PREDICTING DENSITY OF IXODES PACIFICUS NYMPHS IN DENSE WOODLANDS IN MENDOCINO COUNTY, CALIFORNIA, BASED ON GEOGRAPHIC INFORMATION SYSTEMS AND REMOTE SENSING VERSUS FIELD-DERIVED DATA

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Abstract. Ixodes pacificus nymphs are the primary vectors to humans of Borrelia burgdorferi, the etiologic agent of Lyme disease, in California. We used a supervised classification model, based on remote sensing (RS) data from multi-seasonal Landsat TM 5 images, to identify the key habitat in Mendocino County where humans are exposed to I. pacificus nymphs (woodlands carpeted with leaf litter). The model, based on the normalized difference vegetation index (NDVI), brightness, and wetness, separated the nymphal risk habitat (52.6% of the county) from other habitat types with > 93% user and producer accuracies. Next, we determined the density of questing nymphs in 62 woodland-leaf areas located throughout Mendocino County and created forward-stepwise regression models explaining the variation in nymphal density based on traits attainable by a lay-person in the field (e.g., tree species present, deer signs; $r^2 = 0.43$, $P < 0.0001$), or geographic information systems (GIS)/RS-based environmental data ($r^2 = 0.50$, $P < 0.0001$). The GIS/RS model, using July NDVI, November greenness, a coastal influence category, May solar insolation, November hours of sunlight, and dominant hydrologic grouping as input variables, was 22% more accurate in predicting nymphal density at 16 validation sites ($r^2 = 0.72$) than the field-derived data model ($r^2 = 0.50$). The habitat classification and GIS/RS models were combined to create a continuous nymphal density surface for the entirety of Mendocino County. This risk surface showed that 11.9% of the county was classified as habitat posing at least moderate risk of human exposure to nymphs (> 6.4 nymphs per 100 m$^2$). Furthermore, high-risk areas (> 10.5 nymphs per 100 m$^2$; 1.7% of the county) tended to cluster in the central interior and most heavily populated region of Mendocino County, but were rare in the proximity of coastal population centers.

INTRODUCTION

The nymphal stages of the western black-legged tick Ixodes pacificus and the black-legged tick I. scapularis are considered the primary vectors of Borrelia burgdorferi, the causative agent of Lyme disease in North America, in the far western and eastern United States, respectively. Although several studies have indicated that the density of host-seeking nymphal I. scapularis is a good predictor of temporal or spatial Lyme disease risk, attempts to create large-scale predictive models of nymphal density based on environmental geographic information system (GIS)–derived or remote sensing (RS)–derived data have been lacking in North America. The distribution and abundance of various disease vectors, including anopheline mosquitoes, tsetse flies, and ticks, have been modeled based on remotely sensed correlates. Several reviews also provide information on the use of GIS and RS data in relation to vector-borne disease modeling.

Hereafter published data on spatial distribution patterns of I. pacificus in California include county records showing where this tick is established or reported and points data for incidental records of ticks collected from vegetation or during examination of various animals. Unfortunately, neither data set is suitable to create spatially explicit predictive models for nymphal density patterns. Previous studies from Mendocino County, a high-risk area for Lyme disease in California, demonstrated that open grasslands, woodlands carpeted with grass, and chaparral represent risk habitats for exposure to I. pacificus adults, whereas risk of exposure to the nymphal stage is minimal in these habitats (Waggett CE, 2004. Landscape scale patterns in disease ecology: assessing risk of exposure to Lyme borreliosis in a highly endemic region of northern California. Ph.D. dissertation, University of California, Berkeley). In contrast, host-seeking nymphs are readily collected by drag sampling or during normal human activities in woodlands with ground cover dominated by leaves or fir needles (hereinafter called woodland-leaf [WL]), whereas adults rarely are found questing in such areas (Waggett CE, 2004. Landscape scale patterns in disease ecology: assessing risk of exposure to Lyme borreliosis in a highly endemic region of northern California. Ph.D. dissertation, University of California, Berkeley). Moreover, preliminary studies suggested that human risk of exposure to I. pacificus nymphs differs dramatically between WL areas dominated by coniferous redwoods or hardwoods in Mendocino County.

To create a predictive spatial model of nymphal density patterns in Mendocino County, we initiated a study where nymphs were collected from 78 woodland-leaf/fir needle dominated sites representing five major sub-types (redwood, pine, hardwood, hardwood/conifer, and tanoak). We had three main objectives. The first was to create a statistical model explaining the variation in nymphal density based on site-specific characteristics easily attained by a lay-person in the field (e.g., tree species present, elevation, slope, aspect). The second was to create a county-wide model of nymphal density based on GIS/RS-derived data. The third was to compare the predictive capability of the models based on GIS/RS-derived versus field-derived data. In addition, a lack of...
existing GIS-based habitat classifications for northern California that can distinguish between woodlands with a ground cover of leaf litter versus herbaceous vegetation forced us to create such a GIS data layer.

MATERIALS AND METHODS

Study sites. Mendocino County, a climatically and ecologically diverse area encompassing approximately 9,090 km² in northwestern California, extends approximately 130 km along the coast of the Pacific Ocean and up to 80 km inland from the coastline. Climatic conditions and habitat types of Mendocino County were previously described.27–29 Woodland-leaf sampling sites were classified as redwood (n = 10), pine (n = 11), hardwood (n = 19), hardwood/conifer (n = 22), mixed tanoak/madrone or Douglas fir with a redwood influence (n = 4), or tanoak (n = 12). Sites belonging to each of these categories are presented in Figure 1. The WL-redwood habitats were dominated by coast redwoods (Sequoia sempervirens) (≥ 65% of the trees counted in sites were categorized as coast redwood). Other tree species commonly present within this habitat type included California bay (Umbellularia californica), Douglas fir (Pseudotsuga menziesii), and tanoak (Lithocarpus densiflorus). The WL-pine category combines coastal and inland sites where dominant tree species include coastal pine (Pinus spp.) and redwood/Douglas fir (≥ 90% for three coastal sites) and Ponderosa pine (Pinus ponderosa), and Douglas fir (≥ 65% for eight inland pine sites). The WL-hardwood category is defined as sites with ≥ 90% of the trees in sites categorized as hardwoods (Quercus spp. oak, Madrone (Arbutus menziesii), and California Bay (Umbellularia californica), with tanoak rare (< 5%) and conifers absent or present only as an isolated tree or as saplings. In contrast, WL-hardwood/conifer sites included the hardwoods listed above, and conifers (Douglas fir, Ponderosa pine) were present. Redwoods were lacking in these sites or their influence was minimal (i.e., isolated trees or saplings counted in sites). The WL-tanoak sites were comprised of tanoak and redwood or bay and redwood. Quercus spp. oaks were absent or rare within these sites and redwood trees were common in or within 100–200 m of all sites. Four sites did not fit within any of the categories and were classified as mixed tanoak/madrone and Douglas fir with a redwood influence.

Tick sampling and environmental assessments. Ticks were collected by dragging a white flannel blanket, 1 m × 1.25 m, along fixed 15-m transect lines. The blanket was examined for presence of ticks every 15 m. The total sampling effort per sampling occasion represents 50 transects of 15 m² each for a total coverage of 750 m² of dense woodland with a leaf or fir needle litter ground cover. Sampling was conducted twice per site with a first sample from April 28 to May 14, 2004 and a second from May 17 to June 4, 2004. This sampling period corresponds to the peak activity period for I. pacificus nymphs throughout Mendocino County; a previous seasonality study included sites from the extreme southeastern and northwestern parts of the county.27

Presence of deer signs and woodrat nests, exposure, slope, tree species present, and abundance of logs were examined on a single occasion in each site. All animal sightings in the sites were noted for each site visit. The exact location of each sampling area was determined by a Trimble Geo XT (Trimble Corp., Sunnyvale, CA) global positioning system (GPS). Additional site-specific habitat characteristics were derived from layers included in the GIS, as described below.

Construction of the RS habitat classification model. Landsat TM image processing. Landsat TM5 images (path 45, rows 32–33) taken during all seasons (May 11, 2002, July 14, 2002, November 19, 2002, and February 7, 2003) were used. The quality of the images was good with less than 10% cloud cover. Within the clip area to be classified, no clouds were present. Images were georeferenced to a universal transverse mercator (UTM zone 10 NAD 1927) grid based on 14 ground-control points (GCPs) selected from United States Geological Survey (USGS) 7.5-minute quadrangle topographic maps, USGS digital orthophoto quarter quadrangles, and 1:24,000-scale roads and streams digital line graph data derived from 7.5-minute quad maps. Number and selection of GCPs followed guidelines provided by PCI Geomatics (Ontario, CA); GCPs were evenly distributed throughout the scene and represented a wide range in elevation (35–1,437 m). All root mean square errors were less than one pixel (30 × 30 m). The images were orthorectified with a merged 30-meter USGS digital elevation model (DEM) that covered the entire image area. Corrected images were reprojected into TealAlbers

FIGURE 1. Location of sampling sites in Mendocino County, California, classified as redwood (*, n = 10), coastal pine (○, n = 3), inland pine (□, n = 8), hardwood (●, n = 19), mixed hardwood/conifer (■, n = 22), tanoak (+, n = 12), and mixed tanoak/Pacific madrone/Douglas fir/redwood (▲, n = 4). The geographic area of coastal influence, with woodlands where redwoods can be found, is shaded in gray. Location of Mendocino County within California is shown in the inset.
zone 10 NAD 1927. Georeferencing, orthorectification, and supervised classifications were performed using PCI Geomatics version 9.0 software.

**Satellite variables used for supervised classifications.** To determine the best predictor of habitat type, we calculated the normalized difference vegetation index (NDVI) and tasseled cap brightness, greenness, and wetness (BGW), as well as between-scene changes in each, using the TM images for each of the four dates. NDVI combines the red and near-infrared bands (NDVI = [band 4 - band 3]/[band 4 + band 3]). The tasseled cap BGW combine the six non-thermal bands, and were calculated following the method of Crist and others.\(^{30}\) Brightness is related to soil reflectance, greenness is strongly related to amount of vegetation, and wetness is related to canopy and soil moisture.\(^{31,32}\) Differences between images in BGW and NDVI were calculated using the raster calculator in ArcMap (Arc8; Environmental Systems Research Institute, Redlands, CA).

**Supervised classification.** Training site pixels (30 m × 30 m) representing dense woodland habitats with risk of exposure to *I. pacificus* nymphs (total = 417 pixels, including 100 redwood, 50 coastal or inland pine, 50 *Quercus* spp. oak/madrona hardwood, 100 mixed oak/madrona and conifer, 101 tanoak, and 16 mixed madrone/tanoak/conifer pixels), grass- or brush-dominated habitats with risk of exposure to *I. pacificus* adults (total = 300 pixels, including 100 chaparral, 100 open grassland, and 100 woodland-grass pixels), or areas with no or minimal risk of exposure to *I. pacificus* ticks (total = 499 pixels, including 100 pear orchard, 100 vineyard, 100 urban, 99 barren, and 100 water pixels) were created based on data collected in the field using a GPS (except for urban, barren and water; these were readily distinguishable using orthorectified aerial photos). All GPS data were differentially corrected using Trimble Pathfinder software, projected to TealAlbers zone 10 NAD 1927, and imported into ArcMap where they were overlaid on orthorectified aerial photos. Training pixels were then selected in Focus (PCI Geomatics version 9.0 software) using the GPS point-data as a reference. The approximately 18,955 km² clip area to be classified included the entirety of Mendocino County, as well as parts of neighboring counties (Humboldt, Trinity, Tehama, Glenn, Lake, and Sonoma) and Pacific coastal waters. Training sites were distributed throughout this area. Supervised classifications were run for the entire clip area using a maximum likelihood algorithm with a null classification. Several iterations of the model, each changing the input channel values (i.e., using various combinations of seasonal NDVI and BGW values), were run to improve the average and overall accuracy of the model. The model was validated by comparing the model classification with both the training pixels and with validation pixels selected from the field-based GPS data representing perimeters of homogeneous habitats.

**Construction of a regression model of risk of human exposure to *I. pacificus* nymphs based on field-derived variables.** Before modeling nymphal density, we tested for spatial autocorrelation of density data at the county scale using Moran’s I statistic (ArcGIS version 9.0; Environmental Systems Research Institute), and found no significant clustering (Moran’s I = 0.16; Z(I) = 1.6). Density of *I. pacificus* nymphs in Mendocino County woodlands was first predicted based on a forward-stepwise regression model created in JMP (SAS Institute, Cary NC) and based on field-derived environmental data. The build set for this model included density data from the same 62 sites used to create the GIS model (see below). Input variables included habitat category (as described in the Materials and Methods), number of logs or stumps, presence or absence of deer signs (e.g. droppings, game trails, beds, deer sightings), wood rat nests, various tree species (i.e., white alder *Alnus rhombifolia*, California buckeye *Aesculus californica*, California bay, Douglas fir, evergreen *Quercus* spp., big leaf maple *Acer macrophyllum*, deciduous *Quercus* spp. oaks, Pacific madrone, *Pinus* spp. pines, coast redwood, and tanoak), aspect, slope, and elevation. With the exception of aspect, slope, and elevation, these traits are unique to the field-derived data model because they could not be derived from satellite imagery and were not available as GIS layers.

The model was validated by creating a linear regression of the model prediction of nymphal density on the actual tick density at 16 drag sampling sites that were not used in the build set. Validation sites were selected randomly from within each habitat type, but each of the five primary habitat categories was represented by at least three sites. The same 16 validation sites were used for the GIS model.

**Construction of a GIS model of risk of human exposure to *I. pacificus* nymphs.** To predict the density of *I. pacificus* nymphs throughout the woodlands in Mendocino County, we created a forward-stepwise regression model using JMP based on density data from 62 of the 78 sites sampled in 2004 and several independent variables. These included NDVI and tasseled cap BGW for four seasons (May 2002, July 2002, November 2002, and February 2003) derived from Landsat TM 5 images, elevation, slope, and aspect (derived from the USGS 10-meter DEMs using the Spatial Analyst in ArcMap), solar insolation and hours of sun exposure for four dates corresponding with those of the Landsat images (derived from USGS 30-meter DEM using ArcInfo version 8.3; Environmental Systems Research Institute), annual mean precipitation from 1961 to 1990 (Water and Climate Center of the Natural Resources Conservation Service, Portland, OR), base 50F (10°C) annual mean growing degree days (Spatial Climate Analysis Service, Oregon State University, Corvallis, OR), and hydrologic grouping (based on data from United States Department of Agriculture Natural Resources Conservation Service Soil Survey Geographic database).

Hydrologic soil groups typically are classified as groups A (soils with high infiltration rate when thoroughly wet), B (moderate infiltration rate), C (slow infiltration rate), and D (very slow infiltration rate). Our model uses a classification system suitable for soil types represented in Mendocino County; it compares soils with very slow or slow infiltration rates (C and D) with all others (B, BC–BCD compared with CD–D).

In addition, we created a GIS-layer separating coastal woodlands with presence of redwood from inland woodlands without redwood (Figure 1). This was based on data on the geographic distribution of redwood and mixed redwood/Douglas fir from the 1994 California Department of Forestry and Fire Protection Land Cover Mapping and Monitoring Program (http://frap.cdf.ca.gov/data/frapgisdata/select.asp) with a 500-m buffer to produce a smooth surface. Habitats where people are at risk for nymphal exposure (dense woodlands) were separated from all others by creating analysis masks in ArcMap. The resulting best fit model equation was then applied to each risk pixel within Mendocino County. The
model was validated by creating a linear regression of the model prediction of nymphal density on the actual tick density at 16 drag sampling sites that were not used in the build set.

RESULTS

Habitat classification model. Based on a comparison with training sites, average (85.64%) and overall (84.46%) accuracy in separating habitat types with differing risk of exposure to I. pacificus ticks (exposure to nymphs, exposure to adult ticks, or minimal or no risk of tick exposure) was best when input channels included NDVI and brightness from February and NDVI and wetness from July (Table 1). The kappa coefficient, a measure of accuracy that takes into account agreements expected by chance, was 0.77. Comparisons between model predictions and validation points yielded an overall model accuracy of 82.64% (Table 1). Producer accuracies (percentage of validation pixels correctly categorized by the model) ranged from 93.71% for woodland habitats with risk of exposure to I. pacificus nymphs to 82.20% for grass- or brush-dominated habitats with risk of exposure to I. pacificus adults and to 73.48% for habitats with minimal or no risk of tick exposure (Table 1). User accuracies (percentage of model pixels correctly categorized by field validation) ranged from 93.38% for nymphal risk habitats to 82.39% for minimal or no risk habitats and to 76.97% for adult risk habitats.

Based on our model, 36.23% of the included clip area was categorized as woodland habitats with risk of exposure to I. pacificus nymphs, 23.49% as grass- or brush-dominated habitats with risk of exposure to I. pacificus adults, and 33.24% as nymphs (woodlands with leaf or fir needle litter) are I. pacificus adults, and 33.24% as nymphs (woodlands with leaf or fir needle litter) are

Habitat-associated variation in nymphal density. The study yielded 4,312 I. pacificus nymphs and 119 adults (44 females and 75 males). Nymphs were present in 77 of the 78 sites sampled and 1 nymph was collected from leaf litter adjacent to the remaining site. Average nymphal density was highly variable among sites with a range of 0 to 24.6 nymphs per 100 m². The geographic distribution of sites with nymphal density classified as high (>10.50 nymphs per 100 m²), moderate (6.41–10.50 per 100 m²), low (2.51–6.40 per 100 m²), and very low (< 2.5 per 100 m²) are shown in Figure 3. Peak nymphal density was similar between hardwood (mean peak density = 5.34 nymphs per 100 m²) and hardwood/conifer sites (7.43 nymphs per 100 m²), but significantly higher in either hardwood or hardwood/conifer sites relative to all other habitat classes (redwood (1.02 nymphs per 100 m²), pine (1.57 nymphs per 100 m²), and tanoak (1.53 nymphs per 100 m²); \( \chi^2 \geq 10.01, \) degrees of freedom \( [df] = 1, P < 0.0016 \) by Wilcoxon test for all 6 pairwise comparisons). In addition, nymphal density was significantly higher in sites where deciduous Quercus spp., Pacific madrone or California buckeye were present relative to absent \( \chi^2 \geq 5.20, \) df = 1, \( P < 0.02 \) in all three cases), and significantly lower where redwood was present \( \chi^2 = 22.99, \) df = 1, \( P < 0.0001 \). Nymphal density increased between the first and second samplings in 30 sites, decreased in 38 sites, and remained the same in 10 sites. As expected, nymphal density tended to decrease from the first to second sample in the warm and dry hardwood sites in the southeast (15 of 19 sites with a decrease), whereas increases more commonly were observed in cooler and more moist sites to the north and west.

![Figure 2. Habitat classification of Mendocino County based on Landsat TM5 imagery. Habitats with primary risk of exposure to Ixodes pacificus nymphs (woodlands with leaf or fir needle litter) are shown in green, those with primary risk of exposure to I. pacificus adults (chaparral, grass, woodland with grass) are shown in yellow, and habitats with minimal or no risk of exposure to ticks (agricultural, barren, urban or water) are shown in blue. Map also displays major highways. The boundary of Mendocino County is shown in black. This figure appears in color at www.ajtmh.org.]

| Table 1 Training and validation pixel confusion matrices for a Mendocino County, California remote sensing (NDVI/brightness/wetness) model based on a 30 × 30 m pixel size from Landsat TM5 imagery* |
|---|---|---|
| **Model classification**
| **Training site type**
| **Percentage pixels correctly classified**
| W-NY | GCGW-AD | MIN-NO |
| Training pixel matrix |
| W-NY | 376 | 2 | 0 | 99.47 |
| GCGW-AD | 16 | 273 | 103 | 69.64 |
| MIN-NO | 13 | 19 | 378 | 92.19 |
| Null | 12 | 6 | 18 | — |
| Percent correct§ | 90.17 | 91.00 | 75.75 | 84.46¶ |
| Validation pixel matrix |
| W-NY | 536 | 30 | 8 | 93.38 |
| GCGW-AD | 17 | 605 | 164 | 76.97 |
| MIN-NO | 14 | 89 | 482 | 82.39 |
| Null | 5 | 12 | 2 | — |
| Percent correct§ | 93.71 | 82.20 | 73.48 | 82.64¶

* NDVI-normalized difference vegetation index
† Woodland-leaf/fir needle habitats with risk of exposure primarily to Ixodes pacificus nymphs; W-NY = grassland, chaparral, and grassy woodland habitats with risk of exposure primarily to I. pacificus adults; GCGW-AD = other habitats (orchard, vineyard, barren, urban, water) with minimal or no risk of tick exposure; MIN-NO = habitat not categorized by the model Null
‡ User accuracy
§ Overall accuracy, weighted average.
Nymphal density data included in the regression models (H11505 < 0.0001). The model was validated by creating a linear regression of the model prediction on the actual observed peak tick density at 16 drag sampling sites (Table 2; actual observed peak density = 0.21 + (0.754 × predicted peak density), F(1,15) = 35.70, r² = 0.72, P < 0.0001). The resulting best fit model equation was applied to each pixel (WL) within Mendocino County, which amounted to 52.6% of the county. The resulting nymphal density surface yielded 1.7% of the county classified as high-risk (> 10.5 nymphs per 100 m²), 10.2% as medium risk (6.4–10.5), 21.4% as low risk (2.5–6.40), and 19.3% as very low risk (< 2.5) (Figure 4). As shown in Figure 5, high-risk areas for nymphal exposures are common near population centers located in the central interior portion of the county but very rare in the vicinity of the coastal population centers.

**DISCUSSION**

Our habitat classification model based on Landsat TM5 imagery accurately predicted the spatial distributions of habitats in Mendocino County representing risk of exposure to *I. pacificus* nymphs (WL) or adults (grassland, chaparral, grassy woodlands) versus habitats with minimal risk of tick exposure (orchards, vineyards, barren and urban areas). Similar to a previous model focusing on the 2,200-hectare University of California Hopland Research and Extension Center, the nymphal risk WL habitat was identified with user and producer accuracies > 90% at the spatial scale of Mendocino County. In the current model, the best predictors for separat-
ing nymphal- from adult- or minimal risk-habitats included brightness and NDVI from February (deciduous trees without leaves) and wetness and NDVI from July (deciduous trees in full leaf and dry conditions). In July, when photosynthetic rates are high in woodlands but low in the dried-out grasslands, NDVI is useful for separating these two habitats. Conversely, woodlands with leaf versus grass are best distinguished by NDVI during the February leaf-off, grass growth period because of high photosynthetic rates in the grassy woodlands. Furthermore, July wetness is useful to separate woodlands from the drier chaparral and grassland habitats. In accordance with the study of Eisen and others, a multi-seasonal approach was required to adequately separate the target habitats.

Based on the assumption, justified by the results of the current study, that nymphs can be found in all WL habitats in Mendocino County, our model classified 53% of the county as nymphal risk habitat. The large proportion of the county representing nymphal risk habitat help to explain the high incidence of Lyme disease in Mendocino County, relative to other counties in California. Further studies are needed to determine whether the proportion of nymphal risk habitat for spatial units such as counties, zip code tabulation areas, or census tracts can be used as a general predictor of Lyme disease risk in the far western United States.

As in previous studies from Mendocino County, we found tremendous variability in site-specific nymphal densities in dense woodland habitats (0–25 nymphs per 100 m²). This density range is comparable to those reported for I. scapularis in the northeastern United States. In our study, nymphal densities were lowest in cool, moist coastal habitats. We considered the possibility that exposure to nymphs may not be restricted to WL habitats in these moist areas. Therefore, we sampled for nymphs within two grassland sites during the same sampling period as described for woodlands within MacKerricher and Jughandle state parks. Although questing adult ticks were readily collected from the identical sampling transects during both the previous and subsequent winters, no nymphs were found questing in these grasslands during the spring of 2004.

To find environmental factors predictive of variation in nymphal density in woodlands, we first examined associations with habitat type and then created models based on GIS/RS-derived data or factors that can be perceived by humans in the field. Our findings of elevated nymphal densities in habitats with deciduous Quercus spp. oaks (hardwood, hardwood/conifer) and low nymphal densities in habitats with redwood...
(redwood, tanoak, coastal pine) corroborate observations suggested by previous preliminary studies.26,27 Other tree species such as evergreen live oaks, Pacific madrone, and Douglas fir occurred more commonly in both of the above habitat groupings, and were not found to be useful as biomarkers of nymphal density. Presence of redwood was included as a predictor of low nymphal density in the multiple regression model both for data based on GIS/RS (GIS layer of coastal influence where redwoods are present) and for field derived data (presence of redwood trees). These results are similar to trends of depressed infestation rates by immature I. pacificus ticks on small vertebrates captured in redwoods compared with hardwood and hardwood conifer sites throughout Mendocino County.27 Redwood forests, with relatively low temperatures and high humidity compared with the oak woodlands of eastern Mendocino County,27 likely provide suitable conditions for both prolonged nymphal questing activity26,27 and tick development and survival. Conversely, the paucity of animals typically serving as primary hosts for I. pacificus immatures (lizards) and adults (deer) in the redwood habitat probably presents a severe limitation to tick population growth. Both this study and previous studies from Mendocino County,22,27 have recorded positive associations between deer signs and nymphal density, and several studies from oak woodlands in eastern Mendocino County indicate that lizards account for most of the larval and, especially, nymphal feedings.37–39

Our study showed a pattern in which the sites with the highest nymphal densities tended to cluster in the central part of Mendocino County, just to the east of the limit of the area with influence of redwoods (Figure 3). We speculate that tick populations generally are limited in the west by low densities of key hosts and to the east by climatic conditions that are unfavorable (i.e., too hot and dry) for tick survival. However, there seems to be a region in the south-central part of the county where the oak/conifer habitat allows for high densities of tick hosts, but the climatic conditions still have enough of a coastal influence to be highly suitable for the ticks. Further studies are needed to determine if this combination of habitat type and climatic conditions could be used as a general predictor of elevated Lyme disease risk in California.

Both models based on field-derived or GIS/RS data were statistically significant and could be validated using nymphal density data not included in the model build-sets. Overall, the GIS/RS model correctly estimated nymphal density at validation sites 22% more accurately than the field-derived human perception model. In addition to the greater predictive power, relative to the human perception model, the GIS/RS model also can be used to create a predictive nymphal density surface across the entire coverage area. Reliable data on key variables used in the human perception model, such as deer density or presence of specific tree species, are not available across large geographic areas at a spatial resolution useful to produce such a nymphal density surface. Consequently, although both models incurred the cost of initial field sampling, the GIS/RS model provided a cost-effective approach to producing a reliable large-scale nymphal density surface. Nevertheless, the model based on field-derived data produced several bio-markers (e.g., deer signs, presence of deciduous oaks) useful to the general public in identifying areas with elevated risk of nymphal exposure.

Environmental factors predictive of nymphal density in the GIS/RS model included coastal influence (discussed above), NDVI, greenness, solar insolation, and dominant hydrologic group. In the case of hydrologic soil group, density of nymphs was significantly higher in areas with soils characterized by slow or very slow infiltration rates. Previous studies in the midwestern and eastern United States have reported positive associations of tick presence or density with well drained soils, such as sandy and loamy soil types.12,40–42 The difference between the association of soil type and tick density from the eastern United States to California most likely is related to climatic conditions. Rainfall is rare or absent during the peak nymphal questing period of I. pacificus in Mendocino County, whereas precipitation events are more common during the peak activity period of I. scapularis nymphs in the east. Consequently, California soils that hold moisture likely provide more suitable, moister microclimate conditions in the leaf litter than soil types with faster infiltration rates.

The inclusions of NDVI, greenness, solar insolation, and hours of sunlight all follow logically from general associations of tick density and habitat or climatic conditions. The spectral signatures of July NDVI and November greenness combine to reflect the woodland sub-type, which, in turn, is associated with nymphal density. Studies from the eastern United States also have found NDVI or greenness to be useful predictors of tick and/or Lyme disease case distributions.3,11,14 The combination of solar insolation and hours of sunlight included in our model likely reflects microclimatic conditions, where intense solar insolation may be correlated with microhabitats too hot and dry for tick survival, especially in southeastern Mendocino County. For example, Peavey and Lane43 showed that mortality of I. pacificus larvae was far higher in exposed than in more shaded brushy microhabitats.

Due to the lack of reliable fine-scale GIS data of deer and lizard abundance and presence of key tree species such as Quercus spp. oaks and redwood, these important biotic factors could not be included in our model of nymphal density. However, even in the absence of such crucial data, the regression model constructed using GIS/RS data explained 50% of the total variation in nymphal density, and 72% of the variation in validation site density. We attempted to refine our RS classification of woodlands into subtypes used in the habitat evaluation, following the methods described for the supervised classification. However, this proved unsuccessful at the 30 m × 30 m pixel scale used in the Landsat TM5 imagery. For example, a pixel classified in the field as oak/conifer could consist of 25%, 50%, or 75% hardwood and, therefore, produce a wide range of spectral signatures. Use of available finer-scale imagery should improve classification of woodlands sub-types or even individual tree species.

Identifying and partitioning basic risk of exposure to vectors (e.g., I. pacificus nymphs) across large spatial scales, such as counties or states, could be useful in several respects. First, the information is a valuable tool for focusing expensive or labor-intensive tick control efforts (e.g., use of acaricides targeting vegetation or specific hosts) to specific high-risk areas. Second, these kinds of risk surfaces also are helpful as tools for the medical community to identify local areas of elevated risk of exposure to I. pacificus nymphs. Distribution of such risk maps to the public coupled with information on how to avoid exposure to the Lyme disease spirochete (e.g., checking oneself for ticks after exposure to tick habitat, use of acaricides or habitat alteration in the peridomestic environment)
could aid in reducing human disease. These risk maps also could be used by public health agencies to raise awareness of health care providers as to where vector ticks are present and, hence, aid in early and accurate diagnosis of Lyme disease.

Our surface of nymphal density for Mendocino County is a prime example of the usefulness of this approach. Although this county is considered a high-risk area for Lyme disease by California standards, our nymphal density surface (Figure 4) clearly shows that basic risk of nymphal exposure generally is low to the west and minimal within most of the agriculturally developed valleys to the east. Thus, we would expect to see low Lyme disease incidences in the human population centers located along the coast line (Figure 5). Conversely, areas of high nymphal densities are common within 15 km of the Highway 101 corridor, which runs from south to north in the central part of the county. The general distribution of these high-risk areas coincides with the most heavily populated areas of Mendocino County (Figure 5), and this is where we would expect most Mendocino County Lyme disease cases to occur. Finally, producing a similar risk surface for nymphal density in southern California would be a valuable tool to locate the small, isolated areas with elevated risk of nymphal exposure that probably occur in the generally low-risk Lyme disease landscape present in that part of the state.

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