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ARTICLE

Disease Ecology

Climate-associated variation in the within-season dynamics of juvenile ticks in California

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Abstract

Changing climate has driven shifts in species phenology, influencing a range of ecological interactions from plant–pollinator to consumer–resource. Phenological changes in host–parasite systems have implications for pathogen transmission dynamics. The seasonal timing, or phenology, of peak larval and nymphal tick abundance is an important driver of tick-borne pathogen prevalence through its effect on cohort-to-cohort transmission. Tick phenology is tightly linked to climatic factors such as temperature and humidity. Thus, variation in climate within and across regions could lead to differences in phenological patterns. These differences may explain regional variation in tick-borne pathogen prevalence of the Lyme disease-causing *Borrelia* bacteria in vector populations in the United States. For example, one factor thought to contribute to high Lyme disease prevalence in ticks in the eastern United States is the asynchronous phenology of ticks there, where potentially infected nymphal ticks emerge earlier in the season than uninfected larval ticks. This allows the infected nymphal ticks to transmit the pathogen to hosts that are subsequently fed upon by the next generation of larval ticks. In contrast, in the western United States where Lyme disease prevalence is generally much lower, tick phenology is thought to be more synchronous with uninfected larvae emerging slightly before, or at the same time as, potentially infected nymphs, reducing horizontal transmission potential. Sampling larval and nymphal ticks, and their host-feeding phenology, both across large spatial gradients and through time, is challenging, which hampers attempts to conduct detailed studies of phenology to link it with pathogen prevalence. In this study, we demonstrate through intensive within-season sampling that the relative abundance and seasonality of larval and nymphal ticks are highly variable along a latitudinal gradient and likely reflect the variable climate in the far western United States with potential consequences for pathogen transmission. We find that feeding patterns were variable and synchronous feeding of juvenile ticks on key blood meal hosts was associated with mean temperature. By characterizing

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within-season phenological patterns of the Lyme disease vector throughout a climatically heterogeneous region, we can begin to identify areas with high potential for tick-borne disease risk and underlying mechanisms at a finer scale.

KEYWORDS
host-seeking, *Ixodes pacificus*, *Ixodes* spp. ticks, latitudinal gradient, phenology, western fence lizards

INTRODUCTION

Phenological shifts in response to climate have implications for individual performance, population demographics, and interspecific interactions (Renner & Zohner, 2018; Stemkovski et al., 2023; Zettlemoyer & DeMarche, 2022). Understanding how environmental conditions impact the behavior and activity of pathogen vectors—such as ticks and mosquitos—is critical for predicting and responding to the seasonal risk and geographic spread of vector-borne pathogens (Lippi et al., 2021). Predicting vector-borne disease risk has been a challenge for both field and modeling studies due in part to the complexities of measuring variable behavioral responses of vectors and monitoring the dynamics of the multispecies system including the vertebrate populations that support vectors and their pathogens (Estrada-Peña et al., 2021; Ogden & Lindsay, 2016). A lack of standardization in disease (or pathogen) surveillance may obscure patterns within vector-borne disease systems, making detection and quantification of change in disease risk difficult (Randolph, 2010; Semenza et al., 2022). This challenge of monitoring and quantifying vector-borne disease risk in a changing climate is exacerbated by the amount of resources needed to link small-scale field studies with broader scale ecological and epidemiological patterns in order to identify, predict, and manage vector-borne disease risk (MacDonald et al., 2022).

Lyme disease ecology is particularly complex with many potential linkages between climate and transmission dynamics that could influence human disease outcomes under projected climate change. The tick vectors of Lyme disease in the United States, *Ixodes scapularis* and *Ixodes pacificus*, have three post-egg life stages (larva, nymph, adult) that each take a blood meal from a vertebrate host prior to molting into the subsequent life stage (or, in the case of adult female ticks, prior to producing eggs) over their 2- to 3-year life cycles. The seasonality of when larvae and nymphs (juvenile ticks) are actively seeking a host (i.e., "questing") for a blood meal will be referred to as phenology hereafter (Figure 1). Tick phenology patterns are tightly linked with climatic factors such as temperature and humidity (Bacon et al., 2022; Eisen et al., 2017; Ginsberg et al., 2020; MacDonald & Briggs, 2016; MacDonald et al., 2018, 2019, 2020; Ogden et al., 2004, 2018). Variations in temperature can influence tick phenology through effects on developmental rates, seasonal emergence, duration of activity, and survival (Ogden et al., 2004; Padgett & Lane, 2001). Each tick life stage responds differently to environmental cues that determine when they emerge to start questing for a blood meal (Eisen et al., 2004, 2017; Padgett & Lane, 2001). These climatic conditions vary spatially within and across regions, as well as throughout a season, which likely contributes to the variety of tick phenology patterns reported across the United States (Diuk-Wasser et al., 2006; Eisen et al., 2003; Gatewood et al., 2009; Hamer et al., 2012; Kurtenbach et al., 2006; MacDonald, 2018; Ogden et al., 2018).

The sequential order and timing of peak larval and nymphal abundance for cohort-to-cohort transmission is an important factor for pathogen maintenance and disease risk in the Lyme disease system (Gatewood et al., 2009; Hamer et al., 2012; Kurtenbach et al., 2006; Ogden et al., 2007; Voordouw, 2015) (Figure 1). The sequence of nymphs emerging earlier in a season than larvae is thought to facilitate transmission when infected nymphs infect vertebrate hosts that larval ticks subsequently feed on, which then become infected nymphs the following season (Kurtenbach et al., 2006). In the other extreme, if larvae fully emerge before nymphs, then transmission would only occur through interannual maintenance of infection by reservoir hosts. However, in the western United States, where larval and nymphal phenology are more synchronous on a broad spatial scale, local transmission dynamics can be impacted by slight phenological shifts in larval and nymphal peak abundances (Lane et al., 2013; MacDonald & Briggs, 2016). In a system with a short period between nymphal and larval peak abundance, there is less time for the hosts to be infected by nymphs before larvae feed, which reduces the probability of uninfected larvae acquiring an infection from their host. Synchronous feeding—herein characterized by a scenario where two different life stages

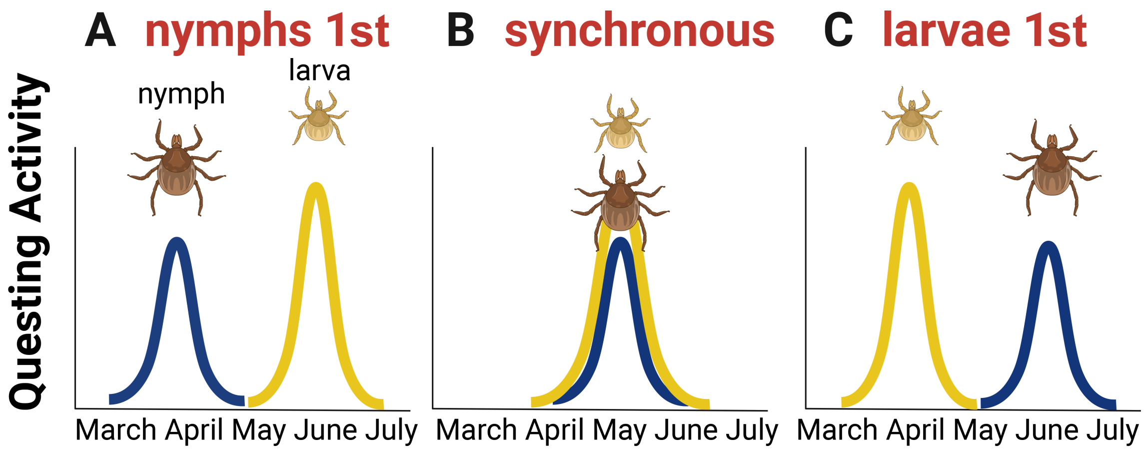

FIGURE 1 Phenological patterns of juvenile tick conceptual diagram. Questing activity is represented by the density curves of ticks (blue, nymphs; gold, larvae). The sequential order of life stage emergence within a given season is hypothesized to drive enzootic transmission dynamics of tick-borne pathogens. The panels represent three scenarios which may amplify the transmission of different pathogens such as (A) horizontal transmission of *Borrelia burgdorferi*, (B) synchronous feeding of *Anaplasma phagocytophilum*, and (C) vertical transmission of *Borrelia miyamotoi*. Created in BioRender; Sambado (2024).

(i.e., larvae and nymphs) are feeding on one individual host—can allow for larvae to become infected from nymphs and increase transmission during a short period. Although transmission may be highest in a system where nymphs emerge first (Kurtenbach et al., 2006) and lowest in a system where larvae emerge slightly before nymphs (Salkeld et al., 2014), if synchronous feeding of both life stages on individual hosts occurs, then some larvae may acquire a pathogen and increase transmission potential (Ogden et al., 2007). In a system where larvae and nymphs are either active at the same time (synchronous) or where larvae emerge before nymphs (asynchronous), synchronous feeding is predicted to yield higher pathogen transmission potential.

Despite the importance of measuring cohort-to-cohort transmission of juvenile ticks—the sequential order of emergence and the time between when each life stage emerges, there are two main challenges that have hindered field-based assessments of tick phenology. The first challenge is implementing a field sampling program that balances the trade-offs of spatial scale and temporal frequency of tick collection; the second is using a sampling method that accurately detects all life stages of ticks (Padgett et al., 2014; Salkeld et al., 2014). Some field design trade-offs include studies that span large spatial scales (capturing climate variability) but often lack rigorous within-season sampling which may not capture the phenology of juvenile life stages or its implications for cohort-to-cohort transmission (Ginsberg et al., 2017; Lane et al., 2013; Padgett et al., 2014). On the other hand, studies that focus on small spatial scales can achieve frequent within-season sampling (producing a detailed quantification of phenology) at a particular site (Eisen et al., 2017; Hacker et al., 2021; Hamer et al., 2012; Levi et al., 2015; Salkeld et al., 2014), but lack the ability to connect broader patterns of climate and tick phenology. Both spatial and temporal sampling of sites with varying climatic conditions will be required to accurately measure how climate impacts tick phenology to then link it with cohort-to-cohort transmission of tick-borne pathogens. The second challenge is that available tick sampling methods vary in their ability to capture different life stages, particularly juvenile ticks, making the comparison of juvenile ticks across large spatial scales complicated. Seasonal activity patterns of larvae and nymphs are a critical component of assessing disease risk, yet are notoriously difficult to collect in their southern range in the Northern Hemisphere because it is more arid, altering tick questing behavior compared to the northern edge of their range (Ginsberg et al., 2017; Hacker et al., 2021; Lane et al., 2013; MacDonald & Briggs, 2016; Padgett et al., 2014). These differences in tick questing behavior introduce potential biases in large-scale and repeated sampling efforts. As a result of these two challenges, studies that attempt to summarize this imperfect data may fall short of the idealized outcome of quantifying the role of tick phenology—and its relationship with climate—in determining pathogen prevalence.

The majority of studies that attempt to link *Ixodes* spp. phenology with pathogen prevalence are focused in the northeastern and midwestern United States (Diuk-Wasser et al., 2006; Gatewood et al., 2009; Ginsberg et al., 2017; Hamer et al., 2012; Kurtenbach et al., 2006; Levi et al., 2015; Ogden et al., 2018). Although these are epidemiologically important regions, the system in the far western United States provides an important contrast and is relevant for understanding how tick-borne pathogens are distributed and maintained. Unlike the other endemic regions, the far western United States is classically thought of as being a synchronous region with larvae emerging slightly before, or at the same time as, nymphs (Eisen et al., 2017; MacDonald, 2018; Salkeld et al., 2014). However, extreme heterogeneity in microclimates and habitat types, as well as latitudinal variation in climate throughout the geographical range of *I. pacificus* which ranges from southern California to southern British Columbia, may lead to a large variation in phenological patterns within this region. This study attempts to characterize the variation in juvenile tick phenology as a potential mechanism behind the highly heterogeneous tick-borne disease risk observed throughout the far western United States.

Here, we address the dual challenges of quantifying juvenile host-seeking phenology to characterize tick phenology more accurately across the climatically heterogeneous landscapes of California. To do so, we collected tick life stage and seasonality data from 33 plots across 11 sites that were sampled five times within one juvenile tick season spanning a 650-km latitudinal gradient. We incorporated remotely sensed climate data to explore variations in tick–host interactions across a latitudinal (i.e., temperature) and coastal to inland (i.e., humidity) gradient to explore potential mechanisms and predictors of variation in tick phenological patterns. Specifically, this study seeks to answer the following questions:

1. What are the regional within-season patterns of tick abundances? Are monthly abundance patterns similar for questing (i.e., drag cloth) and attached tick (i.e., lizard burden) collection methods?
2. How do patterns of within-season tick abundance respond to temperature (latitudinal) and/or humidity (coastal to inland) gradients?
3. Do larvae and nymphs feed synchronously on individual hosts? If so, how frequently, and are there climatic variables associated with synchronous feeding patterns?

If the assumption is that the far western US juvenile tick activity is synchronous, then we would expect there to be no variation in the within-season patterns of monthly tick abundance across the 11 sites despite each site representing a unique combination of temperature and humidity characteristics. However, we hypothesize that juvenile ticks are sensitive to local cues of climate, which will result in variation in within-season tick dynamics and a potential mechanism explaining variable tick-borne disease risk throughout the far western United States.

METHODS

Site selection and field sampling

California has a Mediterranean climate with wet, cool winters that transition to hot, dry summers during high juvenile tick activity in April through June (MacDonald & Briggs, 2016) (Appendix S1: Figures S1 and S2). Our study was designed with this in mind to test the associations of climate and *I. pacificus* abundance and seasonality. Eleven reserves in the University of California Natural Reserve System (UCNRS) were chosen based on the unique temperature and humidity gradient they represent (Figure 2) and had documented nearby populations of *I. pacificus* (MacDonald, 2018; MacDonald & Briggs, 2016; Padgett et al., 2014; Salkeld et al., 2014). Coastal and inland sites were designated based on the average humidity and temperature during the peak host-seeking months of April through June, with coastal sites on average having higher humidity (~5–25 kPa difference) and lower mean temperatures (~5–10°C difference) than inland sites. Gradient classification of each reserve can be found in Appendix S1. The reserves were consecutively sampled once per month between January through June of 2021 to overlap with peak *I. pacificus* activity in California (11 reserves in 12 days each month; exceptions can be found in Appendix S1: Table S1). At each reserve, three plots in oak woodlands or chaparral were repeatedly sampled. From March through June, each plot was sampled roughly every 3 weeks to capture peak activity at all locations (sample dates and plot locations in Appendix S1: Tables S1 and S2). Standard tick dragging was conducted for approximately 500 m^2 at each plot using a 1-m^2 white flannel cloth. The drag cloth was checked every 8–10 m. All collected ticks were put in a vial with 70% ethanol with tweezers and stored at room temperature until species identification in the laboratory (Furman & Loomis, 1984). Ticks collected by this method are labeled as "drag cloth ticks."

To assess the seasonality of juvenile ticks more accurately on their preferential host (Casher et al., 2002; Slowik & Lane, 2009), host-feeding ticks on western fence lizards (*Sceloporus occidentalis*) were surveyed. Lizard burdens were assessed at each reserve during the months of March through June. Lizard surveying began after 11:00 AM at each plot. Lizards were caught using a 0.5-m fishing pole with a dental floss lasso at the tip (Swei et al., 2011). Twenty minutes were dedicated to looking for lizards at each plot. Ticks collected by this method are labeled as "lizard attached ticks." Additional details regarding lizard sampling can be found in the Supplement.

All tick drags and lizard handling was conducted by the same individual throughout the field season to

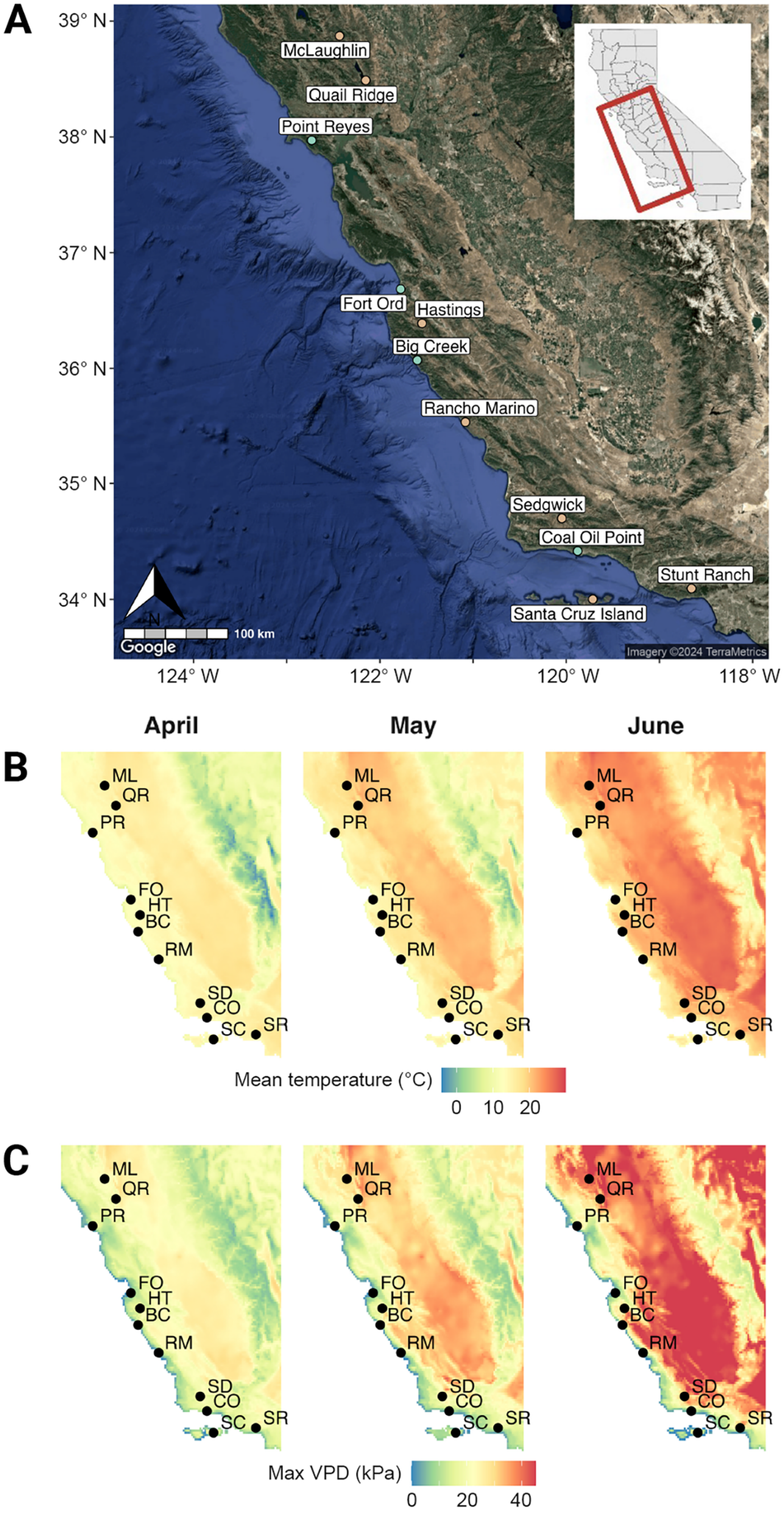

FIGURE 2 Legend on next page.

standardize collection methods under the permit approvals of Department of Fish and Wildlife Scientific Collection Permit (S-193220002-19357-001) and Institutional Animal Care and Use Committee (UCSB number 952).

Remotely sensed climate data

Climate data for each reserve were accessed from the Parameter-elevation Regression on Independent Slopes Model (PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu), which provides estimates of primary climate elements such as mean temperature (tmean, in degrees Celsius), precipitation (ppt, in millimeters), and maximum vapor pressure deficit (VPDmax, in kilopascals) (Daly et al., 2015). Unlike relative humidity, VPD is independent of temperature. Maximum VPD and mean temperature have previously been shown to be significant predictors of tick counts and questing activity (Bacon et al., 2022; Diuk-Wasser et al., 2010; Hahn et al., 2016). In the context of coastal California, where temperatures on average are cooler than inland California, a high maximum VPD can represent a location with relatively high humidity. Data at a 4-km spatial and daily temporal resolution were taken from December 2020 through July of 2021 (Appendix S1: Figure S3) and were selected to match the sampling dates and account for biologically relevant time lags (e.g., December precipitation data for January tick sampling) and was accessed on February 2, 2022. Due to some plots that were less than 4 km apart, climate data were taken for each reserve and not for each plot ($n = 33$) resulting in single climate estimates at a 4-km resolution (Appendix S1: Table S2).

Statistical analyses

A total of 141 sampling events took place between January and mid-June in 2021; the aim was to sample 3 plots in each of 11 reserves, each month for 5 months (Appendix S1: Table S1 for exceptions). Plot-level data were aggregated to reserve due to low sample sizes of drag cloth ticks on some plots. Data were cleaned and analyzed in RStudio version 4.1.0 (Rstudio: Integrated Development Environment for R. Rstudio, PBC, Boston, MA URL http://www.rstudio.com/), and software package information can be found in Appendix S1. All data necessary to create the figures and run the analyses are available from Dryad (https://doi.org/10.5061/dryad.0p2ngf29d).

To characterize regional within-season patterns of tick abundances, we tested for differences in tick abundance either using counts of ticks per 100 m^2 for drags, or the sum of ticks on individual lizards across the latitudinal temperature gradient, and coastal to inland humidity gradient that our sampling design captures (Ginsberg et al., 2021; MacDonald, 2018; Ogden et al., 2018) (Figure 2). Due to unequal variances, two nonparametric tests were used to compare the mean rank of tick abundances. A Kruskal–Wallis test was used for comparison of regions (northern, central, southern), and a Wilcoxon signed-rank test was used for comparison of locations (coastal, inland). A Dunn's test with a Bonferroni correction was used as a post hoc test following the Kruskal–Wallis test. The effect sizes for latitudinal temperature and climatic humidity gradient for the entire study and by month were also calculated. The mean and SD of *I. pacificus* counts were calculated for each sampling month (January, March, April, May, June) by latitudinal region (northern, central, southern) and climatic location (coastal, inland) (Appendix S1: Table S3).

To assess the relationship between tick abundances and the climate gradient within our study design, we analyzed the influence of important climate variables for each *I. pacificus* life stage. Because we are interested in comparing within-season dynamics of ticks along a climatic gradient, and not within a reserve itself which represents a unique combination of climatic features compared to other reserves, we aggregated tick abundance to reserve. Tick abundances—aggregated as counts per month by reserve for each sampling method—were the outcome of interest with explanatory climate variables including daily temperature (maximum, minimum, mean; in degrees Celsius), daily vapor pressure deficit (maximum, minimum; in kilopascals), and total precipitation (in millimeters). Daily climate variables were selected for the day tick dragging occurred. Precipitation was summed for the current month and prior month because tick sampling did not occur on days it rained and to account for a lagged response between rain and tick activity. We assessed the relationship between *I. pacificus* tick counts and climate variables by running a series of separate regression models for each life stage (larva, nymph, adult) to capture potentially unique climate

FIGURE 2 Map of study region illustrating the latitudinal and climatic gradients captured by sampling. (A) Study locations are situated throughout the University of California Natural Reserve System with designation of humidity gradient (teal, coastal; brown, inland). We highlight the shift of two important climate variables: (B) mean temperature and (C) maximum vapor pressure deficit (VPD) across the peak tick season (April–June). Site abbrevations in (B) and (C) are related to sites in (A).

relationships and for each sampling method (drag cloth or lizard burden) since each method had biases in sampling success for all three life stages. Multiple exponential distributions for the generalized linear model (i.e., negative binomial, quasi-poisson, poisson) were fitted to deal with nonnormal data and an overdispersion of tick abundances. To select for the best fit models, a stepwise regression for both forward and backward selection was performed. Explanatory variables were checked for collinearity. Model construction included an exploration of models with the random effect of plot ID to control for potential microclimatic differences at each plot as well as the random effects of reserve and month.

To evaluate whether larvae and nymphs feed synchronously on individual hosts and whether the probability of synchrony is influenced by climate, we analyzed lizard burden outcomes against climate variables. We describe the patterns of larvae and nymphs on an individual host as synchronous feeding instead of cofeeding, the event where an infected and uninfected tick feed spatially close to each other on an individual host (Randolph et al., 1996; Randolph & Rogers, 2000; Voordouw, 2015), because we are looking at the transmission potential, not transmission itself. We explicitly want to understand how certain climate variables are associated with synchronous feeding because it is a unique phenology pattern in the far western United States and could be a mode of cohort-to-cohort transmission of *Borrelia* spp., as well as a potential mechanism for varying pathogen prevalences in California. While lizards are not competent hosts (i.e., do not have the ability to acquire, maintain, and transmit *Borrelia* spp. via tick bite), they can serve as a general proxy for what the juvenile burden proportions are like on competent hosts (such as rodents and birds, which are more difficult to intensively sample) at the same location. Lizards are also the preferred host for both juvenile life stages of *I. pacificus*, so should produce a better estimate of juvenile seasonality than other hosts (Casher et al., 2002).

To understand where transmission potential may be elevated, we focus on synchronous feeding as a metric of potential pathogen risk. We define synchronous feeding as an event where an individual lizard has at least one larva and one nymph attached, which is denoted as a success in the binomial model. If an individual lizard has only larvae or only nymphs attached, then it is denoted as a failure in the binomial model. With our binary outcomes ($1 =$ synchronous feeding, $0 =$ no synchronous feeding), we fit a logit model with the input of climate variables including daily temperature (maximum, minimum, mean; in degrees Celsius) and daily vapor pressure deficit (maximum, minimum; in kilopascals). We included the additional term of reserve to capture variation in the frequency of synchronous events across multiple locations and used a Wald test to test for the overall effect of reserve in the synchrony model. The process of building, fitting, and diagnosing the binomial model was the same to the tick abundance mixed-effect regression model.

RESULTS

Data summary

A total of 2399 *I. pacificus* ticks were collected via drag cloth method ($n = 895$) and lizard burden ($n = 1503$). For the drag cloth method, all life stages were collected, whereas on lizards, only larval ($n = 713$) and nymphal ($n = 791$) *I. pacificus* were collected (Figure 3). A total of 297 individual lizards were assessed for tick burdens.

Tick abundance patterns vary by region

The Kruskal–Wallis and Wilcoxon signed-rank tests showed a significant difference in the mean rank of tick abundances by latitudinal region ($\chi^2 = 7748.7$, $\text{df} = 17$, $p < 0.001$) and climatic location ($W = 45{,}989$, $p \leq 0.001$) for juvenile *I. pacificus* attached to lizards. For latitudinal region, the post hoc Dunn test showed all three regional comparisons were significantly different with central and southern as the most significantly different groupings (z test statistic $= -5.6$, $p < 0.001$) followed by northern and southern (z test statistic $= -4.9$, $p < 0.001$), and central and northern (z test statistic $= 2.1$, $p = 0.003$). Lizard juvenile tick counts were greatest in the northern region and lowest in the southern region. For climatic location, lizard burdens differed by climatic location with coastal reserves having higher mean tick count (3.35 ± 5.52 ticks) than inland reserves (1.97 ± 3.65 ticks). Across the entire study, the effect size for latitudinal region on lizard burdens was moderate ($H = 0.069$) while coastal location was small ($d = 0.29$). However, when looking at the effect size for each month, there were differences in effect sizes for latitudinal region and coastal location gradients that were more prominent with a shift from small to large to small ($H = 0.029$ in April, $H = 0.26$ in May, $H = 0.04$ in June) for latitude gradient and small to moderate ($d = 0.35$ in April, $d = 0.30$ in May, $d = 0.58$ in June) for coastal humidity gradient.

For drag cloth collected ticks, we were unable to run the analyses (i.e., Kruskal–Wallis or Wilcoxon signed-rank test) due to low sample size of juvenile ticks collected by this method across our entire study region, particularly at sites below 36° latitude (Big Creek, Rancho Marino, Sedgewick, Coal Oil Point, Santa Cruz Island, Stunt

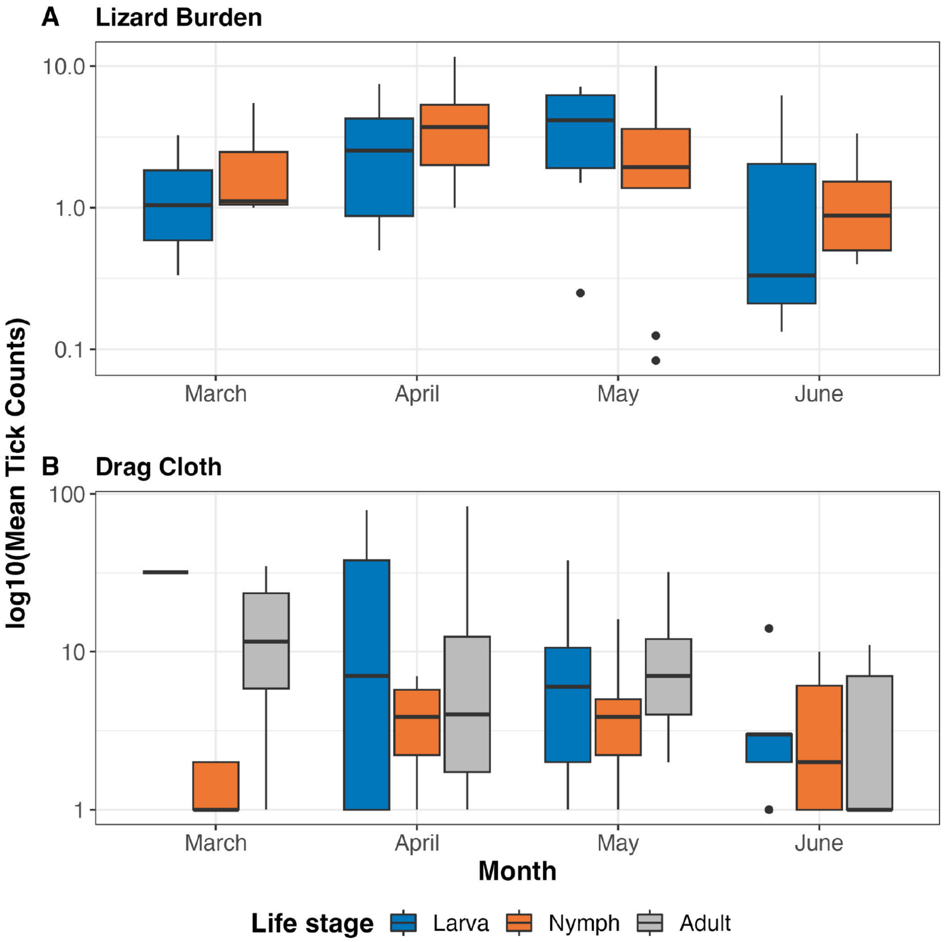

FIGURE 3 Abundance patterns for (A) attached and (B) questing *Ixodes pacificus* ticks vary by collection methods. Attached ticks represent the mean tick burden on an individual lizard per reserve per month. The box spans the first and third quartiles, the median is marked by a thick horizontal line, the whisker represents the minimum and maximum values excluding outliers, and the solid circles represent outliers.

Ranch) where the majority of collected juvenile ticks came from lizard burdens despite drag cloths still collecting adult ticks, which is consistent with other studies (Ginsberg et al., 2021; Lane et al., 2013; MacDonald & Briggs, 2016).

Monthly tick abundance patterns vary by collection method

Peak tick abundances occurred in different months at different sites, suggesting dissimilar phenology patterns across our study system. Aggregating all tick counts by drag cloth sampling illustrated the mean counts of all life stages of *I. pacificus* were highest in April (17.3 ± 35.3 ticks/sampling event [mean ± SD]) followed by March (11.9 ± 12.7 ticks/sampling event), May (8.9 ± 10.6 ticks/sampling event), January (8.4 ± 7.3 ticks/sampling event), and June (4.3 ± 4.3 ticks/sampling event). The peak mean counts of larvae occurred in April (25.2 ± 33.8 ticks/sampling event), of nymphs occurred in May (5.3 ± 5.5 ticks/sampling event), and of adults occurred in April (20.7 ± 44.0 ticks/sampling event). Aggregating all tick counts from lizard burden sampling showed that mean counts of *I. pacificus* were highest in April (3.9 ± 5.6 ticks/sampling event), followed by May (2.7 ± 5.1 ticks/sampling event), March (2.3 ± 3.9 ticks/sampling event), and June (1.4 ± 2.7 ticks/sampling event). The peak mean counts of larvae occurred in May (3.1 ± 6.4 larvae/sampling event), and nymphs occurred in April (4.9 ± 6.0 nymphs/sampling event), which was the opposite of the drag cloth results (Figure 4). And despite lizard surveillance in the months of January through March, there were no lizards observed in January, and by March, only southern, warmer sites had lizards that were observed and collected for lizard burden assessment. All tick count means from drag cloth and lizard burden sampling methods for each region and month can be found in Appendix S1: Table S3.

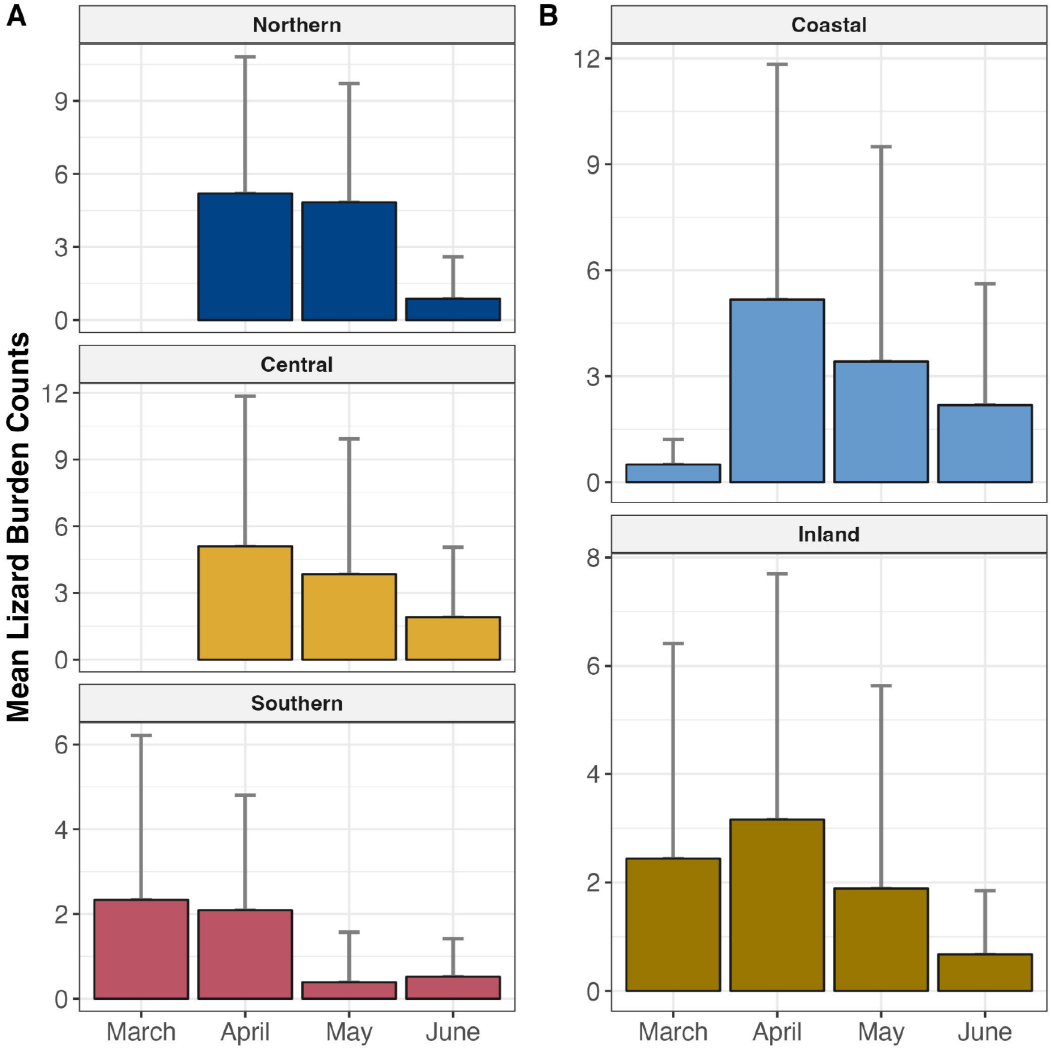

FIGURE 4 Regional within-season patterns of juvenile *Ixodes pacificus* ticks vary by (A) latitudinal (i.e., temperature) and (B) climatic (i.e., humidity) gradients (mean + SD).

Tick abundance patterns are associated with climate gradients

The generalized linear models showed the abundance of each tick life stage responded differently to climate variables at a given month. All tick abundance models were best fitted with a negative binomial distribution. A list of the best fit models for each regression model can be found in Table 1. A brief summary of significant climate variables for each tick life stage by sampling method can be found below.

For lizard burden collected ticks, both larvae and nymphs were negatively associated with mean temperature and positively with VPD. However, larvae were more significantly associated with maximum VPD whereas nymphs were more significantly associated with minimum VPD. For drag collected ticks, each life stage was significantly associated with different climate variables. The best fit model for adult ticks included mean temperature and maximum VPD, with adult ticks responding most significantly to mean temperature (negative direction). Both larva and nymph models were significant ($p < 0.01$) or trending toward significance ($p = 0.07$), respectively, for precipitation inputs. Larvae were positively and significantly associated with summed precipitation from the prior month, whereas nymphs were trending negatively with summed precipitation from the collection month.

Larvae and nymphs feed synchronously on individual hosts, but the frequency of synchrony depends on climate

Juvenile within-season metrics at individual sites, such as the sequential order of life stage emergence, emergence rate, duration of activity, and proportion of synchronous

TABLE 1 The best fit regression models of associations between (A) tick abundance per month or (B) juvenile synchrony per lizard and climate variables.

Method	Life stage	Explanatory variable	Estimate ± SE	*z*	*p*
(A) Tick count per month ~ climate variables + (1|reserve)[a]					
Drag	Larvae	(Intercept)	1.8 ± 0.32	5.8	<0.001***
		ppt prior month	**0.03 ± 0.01**	**2.8**	**0.005****
	Nymphs	(Intercept)	1.3 ± 0.27	4.7	<0.001***
		ppt month	−0.02 ± 0.01	−1.8	0.07
	Adults	(Intercept)	3.8 ± 0.81	4.7	<0.001***
		tmean	**−0.2 ± 0.09**	**−2.3**	**0.02***
		VPDmax	0.06 ± 0.05	1.3	0.2
Lizard	Larvae	(Intercept)	3.4 ± 0.97	3.6	<0.001***
		tmean	**−0.34 ± 0.10**	**−3.5**	**<0.001******
		VPDmax	**0.11 ± 0.04**	**2.8**	**0.005****
	Nymphs	(Intercept)	2.2 ± 0.45	4.9	<0.001***
		tmean	**−0.09 ± 0.04**	**−2.5**	**0.01***
		VPDmin	0.05 ± 0.06	0.8	0.44
(B) Juvenile synchrony event per lizard ~ tmean + reserve[b]					
Lizard	Synchrony	(Intercept)	0.23 ± 0.77	0.3	0.76
		tmean	**−0.13 ± 0.05**	**−2.5**	**0.01***
		ML	**2.9 ± 0.80**	**3.6**	**<0.001******
		QR	**2.7 ± 0.91**	**3.0**	**0.003****
		FO	**1.7 ± 0.53**	**3.3**	**<0.001******
		HT	0.86 ± 0.54	1.6	0.11
		BC	**1.1 ± 0.50**	**2.2**	**0.03***
		RM	**2.0 ± 0.56**	**3.6**	**<0.001******
		SC	0.14 ± 0.74	0.19	0.85
		SD	**1.1 ± 0.56**	**2.1**	**0.04***

Note: Explanatory variables listed are the best fit predictors out of the full set of climate variables, including daily temperature (maximum, minimum, mean; in degrees Celsius), daily vapor pressure deficit (VPD; maximum, minimum; in kilopascals), and precipitation (in millimeters) summed by month of collection (ppt month) and prior to month of collection (ppt prior month). Juvenile synchrony refers to the burden pattern on an individual lizard where a synchronous event (=1) is when a single larvae and nymph are feeding on the same host. Significant covariates are bolded.

[a] Negative binomial distribution with log link function.

[b] Binomial distribution with logit link function. 1, one larva and one nymph feeding on individual lizard; 0, all other lizard burden types (most southern site, Stunt Ranch, as the reference level).

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

events, were highly variable, suggesting multiple phenological patterns across our study area (Figure 5). The sequential order of life stages emerging (i.e., larvae first, nymphs first, synchrony of larvae and nymphs) varied by site. At seven sites (McLaughlin, Fort Ord, Big Creek, Rancho Marino, Santa Cruz Island, Sedgewick, Stunt Ranch), both larvae and nymphs were first observed in the same month (i.e., synchrony). At four sites (Quail Ridge, Point Reyes, Hastings, Coal Oil Point), nymphs were first observed a month or more before larvae (i.e., asynchrony larvae first). And at no sites did we observe larvae a month or more before nymphs (Figure 5). The emergence rate of juvenile ticks (i.e., cumulative proportion at an individual site per month) was variable, with warmer southern sites (e.g., highest mean temperature in March; Stunt Ranch, Sedgewick, Coal Oil Point) reaching higher cumulative proportions before cooler coastal sites (Fort Ord, Big Creek) (Figure 5). The duration of juvenile activity at an individual site was also variable, with some sites having one relatively high abundance month (BC, RM) or several relatively moderate abundance months (Quail Ridge, Hastings, Santa Cruz Island, Sedgewick, Coal Oil Point). The proportion of synchronous events (i.e., one or more

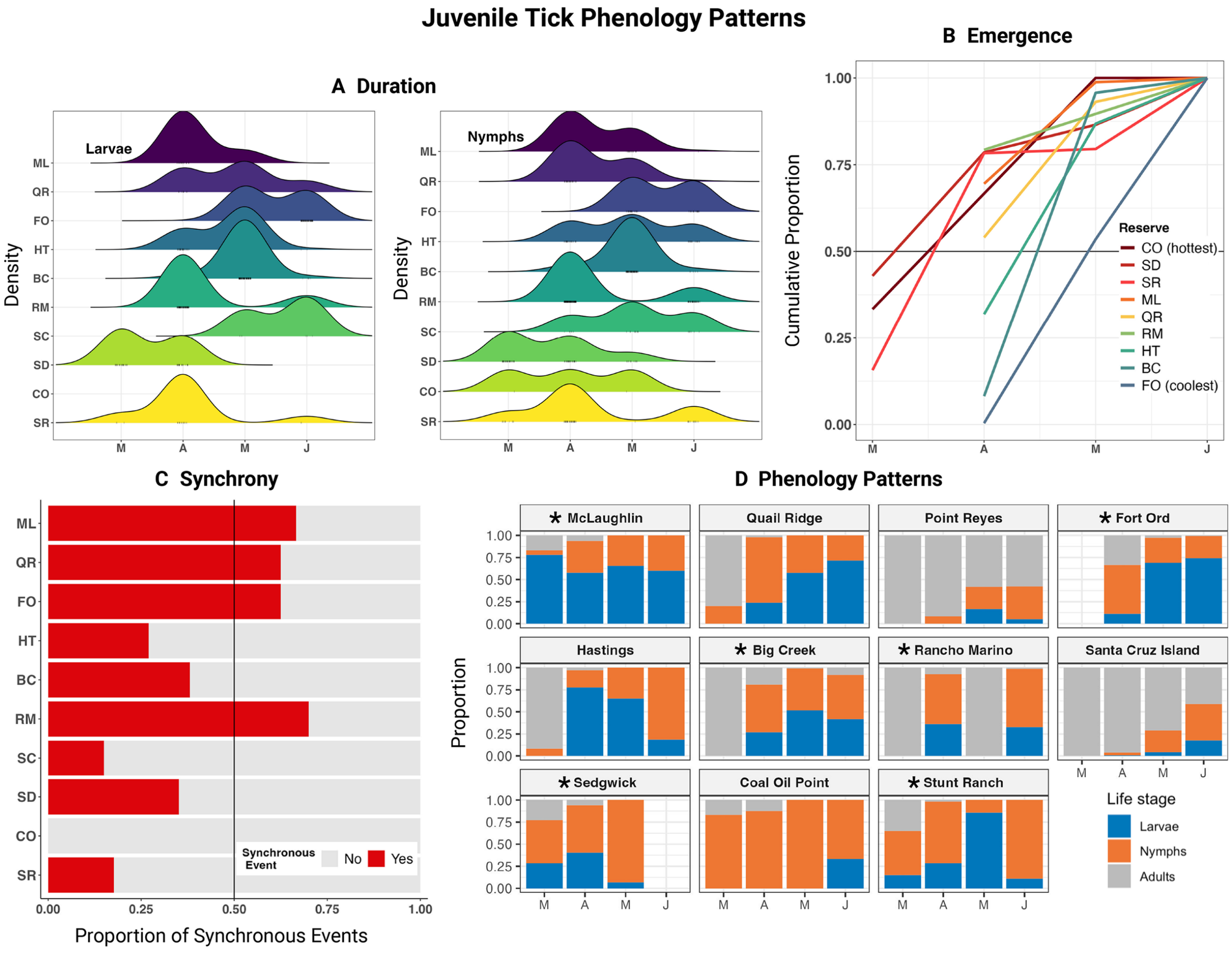

FIGURE 5 Individual reserves, which represent a unique combination of temperature and humidity, vary in their within-season dynamics of juvenile *Ixodes pacificus* from attached lizards. Within-season dynamics such as (A) duration of activity, (B) emergence rate, (C) proportion of synchrony events, and (D) sequential pattern are different for each reserve. (A) Density curves represent the monthly abundance of juvenile ticks during the sampling season (March–June) at each reserve. (B) Cumulative proportion represents the emergence rate of juvenile ticks by reserve during the sampling season. Color of the reserves represents the descending order of mean temperature in March for each reserve (i.e., highest mean temperature in March was Coal Oil Point, lowest was Fort Ord). (C) The proportion of synchronous events (i.e., when both larva and nymph feed on an individual lizard) at each reserve during the sampling season. (D) The sequential order of life stages emerging (*for sites with synchronous emergence). Site abbreviations can be found in Figure 2.

larva and one or more nymphs feeding on an individual lizard at a given site) was also variable, with northern sites (McLaughlin, Qauil Ridge, Fort Ord) having on average more synchronous events than southern sites (Stunt Ranch, Coal Oil Point, Santa Cruz Island) (Figure 5).

The binomial model with the defined success outcome as synchrony of juvenile stages (i.e., at least one larva and one nymph on an individual lizard) showed that the log odds of having a synchronous feeding event was significantly associated with mean temperature and individual reserves varied in their success rate of synchronous events. For every one unit increase in mean temperature, the log odds of synchronous feeding decreases by 0.12 (or an odds of $\exp(\beta) = 0.88$ [95% CI 0.80–0.97]). The overall effect of reserve was significant ($\chi^2 = 31.6$, df $= 9$, $p < 0.001$), meaning the baseline odds of synchronous feeding (i.e., at a given temperature) varied among reserves, which represents a unique combination of temperature and humidity conditions.

DISCUSSION

Environmental conditions strongly influence vector behavior and vector–host contact rates, which influences vector-borne disease risk (MacDonald et al., 2021).

The phenology, or timing of seasonal activity of vectors, can strongly influence transmission dynamics (Alkishe et al., 2021; MacDonald et al., 2020; Ogden et al., 2018). Here, we quantify the phenology of the primary Lyme disease vector in California, both across a temperature (latitudinal) and humidity (coastal to inland) gradient, using host-feeding ticks as a robust way to estimate seasonal juvenile abundance and activity within a season (Table 1). We find that when sampling over a very broad geographic range (Figure 2), there was a higher probability of collecting juvenile ticks on lizards compared to drag cloths (Figure 3), which allowed us to detect differences in phenology across climate gradients (Figure 4). Beyond regional differences, there was variation in the within-season dynamics (i.e., emergence, duration, synchrony) of ticks across sites, highlighting the local variation of juvenile activity. Interestingly, our emergence data (i.e., when a life stage was first observed at an individual site) did not yield evidence for larvae emerging before nymphs, but observed nymphs emerging before larvae at four individual sites (asynchrony), suggesting higher potential of transmission at those particular sites. We found that synchronous feeding of larvae and nymphs on individual hosts does occur, but the success rate (i.e., an individual lizard with both a larva and nymph attached) at which it occurs appears to differ regionally (Appendix S1: Figure S4), suggesting a potential mechanism behind observed differences in tick-borne pathogen prevalence across California.

We do not find evidence for similar juvenile phenology patterns across our 650 km study region. Quantifying the within-season regional patterns of juvenile populations, particularly *I. pacificus*, has been a challenge yet we overcame this challenge by assessing lizard burdens—the preferred host for juvenile *I. pacificus* (Casher et al., 2002; Slowik & Lane, 2009)—alongside drag cloth sampling methods. These two methods produced vastly different results with drag cloth sampling collecting mostly adult ticks, whereas lizard burdens only captured larvae and nymphs (Figure 3). From juvenile tick data collected from lizards, we were able to consistently describe seasonality of larval and nymphal ticks across a large latitudinal gradient and at a finer resolution than in previous studies (Lane et al., 2013; MacDonald, 2018; MacDonald & Briggs, 2016; Salkeld et al., 2014). Consistent with those studies, we found significantly higher abundances of *Ixodes* in cooler northern locations than in warmer southern regions ($\chi^2 = 7748.7$, df $= 17$, $p < 0.001$); however, we also found significant differences between humid coastal and dry inland locations ($W = 45{,}989$, $p \leq 0.001$) potentially signaling that tick populations are responding to other factors than latitudinal differences (e.g., temperature or photoperiod). Yet the overall effect size of latitudinal gradient (moderate, $H = 0.069$) was greater than the humidity gradient (small, $d = 0.29$) on juvenile burdens. This may be due to the less extreme range of mean temperature and maximum humidity at coastal sites (Δ ~11°C; Δ ~4 kPa) compared to northern sites (Δ ~21°C; Δ ~57 kPa) during our study period (Appendix S1: Table S2).

The effect size of latitudinal and coastal gradients becomes more prominent in later months of the study (regional: $H = 0.26$ large in May; coastal: $d = 0.58$ moderate in June), which may represent the more rapid change in temperature and humidity (Figure 2; Appendix S1: Figures S1 and S2) as well as the relatively short juvenile activity season compared to *I. scapularis* (MacDonald & Briggs, 2016). To explore these regional patterns as a function of underlying difference in climate, we found significant associations between the abundances of ticks and our temperature and humidity variables. Mean temperature and maximum vapor pressure deficit were significantly associated with tick abundances in different directions (temperature-negative, vapor pressure deficit-positive), although certain life stages were more strongly associated with abiotic conditions than others (Table 1). We highlight these differences in each life stage because it may also impact when and for how long each life stage is active at a particular location, possibly influencing those local transmission dynamics. Broadly in coastal California with mild mean temperatures, the context of higher maximum vapor pressure deficit may translate to humid environments that increase the amount of time ticks can quest on vegetation (i.e., longer seasonal duration), whereas higher mean temperature may cue ticks to emerge earlier in the season (i.e., quicker emergence rate) but reduce the amount of time questing because of desiccation pressures (MacDonald & Briggs, 2016). Tick phenology, or seasonal activity, could also be influenced by nontemperature-related cues such as photoperiod, which could have an impact on the host-seeking behavior across the latitudinal gradient, or diapause, which we assume was not occurring in the middle of peak host-seeking season, but should be considered in future studies. Additional future studies should incorporate a finer scale of microclimatic conditions with data loggers associated with each collection plot (Figure 2; Appendix S1: Figures S1 and S2).

We found that an increase in mean temperature decreases the probability of a synchronous feeding event (Table 1); feeding synchrony was greater in northern and coastal sites (Figure 5), which are cooler than southern, inland sites. These climatic characteristics may allow for a longer tick season (i.e., ticks still relatively active in June) giving more opportunities for ticks to feed on hosts and amplify pathogen transmission at a specific site. Synchrony is limited in southern, inland sites due to limitation by intense heat, thus reducing the opportunities for ticks to feed on hosts. While the results of our study are consistent with observed patterns of tick infection in California, with higher rates in northwestern California than in central or southern regions of the state (Padgett et al., 2014), we did not explicitly control for or investigate the abundance or composition of reservoir hosts. Future research endeavors that incorporate investigations of infection in tick populations with phenological patterns and vertebrate host dynamics will be better suited to address drivers of Lyme disease risk in California and western North America.

CONCLUSION

The primary Lyme disease vector in the western United States is often described as exhibiting a synchronous phenology, where we would expect to see synchronous feeding of juvenile *I. pacificus* occurring at relatively equal rates across its range. However, we document high variability in the degree of synchrony within the host-seeking season, and show that nymphs are active before larvae in some locations suggesting potential pathogen amplification compared to locations with synchronous phenology. The relative abundance and seasonality of these life stages are highly variable and potentially reflective of the varying climate of California—an endemic, low prevalence Lyme disease region. By more accurately characterizing within-season phenological patterns throughout the state, we can leverage the data to describe spatial patterns of pathogen prevalence in the microclimatically heterogeneous landscape of California and can be applied to other geographic regions as well.

AUTHOR CONTRIBUTIONS

Samantha Sambado, Andrew J. MacDonald, and Cheryl J. Briggs designed the experiment. Samantha Sambado collected and analyzed the data and wrote the initial draft of the manuscript. Andrew J. MacDonald, Andrea Swei, and Cheryl J. Briggs contributed to the writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Sambado et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.0p2ngf29d.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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