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Research Article

Role of bank vole (*Myodes glareolus*) personality on tick burden (*Ixodes* spp.)

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Abstract: Parasitism among individuals in a population often varies more than expected by chance only, leading to parasite aggregation, which is a parameter of paramount importance in parasite population dynamics and particularly in vector-borne epidemiology. However, the origin of this phenomenon is yet not fully elucidated. An increasing body of literature has demonstrated that individuals vary consistently in their behaviour, which is referred to as animal personality. Such behavioural variation could potentially lead to different encounter rates with parasites. To test this hypothesis, the relationship between personality and burden with ticks (*Ixodes* spp.) in the bank vole, *Myodes glareolus* (Schreber), was assessed. Wild rodents (eight females and 18 males) were live-trapped, identified, sexed, weighted, and inspected for ticks. Behavioural profiling was then performed using standardised tests measuring activity/exploration and boldness with a combination of automatically and manually recorded behavioural variables summarised using multivariate analyses. The resulting personality descriptors and questing tick variables were used as explanatory variables in negative binomial generalised linear models of tick burden and Bayesian simulations were performed to better estimate coefficients. Tick burden was associated to body mass and sex, but not to personality descriptors, which was mainly associated to activity/exploration. These results are discussed regarding the complex relationships among individual personality, physiological status, space use and health status.

Keywords: Behavioural profiling, small mammals, parasite aggregation, video analyses

Parasite aggregation is a well-known phenomenon (Crofton 1971, Shaw and Dobson 1995). Since few individuals hosting most of the vector population are involved in most of the transmission events of infectious agents, this phenomenon is of paramount importance in vector-borne disease transmission (Woolhouse et al. 1997, Perkins et al. 2003). This is particularly true in tick-borne disease systems (Milne 1943, Perkins et al. 2003); however, such aggregation in ticks is not yet fully understood (Brunner and Ostfeld 2008). Some individual characteristics such as body mass, sex and home range size are known to influence parasitic burden, as larger males with larger home ranges are generally more parasitised, whereas the spatial aggregation of parasites in the environment seems to be a poor explanatory factor (Boyard et al. 2008, Harrison et al. 2010, Kiffner et al. 2011, Devevey and Brisson 2012, Mysterud et al. 2015, Perez et al. 2017). Nonetheless, other individual characteristics of hosts might be of significance in driving parasitic burden.

In the last decades, increased attention has been paid to population heterogeneity at the genetic and phenotypic levels. For instance, the genetic background can play a significant role in susceptibility to parasites and infections, particularly in relation to immunity (Porto Neto et al. 2011, Schad et al. 2012, Tschirren 2015, Arriero et al. 2017). Individuals in a population can also display behavioural differences consistent in time and contexts, which is referred to as personality (Wolf and Weissing 2012). Such varying behavioural characteristics among individuals can include activity/exploration (i.e., the propensity to explore new areas) and boldness (i.e., curiosity to unknown items and propensity to take risks) (Carter et al. 2013) and can be linked to the level of exposure to parasites. For instance, associations between activity/exploration and space use with tick burden have been demonstrated in Siberian chipmunks, *Tamias sibiricus barberi* (Johnson et Jones) (Boyer et al. 2010).

The bank vole, *Myodes glareolus* (Schreber), is one of the most important reservoir host species of tick-borne infectious agents in Europe (e.g., *Borrelia afzelii*, one of the bacteria responsible for human Lyme borreliosis; Takumi et al. 2019). This rodent species can be heavily infected by larvae of the tick *Ixodes ricinus* (Linnaeus, 1758), the

most common tick species on the continent (Hofmeester et al. 2016, Perez et al. 2017). The existence of different personalities in this species has been demonstrated by several studies (Korpela et al. 2011, Schirmer et al. 2019). However, no studies have yet been conducted on the role of personality on the tick burden in this species. Thus, the present study assessed whether the tick burden of bank voles can be partly explained by individual personality after assessing the role of other factors, namely sex, body mass and questing larvae density at habitat scale. The results and their possible implications on the circulation of tick-borne infectious are discussed.

MATERIALS AND METHODS

Study site

The study site was located on the municipality of Ruffey-le-Château, Doubs Département, Bourgogne-Franche-Comté region, France (47.2750N, 5.7920E). The site was in a communal (public) forest fragment (about 600 × 200 m) dominated by oaks, *Quercus petraea*, and hazel trees, *Corylus* sp., and surrounded by crops, pastures and water bodies. No special authorisation was needed to access the area.

Small mammal trapping

Small mammals were captured using INRA live-traps with plastic dormitory boxes (Aubry 1950). Traps were baited with commercial seeds for rodents, peanut butter, a piece of cod liver, a piece of apple and a hand-fist of hay as litter. Cod liver was used to enhance shrew survival (C. Fritsch, pers. comm.) and the piece of apple to assure animal hydration. A total of 91 traps were set every 5 metres in every direction, shaping a 25 m-sided hexagon covering about 0.2 ha. The percent of understory covered with brambles, ferns, dead wood, dead leaves and bare soil around each trap was recorded.

Trapping was conducted in two sessions. For the first session, traps were set on the 25 June and retrieved on the 1 July, and for the second session, traps were set on the 10th and retrieved on the 14 July 2018. Traps were checked twice a day: in the morning and before dusk. All morning-captured small mammals were brought to the field camp, and food availability was checked, whereas individuals caught before dusk were released immediately to avoid prolonged captivity overnight. Empty traps were reloaded with bait as necessary (every 3 days or less).

Small mammals were identified at the species level, sexed, weighted at 0.5 g (instrumental measurement error), and their reproductive status was recorded (active or not on the base of pregnancy or signs of lactation for females and visibility of testes for males). At first capture, rodents were marked by shaving a unique pattern in their back fur. Only a small surface of their back was shaved, the undercoat was left, and the visible pattern was unlikely to enhance their visibility to predators. According to existent literature, thermal losses were assumed to be negligible given that only a small surface of the animal was shaved and the temperatures were fair at this season (Kenagy and Pearson 2000). Thus, fur shaving was assumed not being harmful to animals. At the second session, only bank voles were brought to the field laboratory, and animals of other species were immediately released after identification.

Small mammal community

Three rodent species were identified on the study site: the bank vole, *Myodes glareolus*, the wood mouse, *Apodemus sylvaticus* (Linnaeus), and the yellow-necked mouse, *Apodemus flavicollis* (Melchior). Some *Apodemus* mice could not be identified and were identified only as *Apodemus* sp. Five *Sorex* spp. and one *Crocidura* sp. shrews were also captured. All shrews were dead except one *Sorex* sp. that probably stayed alive because of the warmth of the bank vole captured in the same trap.

Tick burden evaluation

Bank voles were meticulously inspected for ectoparasites before behavioural profiling with a magnifying glass on the whole body (Perez-Eid 1990). The number of ticks and other ectoparasites was noted for each body part (muzzle, head, ears, legs, belly, back and tail). Because ticks were left on hosts, they were only identified at the stage level when po ssible (visible legs), but it was not possible to identify them at the species level. Ticks are thus referred to as *Ixodes* spp. hereafter.

Bank vole behavioural profiling

Bank vole behavioural profiling was performed at the field camp with a combination of Open Field and Novel Object tests (Larsen et al. 2010). These tests have been prove appropriate to measure activity/exploration in vertebrates (Perals et al. 2017). Bank voles were placed into a rectangular box of 55 × 35 cm for 10 minutes, and after the first 5 minutes, an object (a die) was introduced at the centre of the box. This time is sufficient to produce reliable behavioural measures (Mazzamuto et al. 2019). Voles were filmed and the videos were analysed automatically using ImageJ v. 1.52a (Rasband) with the plug-in MouBeAT (Bello-Arroyo et al. 2018). Some parameters had to be adjusted for each experiment to deal with small changes in framing and enlightening imposed by field conditions, but others were kept at default settings. Two additional variables were measured manually: the number of self-grooming boots (NSGB) and the number of object approaches with stop in front of the object (NOA).

To reduce stress, voles had at least one hour to relax between first manipulation and behavioural profiling. All tests were conducted in the shade, as much as possible under the same lighting conditions and isolated several metres from experimenters to avoid external stimuli (noise, odours, visual contact). To reduce bias caused by odours and the transmission of infectious agents by faeces and urine, the box was cleaned with disinfectant wipes between all tests. Pregnant and lactating females were tested first and released immediately after being tested. Other animals were tested randomly. All animals were released at the place of capture. Time spent in the trap is assumed not to bias the results (Brehm et al. 2020).

Questing ticks

To assess whether tick burden could be influenced by tick distribution in the sampling grid, ticks were collected on 25 June 2018 between 4:00 and 6:30 PM over 48 five-metre-long regularly spaced transects using the dragging method (MacLeod 1932, Vassallo et al. 2000). Briefly, this method consists of drawing a one-m² white flannel cloth on the substrate at a pace of about 0.5 m×s⁻¹ to lure a tick host. All ticks on the cloth were subsequently removed with forceps and placed in 70% ethanol. Because *Ixodes*

ricinus is the dominant tick species in this area and all adult and nymphal ticks found were identified as belonging to this species, larvae were assumed to also be of this species. Transects were placed so that each one could be attributed to two traps, and at least two transects were less than 5 m from a trap. Because larvae were generally aggregated, and to not rely only on one measure, the questing larvae density variables used were the mean number of questing larvae of transects around capture traps in 5-, 10-, 15- and 20-m radius (questing larvae in 5, 10, 15, 20 m hereafter). This variable provides a measure of the abundance of larvae in the area most likely recently frequented by voles before their capture.

Statistical analysis

All statistical analyses were performed with R v. 4.0.3 (R Core Team 2020) and Stan in RStudio v. 1.2.5033 (RStudio Team 2019). Several R packages were used, as specified hereafter. The explanatory behavioural variables considered were as follows: the total travelled distance (TTD), the number of entries, the time spent, the distance travelled, and freezing time (time not moving) spent in the central zone (NEI, TSI, DTI and FTI, respectively), a zone defined as the central 3 × 3 quadrants after dividing the whole area in 5 × 5 equal quadrants (11 × 7 cm); the distance travelled, the time spent, and the freezing time spent outside the central zone (DTO, TSO and FTO, respectively); the average speed (AVS), the NSGB and the NOA (on the last 5 minutes only). Variables were computed for the first (e.g., TTD1) and second (e.g., TTD2) 5-minute parts of the test.

Self-grooming can indicate a stress in rodents (Roth and Katz 1979), but it can also be a response to parasitism (Godinho et al. 2013). To test the effect of parasitism on the self-grooming score, NSGB was modelled, after being log-transformed to reach a normal distribution, as a function of burden with tick larvae and the presence/absence of other parasites in Linear Models (LMs).

To describe the behavioural profile, a principal component analysis (PCA) was performed to summarise the behavioural variables (Carter et al. 2013), using with the R package "ade4" v. 1.7-16 (Chessel et al. 2004, Dray and Dufour 2007, Dray et al. 2007, Bougeard and Dray 2018, Thioulouse et al. 2018). Only axes with inertia > 1 were used as behavioural profile descriptors (BPDs) (Wold et al. 1987). Because most animals were caught only once and tests were performed in priority to new individuals to maximise sampling size, the repeatability of measures could be assessed only for 10 individuals. Repeatability was evaluated by computing the intraclass correlation coefficient (ICC) of measures in the first and second tests with the "psych" R package v. 2.1.9 (Revelle 2021). Because of this small sample size, conservatively, only variables with a positive ICC associated p-value ≤ 0.10 were retained. The effect of the date and the hour of testing on retained behavioural variables was then tested using a MANOVA.

The spatial autocorrelation of tick burden was checked by computing Moran's I for different distances incremented by 2.5-m steps and a corresponding two-sided p-value, using 9,999 permutations for each distance-class with the R package "ncf" v. 1.2-9 (Bjornstad 2020). The spatial coordinates of the trap from which the animal was caught the day of the test was used. The spatial autocorrelation of questing ticks was also tested using the same method. The relationships between explanatory variables were assessed with LMs.

Since the aggregation of ticks on hosts induces overdispersion of the data, different error distributions were tested. Based on the AICc values of linear, Poisson and negative binomial error distribution null models of larval tick burden, using the package "MASS" v. 7.3-53 (Venables and Ripley 2002), the latter was retained in the following analyses (AICc values: 161.5, 196.7 and 142.8, respectively).

First, larval tick burden was modelled in single explanatory variable negative binomial generalised linear models (NBGLMs) as a function of body mass, sex and the retained behavioural descriptor(s). To check the effect of time and questing larvae density on the tick burden of bank voles, it was also modelled in single explanatory variable NBGLMs as a function of date, session, questing larvae in 5, 10, 15 and 20 m, computed based on a distance matrix built using the R package "distances" v. 0.1.8 (Savje 2019). The variable parameters were also estimated using Bayesian negative binomial model simulations in Stan via the R package "brms" v. 2.14.4 with five chains, 5,000 iterations per chain, a warm-up of 1,000 iterations (overall 20,000 iterations) and other parameters as default settings (Bürkner 2017, 2018). Only variables with 0 not included in the 95% coefficient estimate confidence interval (95%CI) were considered significant.

Subsequently, larval tick burden was modelled in a multiple explanatory variable NBGLMs as a function of body mass, sex, BPDs and other variables retained at p < 0.1 in univariate models. Although some interactions among variables are possible, they were not considered to avoid over-fitting due to the small sample size. An AICc-based model selection procedure was used to retain the best models (delta AICc < 2) using the R package "MuMIN" v. 1.43.17 (Barton 2020) and variable significance was evaluated with a type 2 ANOVA (p-value ≤ 0.05), both in a single explanatory variable model and multiple explanatory variable models using the R package "car" v. 3.0-10 (Fox and Weisberg 2019). The parameters of the retained variables in single explanatory variable Bayesian simulations were estimated by multiple explanatory variable Bayesian negative binomial model simulations as described above. Graphs were plotted using the R package "visreg" v. 2.7.0 (Breheny and Burchett 2017).

Data availability statement

The dataset used for the analyses of the study is available in Supporting Information 1. Further details are available upon reasonable request.

Ethical statement

The target species were not protected species, and no intrusive intervention was performed on animals. Thus, according to current French laws in force, no special authorisation or ethical committee approval was needed.

RESULTS

Bank vole behavioural profiling

A total of 8 female and 18 male bank voles were tested for behavioural profiling. Mean body mass did not differ between sexes (mean, median, minimum and maximum values were 23.3, 21.0, 17.5 and 33.5 g for females and

Table 1. Parameter estimates of the best multiple explanatory variable negative binomial generalised linear models of the larval tick burden (*Ixodes* spp.) of bank voles *Myodes glareolus* (Schreber).

Model rank	Variable	Estimate [± SE]	P-value	df	Pseudo-R²	AICc
1	Intercept	-0.839 [± 0.652]	0.198	23	0.347	136.3
	Body mass	0.072 [± 0.023]	0.001			
	Sex[Male]	0.880 [± 0.377]	0.020			
2	Intercept	-0.793 [± 0.616]	0.198	22	0.407	137.0
	Body mass	0.065 [± 0.022]	0.002			
	Sex[Male]	0.818 [± 0.360]	0.021			
	Questing larvae in 5 m	0.031 [± 0.020]	0.105			
3	Intercept	-0.166 [± 0.625]	0.791	24	0.221	138.2
	Body mass	0.072 [± 0.026]	0.004			
Null model	Intercept	1.562 [± 0.206]	< 10-3	25	0	142.8

Summary of parameter estimates with standard error of multiple explanatory variable negative binomial generalised linear models of the larval tick burden of bank voles with *Ixodes* spp. larval tick after the AICc based selection procedure. Only models with delta AICc < 2 and the null model are shown. See text for more details. Note: "df": degrees of freedom.

21.6, 24.2, 8.0 and 33.0 g for males, respectively; LM: estimate[male] = -1.674, p-value = 0.606, df = 24). Body mass was highly repeatable (ICC = 0.957, p-value < 10^{-3}, n = 10). Among these individuals, the reproductive status was confounded with body mass. Females weighting 24.5 g or more (n = 3) and males weighting 16.5 g or more (n = 13) were all active. Reproductive status was thus no further considered hereafter.

As no significant statistical association was observed between parasitism (either ticks or other parasites) and NSGB (p-value > 0.05), self-grooming was assumed to not have been caused by parasite load during the experiment and thus considered as a potential personality measure. According to the ICC tests to assess repeatability (Supporting Information 2), the variables finally used for the PCA (p-value < 0.10, ICC > 0.4) were DTI2, NEI2, TSI2, NSGB2 and NOA. No relationship of date or hour with behavioural variables was detected in MANOVAs (p-value = 0.530 and p-value = 0.510, respectively). Only the two first axes of the PCA were retained as BPD (inertia of axis 1 was 3.04 and accounted for 60.7% of the explained variance; inertia of axis 2 was 1.07 and accounted for 21.5% of the explained variance). According to the correlation circle, axis 1 was negatively associated to DTI2, NEI2 and TSI2, and more weakly to NOA. These variables can be associated to activity/exploration: the more active an animal is, the longer distances it travels (DTI2) and the more likely it is that it enters different zones (TSI2 and NEI2) (e.g., Dingemanse et al. 2007). Axis 2 was mostly negatively associated to NSGB2 and weakly positively to NOA (Supporting Information 3). The NSGB2 can be associated to stress, and thus negatively to boldness (Roth and Katz 1979), whereas NOA is generally positively associated to boldness (Dammhahn and Almeling 2012).

Tick burden and questing ticks

Tick burden ranged from 0 (4 individuals) to 20 *Ixodes* spp. larvae per bank vole (mean = 4.77, median = 3). Tick burden was highly repeatable (ICC = 0.724, p-value = 0.006, n = 10). Additionally, one male and one female had one *Ixodes* spp. nymph and one male had three. Finally,

one female and one male had one *Ixodes* sp. adult female. No larvae were found on most transects (35), but up to 68 larvae were found on one transect (13.6 larvae per m²). However, no significant spatial autocorrelation was detected in questing larvae, nor in attached ones (based on coordinates of capture traps).

Explanatory variables of *Ixodes* spp. tick burden

In univariate NBGLMs, larval tick burden was significantly associated to body mass (estimate = 0.072, p-value = 0.004, pseudo-R² = 0.221, df = 24, AIC = 137.1), sex (estimate[male] = 0.899, p-value = 0.047, pseudo-R² = 0.118, df = 24, AIC = 140.6) and to questing larvae in 5 m (estimate = 0.047, p-value = 0.047, pseudo-R² = 0.117, df = 24, AIC = 140.6). Larval tick burden was neither significantly associated to sampling date, sampling session, questing larvae in 10, 15 and 20 m nor to PCA axis 1 and axis 2 (p > 0.10). According to single explanatory variable Bayesian larval tick burden NBGMs simulations, only the coefficient estimate for body mass had 0 outside its 95% IC (estimate: 0.07; 95% IC: 0.02–0.12; for other variables see Supporting Information 4). This variable could thus be considered as significantly associated to larval tick burden.

According to the AICc selection procedure, the best multiple explanatory variables NGLM of larval tick burden included body mass and sex, the second best model included body mass, sex and questing larvae in 5 m, and the third best model included body mass only. However, only body mass and sex were significantly associated to larval tick burden (Table 1). The Bayesian model simulations were consistent with these results, with 0 outside the 95%CI coefficient estimates for body mass and sex, but not for questing larvae in 5 m (Supporting Information 4). Larval burden significantly increased with body mass by 2.01 times (IC95%: 1.22–3.32) every 10 g, and males were significantly more infested than females with 2.44 (IC95%: 1.05–5.47) more tick larvae (Table 1 and Fig. 1).

DISCUSSION

This study assessed the role of bank vole personality on their tick burden. It was hypothesised that body mass, sex, personality traits associated to home range size, particularly activity/exploration and boldness, modulate encounter rates with *Ixodes* spp. ticks and, thus, tick burden. From behavioural personality profiling based on only four repeatable behavioural measures summarised by a PCA, two reliable gradients of personality traits were observed, mostly corresponding to an activity/exploration gradient (axis 1) and a boldness gradient (axis 2). The *Ixodes* spp. burden of bank voles ranged from 0 to 20 larvae per individual (0 to 21 ticks with all stages together). Although the results support a role of body mass and sex on *Ixodes* spp. tick burden, they do not support a role of personality.

It was hypothesised that activity/exploration increases encounter rate with ticks and, thus, tick burden, but this was not supported by the results. Similarly in great tits, *Parus major* (Linnaeus), Rollins et al. (2021) found a positive relationship between exploratory behaviour and tick infestation probability, but not with tick burden. Similar
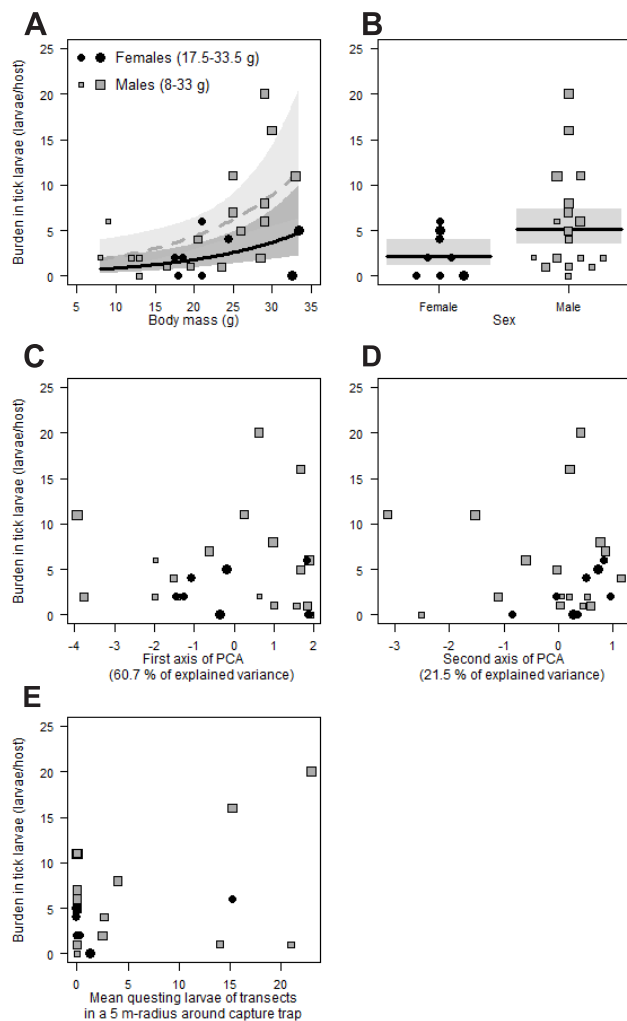
Fig. 1. Larvae of *Ixodes* spp. per bank vole, *Myodes glareolus* (Schreber), as a function of body mass, sex, first and second axes of the PCA performed on behavioural variables, and questing larvae in a 5-m radius. The figure shows burden with larvae of *Ixodes* spp. per bank vole as a function of **A** – body mass, **B** – sex, **C** – first and **D** – second axes of the PCA performed on the retained behavioural measures, and **E** – mean questing larvae of transects in a 5-m radius around the capture trap. Curves in **A** are the fitted burden of *Ixodes* spp. tick larvae by sex (solid line for females and dashed line for males), and in **B**, lines are the estimated burden of *Ixodes* spp. tick larvae for a median body mass of 21 g, both according to the best negative binomial generalised linear model with a 95% confidence interval (lighter colour). Females are represented by circles and males by squares with size proportional to body mass (see legend in **A**).

trends have also been observed by Santicchia et al. (2019) in eastern grey squirrels, *Sciurus carolinensis* Gmelin, with helminth infestation. It is thus possible that personality differently influences tick encounter probability and tick burden (encountered ticks that eventually get attached). It is possible that the more active/exploring individuals do not necessarily use more habitat (Schirmer et al. 2019).

Interestingly, in the study by Schirmer et al. (2019), boldness was positively associated with home range size and distance moved in this species.

Unfortunately, the low number of recaptures and the numerous individuals trapped in the periphery of the sampling grid did not allow the production of reliable home range estimates to compare with tick burden. However, the behavioural profiling used here was not appropriate to disentangle activity/exploration and boldness (for instance, the number of entries in the central zone can be associated both to activity/exploration and boldness). Thus, a behavioural profiling more focused on behaviour associated with boldness would be more relevant as surrogate to home range size.

The positive relationship between body mass and parasitism confirms previous results (e.g., Perez et al. 2017). This relationship can be explained by larger home ranges of heavier individuals, which need more food to meet their energy requirements, as suggested in a recent study (Boratyński et al. 2020). Home range size depends also on factors such as food availability and inter- and intra-species competition (Wolff 1985, Schradin et al. 2010, Liesenjohann et al. 2011) and even on interactions with personality (Wauters et al. 2021), which in turn can modulate tick burden. The habitat was relatively homogeneous in the study area, preventing large differences in home range size due to food availability.

The difference in parasitism between sexes can be explained by differences in body size, immunity and behaviour (Krasnov et al. 2012). As body mass did not significantly differ between females and males in this study, a difference in body mass between sexes to explain a difference in tick burden is not supported. Furthermore, the effect of sex is also significant when considering body mass. An alternative hypothesis is a decrease in immunity in males, associated with testosterone level (Mills et al. 2010). Higher testosterone concentrations have been associated experimentally to higher tick loads in bank voles, which is compatible with the present results (Hughes and Randolph 2001).

Females and males can also differ in their behaviour. Among the behavioural factors possibly responsible for their difference in tick burden is their home range size. Males generally have larger home ranges than females, which might explain their higher tick burden (Korn 1986). Home range size is also dependent of the reproductive status in both sexes, expanding when males are active and reducing for females when breeding (Koskela et al. 1997, Karlsson and Potapov 1998). However, here, the reproductive status was confounded with body mass and the sample size was too small, particularly in females, to study it further. The role of the reproductive status in females and males on tick burden deserves further investigation (see Perez-Eid 1990).

Spatial heterogeneity in tick distribution can also explain tick aggregation on hosts. Questing larvae were indeed heterogeneously distributed in the study area, although no significant spatial autocorrelation was detected. A significant association was found between mean questing larvae around capture traps in a 5-m radius and larval tick burden, but this variable was not significant when also accounting for body mass. However, density of questing

larvae was surveyed only once and only in a fraction of the study area, potentially leading to weakly reliable estimates. The tick distribution at (micro)-habitat level and its role in tick burden would thus deserve more investigation.

This study does not completely exclude a role of bank vole personality on *Ixodes* spp. tick burden. First, these results are based on a low number of individuals and should be considered cautiously. The sample size was sufficient to capture significant differences in tick burden between sexes and a significant relationship of body mass with tick burden, but not with behavioural measures. Results of studies on the relationship between animal personality and parasite load might be misleading if the assessed behaviours are sex- or body mass-dependent. In this case, behavioural profiling provides only a mere approximation of personality traits (compared to precision in body mass measurement, for instance). Thus, more individuals (or several repeated measures of the same individuals) would have been necessary to better capture variations in personality (Dingemanse and Wright 2020).

Furthermore, the behavioural profiling performed here might have missed capturing important aspects of the complexity of personality-tick interaction, with only four retained variables from two combined tests. A heavy parasitic burden could induce behavioural changes. Particularly, blood spoliation by a high tick burden could induce anaemia and reduce animal activity. Conversely, a reduced activity could also be a behavioural response to reduce tick burden (by reducing encounter rate). For instance, one study found that more parasitised white-footed mice, *Peromyscus leucopus* (Rafinesque), dispersed less than the less parasitised ones (Gaitan and Millien 2016), and another one reported a correlation between aggressiveness and tick burden in the long-lived sleepy lizard, *Tiliqua rugosa* (Gray), but the causality could not be inferred (Payne et al. 2021). A more experimental approach comparing the same animal with and without ticks might help to answer this question.

Likewise, a high exposure to ticks increases the infection risk by tick-borne infectious agents, which might affect behaviour. For instance, infection can induce anaemia (e.g., *Babesia microti*; Wiger 1978, Hu et al. 1996, Sasaki et al. 2013) or reduce the immune response (e.g., *Anaplasma phagocytophilum*; Johns et al. 2009). Infection can also increase the susceptibility to other parasites, leading to a cascading health burden (Beldomenico et al. 2008, 2009, Telfer et al. 2010). Infection can be energetically costly and

may be compensated by a behavioural response such as a reduction of activity and home range (e.g., *Borrelia afzelii*; Cayol et al. 2018). Assessing the infection status of individuals would have been useful to better disentangle these mechanisms. It seems thus required to directly estimate home range size to understand its relationship with tick burden and to increase sample size and individual health parameter estimates to evaluate the possible role of reproductive and infection status on tick burden.

More generally, the interactions between parasite infections in small mammals on their behaviour, health, risk of other infections and other ecological interactions, despite their epidemiological interest, are still vastly unknown. Nonetheless, some studies have shown that parasite infection can interact with predation. For instance, helminth infections in *Microtus townsendii* (Bachman) are associated with higher predation risks (Steen et al. 2002). Here, a role of other species, such as wood mice, yellow-necked mice and shrews, which were also trapped, is possible either by affecting the home range size of bank voles by competition and/or by diluting the tick burden (Tersago et al. 2008).

Because tick dispersal is mainly realised by hosts, animal personality can be linked to dispersal in various ways and different personality traits can be selected according to landscape structure, knowledge on host personality could be of paramount importance to better understand the spread of tick-borne infectious agents in the landscape (Cote et al. 2010, Brehm et al. 2019). For instance, landscape fragmentation associated with predation release can favour bolder individuals, which are more prone to encounter ticks and spread both ticks and tick-borne infectious agents. Interactions among host personality, tick dispersal and tick-borne infectious agent spread are, however, probably more complex than it would seem at first sight (Gaitan and Millien 2016). These results show that the relationships among host personality, physiological status and parasitic burden are still largely unclear, calling for further studies.

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Cite this article as: Perez G. 2022: Role of bank vole (*Myodes glareolus*) personality on tick burden (*Ixodes* spp.). Folia Parasitol. 69: 014.