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Research Article

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In the Lyme light: individual trait determinants of *Borrelia burgdorferi* infection in *Peromyscus* mice

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Abstract

Disease ecologists commonly use abiotic factors (e.g. temperature and moisture) or measures of biodiversity (e.g. species richness) to predict Lyme disease transmission patterns, but variance in infection probability among individuals within a population is poorly understood. Most studies assume intraspecific consistency, but recent evidence suggests that individual traits, such as animal personality, may drive differences in encounter rates with infected vectors and pathogen transmission probabilities through differential space use and microhabitat selection, leading to intraspecific variation in infection probability. In addition, because vectors and hosts are nonrandomly distributed across a landscape, land-use changes that modify key habitat features—such as forest management practices—may substantially alter associations between individual traits and infection probability. To address these gaps in our knowledge, we used a large-scale capture–mark–recapture study targeting *Peromyscus* mice in Maine, United States, to test whether personality drives probability of *Borrelia burgdorferi* infection in hosts within managed forest compartments with different silvicultural treatments. Specifically, we tested effects of individual phenotypic traits (physical and behavioral) and environmental traits (microhabitat and forest type) on infection probability within 2 species: *P. leucopus* and *P. maniculatus*. We found evidence that boldness negatively influences infection probability in *P. maniculatus*, and that body mass positively influences infection probability in both species. We found no effect of mouse density, microhabitat, or forest type in our analyses. These results suggest that personalities vary in their functional contributions to the natural cycle of *B. burgdorferi*, and that broader integration of behavioral diversity in disease ecology studies may aid in identifying key transmission zones for this rapidly expanding vector-borne zoonosis.

Key words: behavioral diversity, forest management, *Ixodes scapularis*, Lyme disease, microhabitat, *Peromyscus leucopus*, *Peromyscus maniculatus*, personality, reservoir competence, vector-borne zoonosis.

Lyme disease is one of the most commonly reported vector-borne zoonoses in temperate zones including the United States, Canada, and much of Europe (Kurtenbach et al. 2006; Stone et al. 2017; Rosenberg et al. 2018). In recent years, worldwide incidence rates have increased and the geographic distribution of Lyme disease has expanded, especially in the Northeast, Mid-Atlantic, and upper Midwest regions of the United States; and in England, Wales, and the Scottish Highlands (Stone et al. 2017; Bisanzio et al. 2020; Gardner et al. 2020). In parts of northeastern United States, where the majority of cases can be attributed to the spirochete bacterium *Borrelia burgdorferi* sensu stricto (synonym "*Borreliella burgdorferi*" Adeolu and Gupta 2014; Barbour et al. 2017), this pattern likely reflects climate-driven geographic expansion of the Blacklegged Tick (*Ixodes scapularis*), the primary vector in eastern states (Diuk-Wasser et al. 2010), and of the White-footed Deermouse (*Peromyscus leucopus*), the primary reservoir host for Lyme disease in North America (Roy-Dufresne et al. 2013; Eisen and Eisen 2018). In other parts of the Northeast, where these vector and host species have been endemic for decades, the recent rising incidence could be attributed to land-use changes and rising temperatures that may accelerate vector life cycles and increase vector overwinter survival (Ogden et al. 2014; Alkishe et al. 2021; Volk et al. 2022).

Forest management practices—by manipulating forest age structure, stand composition, canopy cover, and connectivity—have the potential to change disease dynamics within a system. Forest management effectively modifies the amount and availability of resources and habitat features which subsequently affects wildlife community richness and composition (Fisher and Wilkinson 2005; Gasperini et al. 2016; Sozio and Mortelliti 2016) as well as intraspecific behavioral traits (Mortelliti and Brehm 2020). In vector–pathogen systems, forest management practices

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directly impact disease prevalence by altering pathogen and vector habitat quality, host abundance, and movement patterns (Ehrmann et al. 2018; Conte et al. 2021). Forest management practices including invasive plant removal, prescribed burns, and timber harvesting alter critical habitat features and have been strongly linked to *B. burgdorferi* prevalence in vertebrate hosts (Stafford et al. 1998; Williams and Ward 2010; Conte et al. 2021).

The life cycle of *I. scapularis* and transmission of *B. burgdorferi* is inherently complicated, involving multiple vertebrate host species, e.g. small mammals and birds (Dobson 2004). A key point of uncertainty is host species reservoir competence (Kilpatrick et al. 2017). Reservoir competence, typically defined as the probability that a vertebrate host infects a feeding vector, is the product of host species infectivity and infection prevalence (Schauber and Ostfeld 2002; Brunner et al. 2008). Studies investigating infectivity through experimental infection and natural infection prevalence have revealed substantial variation among vertebrate species (Brunner et al. 2008; Keesing et al. 2009; Barbour et al. 2015), but the vast majority of studies investigating reservoir competence assume intraspecific consistency (Ostfeld and Keesing 2000; Ginsberg et al. 2005; Richter et al. 2011). Where individuals vary in exposure rates to ticks and immune response, individual traits may be an important source of variation in infection probability and infectivity (Tompkins et al. 2011). Currently, the magnitude and cause of reservoir competence variation among individuals is poorly studied and focuses mostly on physical traits including sex, age, and body mass, rather than behavioral traits (Barber and Dingemanse 2010; Mysterud et al. 2015; Filion et al. 2020).

Animal personality, defined as consistent individual behavioral differences across time and/or contexts, has become one of the fastest-growing frontiers in behavioral ecology (Merrick and Koprowski 2017) and may be key to understanding differences in infection prevalence and pathogen transmission within species (Réale et al. 2007; Barber and Dingemanse 2010). Personality traits including activity, exploration, boldness, docility, and aggressiveness are known to correlate with animal spatial movement patterns, activity levels, risk avoidance, foraging strategies, habitat and diet preferences, grooming tendencies, and contact rates, which may in turn affect parasite encounter rates and pathogen transmission probabilities (Wolf and Weissing 2012; VanderWaal and Ezenwa 2016; Sih et al. 2018). Studies addressing this interface between personality and disease distribution have found positive associations between boldness in western deer mice (*P. sonoriensis*) and hantavirus infection (Dizney and Dearing 2013), boldness in eastern grey squirrels (*Sciurus carolinensis*) and endoparasitic infection (Santicchia et al. 2019), boldness in eastern chipmunks (*Tamias striatus*) and endoparasitic load (Patterson and Schulte-Hostedde 2011), and negative associations between exploratory behavior in natal multimammate mice (*Mastomys natalensis*) and infection by Morogoro arenavirus (Broecke et al. 2019). Personality may be especially relevant to consider in systems where vectors are highly sensitive to local microhabitat features (Estrada-Peña and de la Fuente 2014) given that different personality types have been shown to vary in their selection of microhabitat at multiple spatial scales (Schirmer et al. 2019; Brehm and Mortelliti 2021). For example, highly active and exploratory eastern deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*) select microhabitats characterized by increased ground cover and light levels (Brehm and Mortelliti 2021), whereas bolder bank voles (*Myodes glareolus*) occupy larger home ranges characterized by lower maximum vegetation height and higher percentage of ground cover (Schirmer et al. 2019). However, previous work has shown that such patterns of habitat selection are context-specific and can be modified by land-use change, such as forest management practices (Brehm and Mortelliti 2021).

To our knowledge, no study has investigated the role of personality in host infection prevalence for Lyme disease or addressed whether associations may be altered by land-use change. A region that may reveal major drivers of spatial and temporal variation of Lyme disease is the state of Maine (United States) which has the highest national incidence rate in humans over the last 3 surveillance years (2017 to 2019; CDC 2021). Concurrently, Maine heavily implements silviculture management practices for an estimated $8.1 billion forestry industry (Bailey and Green 2021). Maine is also currently experiencing an ecological invasion of *P. lecucopus*, which has historically been the predominant reservoir host in the United States and Canada due to its high reservoir competency and comparative abundance to other small mammals in endemic regions (Barbour 2017). However, *P. maniculatus*, the resident species in Central Maine, also appears to be an efficient reservoir (Rand et al. 1993; Larson et al. 2021). Until recently, there existed few regions where the 2 species coincided and contributed to maintenance of *B. burgdorferi* (Barbour 2017) but with the current climate and northern expansion of *P. leucopus*, studies comparing their relative competencies in natural systems are now possible (Roy-Dufresne et al. 2013; Eisen and Eisen 2018).

Our objective in this study is to assess the effects of individual phenotypic traits (physical traits such as body mass and behavioral traits such as personality) and environmental traits on the probability of *B. burgdorferi* infection in 2 mouse species, *P. leucopus* and *P. maniculatus*, within different forest types characterized by different silviculture treatments in Maine, United States. We predict that infection probability will vary at the population, species, and individual level. Firstly, we expect that infection prevalence will vary by forest type due to differences in the abundance and distribution of key microhabitat features—including coarse woody debris and shrub cover—that determine space use by *P. maniculatus* and *P. leucopus* (Brehm and Mortelliti 2021). Specifically, we predict that forest types with more diverse and abundant microhabitat features will provide greater diversification of niche space for reservoir hosts and dilute the overall probability that any one host will become infected, presumably by decreasing competition for important resources and habitat features (Ehrmann et al. 2018). Secondly, although *P. leucopus* and *P. maniculatus* historically rarely co-occur, and few studies have addressed differences in infection probability, we suspect that *P. leucopus* will exhibit higher rates of infection compared to *P. maniculatus*. There is evidence that *P. maniculatus* outcompetes *P. leucopus* for arboreal nesting sites and increased time spent on the ground may disproportionately expose *P. leucopus* to host-seeking ticks (Dooley and Dueser 1990). At the individual level, we predict that body size will be positively related to infection probability in support of previous research on the association (Perkins et al. 2003; Harrison et al. 2010; Mysterud et al. 2015). Lastly, we expect higher infection rates in bolder, more exploratory, and highly active individuals based on the pace-of-life syndrome hypothesis which suggests that disparities in infection probability arise from differences in space use, sociability, and/or immune function (Réale et al. 2010; Sih et al. 2015).

Materials and methods

Study area and trapping.

This study was conducted in the Penobscot Experimental Forest (44°51′N, 68°37′W), Maine (United States), a 1,578-ha mixed conifer–deciduous forest, which hosts a compartment study wherein "management units" have been randomly selected and replicated under varying silviculture treatments to produce different forest types (Brissette and Kenefic 2014). We conducted the study in uniform shelterwood and irregular 2-stage shelterwood forest types and reference sites that have been unmanaged since the late 1800s (Brehm and Mortelliti 2018). In total, we worked in 6 separate sites (3 forest types with 2 replicates each), which average 8.5 ha in size (range 8.1 to 16.2 ha) and positioned trapping grids in each site at least 1.44 km away from all other trapping grids (greater than the daily movements of *Peromyscus* spp.; Bowman et al. 2001; Fig. 1).

We implemented a capture–mark–recapture study consistent with guidelines set by the American Society of Mammalogists (Sikes et al. 2016) and approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC numbers A2015_11_02 and A2018_11_01) from June to October of 2016 to 2021. Within each trapping grid, 100 flagged points spaced 10 m apart were centered within the treatments to minimize edge effects. Longworth traps were set once per month for 3 consecutive days and checked twice daily (just after sunrise and just before sunset) for a total of approximately 54,000 trap-nights (trap-night = number of active traps × number of trap-nights). Traps were baited with oats, sunflower seeds, and freeze-dried mealworms, bedded with poly-fiber for thermoregulation, and set at each flagged point. Previous research in this study system has validated that these sampling methods are not biased toward certain personalities and that trap confinement does not impact subsequent behavioral assays (Brehm and Mortelliti 2018; Brehm et al. 2020).

Behavioral tests and video analysis.

Three standard behavioral tests including an emergence test, an open-field test, and a handling bag test were used to assess boldness, activity and exploration, and docility, respectively (Fig. 2, Supplementary Data SD1; Choleris et al. 2001; Martin and Réale 2008; Gracceva et al. 2014). All behavioral assays were performed in the same sequential order at trapping grids prior to handling

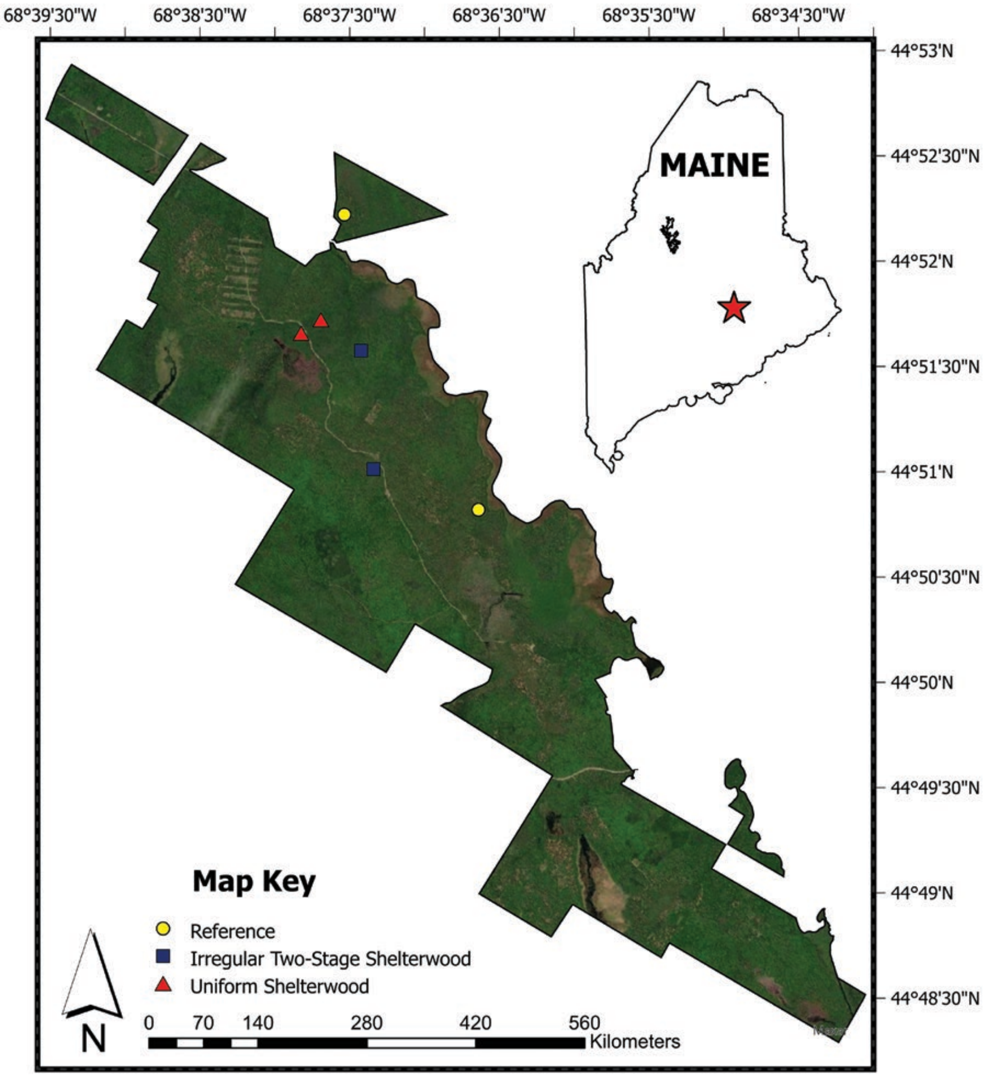

Fig. 1. Map of the Penobscot Experimental Forest in Bradley and Eddington, Maine, United States (PEF; 44°53′N, 68°39′W; site location designated with a star), with locations of unmanaged and managed forest units shown.

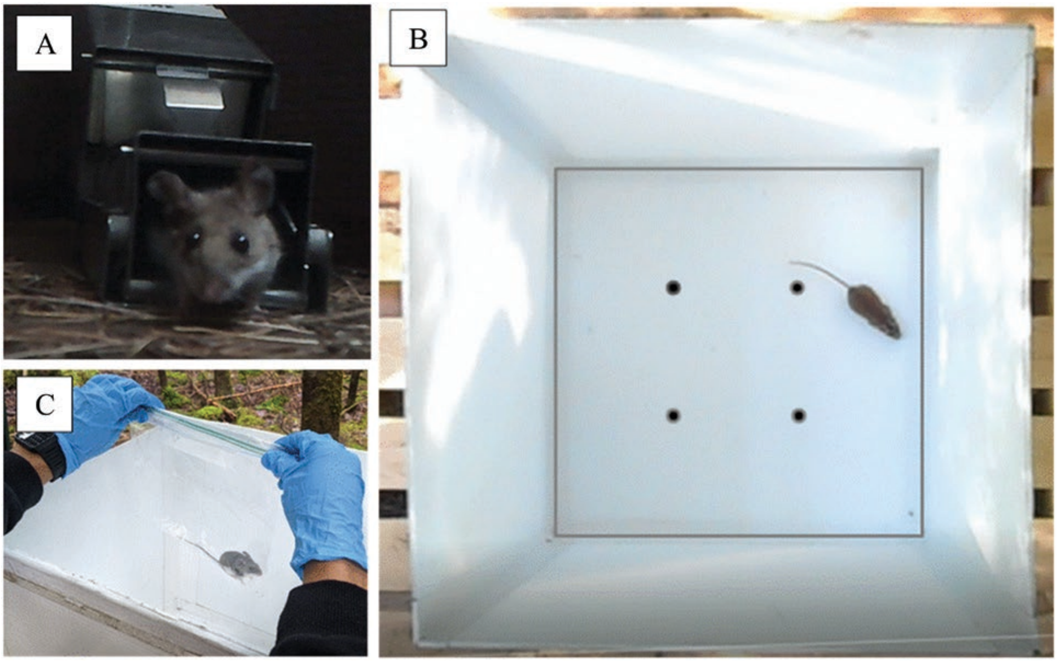

Fig. 2. Three standardized tests used to assess behavioral traits in Peromyscus leucopus and *P. maniculatus*. (A) The 3-min emergence test measures latency of individuals to emerge from the trap tunnel; (B) the 5-min open-field test measures mean speed, proportion of time spent in the center of test or grooming, rear rate and jump rate; and (C) the 1-min handling bag test measures freezing behavior.

and marking, on leveled platforms, and under tarps to control for light levels and canopy cover. All behavioral assays were performed once per month to avoid habituation.

Focal individuals were transferred from the trap of capture to a clean Longworth trap with a 4-L plastic bag for the emergence test. The trap containing the focal individual was placed in a box (46 × 46 × 60 cm) painted brown with a scattering of leaf litter. The door of the trap was then locked open and a digital camera placed on the opposite end of the box facing the tunnel mouth to record the trial (Nikon CoolPix S3700) before the experimenter left the immediate area to avoid disrupting the test. After 3 min, the experimenter returned to capture the focal individual in a 4-L plastic bag and transfer to the open-field test (46 × 46 × 60 cm). The focal individual was released in the center of the arena with a plexiglass cover placed over the box to avoid escape events. A mounted digital camera (Nikon CoolPix S3700) was set to record the trial and the experimenter left the immediate area. After 5 min, the experimenter returned to capture the individual in a clean, clear, 4-L plastic bag, and suspended them in the middle of the open-field area to count the number of seconds the individual spent immobile for 1 min for the handling test. After each trial, all equipment was wiped down with 70% isopropyl alcohol and allowed to dry.

Recorded behavioral trials were played back in the laboratory to quantify individual behavior. For emergence tests, observers recorded latency to end of tunnel, latency of emergence (defined as all feet exiting the Longworth trap), and total time spent at end of the Longworth tunnel. For individuals that did not emerge from the test after 3 min, latency to emerge was set to 3.75 min (1.25× the maximum test length; Brehm and Mortelliti 2021, 2022; Merz et al. 2023). For open-field tests, observers analyzed trials using behavioral tracking software ANY-maze (version 5.1; Stoelting Co; Woods Dale, IL) to record rear rate, jump rate, number of center entries, proportion of time spent grooming, proportion of time spent in the center of the test, and mean speed.

Animal tagging and ear tissue collection.

After all behavioral tests, individuals were anesthetized with isoflurane for subcutaneous insertion of PIT tags (passive integrated transponders; Biomark MiniHPT8), ear tag (National Brand, style 10050-1) application, and measurement of body and tail length. Ear tissue biopsies, approximately 2 mm × 2 mm, were collected from the tip of the ear upon first capture of an individual in 2020 and 2021 with sanitized surgical scissors and stored in a 1.5-mL Eppendorf tube with 1 mL of 70% ethanol stored at −20 °C until DNA extraction, pathogen analysis, and molecular identification of mouse species. Lastly, sex, body mass (using a 100-g Pesola Lightline spring scale), and age class (based on body size and color of pelage) were recorded before releasing individuals at their site of capture.

Microhabitat survey.

In July 2021, detailed microhabitat measurements were taken within a 5-m radius of each flag in all 6 trapping grids (100 sites per grid) to characterize structural components such as fallen logs and woody vegetative cover. Following silviculture disturbance, such habitat features can be substantially altered and can change small mammal microhabitat use (Kellner and Swihart 2014). Measured variables reflect previous literature on small mammal microhabitat use and include total horizontal length (m) of coarse woody debris (CWD) greater than 10 cm in diameter, percent canopy cover, percent cover of herbs and forbs, and percent cover of shrubs and saplings (see Table 1 for brief descriptions of each microhabitat variable; Dueser and Shugart 1978; Price and Kramer 2016; Brehm and Mortelliti 2021).

Peromyscus species and B. burgdorferi pathogen analysis.

Mouse ear tissue samples were bisected and treated with a 1-M solution of Dithiothreitol prior to DNA extraction and purification using the DNeasy Blood and Tissue kit (catalog #69506, Qiagen, Inc., Valencia, California) following Qiagen Protocol. Extracted

Table 1. Predictor variables used in the analysis of *Borrelia burgdorferi* infection probability in *Peromyscus leucopus* and *P. maniculatus*.

Model set	Fixed variable	Variable description
1	Phenotypic variables	
	Sex	male or female
	Mass	weight (g)
	CI	body condition index; calculated scaled-mass index using body length and mass
2	Environmental variables	
	Canopy cover	percent canopy cover calculated using a densiometer ddataaatfacing four cardinal directions
	CWD	total length of coarse woody debris >10 cm in diameter
	DBH	diameter at breast height of largest tree
	Grass	percent cover of herbaceous foliage in a 5-m radius around capture site
	Shrub	percent cover of shrubs and saplings 1 to 2 m tall in a 5-m radius around capture site
	Treatment	silviculture treatment; reference (mature), uniform or irregular 2-stage shelter wood
	Treatment 2	reference (mature) or managed forests
	P. density	total number of mice captured per session per grid
	Session	trapping month of study
	Year	year of study
3	Personality variables	
	Mean speed (MS)	measure of activity (meters/second)
	Proportion time center (PC)	proportion of time spent in center of the open-field arena
	Jump rate (JR)	rate of jumps (jumps/second)
	Rear rate (RR)	rate of rears (rears/second)
	Proportion time groom (PG)	proportion of time spent grooming
	Latency to Emerge (LE)	number of seconds before an individual emerges
	Handling (H)	number seconds individual spent inactive during handling test

samples were then amplified with a quantitative polymerase chain reaction (qPCR) quadruplex at the University of Maine Cooperative Extension Diagnostic and Research Laboratory to detect *P. leucopus* and *B. burgdorferi* sensu lato (Rounsville et al. 2021). Each qPCR reaction contained 2 µL of DNA template (extracted from ear tissues or control samples), 5 µL of Bio-Rad iQ Multiplex Powermix (Hercules, California) iQ Multiplex Powermix, and 3 µL of premixed primers and probes, for a 10-µL reaction size. All samples were loaded in duplicate, and for every 92 samples tested, positive controls containing *P. leucopus* and *B. burgdorferi* DNA, negative PCR controls, and negative extraction controls were also run. The qPCRs were completed on a Quantstudio 5 Real-Time PCR (catalog #A28137, Applied Biosystems, Waltham, Massachusetts) with an initial burn-in at 95 °C for 3 min followed by 45 cycles of annealing–extension (95 °C for 15 s and 60 °C for 1 min). Samples were considered positive if they successfully amplified with a critical threshold (CT) ≤ 35. For samples with unclear results, we reran the sample in quadruplicate and considered the sample positive if at least 2 out of 6 tests positively detected *B. burgdorferi*.

Samples negative for *P. leucopus* were run on separate SYBR reactions to distinguish between unsuccessful extractions and *P. maniculatus* samples. Each PCR reaction contained 2 µL of DNA template, 5 µL of Power SYBR Green (2×, catalog #4367659, Applied Biosystems, Waltham, Massachusetts), 1 µL of premixed primers and probes, and 2 µL of diH$_2$O for a 10-µL reaction size. All samples were loaded in duplicate, and for every 92 samples tested, 2 positive controls containing *P. maniculatus* were included to allow for comparison of positive samples. The PCR was completed on a Bio-Rad CFX96 (catalog #1845097, Bio-Rad, Hercules, California) with an initial burn-in at 95 °C for 3 min followed by 40 cycles of annealing–extension (95 °C for 15 s and 60 °C for 45 s) and a melt curve from 70 to 85 °C in increments of 0.05 °C/s. Samples were considered *P. maniculatus* positive if they dissociated at 80 °C CT.

Statistical analysis.

To determine which variables obtained from the behavioral assays could be considered personality traits, we performed repeatability analyses for each species using package "rptR" (Dingemanse and Dochtermann 2013; Stoffel et al. 2017). For the analysis on *P. leucopus*, we used all individuals captured from 2016 to 2021 (including those with only 1 observation). Using all individuals in the repeatability analysis, compared to only using those with 2 or more observations, allows us to measure variance in behavioral plasticity across the population and yields similar estimates for variance components (Martin et al. 2011). To avoid convergence issues for the repeatability analysis on *P. maniculatus*, we used individuals captured from 2016 to 2021 with 2 or more repeated observations. We ran mixed-effects models on different data sets for each behavioral variable because not all individuals were successfully run through every test and used individual ID as a random effect, and sex, forest type, and trapping month (session) as fixed effects to determine the proportion of behavioral variance attributable to intraindividual differences (Dingemanse and Dochtermann 2013). We also used body condition, calculated using the scaled-mass index method, as a fixed effect (Peig and Green 2010). In brief, the scaled-mass index standardizes body mass according to a fixed linear value of body measurement that is scaled to the standardized major axis regression between body mass and length (Peig and Green 2010). For all models, we used 1,000 parametric bootstraps and 100 permutations to calculate adjusted repeatability and associated confidence intervals. Prior to running repeatability models, each behavioral variable was visually assessed for normality using Q–Q plots, histograms of residuals, and plots fitted against residual values of linear mixed-effect models and generalized linear mixed-effect models. When necessary, we used Box–Cox or logit transformations to normalize response variables (Box and Cox 1964; Yang et al. 2011). Any behavioral trait that excluded zero within its 95% CI was considered a personality trait (Nakagawa and Schielzeth 2010; Table 2).

To account for within-individual variation, we simulated best linear unbiased predictors (BLUP) 1,000 times for each individual and each personality trait using the "arm" package, while controlling for variation due to sex, body condition, forest type, trapping month, and year (consistent with methods used by Dingemanse et al. 2020; Gharnit et al. 2020; Mortelliti and Brehm 2020). Individual mean BLUP value for the target personality variable was then used as personality covariates in our logistic models. We screened all personality variables for correlation, using a threshold of $r < 0.7$ to avoid collinearity during model selection and scaled all continuous variables (z-standardized; Dormann et al. 2013; Supplementary Data SD2). All further mentions of personality will refer to the mean BLUP value and are species-specific.

We used 4 microhabitat measurements (z-standardized) that characterize the structural elements of capture sites and associated measurements with individuals using the single point of capture that corresponded to the date of sample collection. Additional environmental variables used include density of mice—which were calculated as the total number of captured individuals across the season per grid—silviculture treatment, session, and year.

We used logistic regression models in a nested hypothesis testing approach to assess whether personality traits affect individual probability of detected *B. burgdorferi* infection for each species (Burnham and Anderson 2002). For all analyses, individual infective state (positive or negative detection) was used as the response variable, models within 2.0 ΔAICc (Akaike's information criterion corrected for small sample sizes) of the top model were considered to have equal support and we present model-averaged estimates and associated variance estimates (Burnham and Anderson 2002, Burnham et al. 2011). We first tested potential confounding covariates from individual physical traits and environmental variables, carried over best-supported models, and then explicitly tested personality variables. Specifically, we tested sex, body mass, and body condition, and compared models to the null. We retained the top model from this model set and tested it against 10 new models, each with 1 environmental variable added (Table 1). Again, the top model from this model set was retained and tested against 7 new models, each with 1 personality variable added (Table 1). At any point, if more than 1 model scored higher than the null model, additive effects of these variables were tested. Lastly, to assess effect of species on infection probability, we merged *P. leucopus* and *maniculatus* data sets and compared the species model to the null model.

Results

Repeatability of behavioral tests.

From emergence, open-field, and handling bag tests, we examined 91 individual *P. leucopus*, 24 of which had repeated observations and 958 individual *P. maniculatus*, 308 of which had repeated observations, captured from 2016 to 2021. All behavioral variables were significantly repeatable with a mean of 0.50 (range of 0.38 to 0.62) for *P. leucopus* and 0.38 (range of 0.31 to 0.47) for *P. maniculatus* (Table 2). Additional results for the linear mixed-effect models run for each behavioral trait in the repeatability analysis are provided in Supplementary Data SD3.

B. burgdorferi *infection probability.*

Overall infection prevalence was 18.4% for *P. lecuopus* (14/76) and 9.9% for *P. maniculatus* (26/263). We detected infection in 16.7%

Table 2. Adjusted repeatability estimates for target behavioral traits measured in 3 standardized behavioral assays (handling bag, emergence, and open-field tests) in *Peromyscus leucopus* and *P. maniculatus*.

Species	Behavior trait	Mean	Range	RPT	(95% CI)	Observations	Individuals
P. leucopus	Mean speed	0.02	(0, 0.17)	0.60	(0.38, 0.91)	94	82
	Jump rate	0.02	(0, 0.30)	0.58	(0.36, 0.91)	94	82
	Rear rate	0.04	(0, 0.48)	0.46	(0.22, 0.90)	92	82
	Prop groom	0.08	(0, 0.69)	0.43	(0.10, 0.87)	92	81
	Prop center	0.06	(0, 0.31)	0.38	(0.01, 0.87)	92	80
	Latency to emerge	190.35	(1, 225)	0.62	(0.43, 0.90)	96	83
	Handling	49.70	(0, 60)	0.43	(0.15, 0.85)	102	89
P. maniculatus	Mean speed	0.09	(0, 0.29)	0.47	(0.39, 0.53)	836	307
	Jump rate	0.10	(0, 0.60)	0.44	(0.37, 0.51)	840	308
	Rear rate	0.19	(0, 0.65)	0.39	(0.31, 0.46)	840	308
	Prop groom	0.20	(0, 0.97)	0.39	(0.31, 0.46)	839	308
	Prop center	0.02	(0, 0.53)	0.34	(0.26, 0.42)	837	308
	Latency to emerge	49.26	(0, 225)	0.31	(0.22, 0.40)	710	257
	Handling	13.03	(0, 60)	0.36	(0.28, 0.44)	771	275

of *P. leucopus* and 4.5% of *P. maniculatus* captured within uniform shelterwood sites, 22.9% and 13.8% captured in irregular 2-stage shelterwood sites, and 11.8% and 8.0% captured in reference sites (Table 3, Supplementary Data SD4).

Top-ranking models for *P. leucopus* all included body mass (n = 76, β = 1.89, SE = 0.58; Table 4) and the model-averaged prediction showed that as body mass increases, the probability of infection also increases (Fig. 3A). The top-ranking model for *P. maniculatus* (n = 263; Table 4), included body mass (β = 1.89, SE = 0.35; Fig. 3B), trapping month (Session: β = −0.38, SE = 0.35; Session^2: β = −0.99, SE = 0.37), and proportion of time spent in the center of the open-field test, where infection probability increases as proportion time center decreases (β = −0.72, SE = 0.28; Fig. 4). Similar to *P. leucopus* top models, body mass was positively related, but trapping month was quadratically related to infection probability, and proportion time center had a negative effect on infection probability. All other environmental variables reflecting density, microhabitat, and forest type were not within 2.0 ΔAICc of the top model, suggesting lower support for these models. Lastly, in the combined species analysis, there was some support for differential infection probability by species (β = −0.77, SE = 0.36), where *P. maniculatus* infection probability is lower than *P. leucopus* infection probability, but the model was only 2.14 AICc units better supported than the null model and the coefficient of determination was low (R^2 = 0.017).

Discussion

Through a large-scale capture–mark–recapture study, we found that infection probability was strongly related to body mass and trapping month in *P. maniculatus*. We also found evidence of a negative effect of boldness (i.e. proportion of time spent in the center of the open-field test) in *P. maniculatus* on *B. burgdorferi* infection probability. Although there were many high-ranking models that included environmental and personality variables for *P. leucopus*, the main variable driving the relationship was body mass. Lastly, we found no support for an effect of forest type in either species or an effect of reservoir host species.

Personality effects on individual infection probability.

To our knowledge, this is the first study to investigate the role of individual behavioral traits in *B. burgdorferi* infection prevalence. Our results, although preliminary, suggest that shy *P. maniculatus* are more likely to be infected by *B. burgdorferi*. In animal personality research, the shy-bold continuum is commonly interpreted as the tendency of an individual to express risky behaviors (Carter et al. 2013). This negative association between boldness and infection probability contradicts what the pace-of-life hypothesis would predict—“fast” individuals should be associated with high growth rates, early reproduction, and boldness at the cost of low immune responses and high parasite loads (Réale et al. 2007)—as well as what previous studies have found on the effect of boldness on infection by Sin Nombre virus in western deer mice, endoparasitic load in eastern chipmunks, and endoparasitic infection probability in eastern grey squirrels (Patterson and Schulte-Hostedde 2011; Dizney and Dearing 2013; Santicchia et al. 2019). Rather, our results fall more in line with what the risk-of-parasitism hypothesis would predict—bold individuals, due to increased risk of parasite exposure, should have greater immune defenses and thus present lower infection likelihoods (Barber and Dingemanse 2010; Kortet et al. 2010; Jacques-Hamilton et al. 2017). Recent studies report an emerging pattern of heightened immune responses in bold individuals, possibly indicating stronger resistance to infection (Zylberberg et al. 2014; Ezenwa et al. 2016). However, this hypothesis is likely context-dependent, and only operates in situations where there is large enough cost on the infested individual to incur a selective pressure. Of the studies that have investigated the consequence of *B. burgdorferi* infection in *Peromyscus* spp., none have revealed reductions in fitness, substantial pathology, energetic burden, or changes in activity up to 6 weeks postinfection (Schwanz et al. 2011; Voordouw et al. 2015; Barbour 2017).

Alternatively, the negative association between boldness and infection probability could be the result of differential microhabitat use. Previous work has revealed that different personalities choose to occupy distinct microhabitats and thus may be differentially exposed to encounters with infected vectors. For example, shy mice select to occupy areas in unmanaged forests that are characterized by less herbaceous ground cover, i.e. mosses, herbs, and forbs (Brehm and Mortelliti 2021), which have been negatively associated with larval infestation (Adler et al. 1992). There are many alternative mechanisms that remain to be explored, and are likely nonmutually exclusive, but regardless of the mechanism, our result suggests a relationship between boldness and infection probability in *P. maniculatus*. We emphasize that confidence intervals around our estimates were relatively large, which could be the result of small sample size (i.e. overall number of infected individuals), or seroconversion during the season and reservoir competence decay (Schauber and Ostfeld 2002).

Conversely, we found no effect of personality on *P. leucopus* infection probability. Within forested landscapes, although both *P. maniculatus* and *P. leucopus* travel comparable distances in forest-floor microhabitats, *P. maniculatus* tend to outcompete *P. leucopus* in use of arboreal nesting sites (Graves et al. 1988; Dooley and Dueser 1990). Differential nesting habits and constrained microhabitat selection may mitigate variation in infection probability within *P. leucopus* compared to *P. maniculatus*. However, there are few studies on the subject and the lack of association could also be a function of low prevalence coupled with small sample size.

Effects of body mass on infection probability.

In line with our main hypothesis, increased body mass in both *Peromyscus* species corresponded to higher chances of being infected. This result is consistent with previous studies

Table 3. Infection prevalence of *Borrelia burgdorferi* in *Peromyscus leucopus* and *P. maniculatus* across 3 forest types characterized by different silviculture treatments in Maine, United States.

Species	Forest type		
	Uniform shelterwood	Irregular 2-stage shelterwood	Reference (unmanaged)
P. leucopus	16.7% (4/24)	22.9% (8/35)	11.8% (2/17)
P. maniculatus	4.5% (3/66)	13.8% (15/109)	8.0% (7/88)

Table 4. Logistic regression model results ($n = 263$ *Peromyscus maniculatus* observations; $n = 76$ *P. leucopus* observations). The top-ranked models within 10 ΔAICc are shown from each analysis testing probability of *Borrelia burgdorferi* infection. *Peromyscus maniculatus* and genus analyses each had only 1 top model defined as having an ΔAICc score < 2 to all other tested models. *Peromyscus leucopus* had several top models at the second and third model sets, but we chose to advance with the most parsimonious model. Parameter β estimates and SEs are also provided.

	Top-ranked models	**K**	**ΔAICc**	**R^2**
P. leucopus	Mass (β = 2.37, SE = 0.68) + Session (β = 0.91, SE = 0.57) + Session^2 (β = 0.91, SE = 0.45)	4	0.00	0.34
	Mass (β = 1.79, SE = 0.52)	2	0.32	0.27
	Mass (β = 1.88, SE = 0.55) + Shrub 2 (β = 0.41, SE = 0.28)	3	0.59	0.30
	Mass (β = 1.87, SE = 0.54) + MS (β = 0.52, SE = 0.39)	3	0.60	0.30
	Mass (β = 1.81, SE = 0.54) + CWD (β = −0.55, SE = 0.44)	3	0.65	0.30
	Mass (β = 1.95, SE = 0.56) + PC (β = 0.49, SE = 0.38)	3	0.76	0.29
	Mass (β = 1.76, SE = 0.52) + RR (β = 0.40, SE = 0.37)	3	1.32	0.29
	Mass (β = 1.86, SE = 0.55) + Canopy cover (β = 0.44, SE = 0.50)	3	1.62	0.28
	Mass (β = 1.77, SE = 0.52) + H (β = −0.30, SE = 0.33)	3	1.65	0.28
	Mass (β = 1.77, SE = 0.53) + PG (β = 0.30, SE = 0.34)	3	1.69	0.28
	Mass (β = 1.78, SE = 0.52) + LE (β = −0.30, SE = 0.34)	3	1.72	0.28
	Mass (β = 1.79, SE = 0.52) + Year (β = 0.68, SE = 0.88)	3	1.85	0.28
	Mass (β = 1.80, SE = 0.53) + JR (β = 0.16, SE = 0.35)	3	2.28	0.27
	Mass (β = 1.77, SE = 0.52) + P. density (β = −0.13, SE = 0.34)	3	2.34	0.27
	Mass (β = 1.79, SE = 0.52) + Grass (β = 0.11, SE = 0.36)	3	2.40	0.27
	Mass (β = 1.78, SE = 0.53) + TRT2 (Managed β = 0.11, SE = 0.93)	3	2.48	0.27
	Mass (β = 1.79, SE = 0.53) + Session (β = 0.01, SE = 0.35)	3	2.49	0.27
	Mass (β = 1.80, SE = 0.54) + TRT (Irregular β = 0.31, SE = 0.97; Uniform β = −0.29, SE = 1.10	3	4.17	0.28
P. maniculatus	Mass (β = 1.89, SE = 0.35) + Session (β = −0.38, SE = 0.35) + Session^2 (β = −0.99, SE = 0.37) + PC (β = −0.72, SE = 0.28)	5	0	0.41
	Mass (β = 1.82, SE = 0.33) + Session (β = −0.46, SE = 0.35) + Session^2 (β = −1.03, SE = 0.36) + RR (β = −0.47, SE = 0.26)	5	3.87	0.39
	Mass (β = 1.74, SE = 0.31) + Session (β = −0.50, SE = 0.35) + Session^2 (β = −0.94, SE = 0.35)	4	5.07	0.37
	Mass (β = 1.74, SE = 0.31) + Session (β = −0.50, SE = 0.35) + Session^2 (β = −1.01, SE = 0.36) + MS (β = −0.35, SE = 0.28)	5	5.51	0.38
	Mass (β = 1.73, SE = 0.31) + Session (β = −0.50, SE = 0.35) + Session^2 (β = −0.99, SE = 0.36) + JR (β = −0.22, SE = 0.25)	5	6.39	0.37
	Mass (β = 1.71, SE = 0.31) + Session (β = −0.51, SE = 0.35) + Session^2 (β = −1.00, SE = 0.36) + PG (β = 0.23, SE = 0.28)	5	6.46	0.37
	Mass (β = 1.71, SE = 0.31) + Session (β = −0.52, SE = 0.35) + Session^2 (β = −0.96, SE = 0.35) + LE (β = 0.19, SE = 0.25)	5	6.57	0.37
	Mass (β = 1.73, SE = 0.31) + Session (β = −0.50, SE = 0.35) + Session^2 (β = −0.95, SE = 0.36) + H (β = 0.10, SE = 0.25)	5	6.99	0.37
	Mass (β = 1.78, SE = 0.30) + Shrub 2 (β = 0.53, SE = 0.19)	3	7.26	0.34
Peromyscus	Species (β = −0.77, SE = 0.36)	2	0	0.02
	Null	1	2.16	0.00

CWD = coarse wood debris; H = handling time; JR = jump rate; LE = latency to emerge; MS = mean speed; PC = proportion time center; PG = proportion time groom; P. density = *Peromyscus* density; RR = rear rate.

investigating the relationship (Harrison et al. 2010; Kiffner et al. 2011; Mysterud et al. 2015). There are 3 main hypotheses concerning size-based infection in the literature. The first and most direct explanation may be that larger individuals offer larger targets for ticks to parasitize and thus have a greater chance of encountering an infectious vector (Arneberg et al. 1998). Considering that body mass is also often used as an indicator of age in small mammals, this trend could also arise from greater cumulative exposure to infected vectors (Peig and Green 2010). A second hypothesis, generally referred to as the ecoimmunological pace-of-life hypothesis, draws from life-history theory and proposes that the underlying cause of size-biased infection is due to a resource allocation trade-off between growth and immune defense (Moore and Wilson 2002; Perkins et al. 2003; Ostfeld et al. 2014). In other words, individuals that heavily invest in growth and reproduction do so at

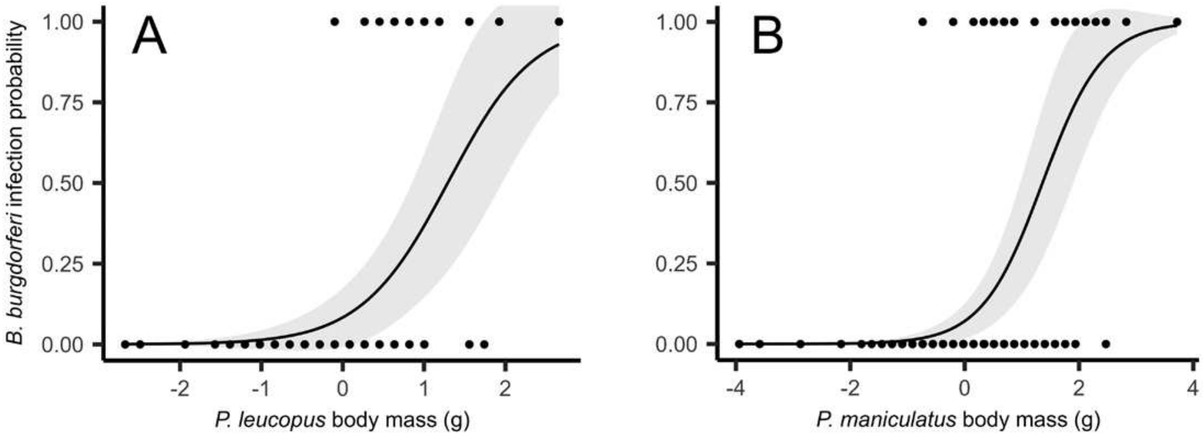

Fig. 3. Effect of body mass (x-axis) on probability of *Borrelia burgdorferi* infection (y-axis) for *Peromyscus leucopus* (A) and *P. maniculatus* (B). Body mass (g) increases probability of infection for both species. The model-averaged prediction for *P. leucopus* and prediction for *P. maniculatus* were obtained from logistic mixed-effects models and the 95% CIs are shown. Predicted probability of infection for *P. maniculatus* is shown for August (trapping session 3) and mean score for proportion time center.

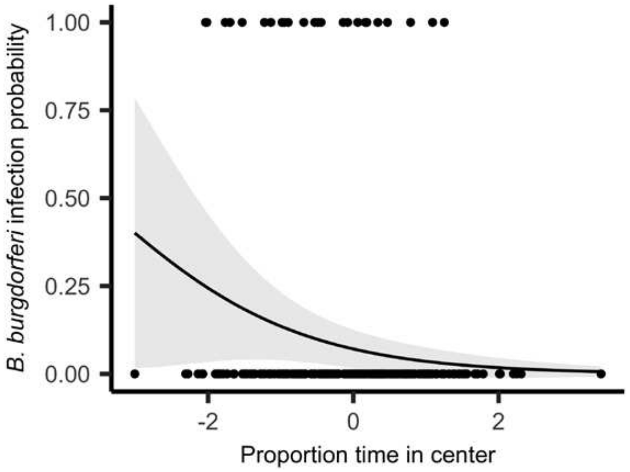

Fig. 4. Effect of personality trait and proportion of time spent in center of open-field test (x-axis) on probability of *Borrelia burgdorferi* infection (y-axis) for *Peromyscus maniculatus*. Proportion of time spent in center (BLUP value) decreases probability of infection. Predictions were obtained from logistic mixed-effects models; 95% CIs are shown. Predicted probability of infection are shown for August (trapping session 3) and mean body mass.

the cost of self-maintenance, including immune function, and should be less resistant to infection (Lee et al. 2008; Hawley and Altizer 2011). A third hypothesis posits that larger individuals have greater competitive ability and select microhabitats that are more conducive to host survival but happen to be also more conducive to tick survival, e.g. habitats with more protective cover and denser vegetation that offer greater protection against predation for mice that simultaneously maintain appropriate moisture levels for host-seeking ticks (Kiffner et al. 2011; Hersh et al. 2014). Although we investigated the effect of several microhabitat features on the probability of infection, a more in-depth analysis on host microhabitat selection with more specific variables that influence tick habitat quality, such as leaf litter depth and soil moisture content, may clarify the mechanism behind the positive effect of body mass on infection probability.

Environmental effects of individual infection probability.

Through our analyses, we found that time of the year was related to infection probability in *P. maniculatus*. The resulting quadratic relationship suggests that there is an increased risk of infection for individuals in the month of August. In Maine, nymphal ticks molt from larvae in the spring and seek hosts throughout the spring and summer (Eisen and Eisen 2018). Mice that have been parasitized by host-seeking ticks throughout the season may present with a higher probability of infection in August due to greater cumulative exposure. It is important to note that our results are limited by a single point of detection and future studies targeting probability of seroconversion and reservoir competence decay could better address the temporal attributes of infection probability.

Contrary to our predictions, there was no observed difference in infection probability among forest types. However, this result runs parallel to findings by Conte et al. (2021) who reported that timber harvesting affected density of host-seeking nymphs, but not nymphal infection prevalence. Although *I. scapularis* distribution has been shown to be spatially autocorrelated at the national and state scale, there appears to be high variability in tick distribution at finer scales (Pardanani and Mather 2004). It may be that the physical environmental variables used in our study do not vary enough or are not at the appropriate response scale for infection prevalence. It may also be that our conifer-dominant sites offer generally poor habitat for ticks. Infection prevalence and tick abundance have been closely associated with depth of deciduous leaf litter and against conifer-dominant sites, purportedly because coniferous forests produce shallower litter and thus less protection again extreme weather conditions (Bunnell et al. 2003; Lubelczyk et al. 2004; James et al. 2013).

Reservoir competence species comparison.

In our analysis, we found little difference between *Peromyscus* species in *B. burgdorferi* infection probability, which is consistent to what Larson et al. (2018) concluded in northern Wisconsin, i.e. although *P. leucopus* was more likely to be infested, infection was similar between the 2 species. Further research on species-specific infectivity and competitive dynamics in varying regions would clarify the relative reservoir competencies of these 2 species of *Peromyscus* mice.

Limitations and future directions.

Although our sample size for personality is large (i.e. 397 individuals) and repeatability estimates were comparable to field and laboratory studies (Bell et al. 2014; Underhill et al. 2021), our results—which report a link between boldness and infection probability—should be considered preliminary. The primary limitation from this study being conducted in a low tick density area was the remarkable scarcity of ticks parasitizing our individuals and the small success rate of infection (11.5%), which constrained the number and complexity of variables we were able to test in our analyses. Zawada et al. (2020) estimate that ear tissue only accounts for 68.4% of detected *B. burgdorferi* infections, which may have contributed to the small sample size of positively infected individuals. Studies that aim to characterize effects of personality on infection probability should target sites where there is greater infection prevalence—possibly in deciduous-dominant forests—and should consider taking both ear and tail snip tissue samples to increase detection to 78.9% (Zawada et al. 2020). Additionally, because abundance of each species covaried with year, we were not able to separate differences in infection probability due to species or year effects. Multiyear studies designed to disentangle temporal from species composition effects would be a critical area for future research. It should also be noted that although *Peromyscus* spp. exhibit no overt pathology, it is possible that infection by *B. burgdorferi* could impose slight sickness behaviors and alter their personality traits (Santicchia et al. 2020). To specifically test this hypothesis, future studies should aim to quantify differences in personality scores pre- and postinfection. Lastly, as this study investigated prevalence of the species complex and not the strict causative agent of Lyme disease in the northeast (*B. burgdorferi*), our conclusions are limited to relationships at the complex level.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Repeatable behavior trait description and interpretation.

Supplementary Data SD2.—Correlation matrix of variables used in logistic model.

Supplementary Data SD3.—Linear mixed-effect model results from repeatability analysis.

Supplementary Data SD4.—Logistic regression data sample summary.

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Author contributions

IY and AM designed research; IY performed field work; IY, AM, and AG wrote the paper; all authors have read, commented, and agreed to the final draft of the manuscript.

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Conflict of interest

The authors declare that they have no conflict of interest.

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