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HIGHLIGHTED STUDENT RESEARCH

Host infection and community composition predict vector burden

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Abstract

Lyme disease is the most prevalent vector-borne disease in the United States, yet critical gaps remain in our understanding of tick and host interactions that shape disease dynamics. Rodents such as deer mice (*Peromyscus* spp.) and dusky-footed woodrats (*Neotoma fuscipes*) are key reservoirs for *Borrelia burgdorferi*, the etiological bacterium of Lyme disease, and can vary greatly in abundance between habitats. The aggregation of *Ixodes pacificus*, the western black-legged tick, on rodent hosts is often assumed to be constant across various habitats and not dependent on the rodent or predator communities; however, this is rarely tested. The factors that determine tick burdens on key reservoir hosts are important in estimating Lyme disease risk because larger tick burdens can amplify pathogen transmission. This study is the first to empirically measure *I. pacificus* larval burdens on competent reservoir hosts as a function of community factors such as rodent diversity, predator diversity, and questing tick abundance. Rodents were live trapped at oak woodland sites to collect tick burdens and tissue samples to test for infection with *Borrelia burgdorferi* sensu lato. We found that *N. fuscipes* tick burdens were negatively correlated with predator diversity, but positively correlated with questing *I. pacificus* larvae. In addition, rodent hosts that were infected with *B. burgdorferi* sensu lato tend to have higher burdens of larval ticks. These results demonstrate that tick burdens can be shaped by variability between individuals, species, and the broader host community with consequences for transmission and prevalence of tick-borne pathogens.

Keywords Zoonotic disease · Biodiversity · *Ixodes pacificus* · *Borrelia burgdorferi* · Predators

Introduction

Vector-borne diseases are disproportionately represented among emerging infectious diseases likely due to their sensitivity to factors such as human land use, climate change, and increased globalization (Sutherst 2004; Jones et al. 2008; Patz et al. 2008; Keesing et al. 2010; Ali et al. 2017; Swei et al. 2020). These global changes lead to biodiversity loss and, in turn, are altering vector–host associations in ways that may promote pathogen transmission rates by increasing the amount of habitat for anthropophilic vectors, decreasing the abundance of diluting hosts, or increasing contact rates between vectors and humans (Lambin et al. 2010; Gottdenker et al. 2011; Gibb et al. 2020). As a result of global changes and biodiversity loss, vector populations and pathogen transmission rates have been responding to changing host community dynamics (LoGiudice et al. 2003; Allan et al. 2003; Wimberly et al. 2014; Buskirk and Ostfeld 2015; Levi et al. 2015). Despite the importance of vector–host relationships, the factors that affect the distribution of vectors attached to their blood meal hosts are not well understood

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This experimental field study documents a positive relationship between larval tick burdens and host-pathogen infection, while predator diversity reduces tick burdens on important reservoir hosts.

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but could have substantial consequences for vector population size and disease transmission dynamics.

Vector blood meal hosts can vary in their reservoir competencies, or in their ability to acquire, maintain, and transmit a pathogen to a feeding vector. When larger tick burdens are on highly competent reservoir hosts, tick infection prevalence and disease risk are predicted to increase (Ostfeld et al. 1996; Levin and Fish 1998; LoGiudice et al. 2003; Slowik and Lane 2009; Swei et al. 2012; Perez et al. 2016). Furthermore, the relative abundance of vectors on their hosts can be affected by changes in host community abundance, host diversity, and vector population density (Ogrzewalska et al. 2011; da Xavier et al. 2012; Young et al. 2015; Hammond et al. 2019). In many tick-borne disease systems, tick burdens of specific hosts can shift based on the composition or abundance of available hosts. For instance, sites with low mouse densities exhibit a larger proportion of ticks feeding on shrews and chipmunks (Shaw et al. 2003; Brisson and Dykhuizen 2006; Brunner and Ostfeld 2008) and when lizard, *Sceloporus occidentalis*, abundance was experimentally reduced, tick burdens increased on *N. fuscipes* (Swei et al. 2011). Therefore, an increased understanding of tick burdens as a function of rodent host community composition is pertinent to understanding tick-borne disease maintenance and transmission. Because each tick life stage takes a single blood meal, there are only three opportunities for ticks to acquire a pathogen from a reservoir host. Therefore, the distribution of the first, or larval, blood meal on hosts are often the focus of many tick-borne disease studies because the subsequent nymph stage is the most important for the transmission of diseases like Lyme disease (Ostfeld et al. 1996; LoGiudice et al. 2003; Shaw et al. 2003; Swei et al. 2012).

In addition to the influence of the rodent community, a growing body of research suggests that predators also play an important function in vector-borne disease transmission, but few studies have directly measured how predators can alter vector populations and pathogen dynamics (Ostfeld and Holt 2004; Moore et al. 2010; Ostfeld et al. 2018). The presence of predators can affect disease transmission directly by lowering host abundances (Levi et al. 2012) and indirectly by reducing foraging behavior of rodents (Keesing et al. 2006; Hofmeester et al. 2017; Moll et al. 2020). Both direct and indirect mechanisms can lead to lower encounter rates with questing ticks. Thus, the presence of predators can reduce transmission rates between infectious ticks and competent hosts. This example supports the 'ecology of fear' hypothesis, which links prey avoidance of predators to a number of behavioral and physiological responses such as reduced foraging time or elevated stress responses (Brown et al. 1999; Ferrero et al. 2011; Moll et al. 2017). There have been a few studies on Sin Nombre virus that have reported a negative impact of predator diversity on mouse infection prevalence (Orrock et al. 2004; Dizney and Ruedas 2009). Furthermore, predator diversity has shown to be associated with reduced nymphal infection prevalence of tick-borne diseases in New York (Ostfeld et al. 2018). However, no study has investigated the impact of predator diversity on the tick burdens of rodent hosts in North America. The western United States provides an ideal setting to study the effects of host and predator diversity on tick-borne diseases and Lyme disease in particular because the predator community is complex and includes an apex predator, the mountain lion (*Puma concolor*). In Europe and the northeastern United States Lyme disease systems, native predator communities are composed of small or meso-carnivores but do not include apex predators such as the mountain lion (Tesky 1995; Culver 2000; Ernest et al. 2003). The current distribution of mountain lions in western North America has the potential to be highly relevant to Lyme disease transmission because their presence could have direct impacts on deer (the reproductive host for adult ticks) and mesopredators (e.g. behavioral changes), as well as indirect impacts on the trophic structure of communities (Levi and Wilmers 2012; Nickel et al. 2019; Suraci et al. 2019a, b; Coon et al. 2020). For example, mountain lions are significant predators of mule deer (*Odocoileus hemionus*), which are important reproductive hosts for adult ticks (Lane and Burgdorfer 1986; Villepique et al. 2011). As a result, the presence of mountain lions has the potential to depress deer populations and indirectly lower tick population densities (Lane and Burgdorfer 1986; Lawrence et al. 2018; MacDonald et al. 2018).

We examined the relationship between host community composition and the distribution of ticks on their hosts in the context of Lyme disease ecology, the most prevalent tick-borne disease in North America (Rosenberg et al. 2018). In the western United States, Lyme disease is transmitted by the western black-legged tick (*I. pacificus*) which feeds on a diverse range of blood meal hosts, especially rodents and lizards in the juvenile stages and deer during the adult stage (Castro and Wright 2007). Lyme disease risk and *I. pacificus* densities are greatest in oak woodland habitats where rodents, mesocarnivores, and top predators are abundant (Eisen et al. 2006; Lawrence et al. 2018). In this study, we evaluated (a) how rodent host and predator community structure influences the distribution of ticks on their blood meal hosts and (b) how these tick burden patterns influence pathogen transmission.

Methods

Site selection

Ten, oak woodland sites were established and sampled as described in Lawrence et al. (2018). Nine sites were established in 2016, and an additional site was added in 2018.

All sites were standardized for abiotic and biotic parameters including the degree of site isolation, mean annual temperature, mean annual precipitation, elevation, slope, aspect, and vegetation cover (≥ 57% oak woodland overstory). The habitat patches ranged in sizes from 2.5 to > 10,000 hectares within the San Francisco Bay Area (For more details see Lawrence et al. 2018). Half-hectare sampling grids were designed within the sites to meet the following criteria: (i) grids were located at least twenty meters away from the forest edge (determined by spatial restrictions of the smallest site), (ii) all grids were located under predominantly oak canopy cover and (iii) direct north facing slopes were avoided due to microclimatic biases (Talleklint-Eisen and Lane 1999).

Rodent trapping and tick collections

Standardized sampling grids were established at each site, consisting of a 7 × 7 trapping grid, with 49 trapping stations set up 11.8 m apart. Rodents were captured with two extra-large Sherman live traps (7.6 × 9.5 × 30.5 cm; H.B. Sherman Traps, Tallahassee, FL, USA) which were positioned at each of the 49 trapping stations facing opposite directions. Sherman traps were baited with oatmeal and peanut butter each evening, and checked the following morning for three consecutive nights at each site during peak larval tick season (beginning of April to mid-May) in 2016 and again in 2018 (Barbour et al. 1985; MacDonald 2018). In 2018, to target squirrels, 11 tomahawk live traps (48.3 × 12.7 × 12.7 in) were also used on five out of the ten sites in addition to the grid of Sherman traps described. Because one new site was established in 2018, 2 years of data are available for 9 sites and one year is available for the tenth site. Most *I. pacificus* hosts are nocturnal, with the exception of lizards and western gray squirrels, both of which do not readily enter Sherman traps (Salkeld and Lane 2010). All captured rodents were identified to species, sexed, weighed, measured, marked with unique ear tags, 2-mm tissue biopsies were taken from the outer pinna of the ear and all attached ticks were collected. Tick examinations occurred for a few minutes with focused attention on the host's head and ears. For tissue collection, rodents were anesthetized with a 50% solution of Isoflurane and 1,3-propanediol. Collected samples were stored in 70% ethanol until further processing in the lab. After processing, all animals were released at the point of capture. All protocols were approved by the Institutional Animal Care and Use Committee (#AU16-05).

Questing ticks were collected using standard dragging methods in which a 1 m^2 white cotton cloth was dragged along linear transects within the 0.5 ha sampling grid totaling 495 m^2 at each sampling site (Salomon et al. 2020). In 2016, drag cloths were checked for ticks every 30 m but in 2018, ticks were checked every 15 m in accordance with updated recommendations from the CDC (Eisen et al. 2018). All ticks were collected and preserved in vials containing 70% ethanol.

Wildlife camera trap data collection

To estimate species richness, relative abundance, and diversity of predators, we installed wildlife cameras at each site within the trapping grid. In 2016, we had a single wildlife camera and in 2018 an additional camera was added to better identify captured animals to species. Motion sensor wildlife cameras (Bushnell Trophy Cam HD) were installed within trapping grids along obvious game trails. Cameras were placed on trees 20–50 cm above the ground. In 2018, the two cameras were positioned on the same tree facing orthogonal directions. Camera traps were set to 'medium' trigger sensitivity and programmed to take three photographs within a 1 s interval with a 30 s delay before a subsequent trigger. Camera traps were active 24 h a day using an infrared flash for night photos. We did not use baits or lures near the camera traps. Cameras were deployed for a total of 40 days between April and May of 2016 and again in 2018 to capture the active predator community during the period of juvenile *I. pacificus* activity, for a total of 80 camera trap days between 2016 and 2018. This camera sampling window was designed to focus on predator and rodent community interactions that occur during the particular phenology of larval *I. pacificus* (Barbour et al. 1985; Lane and Stubbs 1990; Talleklint-Eisen and Lane 1999; Tälleklint-Eisen and Lane 2000; Padgett and Lane 2001; MacDonald 2018).

Borrelia burgdorferi sensu lato testing

Rodent tissue samples were extracted using the DNeasy Tissue Extraction kit (Qiagen, Valencia, California, USA). We made adjustments to the protocol, including the addition of an extra 70% ethanol wash step and the final product was eluted with 100 µl of AE buffer to maximize DNA yield. Extracted DNA was tested with a nested PCR protocol targeting the 5S-23S rRNA intergenic spacer region (Postic et al. 1994; Lane et al. 2004). Samples were then identified as positive or negative for *B. burgdorferi* sensu lato based on gel electrophoresis of the 5S-23S rRNA amplicon, a highly specific target for *B. burgdorferi* sensu lato (Lane et al 2004). Positive samples were then further purified using SeraPure magnetic beads and sequenced on an ABI 3730. Sequences were trimmed and aligned using Geneious v 11.15 software and identified by aligning to reference sequences on NCBI BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Seven samples did not have enough DNA eluate or PCR product to submit for sequencing, but they are included as positives in our analysis based on having a strong PCR amplicon.

Tick species identification and abundance estimates

All ticks collected from rodents and by drag sampling were identified under a dissecting microscope to species and life stage using taxonomic keys (Furman and Loomis 1984; Kleinjan and Lane 2008). Questing tick abundances were calculated as the total number of ticks collected from a 495 m^2 sampling area. Tick burdens were assessed on each individual rodent and mean burdens per species were calculated for each tick species and life stage.

Rodent abundance estimates

Rodent abundances were estimated from the three consecutive days of mark-recapture trapping data in R (v. 0.99.902) using the '*Rcapture'* package (Baillargeon and Rivest 2007). Species abundances were estimated for all ten sites. The best abundance estimate model, for each site was selected based on Akaike information criterion (AIC).

Camera trap relative activity estimates

The relative activity of predators was calculated from photos via camera trap images. Consecutive photographs of the same species were considered independent if taken ≥30 min apart. In 2018, this was cross verified with photographs from the additional camera. If the same species was captured by both cameras within 30 min, then it was considered the same individual. We created a matrix of encounter rates (number of independent photographs per species/trap day) from the independent photographs for all sites. Using this matrix, we calculated numbers of independent photographs per species/trap days. To calculate species richness, relative activity, and Shannon diversity index, we analyzed photographs taken within a time period of 40 consecutive days from April through May in 2016 for a total of 360 trapping days in 2016 (1 camera × 9 sites × 40 days) and again in 2018, totaling 800 days (2 cameras × 10 sites × 40 days) of camera trap data (Lawrence et al. 2018).

Shannon diversity index analysis

Both rodent and predator Shannon diversity index were calculated in R using the '*vegan'* package, for each of the nine sites of 2016 and then additionally for the added tenth site in 2018. Rodent Shannon diversity was calculated from all rodent species captured by live traps. Predator Shannon diversity was calculated from wildlife camera data and based on relative activity. Shannon diversity metrics were used to evaluate the influence of species diversity on response variables (e.g. larval burden) to encapsulate both community richness and evenness and minimize parameters for model testing.

Statistical analyses

Mean *I. pacificus* larval burdens were calculated for all rodent host species on each site and each year (Supplemental Table 1). To test for significant differences between tick burdens between 2016 and 2018, we used Wilcoxon rank sums test. To test for significant differences between tick burdens across collection sites, we used a Kruskal–Wallis test followed by a Dunn's test (Dinno 2015). Power analysis for a multiple regression was used to test whether the rodent sample sizes of each species would be adequate in detecting significant differences in *I. pacificus* larval burdens. Mean *I. pacificus* burdens of *N. fuscipes*, *Peromyscus truei, Peromyscus californicus,* and *Peromyscus maniculatus* were compared using a Kruskal–Wallis test followed by a Dunn's test with a Bonferroni correction. Only *N. fuscipes* and *Peromyscus* spp. tick burdens were further analyzed for community and life history traits on tick burdens by generalized linear model analysis because they were the only reservoir hosts with significant abundances and tick burdens in our data (Swei et al. 2012; Lawrence et al. 2018). We focused on competent reservoir hosts in this study and did not examine another important host for larval *I. pacificus*, *S. occidentalis*, because they are refractory to *B. burgdorferi* (Kuo et al. 2000).

We assessed how tick burdens of individual rodents were correlated with individual factors such as sex, age, and mass for *N. fuscipes* and *Peromyscus* species separately using generalized linear mixed-effect models (GLMM) with site and year as random variables and a negative binomial error distribution. Using the same model selection type, we analyzed which ecological factors predict individual tick burdens of *N. fuscipes* and *Peromyscus* spp. separately with the following fixed factors: rodent Shannon diversity index, rodent richness, *N. fuscipes* abundance, *Peromyscus* spp. abundance, predator Shannon diversity, predator richness, predator relative activity, and questing *I. pacificus* larvae abundance. If we included a Shannon diversity index in a model, then we excluded the respective abundance and richness estimates to prevent multicollinearity in our models. We detected significant differences in rodent community metrics and predator community metrics between years, but not between tick burdens, so we included 'Year' and 'Site' as random effects for the GLMM analyzing community metrics influence on individual tick burdens. Before performing the models, autocorrelation was evaluated using the '*rcoor*' function in the 'Hmisc' package of R (Harrell 2020). Covariates were also scaled to prevent a disproportionate influence of any one particular parameter. A Variance Inflation Factors test was used to check for multicollinearity between parameters of

the final models using the '*VIF*' function in the 'car' package of R (Fox and Weisburg 2011). The final model was selected based on the lowest AIC score. These GLMM analyses were conducted utilizing the *'glmer.nb'* function in the package *'lme4*' (Bates et al. 2015).

To compare if rodents infected with *B. burgdorferi* sensu lato had significantly higher *I. pacificus* larval burdens than uninfected rodents, a nonparametric Wilcoxon rank sum test was calculated. Similarly, a Wilcoxon rank sum test was used to test if *N. fuscipes* was more likely to be infected with *B. burgdorferi* sensu lato. To examine whether *B. burgdorferi* sensu lato infection status of a rodent is correlated with *I. pacificus* larval burdens, a GLMM was used with the following parameters: site, year, and rodent species set as random effects, *Borrelia burgdorferi* sensu lato infection status (a two level variable, positive or negative) was the fixed effect, individual host *I. pacificus* larval burden was the response variable and a negative binomial error distribution was used.

Results

We conducted a total of 5751 trapping events across two years using two types of traps (Sherman and Tomahawk), resulting in the capture and analysis of 512 individual rodents. The rodent species we sampled included: *P. truei*, *N. fuscipes*, *P. californicus*, *P. maniculatus*, *Microtus californicus*, *Reithrodontomys megalotis,* and two captures of invasive species (*Rattus rattus* and *Rattus norvegicus*). Overall, wildlife cameras captured approximately 5694 photographs of animals. Of the photos, eight predator species were identified including: *Puma concolor* (mountain lion), *Canis latrans* (coyote)*, Lynx rufus* (bobcat)*, Urocyon cinereoargenteus* (gray fox), *Procyon lotor* (raccoon), *Mephitis mephitis* (striped skunk)*, Didelphis virginiana* (Virginia opossum), and *Felis catus* (domestic cat). We found that predator and rodent diversity metrics were significantly different between both years sampled ($p < 0.001$), while tick burdens of rodents and *B. burgdorferi* sensu lato infection prevalence of rodents were not statistically different between years (Supplementary Table 1).

We collected a total of 905 ticks attached to 5 different rodent species. Five different species of attached ticks were collected but the majority (84%) were larval *I. pacificus* ($n = 757$; Supplemental Table 2). Drag sampling yielded a total of 4598 questing ticks. The majority of questing ticks sampled were larval *I. pacificus* ($n = 3840$).

Larval burdens of *I. pacificus* were significantly higher on *N. fuscipes* than *P. truei* ($p < 0.0001$) and *P. californicus* ($p = 0.0011$) (*N. fuscipes* mean = 3.53, SE = 0.45; Fig. 1). There were no significant differences in mean *I. pacificus* larval burdens between any other species or within a species between 2016 and 2018. Rodents that were infected with *B. burgdorferi* had significantly higher *I. pacificus* larval burdens (mean = 3.19, SE = 0.72, $p < 0.001$), compared to uninfected hosts (mean = 1.25, SE = 0.16, Fig. 2). *Neotoma fuscipes* were significantly more likely to be infected with *B. burgdorferi* than any *Peromyscus* species, X^2 (1, $N = 473$) = 15.7, $p < 0.001$.

Testing for *Borrelia burgdorferi* sensu lato by PCR resulted in an overall infection prevalence of 10.6% ($N = 489$ tested) in rodents from both years. All positive samples were confirmed visually by gel electrophoresis and some were sequenced and identified by sequence alignment to the GenBank database (Clark et al. 2016). Species identified from the BLAST search included *B. burgdorferi* or *B. bissettiae*, both members of the *B. burgdorferi* sensu lato complex (Rudenko et al. 2011). Sequences of *B. burgdorferi* sensu lato were deposited in Bankit-NCBI (Supplemental Table 3).

Mass of *N. fuscipes* is positively correlated with their *I. pacificus* larval burdens, but not sex (Table 1). The opposite pattern was found for *Peromyscus* spp., sex, but not mass,

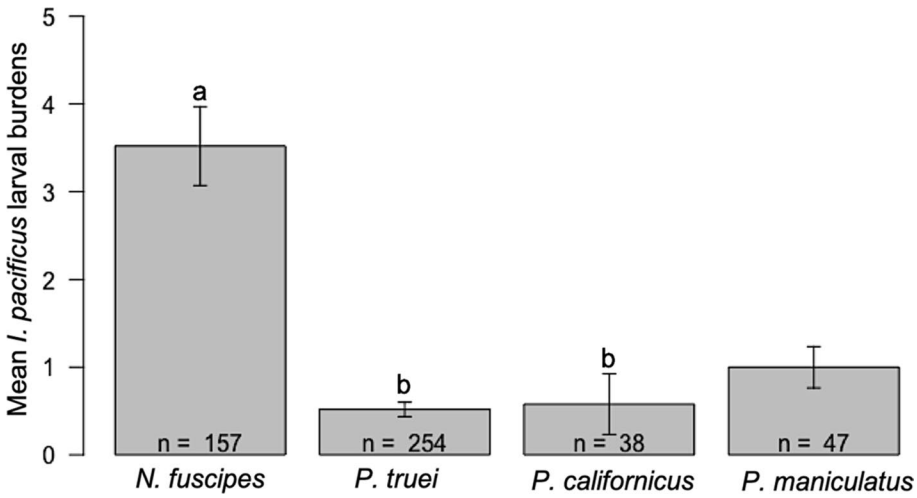

Fig. 1 Bar graph of *I. pacificus* larval burdens (mean ± SE) on the most frequently encountered rodent species (*Neotoma fuscipes*, *Peromyscus truei*, *Peromyscus californicus*, and *Peromyscus maniculatus*). Mean burdens and the standard error of the mean were calculated for each species across all sites and both years. Error bars represent the standard error of the mean and host sample size is presented inside the corresponding bar. Statistical significance ($p < 0.001$) is indicated by different letters above the bars

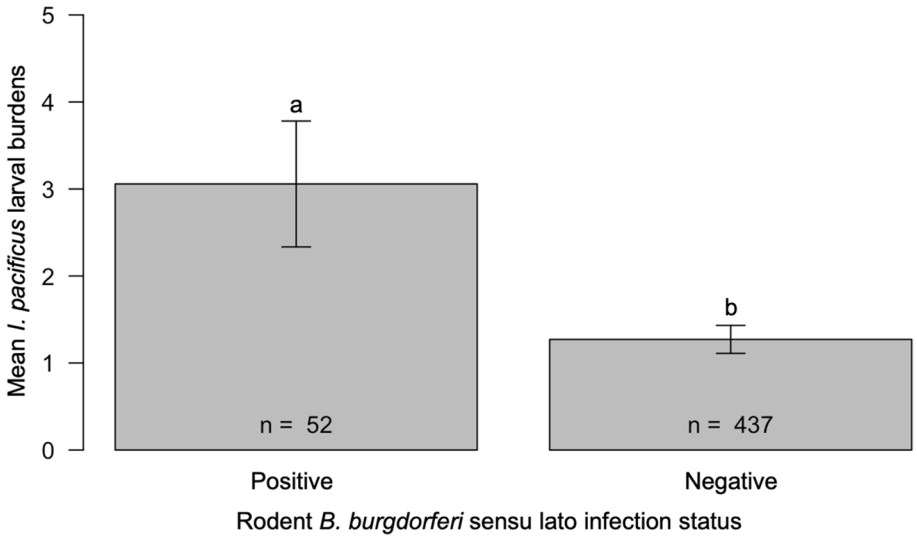

Fig. 2 Bar graph of *I. pacificus* larval burdens (mean ± SE) on all sampled rodents (*Neotoma fuscipes*, *Peromyscus truei*, *Peromyscus californicus*, *Peromyscus maniculatus*, *Microtus californicus*, *Rattus norvegicus*, *Rattus rattus*, *Reithrodontomys megalotis*) that were either uninfected or infected with *B. burgdorferi* sensu lato. Statistical significance ($p < 0.001$) is indicated by letters above the bars. Sample size for each group is presented inside bars and error bars represent the standard error of the mean

Table 1 Generalized linear mixed-effect model results of individual life history traits as predictors of *N. fuscipes* and *Peromyscus* spp. larval tick burdens with site and year set as random variables

Variable	Estimate	Standard error	*z* value	*p* value
N. fuscipes				
Intercept	− 3.44	1.31	− 2.63	0.009**
Mass	1.44	0.49	2.96	0.003**
Peromyscus spp.				
Intercept	− 1.24	0.50	− 2.50	0.014*
Sex (Males)	0.64	0.22	2.87	0.004**
Age (Juveniles)	0.71	0.50	− 1.512	0.13

Model error distribution was negative binomial with a log link function. The best-fit model was selected based on lowest AIC scores

Significance codes as indicated are "*" <0.05, "**" <0.01

Table 2 Generalized linear mixed-effect model results of the community drivers of larval *I. pacificus* burdens on *Neotoma fuscipes* site and year were included as a random effect

Variable	Estimate	Standard error	*z* value	*p* value
N. fuscipes				
Intercept	0.17	0.41	0.42	0.68
Predator richness	− 0.62	0.16	− 3.92	8.95e−5***
Questing *I. pacificus* larvae abundance	0.96	0.22	4.34	1.43e−5***

Data distribution used a negative binomial model with a log link function. The best-fit model was selected based on lowest AIC scores

Significance codes as indicated are "***" <0.001

Table 3 Generalized linear mixed-effect model results testing the relationship between larval tick burden and the probability of *B. burgdorferi* infection in reservoir hosts

Variable	Estimate	Standard error	*z* value	*p* value
Intercept	− 1.10	0.60	− 1.85	0.07
B. burgdorferi sensu lato infection status	0.60	0.25	2.40	0.02 *

Borrelia burgdorferi sensu lato host infection status was set as a fixed effect and random effects included host species, year, and site. Model error distribution was negative binomial with a log link function. *Ixodes pacificus* larval burdens was the response variable because larval ticks are uninfected, and, therefore, not responsible for causing *B. burgdorferi* infection

Significance codes as indicated are "*" <0.05, "**" <0.01

was correlated with *I. pacificus* larval burdens, where males tend to have higher burdens (Table 1). Model analyses of community factors driving larval *I. pacificus* burdens on *N. fuscipes* showed that questing *I. pacificus* larvae abundance was positively correlated, while predator richness was negatively correlated with tick burdens (Table 2). Larval burdens of *Peromyscus* species were not significantly correlated with any host community composition factors. Lastly, GLMM analysis found that higher *I. pacificus* larval burdens on rodents were a positive predictor of rodent infection with *B. burgdorferi* sensu lato ($p < 0.01$, Table 3).

Discussion

Our study involving two years of empirical data on ticks and their host community demonstrates that *I. pacificus* larval burdens vary depending on host species, host infection status, tick abundance, and predator community structure. We found that larval burdens were consistently higher on *N. fuscipes*, a key reservoir host in the California Lyme disease system, relative to other small mammal hosts that we sampled (Lane and Brown 1991; Brown and Lane 1994; Eisen et al. 2004; Brown et al. 2006; Swei et al. 2012). Our

statistical analyses found that *N. fuscipes* larval burden is negatively correlated with predator diversity and positively correlated with the abundance of questing larval ticks. In contrast, *Peromyscus* spp. exhibited significantly lower larval burdens than *N. fuscipes*, and were not clearly driven by any host community characteristics that we examined.

The distribution of larvae on reservoir hosts in a community is critical for predicting the risk of disease. The larval blood meal is the first opportunity for pathogen acquisition by the tick because *B. burgdorferi* is not transovarially transmitted, so all larvae are uninfected. However, *B. burgdorferi* is maintained in ticks transstadially. Additionally, we know that the larval blood meal hosts range in reservoir competency for *B. burgdorferi*. Therefore, monitoring the larval blood meal is extremely significant to estimate disease prevalence in the nymphal stage, which is the most medically important for Lyme disease transmission to humans (LoGiudice et al. 2003; Ostfeld et al. 2006; Calabrese et al. 2011; Swei et al. 2012). These results indicate the importance of community interactions in the transmission and maintenance of Lyme disease. In particular, most ectoparasite studies find that host abundance influences the burdens on hosts (Brunner and Ostfeld 2008; Young et al. 2015; Mowry et al. 2019) but we did not find a significant relationship between rodent abundances and tick burdens.

Our finding that predator diversity and questing larval abundance significantly influence larval burdens on the Lyme disease reservoir host suggests that *N. fuscipes* has reduced encounter rates with ticks as predicted by the 'ecology of fear' idea (Brown et al. 1999). Early formulation of this theory found evidence that predator activity can induce prey to minimize foraging time or initiate a physiological stress response (Brown et al. 1999; Orrock et al. 2004; Dickman and Doncaster 2009; Embar et al. 2014). Here, we describe evidence that predator diversity can also modify rodent behavior resulting in reduced rodent movement or contact with vectors, which reduces pathogen transmission (Tables 2 and 3). These types of behavioral modifications have been documented in other ectoparasite systems (Hofmeester et al. 2017; Moll et al. 2020), which lead to lower encounter rates between ectoparasites and hosts, and a reduction in ectoparasite burdens. Notably, a study conducted in the Netherlands found that higher predator activity reduced the burdens of *Ixodes ricinus* on Lyme disease reservoir hosts (Hofmeester et al. 2017), resulting in lower tick abundances and a lower density of *B. burgdorferi*-infected nymphs within the plot. Although we used different methods to monitor predator activity, we also found that a similar top-down pressure, measured as relative predator diversity, occurred in rodent communities where *I. pacificus* occurs (Table 2). In contrast, tick burdens on *Peromyscus* spp. were not impacted by predator diversity, which may indicate that *Peromyscus* species do not modify their behavior in response to greater predator diversity, while *N. fuscipes* modifies its behavior in response to predator species in unique ways that are specific to individual predator species (Banks 1998; Banks et al. 2003; Suraci et al. 2019b). In addition, the local abundance of questing *I. pacificus* larvae was not a predictor of *Peromyscus* burdens. These results are consistent with prior work showing that when larval densities increased, tick burdens increased on *N. fuscipes* but not on a sympatric *P. maniculatus* population (Swei et al. 2011). In the western United States, tick burdens on *Peromyscus* species do not reach the levels that are reported in the northeastern United States and indeed, seem to be limited, but the mechanism of this limitation is not clear but could be due to tick host preference (Slowik and Lane 2009; Salkeld and Lane 2010; Swei et al. 2011; Mihalca et al. 2012), reduced *Peromyscus* encounter rates with ticks, or *Peromyscus* grooming behavior that may limit tick burdens (Wolff and Cicirello 1991; Wolff 1996; Eisenberg 1962; Bardi et al. 2011; Swei et al. 2012). Confirmation of these results suggest that the role of predators in regulating vector-borne disease is species specific but likely important and warrants further investigation.

Our analyses generally support the results of prior studies that sought to characterize the distribution of ectoparasites on hosts based on host physiological metrics (Brunner and Ostfeld 2008). We found strong evidence that *I. pacificus* larvae are highly aggregated on a limited number of individual hosts while the majority of the rodent population have little to no attached ticks (Fig. 3). These findings are consistent with several parasite aggregation studies (Davidar et al. 1989; Mannelli et al. 1993; Brunner and Ostfeld 2008) and are consistent with the '80/20 rule' of parasite distribution (Poulin 2007). We found that mean tick burdens were significantly higher on *N. fuscipes* compared to other rodent species sampled in our study including all three *Peromyscus* species, highlighting the importance of *N. fuscipes* as a highly competent blood meal host and pathogen reservoir of *B. burgdorferi* (Brown and Lane 1996; Slowik and Lane 2009; Swei et al. 2012). Accordingly, the potential role of *N. fuscipes* in the enzootic maintenance of *B. burgdorferi* remains important, and factors that raise their tick burdens (e.g., reduced predator diversity) could have important repercussions for disease transmission. In particular, because *I. pacificus* larvae emerge earlier in the season than nymphal ticks (Padgett and Lane 2001; MacDonald 2018), long-lived hosts that can maintain an interannual infection of *B. burgdorferi*, such as *N. fuscipes*, are especially important for the enzootic maintenance of *B. burgdorferi.*

The mechanisms for the species-specific differences in tick burdens that we report are unclear. It is possible that larvae either prefer *N. fuscipes*, or perhaps *N. fuscipes* encounter questing larvae more often relative to *Peromyscus* species. When we modeled the impact of mass, age, and sex on the tick burdens of rodent hosts, we found that

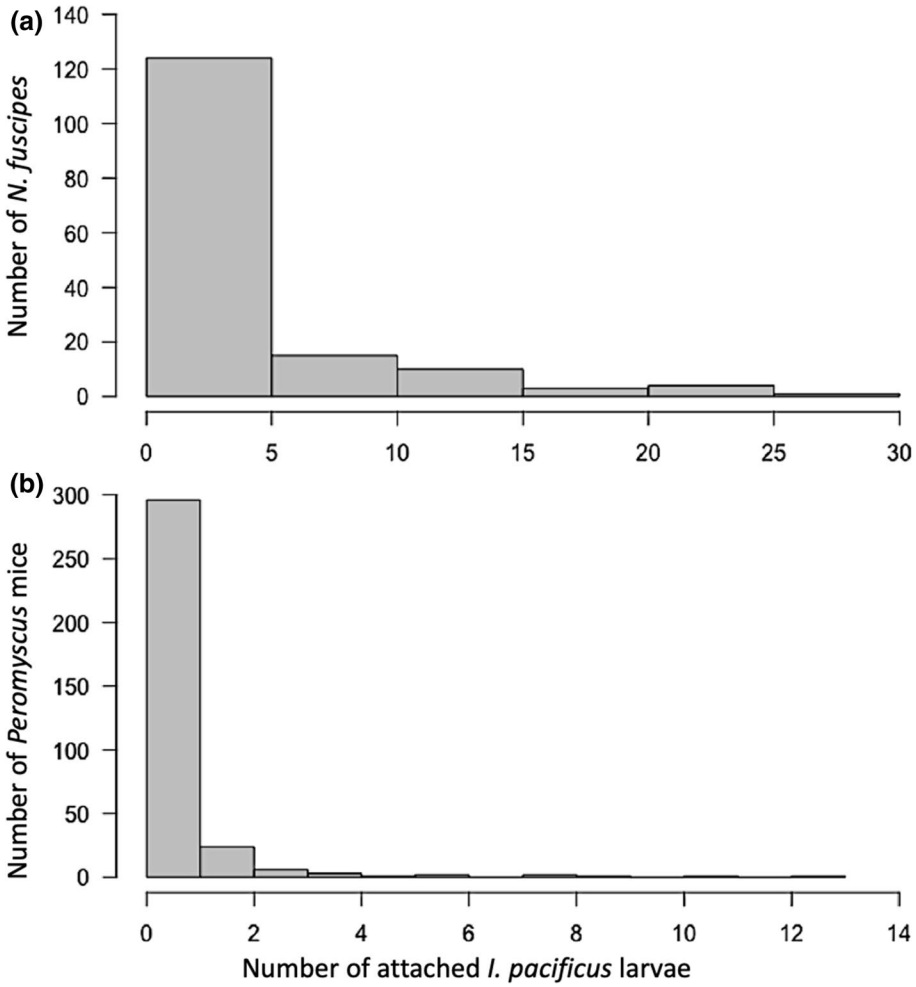

Fig. 3 Histogram of the number of *I. pacificus* larvae attached to (**a**) *Neotoma fuscipes* and (**b**) *Peromyscus* species across all sites and both years

mass but not sex or age was a significant predictor of tick burden on *N. fuscipes* (Table 2). Unlike other tick burden studies of other reservoir species, our results show that male *N. fuscipes* did not have higher burdens compared to females (Brunner and Ostfeld 2008; Harrison et al. 2010; Devevey and Brisson 2012; Mysterud et al. 2015). Life history traits may also contribute to species-specific differences in larval burdens. For instance, *Peromyscus* spp. are social rodents that live communally in nests and groom each other which may be one mechanism by which their tick burdens are kept low (Eisenberg 1962; Wolff and Cicirello 1991; Wolff 1996; Bardi et al. 2011). In contrast, *N. fuscipes* are more territorial, have larger territories, and live at lower densities (Egoscue 1962; Kinsey 1976; Cranford 1977; Wallen 1982). The positive relationship between questing *I. pacificus* and *N. fuscipes* tick burdens may also be driven by *N. fuscipes* construction and use of nests made of sticks and other vegetation, which may create more suitable tick microhabitat (Whitford and Steinberger 2010) and increase parasite–host contact rates.

We found that rodents that are infected with *B. burgdorferi* sensu lato, had higher larval burdens of *I. pacificus* (Table 3). While these results might initially seem intuitive, it is important to note that the ticks we assessed were larvae so were not the cause of infection. Therefore, it is not the case that higher tick burdens are directly driving higher pathogen transmission in the host. Instead, these results may indicate that infected hosts are either encountering more larvae through behavioral changes, are more attractive to host-seeking larvae, or perhaps, are less able or willing to remove their ectoparasite burden if infected (Ostfeld et al. 2018). A similar pattern was reported by Ostfeld et al. (2018) who also reported that *B. burgdorferi*-infected *Peromyscus leucopus* had higher larval burdens and attributed this finding to reduced grooming activity. Experiments to test the specific mechanism underlying this pattern will be important for understanding how *B. burgdorferi* infection may be altering host behavior in a way that promotes pathogen transmission into naïve tick vectors.

In this study, we demonstrate that host species identity, questing tick abundance, and predator–prey interactions can shape vector distributions on pathogen reservoir hosts. The relationship between ticks and their hosts is complex, but we show that community-level factors that alter host structure

can significantly impact vector aggregation on blood meal hosts and consequently, pathogen transmission dynamics. This study demonstrates that efforts to better understand the complex function of predator diversity in maintaining and mitigating pathogen transmission are an important component of tackling the emerging threat of vector-borne diseases.

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Author contribution statement AL, SS, AC and JS collaboratively conducted field work and processed the samples, JS and AS analyzed data and wrote the manuscript; all authors provided edits of the manuscript.

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Compliance with ethical standards

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

Ethical approval All procedures performed in this study involving animals were in accordance with the ethical standards of the California Department of Fish and Wildlife and the San Francisco State Animal Care and Use Committee (IACUC AU15-06).

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