a Poisson distribution with mean Λ_j :

$$206 \quad N_j \sim P(\Lambda_j)$$

207 The expected number of ticks on fawn j is supposed to be the result of a process of accumulation of ticks,
208 i.e. is equal to the integration over time t of an instantaneous risk function $\lambda_j(t)$:

$$209 \quad \Lambda_j = \int_0^{a_j} \lambda_j(t) dt$$

210 where a_j is the age of fawn j at the time of capture. We modelled this instantaneous risk of infection of a
211 fawn having t days old with:

$$212 \quad \lambda_j(t) = \zeta_j \times \mu(\mathbf{x}_j) \times s_j(t) \times \exp(\gamma_v \times I(t > 5)) \quad (1)$$

213 The instantaneous rate of infestation of a given fawn is therefore the product of an instantaneous rate of
214 infestation per unit of body size area $\mu(\mathbf{x}_j)$ -- which itself is supposed to depend on environmental variables
215 characterizing the capture \mathbf{x}_j (see below) --, of the body size $s_j(t)$ of the fawn j at times t , and of a random
216 individual effect ζ_j . These random effects follow a gamma distribution $G(1/\varphi, \varphi)$, with φ a dispersion
217 parameter to be estimated, and account for the fact that different fawns have different sensibilities to ticks.

218 As we said before, we considered a mean duration of blood meal of 5 days. Then, after 5 days, the ticks that
219 infested the fawn on its first day of life start to detach themselves and fall off, which is expected to lead to
220 a decrease in the observed infestation rate, as the number of ticks infesting a fawn may be partly
221 compensated by the number of ticks quitting the animal. Thus, the instantaneous rate of infection is supposed
222 to be different for fawns aged up to 5 days old and for older fawns (this rate is multiplied by $\exp(\gamma_v)$ after
223 that) – in this equation, $I(t>5)$ takes the value 1 when the fawn is older than 5 days old and 0 otherwise.

224 To fit this model, we had to develop a submodel for the instantaneous rate of infestation per unit of body
225 size area $\mu(\mathbf{x}_j)$ – which is independent of age – and another submodel for the changes of the body surface
226 area $s_j(t)$ of fawn j with time – which varies with age.

227 For the latter, we could use the data collected on captured fawns to model the relationship between the age
228 at capture a_j and the body surface area at capture $s_j(a_j)$. Our data suggested that the following quadratic
229 regression model was reasonable to describe the growth of the roe deer fawn during its first 8 days of life
230 (see supplementary material):

$$231 \quad s_j(t) = \beta_0 + \beta_1 \times t + \beta_2 \times t^2 + \epsilon_j$$

232 where ϵ_j is a gaussian residual with zero mean and standard deviation σ_s .

233 Moreover, we proposed the following loglinear submodel for the instantaneous rate of infestation per unit
234 of body size area:

$$235 \quad \log \mu(x_j) = \alpha_0 + \delta_{u(j)} + \sum_{k=1}^p \gamma_k x_{jk} \quad (2)$$

236 where α_0 is the intercept, $\delta_{u(j)}$ is a gaussian random effect characterizing the year $u(j)$ of capture of fawn j ,
237 and γ_k are coefficients characterizing the effect of environmental variables x_{jk} . Note that preliminary versions
238 of our model revealed that the variance of the year random effects $\delta_{u(j)}$ varied a lot across periods. We
239 distinguished three periods based on the dynamics of the forest structure: (i) period 1 corresponded to the
240 period before the Lothar hurricane (between 1992–1999), (ii) period 2 corresponded to the 10 years

241 following this hurricane (between 2000 and 2009), (iii) period 3 corresponded to the later years (2010 to
242 2018). We estimated one variance parameter $\sigma_u^{(p)}$ of the year random effects for each period p . During the
243 step of model building, we tested the effect of several variables x_{jk} on the infestation rate: (i) humidity, (ii)
244 temperature, (iii) roe deer density and (iv) habitat type. We kept in the model only the most influential
245 variables.

246 One difficulty with this model is that we did not know the exact number N_i of ticks on the fawn j but rather
247 the tick-burden class. However, given A_j we could calculate the probability of all the possible values of N_i
248 within a given class (since N_i follows a Poisson distribution), and therefore, we could calculate the
249 probability of each burden class by summing the probabilities of all values of N_i in this class (see
250 supplementary material for more details).

251 We estimated the posterior distribution of the vector of parameters of the model, i.e. $\theta =$
252 $(\beta_0, \beta_1, \beta_2, \phi, \sigma_s, \{\sigma_u^{(p)}\}, \{\delta_u\}, \alpha_0, \gamma_v, \{\gamma_k\})$. We fitted our model using MCMC using the package NIMBLE ([65]
253 see supplementary material for technical details) for the R software, using 4 chains of 50 000 iterations after
254 a burn-in period of 1000 samples. To save some memory space, we thinned the chains by selecting one
255 sample every 20 iterations. We checked the mixing properties of the chains both visually and using the
256 diagnostic of [67]. We checked the goodness of fit by using the approach recommended by Gelman and
257 Meng [68]. Each MCMC iteration generated a sampled value $\theta^{(r)}$ of the parameter vector θ . For each
258 simulated value $\theta^{(r)}$, we simulated a virtual dataset and calculated a summary statistic on it; we then
259 compared the observed statistics with the distribution of simulated values. We used several summary
260 statistics: the number of fawns in each of the three tick-burden classes in total, for each possible age, and in
261 each year. In all cases, the observed values were within the limits of the 95% credible intervals.

262 Results

263 In total, we collected data of tick infestation on 1043 fawns. Age of individuals was estimated between 1
264 and 20 days (mean \pm SD = 4.01 ± 3.05 ; min = 1, max = 20) during the 1992-2018 period. Only fawns aged

265 between 1 and 8 days were kept for our analysis, as older fawns were rare in our data (8% of the total
 266 dataset). For the following analyses, we only used data from the 965 fawns less than 8 days old (mean =
 267 3.35 +/- 2.02) when captured (Fig 3). Among them, 696 fawns had <10 ticks (26 fawns/year in average, SD
 268 = 11), 167 had 10 to 19 ticks (7 fawns/year, SD = 3) and 102 had ≥ 20 ticks (4 fawns/year, SD = 3).

269 **Fig 3. Number of fawns studied per year in the Trois-Fontaines Forest between 1992 and 2018.**

270 The three gray scales correspond to the three tick burden classes (gray light = less than 10 ticks; dark gray
 271 = between 10 and 20 ticks; black = more than 20 ticks).

272 The model including an effect of the variables « >5 days old », « humidity » and random effect of the
 273 « year » was considered as the best model for the infestation rate of fawns. We did not highlight any effect
 274 of the temperature (coefficient = 0.00 [-0.04; 0.04]_{95%CI}) and of the roe deer density (coefficient = 0.002 [-
 275 0.001; 0.005]_{95%CI}) on the instantaneous infestation rate per unit of body surface area. Moreover, all the
 276 coefficients associated to habitat types were characterized by 95% CI including 0 – they were all
 277 characterized by a point estimate comprised between -0.1 and 0.1 and by a standard error equal to 0.11, see
 278 supplementary material). All the estimated parameters of the final model are presented in table 1.

279 **Table 1. Estimated top parameters for the final model of the infestation of fawns by ticks in the Trois-**
 280 **Fontaines Forest. For each parameter, we give the notation used in the text, a short description, the**
 281 **point estimate (corresponding to the mean of the posterior distribution) and the 95% credible**
 282 **interval.**

Description	Notation	Est.	95% CI
Intercept in infestation rate log-linear model	α_0	2.853	2.68 ; 3.02
	β_0	0.176	0.174 ; 0.178
Parameters of the growth model	β_1	0.014	0.013 ; 0.014
	β_2	-0.001	-0.001 ; -0.001
	σ_s	0.021	0.02 ; 0.022
Effect of >5 days old	γ_v	-17.7	-46.6 ; -2.6
Dispersion parameter of individuals random effects on the infection rate	ϕ	0.68	0.53 ; 0.85

Effect of humidity in infestation rate log-linear model	γ_k	0.01	-0.006 ; 0.025
	$\sigma_u^{(1992-1999)}$	0.438	0.044 ; 1.141
Standard deviation $\sigma_u^{(p)}$ of the years random effects in infestation rate log-linear model for each period p	$\sigma_u^{(2000-2009)}$	0.822	0.422 ; 1.543
	$\sigma_u^{(2010-2018)}$	0.165	0.011 ; 0.462

283

284 During the first few days of life, fawns acquire ticks as they grow. Note that the coefficient γ_v , characterizing

285 the rate of infestation for old fawns, was particularly low: this indicates that the instantaneous risk of

286 infestation becomes equal to zero after the first 5 days of life (Fig 4).

287 **Fig 4. Mean number of ticks expected under our final model (see text) on an average sized fawn of a**

288 **given age in the Trois-Fontaines Forest during an “average” year (i.e. a fictious year characterized**

289 **by a random effect equal to 0).**

290 Each thin black curve corresponds to the expected number of ticks obtained for one MCMC iteration (we

291 have 10000 iterations displayed on this plot). The yellow curve corresponds to the mean curve.

292 The effect of humidity seemed only marginally significant (coefficient = 0.010 [-0.006; 0.025]_{95%CI}). When

293 we compared the model including the effect of humidity with a model excluding it with the Watanabe-

294 Akaike Information Criterion (WAIC; [67]), we could not detect any significant difference between the two

295 models (model with humidity: WAIC = 1373.8, SE = 1.57; model without humidity: WAIC = 1374.6, SE =

296 1.57), so that the two models were equally likely according to this criterion. We therefore decided to keep

297 humidity in the model.

298 The mean infestation rate was highly variable between years during the 10 years following the hurricane

299 Lothar. Note that this between-year variation was particularly low from 2010 to 2018, the period prior to

300 the hurricane Lothar being intermediate (Fig 5).

301 **Fig 5. Posterior distribution of the (random) effects $\delta_{u(j)}$ of the year on the instantaneous infestation**

302 **rate per unit of body size area of fawns by ticks in the Trois-Fontaines Forest.**

303 The vertical red lines delimit the three periods: (i) period 1 corresponded to the period before hurricane

304 Lothar (between 1992–1999), (ii) period 2 corresponded to the 10 years following this hurricane (between

305 2000 and 2009), (iii) period 3 corresponded to the later years (2010 to 2018). For a given year, the posterior

306 distribution is represented by a boxplot superposed to a violin plot (i.e. for a given random effect, a kernel

307 smoothing of the MCMC simulations of a random year effect rotated and put on both sides of a vertical line,
308 mirroring each other).

309 A substantial amount of variation in our data remain unexplained. Indeed, the coefficient φ characterizing
310 the Gamma distribution of the individual random effects was lower than 1. The parameter φ is inversely
311 related to the variance of the Gamma distribution (with a mean = 1 and a variance = $1/\varphi$). A small value of
312 φ indicates that the unexplained between-individual random differences in sensibilities are large. And
313 indeed, the Spearman correlation coefficient between the observed dataset and the datasets simulated under
314 our model to assess the goodness of fit of the model was rather small ($\rho = 0.17 [0.1; 0.24]_{95\%CI}$), confirming
315 that there was still a lot of unexplained variability in our data.

316 Discussion

317 The number of ticks on fawns below the age of 8 days was frequently low. Only 28% of total observations
318 ($n = 965$) had 10 ticks and more, and 72% of observations had less than 9 ticks (Fig 3). The hiding strategy
319 of roe deer fawns in their first days of life may be effective towards avoiding parasites such as ticks. Indeed,
320 to increase their chance of survival, they stay hidden in the vegetation to minimize the risk of predation [49].
321 As a result, they have low mobility in the first days of life, leading to a low probability to touch the
322 vegetation where ticks are questing. From the 6th day of life, our study suggests that the level of tick burden
323 becomes constant (Fig 4). This could be explained by the depletion of questing ticks in the habitat of fawns
324 and the turnover of ticks feeding on fawns. Indeed, as ticks take their blood meal on hosts for few days (i.e.,
325 in average 3 days for nymphs and larvae and 7 days for adults; [16]) before falling to the ground, where
326 they molt or lay eggs [15], the number of ticks gained after this age is probably counterbalanced by the
327 number of ticks that detach themselves and fall off.

328 Factors linked to environmental conditions therefore seem to partly drive the between-individual
329 heterogeneity of infestation by ticks. As expected, the humidity rate was positively related to the tick number
330 on fawns. Based on our model, a 20% increase of humidity leads to an increase of 1.2 ticks on fawns in
331 average (i.e., a humidity coefficient equal to 0.01 which is equivalent to a mean number of ticks multiplied

332 by $\exp(0.01 \times 20) = 1.2$). This result is in agreement with the positive influence of the relative humidity on
333 *I. ricinus* survival and activity, which can lead to a greater presence of questing ticks in the environment
334 [21,22]. Ticks need at least 70-80% humidity to survive off-host [7]. In this study, the humidity effect was
335 only marginally significant. Our model showed that a 20% increase in humidity (which is large, since
336 humidity varied between 57% and 90% in our area) leads to an increase of 20% of the number of ticks.
337 Since there was in average between 10 and 15 ticks per animal (Fig 4), a 20% increase in the number of
338 ticks corresponds to only 2 to 3 more ticks in average. This may explain our difficulty to identify clearly
339 this effect with our three broad classes of tick-burden.

340 Tick development and questing activity are strongly temperature dependent [17,24]. Ticks do not tolerate
341 dry and hot conditions due to the risk of desiccation, and below 1°C, they are not active and most of the
342 time goes into wintering [22,24,68]. Thus, climatic conditions are decisive for the survival, development
343 and activity of *Ixodes ricinus*, and this depends on geographic locations and habitat characteristics. We
344 therefore expected to detect an effect of the temperature on the infestation rate. However, no relationship
345 was observed, which could be explained by the lack of power caused by the absence of a precise measure
346 of the number of ticks on fawns.

347 Similarly, we were not able to identify any effect of the habitat structure on the infestation rate of fawns in
348 our study, and could not validate our second hypothesis. However, it is known that habitat structure can
349 impact tick abundance and distribution, particularly in forest habitat [17]. Indeed, forest vegetation provides
350 a more stable microclimate compared to open habitats, with less extreme variation in climate and mortality
351 risk for ticks [69]. Ground vegetation retains moisture and provides shade, which are very important for tick
352 survival and their water balance. It explains why ticks are mainly found in leaf litter and low layer of
353 vegetation in forests [7,25,43]. Indeed, a forest with important overstory and shrub cover creates a favorable
354 microclimate, and a great depth of litter, and constitutes ideal conditions for their survival [29]. In this study,
355 our inability to isolate any effect of the habitat structure is probably due to the inappropriate scale of habitat
356 measurement: we mapped the vegetation at the resolution of the forest plot, which is probably too large to

357 identify such an effect. Actually, the characteristics at the microhabitat level – i.e., whether the vegetation
358 structure within a few meters around the fawn provides the fawn a thermal protection [72] and low light
359 penetration [73] -- would be more accurate to see differences of infestation rate in terms of vegetation
360 structure. Thus, to better understand how weather factors affect the infestation rate of fawns in a forest
361 habitat, we should look at the tick during their free stages of life in our study area, at a finer spatial scale
362 and consider microclimate conditions.

363 The level of tick burden on fawns varied according to the decade of our study (Fig 5). The average infestation
364 rate thus exhibits low inter-annual variability during the periods 1992-1999 and 2011-2018. However, there
365 is a stronger interannual variability over the period 2000-2010. This could be linked to the hurricane Lothar,
366 which took place in December 1999. This event has considerably changed the forest structure, by creating
367 numerous openings patches, modifying forest dynamics and habitat use by roe deer [60]. Prior to the
368 hurricane, the Trois-Fontaines forest appeared homogeneous with no strongly different habitat types. After
369 the hurricane, microhabitats and microclimatic conditions became more spatially heterogeneous [71]. Thus,
370 fawns captured between 2000 and 2010 were probably found in habitats with very different characteristics,
371 which influenced the estimated infestation rate of individuals by ticks. Knowing that deer are hosts for both
372 adult and nymph ticks, we first thought that this high interannual variability in infestation rate could have
373 been caused by a variation in roe deer density [72]. Since deer, mainly red deer and roe deer, are the main
374 host of adult *I. ricinus* ticks, their density and distribution can be strong drivers of the location of ticks in
375 the environment [10]. Large-scale exclusion of deer dramatically reduces the abundance of infectious stage
376 of ticks in the environment [73]. However, contrary to our initial hypothesis, we did not find a link between
377 this factor and the level of tick infestation. As stated by Carpi *et al.* [77], the tick infestation of roe deer is
378 not necessarily dependent of the roe deer density. Tick populations can be maintained with a small density
379 of deer, and ticks in the environment did not automatically increase with the abundance of deer [44,75].
380 Furthermore, during its life cycle, *Ixodes ricinus* can parasitize a large number of vertebrates including
381 mammals (e.g., fox, rabbit, squirrel, etc.) or even birds (e.g., blackbird, pheasant, harrier, etc.) [30]. Thus,

382 to better understand the effect of host density, we should in theory consider the density of all possible hosts
383 of this tick species, which is difficult to monitor.

384 In summary, the level of tick burden became constant when fawns were 5 days old and more. Humidity was
385 significant but no effects of temperature, vegetation structure or roe deer density were found on the tick
386 burden of fawns. However, we noticed a strong heterogeneity of tick burden between years suggesting other
387 variables could be involved, such as local density of various host species or habitat characteristics of fawns
388 (i.e., bedding sites), which may be important for tick activity. Studies at finer scales need to be carried out
389 to understand why some fawns are more parasitized than others. This would require additional data on ticks
390 in the environment, at different times of the year, which would allow a more precise study to improve our
391 understanding of tick infection in ungulate newborns.

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