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Truncated seasonal activity patterns of the western blacklegged tick (*Ixodes pacificus*) in central and southern California

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ABSTRACT

Patterns of seasonal activity and density of host-seeking western blacklegged ticks, *Ixodes pacificus*, were investigated in central and southern California. Weekly to monthly drag sampling was undertaken at two sites in Santa Barbara County and one site in Los Angeles County over multiple years. Adult *I. pacificus* became active in the winter (late November) and were rare or absent by late April to early May. Nymphal ticks became active in early to late February, were absent by early May to early June, and were rarely encountered using the drag method throughout their period of peak seasonal activity. Larval ticks became active earlier in the season, or at the same time as nymphs (early to late February) and were absent by early May. These results suggest a highly truncated period of *I. pacificus* seasonal questing activity, particularly apparent in the juvenile tick stages, in central and southern California relative to observed patterns in Lyme-endemic northwestern California. Notably, the highly truncated period of questing activity of the juvenile stages has important implications for pathogen transmission dynamics in that there exists only a brief window for horizontally transmitted pathogens to be acquired by one tick cohort and subsequently transmitted, through hosts, to the next tick cohort in this system. The broader patterns observed also suggest low human risk of tick-borne disease in central and southern California, and have implications for reduced tick-borne disease risk in the western US more generally under projected climate change.

Introduction

Globally, there has been an increase in the rate of emergence of vector-borne zoonotic diseases in recent decades, presenting new challenges and threats to public health (Jones et al., 2008; Kilpatrick and Randolph, 2012). A number of large-scale anthropogenic changes, such as land use and climate change, are contributing to the amplification of emerging infectious zoonotic diseases. For example, the distribution of vector species may shift or expand as a result of climate change, and lead to subsequent shifts in vector-borne disease burden (Bounoua et al., 2013; Ogden et al., 2008b). In the case of pathogens with complex transmission cycles involving multiple hosts and vector life stages, changing host ecology resulting from land use or environmental change may also alter human disease risk through vector abundance (Ogden et al., 2014), infection prevalence with the pathogen (Allan et al., 2003; Patz et al., 2004), or vector activity patterns (Ogden et al., 2008a). Thus, understanding when and where vector species are active and how these patterns may be expected to change given ongoing climate or environmental change is crucial to prevention and control of vector-borne diseases.

Lyme disease is the most commonly reported vector-borne disease in the United States, and is increasing in incidence and geographic range (Bacon et al., 2008). In the United States, Lyme disease is caused by an infection with *Borrelia burgdorferi*, a spirochete that is transmitted to humans by blacklegged ticks—*Ixodes scapularis* in the eastern United States and *Ixodes pacificus* in the western United States. In addition to *B. burgdorferi*, both blacklegged and western blacklegged ticks vector a number of other emerging pathogens including the causative agents of tick-borne relapsing fever (*Borrelia miyamotoi*), anaplasmosis (*Anaplasma phagocytophilum*), and babesiosis (*Babesia* spp.). *Ixodes* spp. ticks have a four-stage life cycle, comprised of the egg stage and the parasitic larval, nymphal and adult stages, and maintain enzootic transmission of *B. burgdorferi* in complex cycles involving many different vertebrate hosts (Gray et al., 2002; Kurtenbach et al., 2006). *B. burgdorferi* is not transmitted transovarially and can be acquired by larval and nymphal ticks only through blood meals taken from infected hosts, and thus infections may be transmitted only by infected nymphal or adult female ticks (Clover and Lane, 1995; Falco et al., 1999; Gray et al., 2002; Kurtenbach et al., 2006). Seasonal activity and density of potentially

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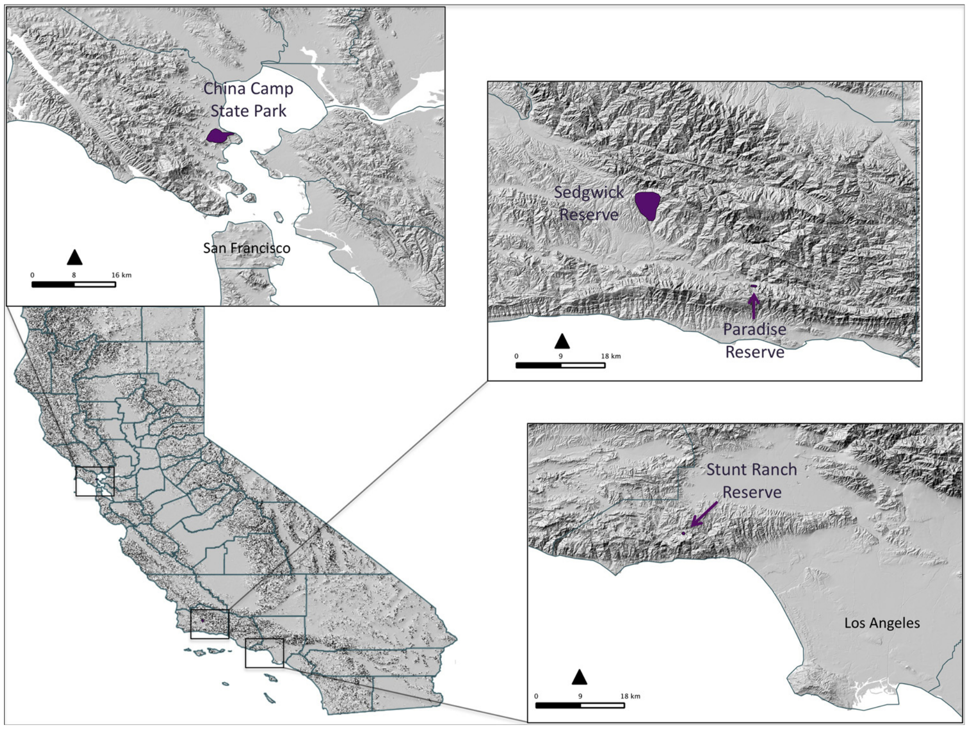

Fig. 1. Map of tick sampling sites in northwestern, and southern California. California hillshade data layer was obtained from Cal-Atlas (www.atlas.ca.gov/download.html) through https://koordinates.com.

infectious tick life stages are thus critical components of Lyme disease risk.

In the eastern US where human Lyme disease is most common, larval *I. scapularis* peak in activity in the early fall (August–October) in the northeastern US, and in the summer months (June–August) in the upper Midwestern US, while nymphal *I. scapularis* peak in activity during the summer months (June–August) and adult *I. scapularis* have bimodal peaks in activity during the fall and spring (Falco et al., 1999; Gatewood et al., 2009; Hamer et al., 2012; Ostfeld et al., 1996). Consequently, because nymphal *Ixodes* spp. are the primary vector, peak Lyme disease transmission in the eastern US occurs during the summer months when nymphal ticks are most active (Falco et al., 1999), and Lyme disease risk is absent during the winter months when much of the northeast and upper Midwest is blanketed in snow or experiencing temperatures consistently below 0 °C. In contrast, in western North America, the area of highest risk for acquiring Lyme disease is northwestern California, where vector ticks have been found to be active throughout the year, presenting a year-round risk of Lyme disease transmission (Salkeld et al., 2014).

In central and southern California, infected *I. pacificus* ticks have been identified, but transmission of *B. burgdorferi* to humans is less common (Padgett et al., 2014). A handful of previous studies suggest that infection prevalence in vector tick populations in central and southern California – with both *B. burgdorferi* as well as the relapsing fever spirochete, *B. miyamotoi* – is low (Lane et al., 2013; Padgett et al., 2014), which is likely contributing significantly to the low rate of transmission to humans in this region. However, the underlying mechanism producing low infection prevalence in southern California tick populations is not well understood. Here we examine one possible mechanism, namely the seasonal activity patterns of the western blacklegged tick, and investigate whether this vector species exhibits a truncated period of seasonal activity in southern California. We report on seasonal activity patterns of *I. pacificus* in sites in Santa Barbara County and Los Angeles County, California in which weekly to monthly tick collection was undertaken over multiple years. We show that *I. pacificus* activity patterns, particularly of the juvenile stages, are truncated relative to those observed in northwestern California. We discuss possible causes of these observed patterns, implications for human tick-borne disease risk in central and southern California, as well as implications for tick-borne disease risk under projected climate change in the western US.

Materials and methods

I. pacificus ticks were collected at three sites in Santa Barbara and Los Angeles County, California to determine seasonal activity patterns and timing of peak density in central and southern California. Santa Barbara County collection locations included Sedgwick Reserve, part of the University of California Natural Reserve System and located in the Santa Ynez Valley, and Paradise Reserve located in the Los Padres National Forest on the north side of the Santa Ynez Mountains (Fig. 1). Collection sites in Sedgwick Reserve were characterized by oak woodland, consisting of coast live oak (*Quercus agrifolia*), blue oak (*Quercus douglasii*) and occasional valley oak (*Quercus lobata*). The understory was dominated by introduced grasses including brome (*Bromus* spp.), wild oats (*Avena* spp.) and occasional native bunch grasses, as well as common vetch (*Vicia sativa*) and California sagebrush (*Artemisia californica*). Collection sites in Paradise Reserve were characterized by similar plant communities, notably coast live oak woodland with occasional California bay-laurel (*Umbellaria californica*) and an understory dominated by introduced grasses and western poison-oak (*Toxicodendron diversilobum*). In Los Angeles County, ticks were collected from Stunt Ranch Reserve, also a part of the University of California Natural Reserve System, in the Santa Monica Mountains (Fig. 1). Collection sites in Stunt Ranch Reserve were also characterized by coast live oak woodland with an understory dominated by introduced grasses and western poison-oak.

Tick sampling for all parasitic life stages: Southern California

Western blacklegged ticks were collected at Sedgwick, Paradise and Stunt Ranch Reserves using the flagging method, in which a 1 m^2 white flannel cloth is dragged over understory vegetation and leaf litter, and attached, questing ticks are counted and removed (e.g. Daniels et al., 2000). Adult ticks were primarily encountered on understory shrubs and grasses, and juvenile ticks were only encountered in patches of leaf litter, so two distinct habitat types were sampled for the different stages. Adult ticks were collected from understory shrubs and grasses along established transects at each reserve, and an area of 500 m^2 of oak woodland was sampled during each sampling event. Adult ticks were collected weekly to biweekly from sites established at Sedgwick Reserve from December 2012 to December 2013, and monthly from January 2014 through June 2014. Adult ticks were collected from Paradise Reserve weekly to monthly from November 2013 through June 2015, and from Stunt Ranch Reserve approximately monthly from December 2013 through June 2014, and from December 2014 through June 2015.

Larval and nymphal ticks were collected using the same flagging method as adult ticks, with flagging effort focused on dense patches of leaf litter. Juvenile ticks were collected at each reserve on the same sampling schedule as adult ticks, and an area of 200 m^2 of leaf litter was sampled in oak understory each time (a smaller area was sampled for juvenile ticks than adults due to the general rarity and patchiness of dense leaf litter habitat in these southern California oak woodland sites). Juvenile ticks were not found to be questing on vegetation above the surface of the leaf litter, so no juvenile ticks were encountered or collected on adult tick transects. Adult ticks were, however, occasionally collected in patches of leaf litter in which juvenile tick sampling took place. These adult ticks were not included in the analysis in order to maintain consistency in area sampled for the various parasitic life stages for the duration of the study.

Tick seasonality data: Northwestern California

We compared our data from southern California collection sites to previously published data from northern California. Northwestern California tick data are from China Camp State Park in Marin County and were published in a recent study by Salkeld et al. (2014). In this study, all parasitic life stages were sampled concurrently over multiple years, producing estimates of tick density through time. This is the only published study from northern California with comparable data to the present study for all parasitic life stages, and data were provided in raw form to be re-analyzed. Details of the sampling methodology are described in Salkeld et al. (2014). Sampling methodology in southern California sites matched the methodology used in northern California, though total area sampled over the duration of the studies differed between sites (e.g., due to the number of times each site was sampled). For comparison between sampling locations, density of ticks was calculated for each stage over time for each site, and standardized between sites.

Weather station data

Weather station data (precipitation, temperature and relative humidity) were obtained from the nearest weather station to each sampling location in this study—from the Point San Pedro weather station (http://www.ipm.ucdavis.edu/WEATHER/wxactstnames.html) adjacent to China Camp State Park in Marin County, from the UCSB department of geography weather station (http://www.geog.ucsb.edu/ideas/) at Sedgwick Reserve for both Sedgwick and Paradise Reserves in Santa Barbara County, and from the Stunt Ranch Reserve weather station in Los Angeles County (http://www.wrcc.dri.edu/weather/ucsr.html). The variables chosen – seasonal temperature, relative humidity and timing of precipitation events – are thought to regulate the life cycle of *I. pacificus* (Padgett and Lane, 2001; Salkeld et al., 2014), and are included to illustrate broad climatic differences between the two regions that may be driving seasonal activity patterns of questing *I. pacificus* ticks.

Statistical analyses

The Welch's *t*-test (for unequal variances and unequal sample sizes) was employed to determine whether mean peak density of each parasitic life stage of *I. pacificus* was significantly lower at the southern California sampling locations than at China Camp State Park. The Welch's *t*-test was chosen due to the unequal number of samples taken from each study site over the duration of the two years of sampling.

Results

Adult tick activity (Santa Barbara and Los Angeles Counties)

At Sedgwick Reserve in the Santa Ynez Valley, the earliest observation of questing adult *I. pacificus* was in mid-December—12/15/2013, and peak density occurred in February–March (Fig. 2c; Tables 1 and 2). At Paradise Reserve on the north side of the Santa Ynez Mountains, earliest observation was in late November—11/23/2013, and peak density occurred in February-March, though there appeared to be bimodal peaks in January and May of 2014 (Fig. 2b; Tables 1 and 2). At Stunt Ranch Reserve in the Santa Monica Mountains, adult ticks became active in late December 2013 and 2014, peaked in density in February-March, and were no longer active by late April to early May (Fig. 2d; Tables 1 and 2). Peak density of adult ticks was significantly lower at Sedgwick Reserve ($t(17.118) = 4.6154$, $p < 0.001$), Paradise Reserve ($t(17.583) = 4.1437$, $p < 0.001$) and Stunt Ranch Reserve ($t(17.956) = 4.4816$, $p < 0.001$) than at China Camp State Park in northern California. As in previous studies (Salkeld et al., 2014), adult tick activity generally began following the first substantial rains of the wet season, with adult ticks becoming rare or absent following the last major rain events of the season. For this study, adult *I. pacificus* became rare or absent by late April to early May at all sites sampled in central and southern California, which mirrored patterns of precipitation, with final major rain events occurring in late March to early April.

Immature tick activity (Santa Barbara and Los Angeles County)

Nymphal *I. pacificus* were first observed in late February and absent by mid-April at Sedgwick Reserve (Fig. 3c). At Paradise Reserve, patterns were similar with first observations occurring in early March, and questing nymphs absent by mid-May (Fig. 3b). At Stunt Ranch Reserve, nymphs were first observed in early March and active through early June (Fig. 3d). Density of nymphal ticks was significantly lower at Sedgwick ($t(26.994) = 2.3209$, $p < 0.05$), Paradise ($t(24.248) = 2.2309$, $p < 0.05$), and Stunt Ranch ($t(18.827) = 3.861$, $p < 0.001$) Reserves than at China Camp State Park in northern California. Questing nymphal ticks were rare throughout the entire season at all southern California sites (Table 2), with no clear peaks in activity when density of ticks was substantially higher than at other times of the year.

Patterns of larval tick activity were similar to those of nymphal ticks, with first observations occurring in late February and questing larval ticks absent by mid-May at Sedgwick Reserve (Fig. 4c). At Paradise Reserve, questing larval ticks were first observed in early March and were absent by mid-May (Fig. 4b). At Stunt Ranch

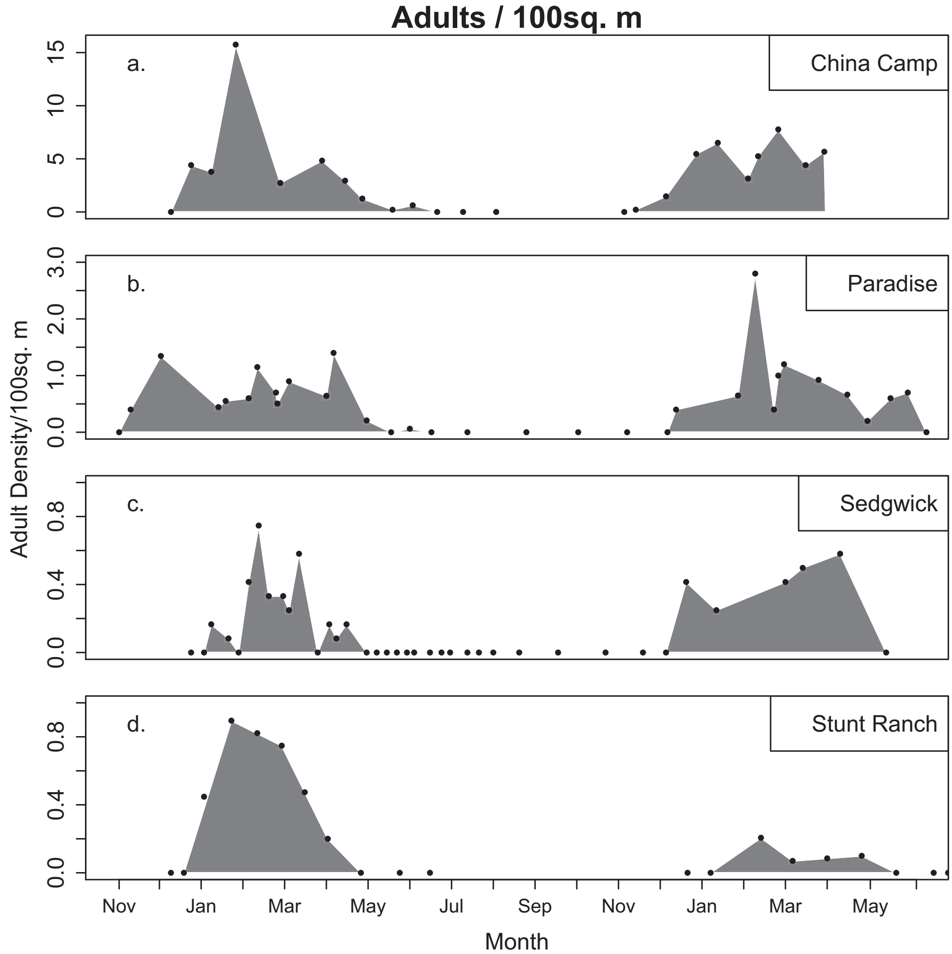

Fig. 2. Seasonal activity patterns of adult western blacklegged ticks, *Ixodes pacificus*, in California sampling sites. Polygons represent tick density through time, and points represent sampling events. (a) Adult *I. pacificus* ticks per 100 m^2 collected at China Camp State Park, 2011–2012; (b) adult *I. pacificus* ticks per 100 m^2 collected at Paradise Reserve, 2014–2015; (c) adult *I. pacificus* ticks per 100 m^2 collected at Sedgwick Reserve, 2013–2014; and (d) adult *I. pacificus* ticks per 100 m^2 collected at Stunt Ranch Reserve, 2014–2015. Note that the *y*-axes are scaled differently, illustrating marked differences in tick density between the northern site and the southern sites. Data are not available from China Camp State Park after March 19, 2012, where density appears to drop precipitously to zero in panel (a) of the figure.

Reserve, larval ticks were first active by early to late February and absent by early to late May (Fig. 4d). Peak density of larval ticks was significantly lower at Sedgwick ($t(15.051) = 1.9921$, $p < 0.05$), Paradise ($t(10.042) = 3.0555$, $p < 0.01$), and Stunt Ranch ($t(12.848) = 2.4215$, $p < 0.05$) Reserves than at China Camp State Park in northern California. Timing of peak larval activity varied between years and sampling locations, though consistently fell within the months of March and April (Table 1).

Abiotic conditions differed substantially between northern and southern California collection locations, and weather station data show that average relative humidity was ~10% higher at China Camp State Park (71.48%) in Marin County than at Sedgwick Reserve (61.71%) in Santa Barbara County, and ~23% higher at China Camp State Park than Stunt Ranch Reserve (48.70%), throughout the duration of the tick sampling periods at each site (Fig. 5a). Similarly, average maximum temperature was ~5 °C lower at China

Table 1
Summary of observed seasonal patterns of questing *Ixodes pacificus* in southern California sites, and China Camp State Park in northwestern California. Length of season for each stage is presented including number of days that each season lasted at each site, as well as dates of peak density—sites sampled over multiple seasons have two numbers in parentheses, indicating the number of days each season lasted.

Sampling location	Date of investigation	Adult season (# of days)	Nymphal season (# of days)	Peak nymphal density	Larval season (# of days)	Peak larval density
China Camp State Park (Marin Co.)	April 2010–March 2012	November–Mid June (210)	Early February–August (175, 158)	April–June	April–June (81, 80)	May
Paradise Reserve (Santa Barbara Co.)	November 2013–June 2015	Late November–April (194, 161)	Early March–Mid May (63, 34)	March–April	Early March–Mid May (63, 62)	March
Sedgwick Reserve (Santa Barbara Co.)	December 2012–June 2014	Mid December–April (94, 107)	Late February–Mid April (47, 38)	March–April	Late February–Mid May (47, 38)	March
Stunt Ranch Reserve (Los Angeles Co.)	December 2013–June 2015	December–April (67, 70)	Early March–Early June (82, 98)	March–April	Early February–May (117, 72)	February–March

Table 2
Peak density per 100 m^2 of each parasitic life stage (mean and standard deviation over sampling events during seasonal peak activity are presented in parentheses), and total number of collected adults, nymphs and larvae per site over the course of the two years sampled for each site. Density of adults is expressed as average density per 100 m^2 of understory vegetation, and juvenile tick density is expressed as average density per 100 m^2 of leaf litter, following the sampling protocol employed. Total area sampled differs between sites, thus density and total number of ticks collected do not scale by the same factor across all sites sampled.

Sampling location	Adult peak density/100 m^2 (Mean, SD)	Total adults collected	Nymph peak density/100 m^2 (Mean, SD)	Total nymphs collected	Larva peak density/100 m^2 (Mean, SD)	Total larvae collected
China Camp State Park (Marin Co.)	15.75 (5.03, 3.46)	364	21 (8.33, 5.28)	336	500 (232.08, 151.38)	277
Paradise Reserve (Santa Barbara Co.)	2.8 (0.86, 0.54)	194	3.6 (1.18, 1.22)	34	27.5 (8.64, 8.57)	125
Sedgwick Reserve (Santa Barbara Co.)	0.75 (0.44, 0.15)	132	3.4 (2.86, 2.54)	58	76 (61.00, 83.42)	308
Stunt Ranch Reserve (Los Angeles Co.)	0.9 (0.51, 0.36)	52	1.6 (0.97, 0.50)	34	146.4 (46.65, 67.08)	1020

Camp State Park (20.32 °C) than at Sedgwick Reserve (25.01 °C), and ~6 °C lower at China Camp State Park than at Stunt Ranch Reserve (26.76 °C), over the same period (Fig. 5b). Further, seasonal trends of relative humidity and temperature illustrate that the differences between northwestern and southern sites are particularly apparent during the seasonal summer drought. Finally, timing between precipitation events was shorter at China Camp State Park than at Sedgwick or Stunt Ranch Reserves over the duration of each respective study period (Fig. 6a–c). The first rains of the season occurred earlier and last rains of the season occurred later at China Camp State Park than at either Sedgwick or Stunt Ranch Reserves, which experience a more protracted summer drought.

Discussion

In this study, the season for questing adult *I. pacificus* ticks in Los Angeles and Santa Barbara counties began in late November to late-December, depending on the sampling location, peaked between January and May, and ended by late April to early May. Differences between sampling locations are likely due to the microclimatic

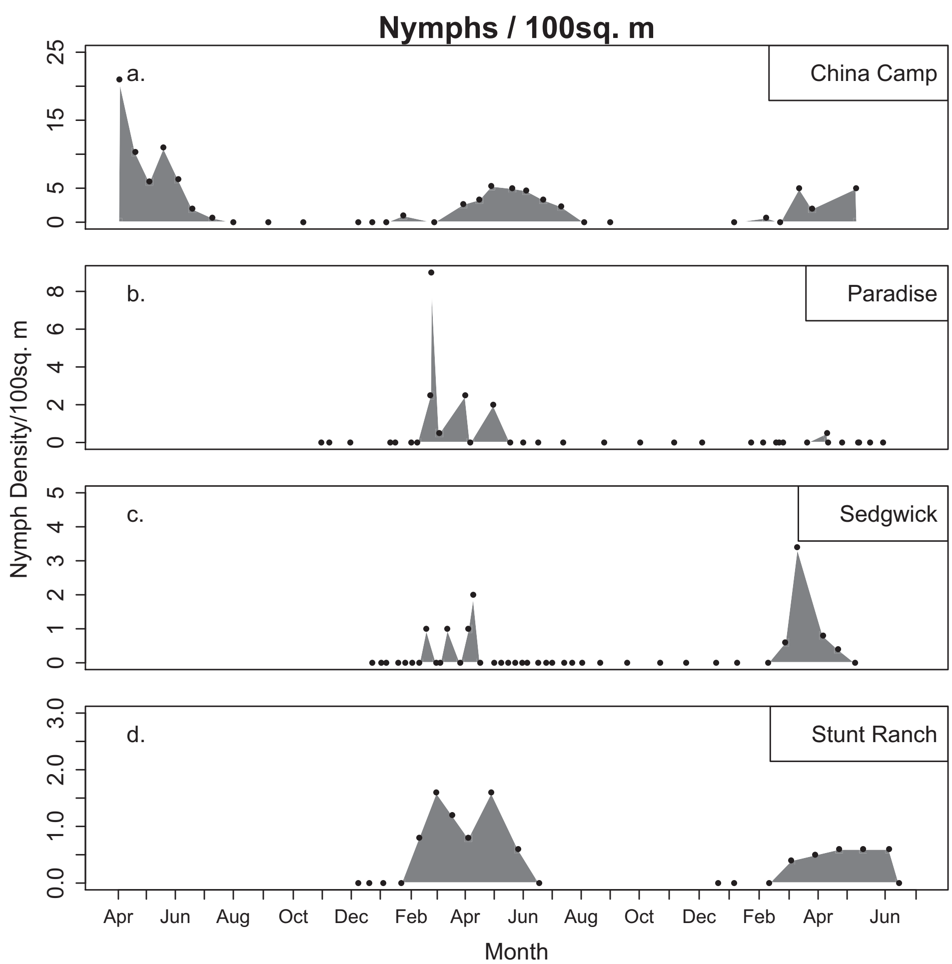

Fig. 3. Seasonal activity patterns of nymphal western blacklegged ticks, *Ixodes pacificus*, in California sampling sites. Polygons represent tick density through time, and points represent sampling events. (a) Nymphal *I. pacificus* ticks per 100 m^2 collected at China Camp State Park, 2010–2012; (b) nymphal *I. pacificus* ticks per 100 m^2 collected at Paradise Reserve, 2014–2015; (c) nymphal *I. pacificus* ticks per 100 m^2 collected at Sedgwick Reserve, 2013–2014; and (d) nymphal *I. pacificus* ticks per 100 m^2 collected at Stunt Ranch Reserve, 2014–2015. Note that the *y*-axes are scaled differently, illustrating marked differences in tick density between the northern site and the southern sites. Data are not available from China Camp State Park after May 2, 2012, where density appears to drop precipitously to zero in panel (a) of the figure.

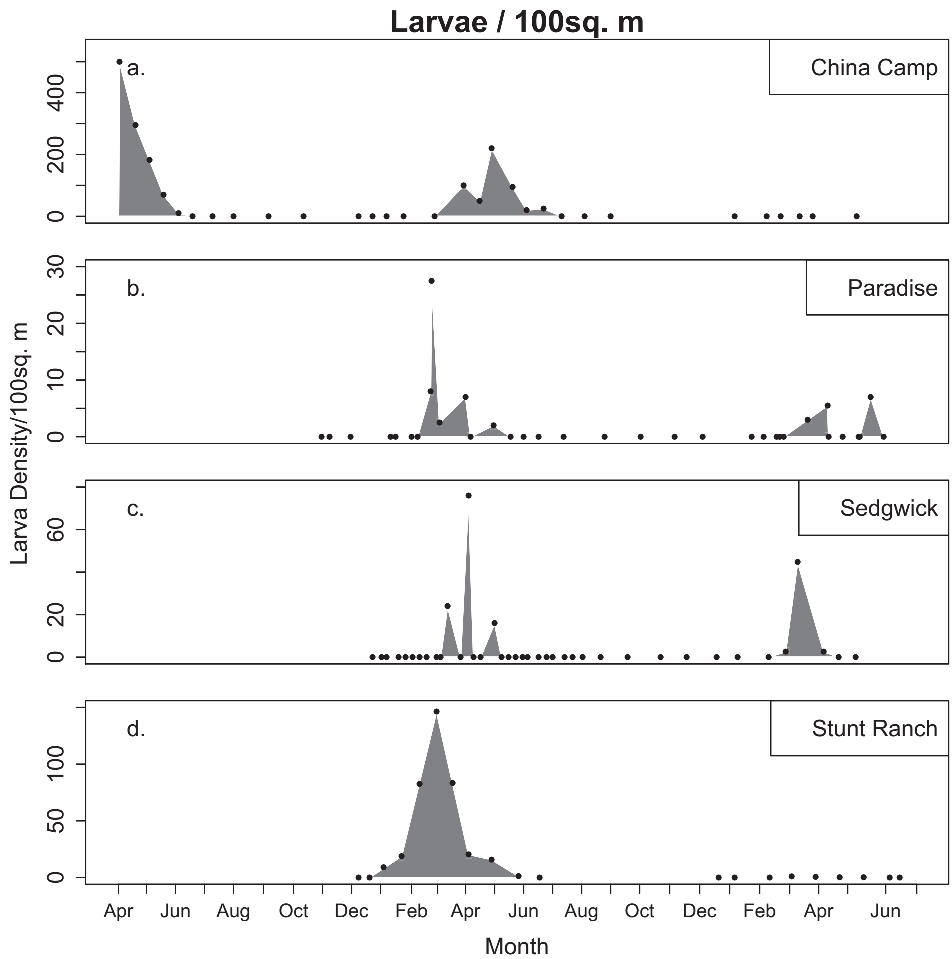

Fig. 4. Seasonal activity patterns of larval western blacklegged ticks, *Ixodes pacificus*, in California sampling sites. Polygons represent tick density through time, and points represent sampling events. (a) Larval *I. pacificus* ticks per 100 m^2 collected at China Camp State Park, 2010–2012; (b) larval *I. pacificus* ticks per 100 m^2 collected at Paradise Reserve, 2014–2015; (c) larval *I. pacificus* ticks per 100 m^2 collected at Sedgwick Reserve, 2013–2014; and (d) larval *I. pacificus* ticks per 100 m^2 collected at Stunt Ranch Reserve, 2014–2015. Note that the *y*-axes are scaled differently, illustrating marked differences in tick density between the northern site and the southern sites.

conditions within each site, which have previously been shown to drive local-scale differences in tick density (Eisen et al., 2003). The observed patterns of adult tick activity generally follow those reported from northwestern California (Salkeld et al., 2014), though activity in central and southern California consistently begins later in the season and ends earlier than in northwestern California (Fig. 2), displaying a truncated pattern. Furthermore, density of adult ticks is much lower at sites sampled in Santa Barbara and Los Angeles County than in sites sampled in northwestern California (Salkeld et al., 2014) (Fig. 2; Table 2).

Seasonal activity patterns of juvenile *I. pacificus* were also found to be truncated relative to those reported for China Camp State Park, as well as other study sites in northwestern California (Salkeld et al., 2014) (Figs. 3 and 4; Table 1). Nymphal tick activity reported in northwestern California began as early as the beginning of February, lasting throughout the summer months and in some cases as late as October (Salkeld et al., 2014). In southern California sites, nymphal ticks were found to be active only from late February through early June. Larval *I. pacificus* displayed a similarly abbreviated pattern of seasonal activity as nymphal ticks in southern California sites. In a previous study conducted in southern California (Lane et al., 2013) during the months of March, April and May of 2010, juvenile *I. pacificus* activity was found to be broadly similar to seasonal patterns of activity reported for northern California, based on flagging and tick removal from western fence lizards (*Sceloporus occidentalis*), which are a primary host for juvenile *I. pacificus* in northern California (Lane and Loye, 1989). However, due to the short duration of sampling for juvenile ticks in this study, seasonal trends could not easily be discerned.

Ixodid ticks, especially those species that spend a significant proportion of their life-cycle off-host, are highly susceptible to adverse abiotic conditions (e.g. high temperatures and low humidity), and avoid such conditions by entering states of inactivity or behavioral diapause (Needham and Teel, 1991; Padgett and Lane, 2001). *I. pacificus*, which spends >90% of its three year life cycle off-host, has been found to be particularly susceptible to high temperatures and low humidity and precipitation, which likely drive seasonal activity patterns of this tick (Eisen et al., 2002, 2003; Padgett and Lane, 2001; Swei et al., 2011). Thus, while the variation in patterns of seasonal activity between the sites sampled in northwestern and southern California may be due to interannual differences in weather and abiotic conditions (Figs. 5 and 6; Table 1), especially given the drought conditions that California experienced during the course of the present study, broader climatic differences between northern and southern California are consistent. Therefore, they may be expected to produce consistent differences in tick density and seasonal activity between the two regions (Eisen et al., 2003). This effect of climate could manifest as a direct negative effect on tick survivorship during off-host

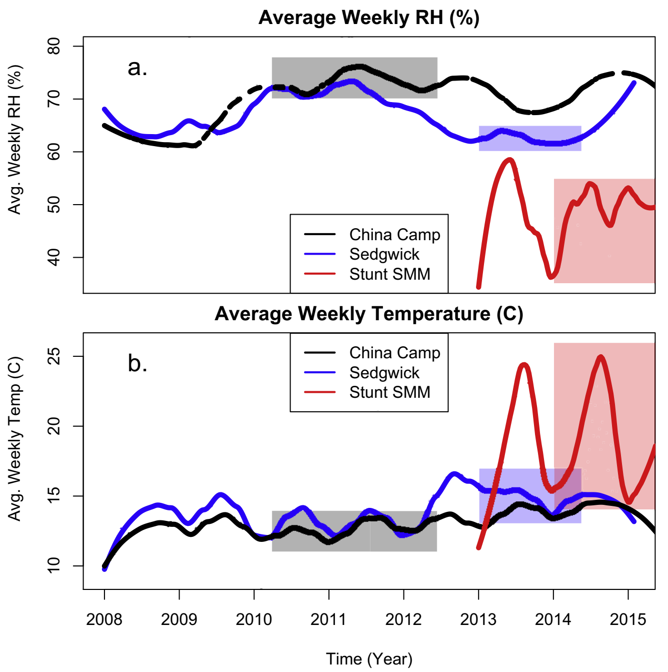

Fig. 5. Weather station data from Sedgwick, Stunt Ranch and China Camp State Park collection sites. (a) Average weekly relative humidity (%) from 2008 to 2015; solid lines represent a smoothing loess for each site illustrating seasonal patterns. (b) Average weekly temperature (°C) from 2008 to 2015; solid lines represent a smoothing loess for each site illustrating seasonal patterns. Shaded boxes overlying the data in each panel of the figure illustrate the dates over which tick sampling took place at each of the three sites. Weather station data is not available prior to 2013 at Stunt Ranch, and no data is available for Paradise Reserve.

periods throughout the protracted summer drought, or could be indirect through a negative effect on the densities of vertebrate hosts resulting in fewer successful juvenile tick blood meals in southern California.

The observed patterns of seasonal activity in central and southern California thus have potential implications for tick-borne disease risk in the western US under future climate change. In California, temperatures are expected to increase by 1.5 °C to 5.8 °C, depending on emissions scenarios and the climate model used, by the end of the century (Cayan et al., 2008; Hayhoe et al., 2004). Much of this warming is expected to occur during the summer months (Hayhoe et al., 2004). Additionally, average precipitation is expected to decline in California, primarily in the winter months (Hayhoe et al., 2004). These projected impacts of climate change in California are predicted to be more pronounced in northern and north pacific coastal regions of the state (Cayan et al., 2008; Hayhoe et al., 2004), where tick-borne disease risk is currently higher (Eisen et al., 2006b; Salkeld et al., 2014), than elsewhere in the state. If climate change leads to hotter, longer summers and drier winters in northwestern California, more closely approximating the current climate in southern California, this could lead to reduced tick-borne disease risk in northwestern California via climate impacts on tick density and seasonal activity (Eisen et al., 2003, 2006a,b). This prediction contrasts with those made for tick-borne disease in the eastern US (e.g., Ogden et al., 2014), as well as with the often reported result that climate change will exacerbate infectious disease burden and increase risks to human health (Patz et al., 2005; Altizer et al., 2013). Interactions between climate change and infectious disease are complex, and impacts will vary regionally and by disease agent (Lafferty, 2009; Holt et al., 2009).

However, given the uncertainties surrounding the magnitude and direction of climate change impacts, as well as uncertainty surrounding species adaptation to changing climate – in this case ticks and their vertebrate hosts, particularly reservoir hosts for *B. burgdorferi* and other pathogens – impacts of climate change on tick-borne disease risk in California remain challenging to predict. Future studies should examine patterns of tick activity and density, host-feeding, and infection prevalence across California's extensive latitudinal and climate gradients, to better inform our understanding of current, as well as predictions of future, tick-borne disease risk in California.

The truncated period of seasonal activity of the juvenile stages in particular, also has important implications for enzootic pathogen transmission dynamics in southern California. *I. pacificus* has three parasitic life stages, and one opportunity for pathogen acquisition during the larval stage before molting into the epidemiologically important nymphal stage. Given the highly reduced period of activity of the larval stage in this study, there exists a shorter period of time and fewer opportunities for larval ticks to feed successfully on an infected host. This could lead to lower infection rates in the nymphal stage, as observed in previous studies (Lane et al., 2013; Padgett et al., 2014), than in northwestern California as well as lower risk of human infection. However, to determine whether this mechanism is indeed operating, additional studies are needed that explore the seasonality of host feeding across various species of hosts including reservoir hosts as well as western fence lizards, a dilution host in this system (Lane and Quistad, 1998). Additionally, the proportion of blood meals coming from reservoir hosts may differ between southern and northern California, which may also be playing an important role in the ecology of tick-borne pathogens in this region.

The low number of nymphs retrieved in the central and southern California study sites may be due to regional behavioral differences in tick questing. For example, other studies have yielded similar results in which nymphal *I. scapularis* in the southeast exhibit different questing behavior than *I. scapularis* in the northeast (Arsnoe et al., 2015), and nymphal *I. pacificus* in southern California were found at similarly low densities by flagging, which did not track densities of host feeding nymphs on western fence lizards (Lane et al., 2013). Thus, while southern California nymphal ticks may be active below the surface of the leaf litter or exhibit more nidicolous questing behavior than in northern California, they are not found at high densities using the drag method, which closely approximates human risk of tick encounter. Such low encounter rates using the drag method with nymphal ticks, the most epidemiologically important tick life stage for pathogen transmission to humans, coupled with low rates of enzootic pathogen transmission and tick infection prevalence (Lane et al., 2013; Padgett et al., 2014) suggests that human risk of tick-borne disease is exceedingly low in central and southern California. If human cases of Lyme disease are acquired in southern California, dates of onset are expected to fall within a brief window between early March to early June, given observed nymphal *I. pacificus* questing activity in this region, and the average delay in occurrence of 10 days following tick bite of erythema migrans rash, the characteristic skin lesion associated with human Lyme disease (Nadelman et al., 1996).

In conclusion, based on this and other recent studies (Lane et al., 2013; Padgett et al., 2014), risk of *I. pacificus* tick encounter and human tick-borne disease appear to be comparatively low in southern California. The period of seasonal activity of questing *I. pacificus*, particularly the juvenile stages, was truncated in this study in the three sites sampled in southern California relative to activity patterns reported from one recent study, as well as historical data and long-term monitoring of sites in northwestern California (Salkeld et al., 2014). Additionally, density of questing nymphal ticks – the most important life stage for human disease risk – collected using the flagging method, which is a good proxy for risk of human tick encounter, was found to be very low in various sites across central and southern California (Lane et al., 2013; and the present study).

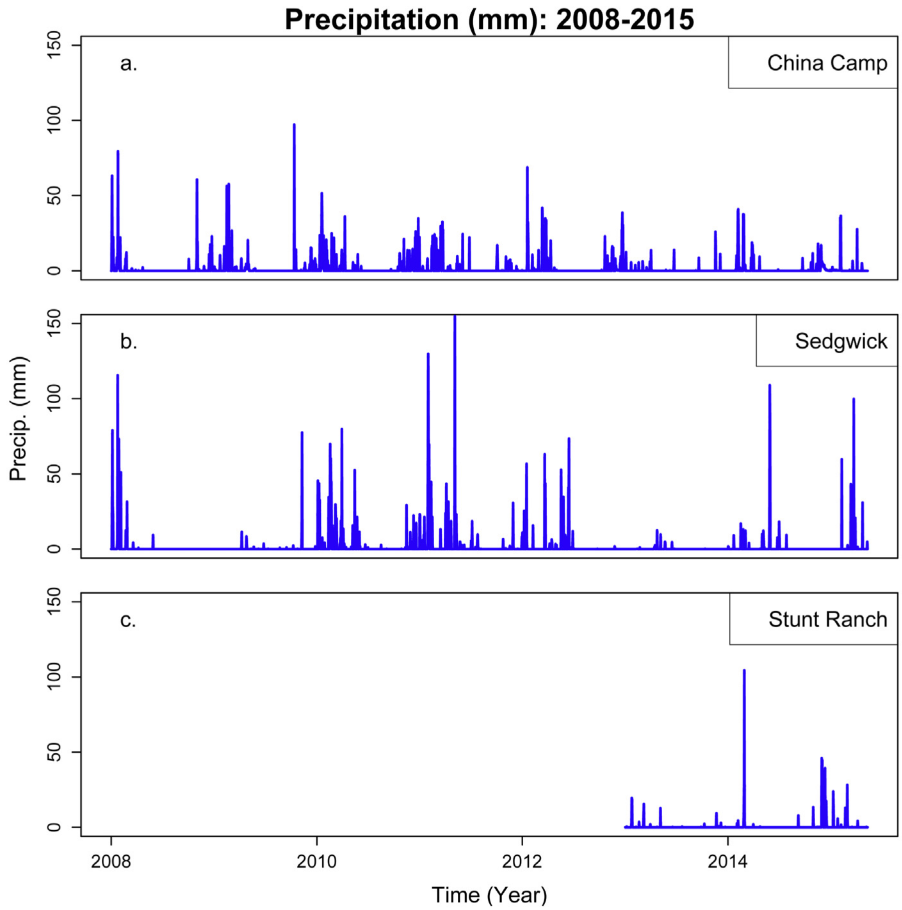

Fig. 6. Seasonal precipitation (mm) from 2008 to 2015: (a) China Camp State Park, (b) Sedgwick Reserve, and (c) Stunt Ranch Reserve. Timing between rain events is longer at both Sedgwick and Stunt Ranch Reserves producing a more protracted summer drought at these sites than is experienced at China Camp State Park in northwestern California. Data are not available for Stunt Ranch Reserve prior to 2013, and no data are available for Paradise Reserve.

Given the potential role of weather and climate, including seasonal precipitation patterns, relative humidity and temperature, in producing the observed differences in density and seasonal activity between regions in California (Eisen et al., 2003, 2006a,b), these results also have implications for reduced tick-borne disease risk under future climate change in the western United States.

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