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Habitat-related variation in infestation of lizards and rodents with *Ixodes* ticks in dense woodlands in Mendocino County, California

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Abstract. During the spring and early summer of 2002, we examined the relative importance of *Borrelia*-refractory lizards (*Sceloporus occidentalis*, *Elgaria* spp.) versus potential *Borrelia burgdorferi* sensu lato (s.l.)-reservoirs (rodents) as hosts for *Ixodes pacificus* immatures in 14 woodland areas (six oak, five mixed oak/Douglas fir, and three redwood/tanoak areas) distributed throughout Mendocino County, California. Lizards were estimated to serve as hosts for 93–98% of all larvae and ≥99.6% of all nymphs infesting lizards or rodents in oak woodlands and oak/Douglas fir sites in the southern part of the county. In redwood/tanoak woodlands and oak/Douglas fir sites in northern Mendocino County, the contribution of rodents to larval feedings reached 36–69% but lizards still accounted for 94–100% of nymphal bloodmeals. From late April to mid-June, *I. pacificus* larvae were recovered from 95 to 96% of lizards and dusky-footed woodrats (*Neotoma fuscipes*) and from 59% of *Peromyscus* spp. mice. In contrast, 99% of lizards but few woodrats (15%) and none of the mice were infested by nymphs. Comparisons of tick loads for 19 lizard–*Peromyscus* spp. mouse pairings, where the lizard and mouse were captured within 10 m of each other, revealed that the lizards harbored 36 times more larvae and >190 times more nymphs than the mice. In oak woodlands, loads of *I. pacificus* larvae decreased from late April/early May to late June for *S. occidentalis* lizards but increased for *Peromyscus* spp. mice. We conclude that the relative utilization of *Borrelia*-refractory lizards, as compared to rodents, by *I. pacificus* larvae was far higher in dry oak woodlands than in moister habitats such as redwood/tanoak and oak/Douglas fir woodlands in northern Mendocino County. Non-lizard-infesting potential enzootic vectors of *B. burgdorferi* s.l. (*I. angustus* and *I. spinipalpis*) were recorded from rodents in three of six oak woodland areas, two of five oak/Douglas fir woodland areas, and two of three redwood/tanoak woodland areas.

Introduction

The western black-legged tick, *Ixodes pacificus*, parasitizes a wide range of vertebrates including birds, lizards, and mammals (Furman and Loomis 1984). Moreover, local rates of infection with human pathogens (such as the causative agent of Lyme disease, *Borrelia burgdorferi*) in nymphal or adult ticks depend on the relative contributions of various vertebrates as hosts for the preceding larval and nymphal stages. Several rodent species (*Dipodomys californicus*, *Neotoma fuscipes*, *Peromyscus* spp. mice) are capable of acting as sources of *B. burgdorferi* sensu lato (s.l.)-infection to feeding *I. pacificus* immatures (e.g., Lane and Brown 1991;

Brown and Lane 1992, 1996; Peavey and Lane 1995), whereas *Borrelia*-refractory hosts include at least two species of lizards (*Sceloporus occidentalis*, *Elgaria multicarinata*) (Lane and Quistad 1998; Wright et al. 1998). Consequently, high utilization of these lizards by larvae or nymphs should result in low infection prevalences in the subsequent tick stages.

The only previous quantification of the specific contribution of rodents versus lizards as hosts for *I. pacificus* immatures was carried out in a single chaparral site in the spring of 1993 at the University of California Hopland Research and Extension Center (HREC), Mendocino County, California (Casher et al. 2002). The western fence lizard (*S. occidentalis*) was estimated to account for 78–88% of all larval and 98–99% of all nymphal feedings on lizards and rodents in this habitat. However, other studies revealed that dense woodlands with a leaf/fir-needle groundcover, rather than chaparral, constitute the primary risk-habitat for exposure to *B. burgdorferi*-infected *I. pacificus* ticks in north coastal California (e.g., Clover and Lane 1995; Tälleklint-Eisen and Lane 1999).

The primary aim of this study was to evaluate the variability in relative importance of rodents versus lizards as hosts for *I. pacificus* immatures in 14 woodland areas distributed throughout Mendocino County and representing three common habitat types (oak, mixed oak/conifer, redwood/tanoak). Subsidiary aims included determining the species composition of *Ixodes* ticks infesting mammals in woodland habitats, and comparing infestation levels of *I. pacificus* immatures on rodents versus lizards captured within the same microhabitats.

Materials and methods

Study areas

The study encompassed 14 woodland sites located throughout inland Mendocino County (Figure 1). General sampling areas included HREC (four sites), Montgomery Woods State Reserve (MWSR, one site), Hendy Woods State Park (Hendy Woods, one site), Angelo Coast Range Reserve (Angelo, two sites), a private ranch community located northwest of Ukiah (CHR, three sites), and private properties in the Potter Valley (two sites) and Willits (one site) areas. All sites were located in dense woodlands with a leaf, fir-needle litter or a combination of leaf and fir litter groundcover.

Sampling sites represented three common habitat types in north coastal California (Figure 1). Dry hardwood habitats (*Quercus* spp. oaks and Pacific madrone [*Arbutus menziesii*]) predominate in southeastern Mendocino County, whereas the moister western part of the county typically harbors Coast redwood (*Sequoia sempervirens*) habitats with tanoak (*Lithocarpus densiflorus*) and Douglas fir (*Pseudotsuga menziesii*) (Mayer and Laudenslayer 1988). The central part of Mendocino County usually harbors a mixture of hardwoods and conifers (primarily Douglas fir). The three above-mentioned habitat types will henceforth be referred to as oak, redwood/tanoak, and oak/Douglas fir woodland, respectively.

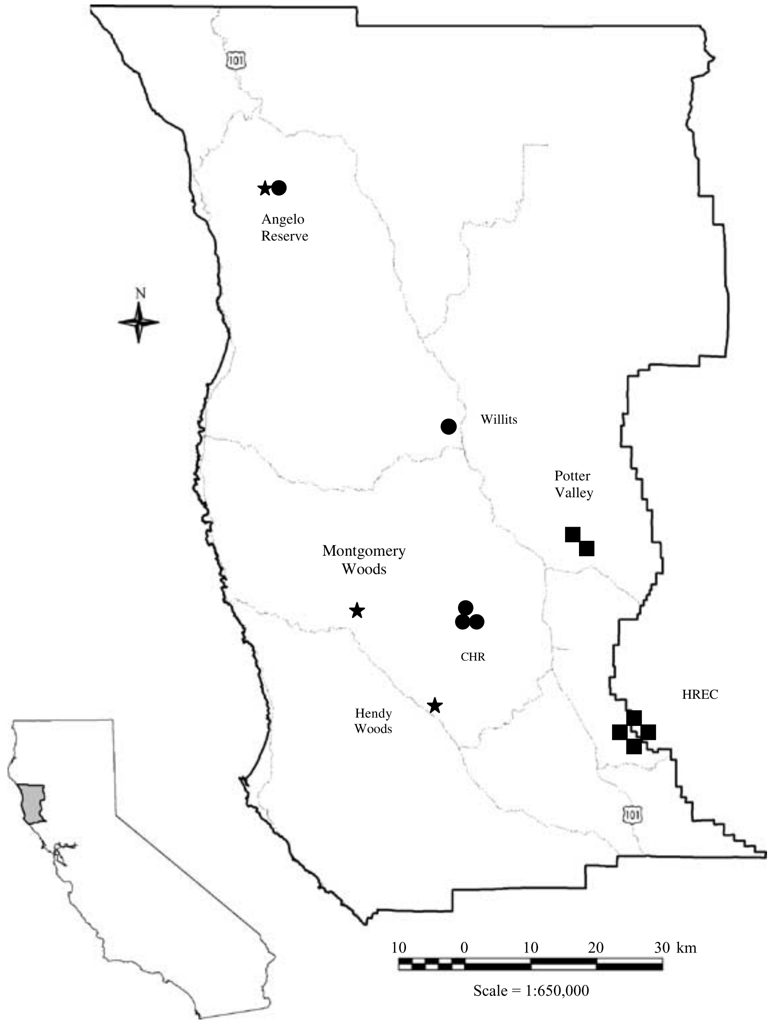

Figure 1. Geographical location of study sites within Mendocino County, northwestern California. Habitat types examined include oak woodland (■), oak/Douglas fir woodland (●), redwood/tanoak woodland (⋆).

Vertebrate trapping/capture and processing

A 4-day small mammal trapping session was carried out once per site from 23 April to 4 May 2002 at HREC, 7–10 May at Potter Valley, 14–25 May at CHR, 28–31 May at Willits, 4–7 June at Angelo and 11–14 June at MWSR and Hendy Woods. The sites at HREC were resampled during 25–28 June. The sampling schedule was designed to coincide, as closely as possible, with the peak activity of questing *I. pacificus* immatures in the above-mentioned areas (see Eisen et al. 2001, 2002, 2003a). Trapping areas ranged in size from 0.65 to 1.61 ha (including a 10-m perimeter around the outer traps in a rectangular grid and 10-m perimeters on each side of a trap line; Table 1), and held 48–120 Sherman live traps (8 cm × 8–10 cm × 23–30 cm; H.B. Sherman Traps Inc., Tallahassee, FL) spaced 10 m apart. Every 10th trap station also held a Tomahawk trap (15 cm × 15 cm × 50 cm; Tomahawk Live Trap, Tomahawk, WI). The traps, baited with a mixture of rolled corn, oats, barley, and cane molasses, were kept open from approximately 15:00 to 08:00 hours.

Captured mammals were anesthetized by intraperitoneal injections with a mixture of ketamine (Ketaset, 100 mg/kg; Fort Dodge Animal Health, Fort Dodge, IA) and medetomidine hydrochloride (Domitor®, 1 mg/kg; Pfizer, Exton, PA). In the case of woodrats and chipmunks, the injections were preceded by a light anesthesia induced by inhalation of isoflurane (IsoFlo®, Abbott Laboratories, North Chicago, IL). The animals were identified to species, sex, reproductive status, and age (juvenile v.s. adult), measured, ear-tagged (National Band and Tag Co., Newport, KY) and examined for presence of ticks. After processing, the anesthesia was reversed by injection of atipamezole hydrochloride (Antisedan®, 5 mg/kg; Pfizer, Exton, PA). After regaining full mobility, which usually occurred within 1–2 h, the mammals were released at the site-of-capture. A subset of the rodents was transferred to tick drop-off cages after the field examination, transported to the University of California at Berkeley Northwest Animal Facility, and held in captivity for 1 week prior to being released at the site-of-capture. Fed ticks detaching from these animals were collected daily.

During the mammalian trapping periods we also estimated the relative abundance of alligator lizards (*E. multicarinata* or *E. coeruleus*) and western fence lizards in each site, including a 10 m perimeter around the site border. Visual searches for lizards were conducted over a 3-day period (1 person-hour per day and site). To maximize the efficiency of this method, searches were conducted only when ambient air temperatures were suitable for lizard activity (20–30 °C). Observed lizards were marked with dilute latex paint (3:1 water to paint; different colors for each day) using a hand-held tree marking gun (Idico Products Co., Miami, FL). A subset of the observed lizards were noosed or captured by hand, identified to species, sex, and age, marked with paint, and examined for ticks. Western fence lizards were considered adults when their snout-to-vent length was $\geq$60 mm.

Ticks removed from mammals or lizards were preserved in 70% ethanol. Larval ticks originating from mammals were cleared for 1 h in 10% potassium hydroxide, slide-mounted in Hoyer's medium and examined by microscopy at 100–400× magnification. Records of *I. spinipalpis* includes *I. neotomae*, which recently was relegated to a junior synonym of *I. spinipalpis* (Norris et al. 1997).

Environmental assessments

For each of the 14 sites, elevation was measured using a Pretel Altiplus A2 altimeter accurate to an increment of 5 m (Suunto, Carlbad, CA), and topographic

Table 1. Relative contribution of potential *B. burgdorferi* s.l.-reservoirs (rodents) versus *Borrelia*-refractory hosts (lizards) as hosts for *I. pacificus* larvae and nymphs.

Habitat type and site	Size of examined area (ha)	Estimated density per ha		Mean no. *I. pacificus* ticks per host				Percentage contribution to tick feeding			
		Rodents[a]	Lizards[b]	Rodents		Lizards		Rodents[c]		Lizards[d]	
				Larvae	Nymphs	Larvae	Nymphs	Larvae	Nymphs	Larvae	Nymphs
Oak woodland											
HREC-Beasley	0.76	6.7	19.6	1.8	0	16.5	20.9	4.9	0	95.1	100
HREC-James II	0.76	10.7	18.3	0.7	0	9.8	21.8	5.4	0	94.6	100
HREC-P.wood	0.80	2.5[e]	16.3[e]	4.0	0	16.3	15.6	4.9	0	95.1	100
HREC-Tank	0.81	29.9	64.2	1.2	0	18.6	8.3	4.0	0	96.0	100
Potter V.-Pond	0.79	18.0	50.4	2.7	0.11	17.5	13.0	7.0	0.4	93.0	99.6
Potter V.-Ravine	1.56	7.7[e]	16.7[e]	2.0	0	56.2	17.6	2.2	0	97.8	100
Mean per site	0.91	12.6	30.9	2.1	0.02	22.5	16.2	4.7	0.1	95.3	99.9
Oak/Douglas fir woodland											
CHR-3	0.90	10.0	34.9	1.5	0	30.3	16.3	1.9	0	98.1	100
CHR-5	1.41	11.3[e]	27.0[e]	1.1	0	34.1	22.2	1.8	0	98.2	100
CHR-9	0.90	7.0	29.7	10.8	0	46.4	37.5	7.0	0	93.0	100
Willits	1.37	43.3	3.9	2.7	0.03	18.5	15.0	68.7	2.9	31.3	97.1
Angelo-Creek	1.61	29.5	14.2	0.9	0	4.5	6.6	36.2	0	63.8	100
Mean per site	1.24	20.2	21.9	3.4	0.01	26.8	19.5	23.1	0.6	76.9	99.4

Table 1. (continued).

Habitat type and site	Size of examined area (ha)	Estimated density per ha		Mean no. *I. pacificus* ticks per host				Percentage contribution to tick feeding			
		Rodents[a]	Lizards[b]	Rodents		Lizards		Rodents[c]		Lizards[d]	
				Larvae	Nymphs	Larvae	Nymphs	Larvae	Nymphs	Larvae	Nymphs
Redwood/tanoak woodland											
Angelo-Redw.	0.65	21.5[e]	0[e]	0.9	0	–	–	100	–	0	–
Hendy Woods	0.91	11.0[e]	2.2[e]	0.5	0.1	2.5	11.0	57.8	5.9	42.2	94.1
Montg. Woods	0.91	4.4[e]	1.1[e]	4.2	0.2	ND[f]	ND	ND	ND	ND	ND
Mean per site	0.82	12.3	1.1	1.9	0.1	NA[g]	NA	NA	NA	NA	NA

[a]Including *Microtus californicus*, *N. fuscipes*, *Peromyscus boylii*, *P. maniculatus*, *P. truei*, and *Tamias senex/ochrogenys*. All three species of *Peromyscus* mice and *N. fuscipes* are known experimental reservoirs for *B. burgdorferi* s.l. (Brown and Lane 1992, 1996; Peavey and Lane 1995). In the case of *Microtus* and *Tamias*, other North American species within the genera are capable of acting as reservoirs for *B. burgdorferi* (e.g., Mather et al. 1989; Markowski et al. 1998).

[b]Including adults of *S. occidentalis*, *E. multicarinata*, and *E. coeruleus*.

[c]Site-specific contributions of rodents calculated as: (rodent density × mean tick infestation × 1.37 [correction factor for 73% field detection efficiency])/((rodent density × mean tick infestation × 1.37) + (lizard density × mean tick infestation)).

[d]Site-specific contributions of lizards calculated as: (lizard density × mean tick infestation)/((lizard density × mean tick infestation) + (rodent density × mean tick infestation × 1.37)).

[e]Density estimate restricted to minimum number of animals known alive.

[f]ND, not determined. The single lizard observed could not be captured and examined for ticks.

[g]NA, not applicable. Available data on tick infestation of lizards were not sufficient for a habitat-wide estimation.

Table 2. Efficiency of field-inspection to detect subadult *Ixodes* spp. ticks infesting *N. fuscipes* woodrats and *Peromyscus* spp. mice.

Tick species and host species (no. hosts examined)	No. larvae/nymphs recovered			Percentage field detection efficiency for subadult ticks (larvae/nymphs)[b]
	Field[a]	Laboratory[a]	Total	
Ixodes pacificus				
N. fuscipes (7)	28/1	11/0	39/1	73 (72/100)
P. boylii (13)	12/0	3/0	15/0	80 (80/NA[c])
P. maniculatus (8)	9/0	4/0	13/0	69 (69/NA)
P. truei (6)	16/0	6/0	22/0	73 (73/NA)
Total (34)	65/1	24/0	89/1	73 (73/100)
Ixodes spinipalpis *and* I. woodi				
N. fus/P. boy (7)	5/2	0/2	5/4	78 (100/50)

[a]All detected attached ticks were removed from rodents during initial field inspections. Directly after these inspections, rodents were placed in drop-off cages and kept in the laboratory for at least 7 days to recover ticks that were not detected during field inspections.
[b]Calculated as the number of ticks detected in the field divided by the total number of ticks recovered in the field and laboratory.
[c]NA, not applicable.

exposure was determined using a compass. Slope was assessed as either flat, mild, moderate or steep. We recorded the number and species of trees and the number and dimensions of logs between each trap station, and average litter depth and habitat type (e.g., woodland or ecotone) at each trap station. Presence of deer sign (e.g., trails, beds, pellet groups, deer sightings), and sightings of other mammals were noted. In addition, local habitat diversity was assessed by recording habitat type (i.e., dense woodland with leaf litter, woodland grass, chaparral, rock outcrop, garden or lawn, water, road, building or other) every 10 m for 100 m in each of the cardinal directions. An overall percentage of each habitat was then calculated per site.

Data analysis

The relative contributions of rodents versus lizards as hosts for *I. pacificus* larvae and nymphs were calculated from site-specific data on levels of tick infestation and host densities (see Table 1). Data on tick infestation were based on field-inspections and corrected for a lower efficiency to detect attached ticks on mammals; all attached ticks are readily visible on lizards, whereas, as shown in Table 2, our field-inspections yielded, on average, 73% of the *I. pacificus* immatures infesting *Peromyscus* spp. mice or dusky-footed woodrats (*N. fuscipes*).

Because sample sizes generally were too low to estimate abundances using mark–release–recapture data, site-specific densities of mammals or lizards were calculated from linear regressions of the number of daily observations of new individuals (y) on the number of individuals previously marked (x). Total population sizes were estimated as the intersect of the regression line with the horizontal axis. In sites where the data did not allow for regression analyses for both mammals and lizards, population sizes for both groups were estimated as the minimum number of individuals known alive. Because the vertebrate abundances were used only in within-site comparisons, the different methods of estimating abundance between sites did not present a problem. Statistical analyses were carried out using the JMP® statistical package (SAS Institute Inc. 1998), and the results were considered significant when $P \leq 0.05$.

Animal health

Animal capture and handling procedures followed protocols on file with the Animal Care and Use Committee at the University of California at Berkeley and were approved by the California Department of Fish and Game.

Results

Small mammals and associated ticks

A total of 4389 trap-nights from late April to mid-June 2002 in oak, oak/Douglas fir, and redwood/tanoak woodlands, with an overall trapping success of 4.9%, yielded 213 individual small mammals (Table 3). Site-specific trapping success ranged from 1 to 13% (data not shown). *Peromyscus* spp. mice (the brush mouse, *P. boylii*; the deer mouse, *P. maniculatus*; the piñon mouse, *P. truei*) were present in all sites examined (data not shown) and accounted for 76–88% of all mammals captured within a specific habitat type (Table 3). *Neotoma fuscipes* was encountered in all habitat types though it was recorded only from 33–50% of the sites examined in a specific habitat type. Low numbers of California meadow voles (*M. californicus*) and *Tamias* spp. chipmunks (the shadow chipmunk, *T. senex*, or the redwood chipmunk, *T. ochrogenys*: these species are indistinguishable under field conditions) were trapped in oak/Douglas fir and redwood/tanoak woodlands. Sonoma chipmunks (*T. sonomae*) were observed within or adjacent to two oak woodland sites. Finally, incidental captures included two juvenile opossums (*Didelphis virginiana*), a northern flying squirrel (*Glaucomys sabrinus*), and a western gray squirrel (*Sciurus griseus*) (data not shown).

Mammals were infested by four species of *Ixodes* ticks (Table 3; *I. angustus*, *I. pacificus*, *I. spinipalpis*, *I. woodi*) and *Dermacentor occidentalis*. Data for *D. occidentalis* are not presented because, in most cases, the sampling periods preceded the onset of seasonal activity by the subadult stages. *Ixodes pacificus* occurred in all 14 sites examined. Subadult *I. pacificus* were recorded from all host species examined and accounted for 92% of all *Ixodes* spp. ticks collected from mammals (Table 3). *Ixodes angustus* was recorded from all three redwood/tanoak

Table 3. Species composition of captured rodents and lizards, and total number of associated *Ixodes* spp. ticks recovered in dense woodlands, Mendocino County, 22 April – 14 June, 2002.

Habitat type[a] and host species[b] (no. hosts examined)	Total no. larval/nymphal/adult ticks recovered[c]			
	I. angustus	*I. pacificus*	*I. spinipalpis*	*I. woodi*
Oak woodland				
N. fus (9)	0/0/0	53/1/0	7/1/0	15/9/0
P. boy (28)	0/0/0	28/0/0	0/0/0	8/0/0
P. man (5)	0/0/0	14/0/0	0/0/0	0/0/0
P. tru (16)	0/0/0	82/1/0	3/0/0	0/0/0
Mammals (58)	0/0/0	177/2/0	10/1/0	23/9/0
Elg. spp. (3)	0/0/0	38/30/0	0/0/0	0/0/0
Sce. occ (75)	0/0/0	1934/1209/0	0/0/0	0/0/0
Lizards (78)	0/0/0	1972/1239/0	0/0/0	0/0/0
Oak/Douglas fir woodland				
M. cal (1)	0/0/0	2/0/0	0/0/0	0/0/0
N. fus (8)	0/0/0	102/1/0	0/1/0	0/0/0
P. boy (24)	0/0/0	37/0/0	0/0/0	0/0/0
P. man (72)	1/0/1	198/0/0	1/1/0	0/0/0
P. tru (15)	0/0/0	70/0/0	0/0/0	0/0/0
Tam. spp. (2)	0/0/0	6/0/0	0/0/0	0/0/0
Mammals (126)	1/0/1	415/1/0	1/2/0	0/0/0
Elg. spp. (6)	0/0/0	468/194/0	0/0/0	0/0/0
Sce. occ (50)	0/0/0	1191/919/0	0/0/0	0/0/0
Lizards (56)	0/0/0	1659/1113/0	0/0/0	0/0/0
Redwood/tanoak woodland				
M. cal (3)	3/0/0	4/0/0	0/0/0	0/0/0
N. fus (3)	0/0/0	3/1/0	0/1/0	0/0/0
P. boy (4)	0/0/0	4/0/0	0/0/0	0/0/0
P. man (15)	1/0/1	11/0/0	0/1/0	0/0/0
P. tru (3)	0/0/0	2/0/0	0/0/0	0/0/0
Tam. spp. (1)	0/1/0	19/1/0	0/0/0	0/0/0
Mammals (29)	4/1/1	42/2/0	0/2/0	0/0/0
Elg. spp. (2)	0/0/0	5/22/0	0/0/0	0/0/0
Lizards (2)	0/0/0	5/22/0	0/0/0	0/0/0

[a]Including six oak woodland, five oak/Douglas fir woodland, and three redwood/tanoak woodland sites.
[b]Mammals; M. cal (*Microtus californicus*), N. fus (*Neotoma fuscipes*), P. boy (*Peromyscus boylii*), P. man (*P. maniculatus*), P. tru (*P. truei*), Tam. spp. (*Tamias senex/T. ochrogenys*). Lizards; Elg. spp. (*Elgaria multicarinata* or *E. coeruleus*), Sce. occ (*Sceloporus occidentalis*).
[c]Including all ticks recovered in the field or laboratory.

sites (Angelo-Redwood, Hendy Woods, MWSR) and one oak/Douglas fir woodland site in the northern part of the county (Angelo-Creek). Hosts of *I. angustus* included *M. californicus*, *P. maniculatus*, and *T. senex/ochrogenys* (Table 3).

Ixodes spinipalpis was recorded from three of six oak woodland sites (both Potter Valley sites and HREC-Beasley), one oak/Douglas fir woodland site (Willits), and one redwood/tanoak woodland site (Hendy Woods). Hosts of *I. spinipalpis* included *N. fuscipes*, *P. maniculatus*, and *P. truei* (Table 3). Notably, *I. spinipalpis* ticks were found in four of six sites with *N. fuscipes* present, as compared to one of eight sites without *N. fuscipes* (data not shown). *Ixodes woodi* was collected from a single oak woodland site (HREC-Tank), where it infested all of five *N. fuscipes* and 23% of 13 *Peromyscus* spp. mice examined (Table 3). Two of 697 *Ixodes* spp. ticks (0.3%) could not be identified to species.

Simultaneous infestation by two of the above-mentioned ticks was recorded for seven *Peromyscus* spp. mice (one with *I. pacificus*/*I. angustus*, four with *I. pacificus*/*I. spinipalpis*, one with *I. pacificus*/*I. woodi*, and one with *I. angustus*/*I. spinipalpis*), 10 dusky-footed woodrats (five each with *I. pacificus*/*I. spinipalpis* and *I. pacificus*/*I. woodi*), one California meadow vole (*I. pacificus*/*I. angustus*), and a chipmunk (*I. pacificus*/*I. angustus*).

Lizards and associated ticks

Visual searches focused on *S. occidentalis* and *Elgaria* spp. alligator lizards. Other observed lizards included five western skinks (*Eumeces skiltonianus*). *Sceloporus occidentalis* was far more abundant than *Elgaria* spp. lizards in oak woodland and in most oak/Douglas fir sites, but rare in north-facing oak/Douglas fir sites with closed canopies (e.g., Willits) and absent from the redwood/tanoak habitat (Table 3, site-specific data not shown). From late April to mid-June, 125 *S. occidentalis* and 11 *Elgaria* spp. lizards were examined for tick infestation. The only tick species infesting these lizards was *I. pacificus* (Table 3).

Infestation by I. pacificus

Overall, *I. pacificus* larvae were recorded from 96% of 136 lizards and 95% of 20 *N. fuscipes*, but only from 59% of 182 *Peromyscus* spp. mice examined (Table 4; Fisher's exact two-tailed test, mice v.s. lizards or woodrats, $P < 0.01$ in both cases). Nymphal ticks were found on 99% of the lizards but only on 15% of the *N. fuscipes* and none of the *Peromyscus* spp. mice (Table 4; lizards v.s. woodrats or mice, $P < 0.001$ in both cases).

In oak and oak/Douglas fir woodlands, *S. occidentalis*, as compared to rodents, carried 3- to 25-fold greater mean larval and 140- to more than 180-fold greater mean nymphal loads (Table 4). Notably, the median nymphal infestation was 0 for both woodrats and *Peromyscus* spp. mice in all habitat types (Table 4). To account for spatial variation in density of questing ticks within sampling sites, statistical comparisons of *I. pacificus* loads on lizards versus rodents were restricted to include 19 lizard–*Peromyscus* spp. mouse pairings, where the lizard and mouse were

Table 4. Infestation of selected vertebrates by *I. pacificus* in dense woodlands, Mendocino County, 22 April – 14 June 2002.

Habitat type[a] and host species[b] (no. hosts examined)	Percentage hosts with		Mean		Level of infestation[c]			
					Mean intensity		Median	
	Larvae	Nymphs	Larvae	Nymphs	Larvae	Nymphs	Larvae	Nymphs
Oak woodlands								
N. fus (9)	100	11	5.6	0.1	5.6	1.0	4.0	0
Per. spp. (49)	53	0	1.0	0	1.8	0	0	0
Sce. occ (75)	94	98	25.8	16.1	25.8	16.1	10.0	11.0
Elg. spp. (3)	100	100	12.7	10.0	12.7	10.0	16.0	11.0
Oak/Douglas fir woodlands								
N. fus (8)	100	13	8.3	0.1	8.3	1.0	8.0	0
Per. spp. (111)	66	0	1.7	0	2.6	0	1.0	0
Sce. occ (50)	96	98	23.2	18.4	23.2	18.4	16.5	16.0
Elg. spp. (6)	100	100	78.0	32.3	78.0	32.3	48.5	19.5
Redwood/tanoak woodlands								
N. fus (3)	67	33	0.7	0.3	1.0	0.5	1.0	0
Per. spp. (22)	41	0	0.8	0	1.9	0	0	0
Elg. spp. (2)	50	100	2.5	11.0	2.5	11.0	2.5	11.0

[a]Including six oak woodland, five oak/Douglas fir woodland, and three redwood/tanoak woodland sites.
[b]N. fus (*Neotoma fuscipes*), Per. spp. (*Peromyscus boylii*, *P. maniculatus*, or *P. truei*), Sce. occ (*Sceloporus occidentalis*), Elg. spp. (*Elgaria multicarinata* or *E. coeruleus*).
[c]Including data only from field examinations. Mean and median includes all animals. Mean intensity includes only infested animals.

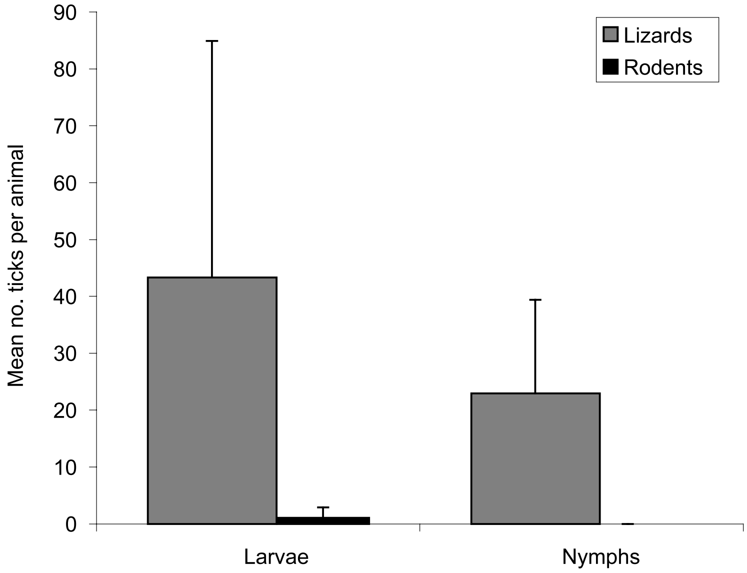

Figure 2. Mean (S.D.) number of *I. pacificus* larvae or nymphs infesting lizards (*S. occidentalis*, *Elgaria* spp.) versus *Peromyscus* spp. mice. Data based on 19 lizard-mouse pairings where the lizard and mouse were captured within 10 m of each other.

captured within 10 m of each other in oak/Douglas fir woodlands. This analysis revealed that lizards harbored 36 times more larvae and >190 times more nymphs than *Peromyscus* spp. mice (Figure 2; Wilcoxon's test with normal approximation, $t_s \geq 4.72$, df = 36, $P < 0.001$ in both cases).

We also were able to compare infestation levels by *I. pacificus* larvae on *S. occidentalis* and *Peromyscus* spp. mice during 23 April–5 May versus 25–28 June at the HREC Beasley, Tank, and James II sites (Figure 3). From late April/early May to late June, the proportion of hosts infested by larvae remained stable for *S. occidentalis* (95 vs. 90% infested) but tended to increase for *Peromyscus* spp. mice (27 vs. 57% infested; $P = 0.07$). Over the same period, larval loads decreased four-fold on *S. occidentalis* ($t_s = -4.35$, df = 67, $P < 0.001$) but increased three-fold on *Peromyscus* spp. mice ($t_s = 2.25$, df = 43, $P = 0.02$).

Efficiency of field-inspections to detect attached ticks

The efficiency of field-inspections to detect *I. pacificus* immatures on rodents ranged from 69% for *P. maniculatus* to 80% for *P. boylii*, with an average of 73% for all four rodent species included (Table 2). Although the sample size was small, a similar detection efficiency (78%) was indicated for nidicolous *Ixodes* ticks (*I. spinipalpis* and *I. woodi*) (Table 2).

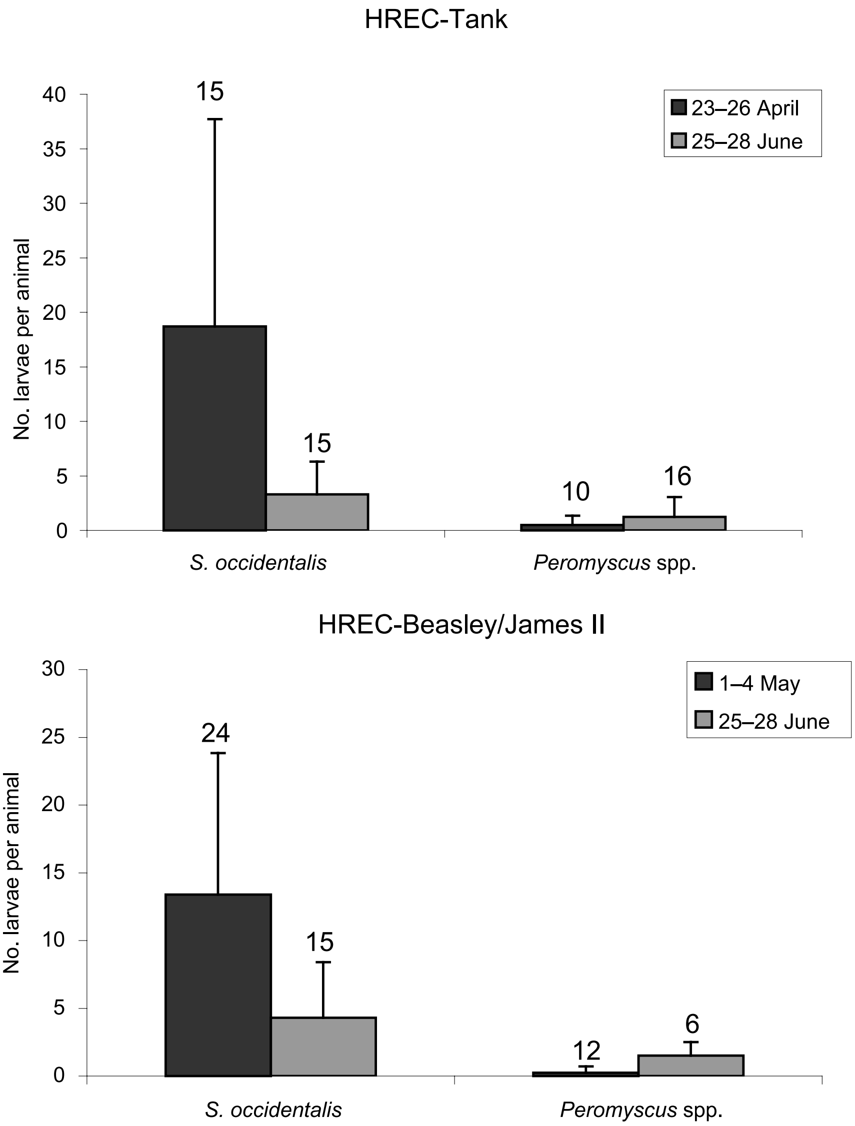

Figure 3. Mean (S.D.) number of *I. pacificus* larvae infesting *S. occidentalis* lizards or *Peromyscus* spp. mice during 23 April–5 May versus 25–28 June at HREC-Tank and HREC Beasley/James II.

Relative contribution of potential Borrelia-*reservoirs (rodents/chipmunks) versus* Borrelia-*refractory lizards as hosts of* I. pacificus *immatures*

Site-specific relative contributions of rodents versus lizards as hosts of *I. pacificus* immatures are shown in Table 1. In oak woodland sites and oak/Douglas fir sites at

CHR, lizards were estimated to serve as hosts for 93–98% of all larvae and ≥99.6% of all nymphs infesting lizards or rodents. In contrast, the estimated contribution of rodents as larval hosts reached 36–69% in two oak/Douglas fir sites in northern Mendocino County (Willits, Angelo) and the redwood/tanoak site at Hendy Woods. However, lizards still accounted for 94–100% of all nymphal feedings in these sites. Overall, the proportion of larvae infesting rodents increased from 4.7% in oak woodland to 23.1% in oak/Douglas fir woodland and >50% in redwood/tanoak woodland, whereas the vast majority of nymphs infested lizards in all habitat types (Tables 1 and 3).

Environmental correlates of host abundance and I. pacificus *loads*

The estimated density of lizards was positively associated with the proportion of woodland ecotone, relative to woodland, present within the sampling boundaries ($F_{1,12} = 16.86$; $P = 0.002$, $r^2 = 0.58$) and negatively associated with the percentage of surrounding habitat categorized as dense woodland with a closed canopy cover ($F_{1,12} = 6.92$, $P = 0.02$, $r^2 = 0.37$). With regards to tick load, the mean number of larvae per lizard decreased as the proportion of surrounding habitat categorized as leaf litter increased ($F_{1,10} = 4.85$, $P = 0.05$, $r^2 = 0.32$). Further, the mean number of nymphs per lizard increased with elevation ($F_{1,10} = 4.94$, $P = 0.05$, $r^2 = 0.33$). No other environmental correlates (see Materials and methods section) were significantly correlated with lizard or rodent density or tick loads on lizards or rodents.

Discussion

Vertebrate and tick species composition

As in earlier studies of rodent species composition in chaparral and woodland-grass habitats in northern California, dusky-footed woodrats and, especially, *Peromyscus* spp. mice predominated in woodland habitats (e.g., Lane et al. 1981; Lane 1990; Lane and Loye 1991; Casher et al. 2002; Table 3). Rodents present in chaparral or woodland-grass habitats, but apparently rare or absent in dense woodlands, include the California meadow vole, the California kangaroo rat (*D. californicus*), and the western harvest mouse (*Reithrodontomys megalotis*) (Casher et al. 2002; Table 3). As expected from previous studies on lizards in California, the western fence lizard was the most commonly encountered species in oak and oak/Douglas fir habitats (Block and Morrison 1998; Table 3). However, alligator lizards predominated in shady oak woodland microhabitats and oak/Douglas fir sites with northern exposures, and were the only lizards present in the moist and cool redwood/tanoak woodlands.

As shown in Table 3, rodents yielded three species of *Ixodes* ticks previously shown to be vectors of *B. burgdorferi* s.l.: *Ixodes angustus*, *I. pacificus*, and *I. spinipalpis* (Brown and Lane 1992; Lane et al. 1994; Keirans et al. 1996; Peavey et al. 2000). *Ixodes pacificus* occurred in all sites examined, at least two vectors were recorded from eight of the 14 sites, and all three vectors were present in the Hendy Woods site. In addition, *I. woodi*, a tick species not yet experimentally evaluated as a vector of *B. burgdorferi* s.l., commonly infested rodents in an oak woodland site at HREC. Simultaneous infestation by two of the above-mentioned four ticks was recorded for 19 of 213 (8.9%) examined mammals. In accordance with a previous study focusing on chaparral and woodland-grass habitats (Casher et al. 2002), we found that most *I. spinipalpis* and *I. woodi* ticks encountered in dense woodlands were associated with dusky-footed woodrats (63 and 75% of ticks collected from woodrats, respectively). County-wide, *I. spinipalpis* was recorded from all three woodland habitats examined, but presence of this tick was usually related to that of the dusky-footed woodrat.

Although *I. pacificus* is the *B. burgdorferi* s.l.-vector most commonly infesting rodents in all examined habitat types in northern California, rodents, especially *Peromyscus* spp. mice, typically are infested by larvae but very few nymphs (e.g., Lane 1990; Lane and Loye 1991; Peavey et al. 1997; Wright et al. 2000; Casher et al. 2002; Table 3). Because questing *I. pacificus* larvae rarely are infected with *B. burgdorferi* s.l. (Lane and Burgdorfer 1987; Schoeler and Lane 1993), the potential of *I. pacificus* to serve as an efficient enzootic spirochetal vector remains unclear.

Patterns of infestation by I. pacificus

Within a given habitat, western fence lizards typically carry greater loads of *I. pacificus* immatures than rodents (e.g., Casher et al. 2002; Table 4). This observation was similar to the southeastern United States where *I. scapularis* immatures infest lizards more heavily than rodents (Apperson et al. 1993). As the distribution of questing immature *Ixodes* ticks typically is highly aggregated (e.g., Daniels and Fish 1990; Tälleklint-Eisen and Lane 2000), tick loads are probably related, in part, to host movement patterns. To control for aggregated tick distributions when comparing *I. pacificus* loads on lizards versus *Peromyscus* spp. mice, we used data from lizard-mouse pairings where the animals were captured within 10 m of each other. The finding that lizards still carried 36 times more larvae and >190 times more nymphs than the mice suggests that some aspect of lizard behavior (e.g., choice of resting microhabitat) results in increased exposure to *I. pacificus* immatures. Alternatively, *I. pacificus* immatures, especially the nymphs, may avoid feeding on rodents; low attachment rates (0–12%) for *I. pacificus* nymphs experimentally exposed to *Peromyscus* spp. mice have been recorded in several laboratory studies (Peavey and Lane 1995; Richter et al. 1996; Eisen et al. 2003b).

Earlier studies indicated that the proportion of western fence lizards infested by *I. pacificus* larvae at HREC in the spring typically exceeds 70% in chaparral and 80% in oak woodlands (e.g., Lane and Loye 1989; Eisen et al. 2001; Casher et al. 2002). In the present county-wide study, 96% of 125 western fence lizards examined were infested by *I. pacificus* larvae. This infestation level is quite impressive, considering that the micro-distribution of questing *Ixodes* larvae (reflecting where fed female ticks deposit their single egg batches) is highly aggregated and that larval dispersion from the hatch site of closely related ticks (*I. ricinus* and *I. scapularis*) is limited to a few meters (e.g., Lees and Milne 1951; Daniels and Fish 1990). Thus, larval infestation rates approaching 100% for western fence lizards suggests the presence of at least one larval focus within the home range of each individual lizard (generally $<80\,m^2$; Davis and Ford 1983). Alternatively, larval batches could have been concentrated in the ecotones, where lizards were most commonly captured. We noted that the mean number of larvae per lizard was negatively associated with an estimate of leaf litter patch size (i.e., the proportion of surrounding area categorized as leaf litter). Within small patches, the ratio of ecotone to contiguous dense leaf litter is high. Therefore, the amount of preferred habitat for lizards and possibly for larvae (e.g., ecotones) is higher in small, relative to large, leaf litter patches, which may increase the encounter rate between lizards and larvae in small patches.

Previous studies at HREC indicated that larval loads on western fence lizards declined from May to late June (Lane and Loye 1989; Eisen et al. 2001), presumably as a result of increasing desiccation-related mortality of questing larvae in late spring. In the present study, larval loads at HREC decreased significantly from late April/early May to late June for western fence lizards but increased for *Peromyscus* spp. mice. This indicates that the decrease in larval loads on the lizards may be related to changes in host or tick behavior, rather than declining numbers of questing larvae. For example, as temperatures increase in the late spring, habitat usage by the western fence lizard tends to shift from primarily terrestrial to semi-arboreal in oak woodlands (R.J.E. and L.E., personal observation). Increasingly hot and dry conditions in late spring also may force a shift in the diel questing activity of larval ticks, resulting in an increased risk of exposure for nocturnally active rodents and a decreased risk for diurnally active lizards. We conclude that further studies on the microhabitat usage of rodents, lizards, and *I. pacificus* immatures in spring and early summer are needed to explain the observed interactions at the tick–host interface.

Relative contribution of rodents versus lizards as hosts of I. pacificus *immatures*

The utilization rate of lizards by *I. pacificus* larvae, as compared to potential *B. burgdorferi* s.l.-reservoirs (rodents), differed dramatically between habitat types in Mendocino County. The results from oak/Douglas fir woodlands in the southern part of the county (CHR-sites) and oak woodlands were similar to those of a previous study in chaparral at HREC (Casher et al. 2002) with lizards (primarily *S. occidentalis*) accounting for 88–98% of all larval feedings on lizards or rodents. In contrast, oak/Douglas fir sites in northern Mendocino County (Willits, Angelo) and redwood/tanoak woodlands typically harbored low numbers of alligator lizards (1–3 per site), and western fence lizards were rare or absent. Consequently, the relative contribution of rodents as larval hosts exceeded 50% in most of these sites. A future study will determine how closely these differing patterns of host utilization by *I. pacificus* larvae are correlated with the prevalence of infection with human disease agents in questing nymphs of the same generational cohort.

The within-site distribution of lizards in oak/Douglas fir woodlands in southern Mendocino County and oak woodlands typically was highly aggregated (data not shown), with clusters of western fence lizards occupying microhabitats with open canopies and only alligator lizards utilizing the more shady parts of the sites. Thus, the contribution of lizards as larval hosts probably ranges from negligible to very high in different parts of a given site. Consequently, pockets of nymphs with high infection prevalences could occur even within areas where, site-wide, *Borrelia*-refractory lizards are estimated to account for the vast majority of all larval feedings.

The utilization rate by *I. pacificus* nymphs of lizards, as compared to rodents, exceeded 99% in 10 of 12 cases and 94% in all 12 sites where host usage could be quantified (Table 1). This concurs with previous estimates from chaparral and woodland-grass habitats at HREC (Casher et al. 2002), and strengthens the hypothesis that observed decreases in *B. burgdorferi* s.l. infection rates from *I. pacificus* nymphs to adults of the same generational cohort (e.g., Lane et al. 2001, R.J.E, L.E., J. Mun and R.S.L, unpublished data) results from a near exclusive usage of *Borrelia*-refractory lizard hosts by the nymphal stage. *Sceloporus occidentalis* and *E. multicarinata* harbor a borreliacidal factor in their blood, and *B. burgdorferi*-infected ticks lose their infection after bloodmeals on these hosts (Lane and Quistad 1998; Wright et al. 1998). Moreover, two oak/Douglas fir sites in northern Mendocino County (Angelo and Willits) provided striking examples of differential host usage by *I. pacificus* larvae and nymphs; the relative contribution of potential *B. burgdorferi* s.l.-reservoirs (rodents) in these areas decreased from 36–69% of larval to 0–3% of nymphal feedings.

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