Anaplasma phagocytophilum Infection in Small Mammal Hosts of Ixodes Ticks, Western United States

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A total of 2,121 small mammals in California were assessed for Anaplasma phagocytophilum from 2006 through 2008. Odds ratios were >1 for 4 sciurids species and dusky-footed woodrats. High seroprevalence was observed in northern sites. Ten tick species were identified. Heavily infested rodent species included meadow voles, woodrats, deer mice, and redwood chipmunks.

Anaplasma phagocytophilum is a tick-transmitted pathogen that causes granulocytic anaplasmosis in humans, horses, and dogs (1–3). Anaplasma phagocytophilum is maintained in rodent-Ixodes spp. tick cycles, including the western black-legged tick (Ixodes pacificus) in the western United States (4). Transovarial transmission does not occur, and I. pacificus feeds only 1 time per stage, so infection must be acquired by a juvenile tick feeding on an infected mammal. Suggested reservoirs in the West include the dusky-footed woodrat (Neotoma fuscipes), for which chronic infection has been observed, and the western gray squirrel (Sciurus griseus), which are frequently infected in nature (5,6). The northern coast range and Sierra Nevada foothills of California (4,7), where abundant rodents include deer mice (Peromyscus spp.), woodrats, and chipmunks (Tamias spp.), have moderate to high levels of granulocytic anaplasmosis. We sought to evaluate granulocytic anaplasmosis exposure and infection and describe the Ixodes spp. tick fauna in small mammals from central and northern coastal California.

The Study
Small mammals were caught in live traps (HB Sherman, Tallahassee, FL, USA, and Tomahawk Live Trap, Tomahawk, WI, USA) at 9 sites or collected as carcasses on roads (online Technical Appendix, available from www.cdc.gov/EID/content/14/7/1147-Techapp.pdf) from 2006 to 2008. Traps were set at locations of observed active rodent use or dens and baited with peanut butter and oats or corn, oats, and barley. Rodents were anesthetized with ketamine and xylazine delivered subcutaneously, examined for ectoparasites, and bled by retro-orbital abraison or femoral venipuncture. The blood was anticoagulated with EDTA. Shrew (Sorex spp.) carcasses were retrieved when found in traps, kept cold, and then sampled in the laboratory. Live shrews were examined for ticks but released without further processing. All carcasses were identified to species, age, and sex; examined for ectoparasites; and then dissected for coagulated heart blood and spleen. Ectoparasites were preserved in 70% ethanol for identification. Data were included for animals from 3 previous studies (5,8,9).

Plasma anti–A. phagocytophilum immunoglobulin G (Ig) was assayed by an indirect immunofluorescent antibody assay (3), by using A. phagocytophilum–infected HL-60 cells as substrate and fluorescein isothiocyanate–labeled goat anti-rat heavy and light chain IgG (Kirkegaard and Perry, Gaithersburg, MD, USA). This assay does not distinguish exposure to A. phagocytophilum from A. platys, but the PCR was specific for A. phagocytophilum. PCR was performed for all flying (Glaucomys sabrinus), Douglas (Tamiasciurus douglasii), and gray squirrels; all chipmunks from Santa Cruz and Marin Counties; a random subset of chipmunks from Humboldt Redwoods State Park and Hendy Woods State Park; and a random subset of individual mammals of other species. DNA was extracted from whole blood by using a kit (DNAeasy Tissue kit, QIAGEN, Valencia, CA, USA), and real-time PCR was performed as described previously (5).

Data were analyzed with “R” (www.r-project.org), with a cutoff for statistical significance of p = 0.05. Differences in seroprevalence among small mammal species and between sexes were assessed by χ2 test. Individual small mammals’ risk for A. phagocytophilum exposure and infection were assessed as a function of sex, species, and location by calculating odds ratios (OR) and 95% confidence intervals (CI). Multivariate logistic regression was performed to evaluate seropositivity as a function of site, host species, and interactions to evaluate possible interaction and confounding between the variables.

A total of 2,121 small mammals, including 2,100 rodents, 20 shrews, and 1 lagomorph, were evaluated for exposure to and infection with A. phagocytophilum and infection with Ixodes spp. ticks (Table 1). The overall seroprevalence was 15.2% (95% CI 13.6–16.9). Highest values and ORs >1 occurred in dusky-footed woodrats, tree squirrels, and some chipmunk species (Table 1; online Technical Appendix). The PCR prevalence among rodents

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tested was 3.8% (N = 652, 95% CI 2.9–5.3); highest values were reported in tree squirrels and some chipmunk species (Table 1). Although deer mice have been reported to be exposed to *A. phagocytophilum* ([10], [11]), we found little evidence of this in our study. Woodrats at northern sites tended to be infected, while sciurids (excluding ground squirrels) showed high rates of exposure at multiple sites, consistent with previous reports ([5]). A total of 60% of eastern gray squirrels from Connecticut were seropositive with reservoir competence documented by producing PCR-positive ticks after feeding on infected squirrels ([12]). A PCR-positive eastern chipmunk (*Tamias striatus*) was reported from Minnesota ([13]).

Location was an important determinant of exposure to infection, with high seroprevalence in the Hoopa Valley Indian Reservation and Hendy Woods State Park (Table 2). ORs significantly <1 were observed for Samuel P. Taylor State Park and the Morro Bay area, and 5 sites in the far northern coast range and Quincy in the Sierra Nevada had ORs >1 (online Technical Appendix). Statistical analysis failed to document a significant interaction between site and host species, but confounding was apparent, with overrepresentation of gray squirrels and woodrats in some high prevalence sites (online Technical Appendix). PCR prevalence was high at Sutter Buttes State Park and Siskiyou County (both with low sample size) and Big Basin State Park and Hendy Woods State Park, each ≈12% (Table 2). Results are consistent with prior reports for horses and dogs ([4]). Previous spatial analysis documented increased *A. phagocytophilum* risk in redwood, montane hardwood, and blue oak/foothill pine habitats ([14]). In our dataset, obvious habitat differences would not account for differences in disease exposure, given the presence of live oak, tanoak, redwood, and Douglas fir at many sites. Further ecologic studies to identify differing ecologic factors among these sites would be useful.

Tick species observed in our study sites include possible enzootic vectors and several human-biting species, including *I. pacificus* and *I. angustus* (online Technical Appendix). Host species from which relatively large col-

### Table 1. Seroprevalence and PCR prevalence of *Anaplasma phagocytophilum* among small mammal species, northern and central coastal California*

| Mammal species               | A. phagocytophilum IFA | A. phagocytophilum msp2 PCR |
|------------------------------|------------------------|-----------------------------|
|                              | Seropositive | Seroprevalence 95% CI | PCR positive | PCR prevalence 95% CI |
| Clethrionomys californicus   | 1           | 12.50 (0.6–53.3)      | 0            | 0–53.7               |
| Glaucomys sabrinus           | 2           | 14.29 (2.5–43.9)      | 1            | 16.7                  |
| Mus musculus                 | 0           | 0.00 (0–25.3)         | 0            | 0–34.4               |
| Microtus californicus        | 2           | 5.88 (1.0–21.1)       | 0            | 0–17.8               |
| Neotoma cinerea              | 0           | 0.00 (0–94.5)         | 0            | 0–94.5               |
| N. fuscipes                  | 167         | 50.15 (44.7–55.6)     | 8            | 4.3–20.8             |
| N. macrotis                  | 2           | 3.03 (5.3–11.5)       | 1            | 1.8 (0.09–10.6)      |
| All Neotoma                  | 169         | 42.25 (37.4–47.3)     | 9            | 3.7–18.7             |
| Peromyscus boylii            | 3           | 8.82 (2.3–24.8)       | 1            | 4.0–22.3             |
| P. californicus              | 2           | 0.67 (0.1–2.7)        | 0            | 0–3.8                |
| P. maniculatus               | 18          | 3.46 (2.1–5.5)        | 0            | 0–6.6                |
| P. truei                     | 1           | 2.56 (0.1–15.1)       | NT           | NT                   |
| Peromyscus spp.              | 0           | 0.00 (0–53.7)         | NT           | NT                   |
| All Peromyscus               | 24          | 2.68 (1.8–4.0)        | 1            | 0.45–2.9             |
| Rattus rattus                | 0           | 0.00 (0–37)           | 0            | 0–37.1               |
| Reithrodontomys megalotis    | 0           | 0.00 (0–17.2)         | 1            | 6.3 (0.3–32.3)       |
| Spermophilus beechei         | 0           | 0.00 (0–4.2)          | 0            | 0–20.0               |
| S. lateralis                 | 2           | 22.22 (3.9–59.9)      | NT           | NT                   |
| Sciurus carolinensis         | 111         | 57.89 (34.0–78.9)     | 3            | 18.8–50.4            |
| S. griseus                   | 34          | 70.83 (55.7–82.6)     | 6            | 15.8–6.6             |
| S. niger                     | 1           | 100.00 (55.0–100.0)   | 0            | 0–94.5               |
| All Sciurus                  | 46          | 47.83 (33.1–62.9)     | 9            | 16.4 (8.2–29.3)      |
| Sorex spp.                   | 0           | 0.00 (0–37.0)         | 0            | 0–94.5               |
| Sylvilagus bachmani          | 0           | 0.00 (0–94.5)         | NT           | NT                   |
| Tamias amoenus               | 6           | 6.82 (2.8–14.8)       | NT           | NT                   |
| T. merriami                  | 0           | 0.00 (0–48.3)         | 0            | 0–40.2               |
| T. minimus                   | 0           | 0.00 (0–4.9)          | NT           | NT                   |
| T. senex                     | 5           | 4.81 (1.8–11.4)       | NT           | NT                   |
| T. speciosus                 | 4           | 33.33 (11.3–64.6)     | NT           | NT                   |
| T. sonomais                  | 1           | 14.29 (0.7–58.0)      | 2            | 50.0 (15.0–85.0)     |
| T. ochrogenys                | 30          | 27.52 (19.6–37.0)     | 2            | 6.9 (1.2–24.2)       |
| Tamias spp.                  | 2           | 8.33 (1.5–28.5)       | NT           | NT                   |
| All Tamias                  | 48          | 13.45 (10.2–17.5)     | 4            | 34.0 (3.2–24.1)      |
| *Tamiasciurus douglasii*     | 6           | 40.00 (17.5–67.1)     | 0            | 0–60.4               |

| Total | 300 | 15.24 (13.7–16.9) | 33 | 3.8 | 2.9–5.3 |

*IFA, immunofluorescence assay; CI, confidence interval; NT, not tested.*
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collections were obtained included meadow voles, woodrats, deer mice, tree squirrels, and redwood chipmunks (T. ochrogenys). Tick diversity was highest on redwood chipmunks and in more northerly sites (online Technical Appendix). *I. angustus*, primarily a nidicolous tick of rodents but occasionally bites humans and is a competent vector for *Borrelia burgdorferi* sensu stricto (15), occurred on most rodent species. *I. spinipalpis*, which occurred on woodrats, deer mice, squirrels, and chipmunks, functions as a primary vector for *B. bissettii* in a woodrat enzootic cycle (16), and *Neotoma mexicana* and *I. spinipalpis* have an enzootic cycle in Colorado for *A. phagocytophilum*.

Conclusions

We show that a strong distinction can be made in possible reservoir capacity among rodent species, with many, such as deer mice and voles, only contributing to the ecology of granulocytic anaplasmosis through their support of ticks but not *A. phagocytophilum* infection. Others, including tree squirrels and woodrats, are frequently infected, in addition to supporting ticks. Considerable similarities exist between the ecology of *A. phagocytophilum* and *B. burgdorferi* in the West, although the large diversity of genospecies that exists for *B. burgdorferi* has not been reported for *A. phagocytophilum*. These data provide a starting point for future work to clarify the reservoir competence of small mammals for *A. phagocytophilum* and to determine how ecological interactions among small mammals, other vertebrate hosts, multiple possible vectors, and both *B. burgdorferi* and *A. phagocytophilum* could affect the enzootic persistence of these pathogens and risk to humans and animals.

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References

1. Greig B, Asanovich KM, Armstrong PJ, Dumler JS. Geographic, clinical, serologic, and molecular evidence of granulocytic ehrlichiosis, a likely zoonotic disease, in Minnesota and Wisconsin dogs. J Clin Microbiol. 1996;34:44–8.
2. Madigan JE. Equine ehrlichiosis. Vet Clin North Am Equine Pract. 1993;9:423–8.
3. Dumler JS, Asanovich KM, Bakken JS, Richter P, Kinsey R, Madigan JE. Serologic cross-reactions among *Ehrlichia equi*, *Ehrlichia phagocytophila*, and human granulocytic ehrlichia. J Clin Microbiol. 1995;33:1098–103.
4. Foley JE, Foley P, Brown RN, Lane RS, Dumler JS, Madigan JE. Ecology of granulocytic ehrlichiosis and Lyme disease in the western United States. J Vector Ecol. 2004;29:41–50.

5. Nieto NC, Foley J. Evaluation of squirrels as ecologically significant hosts for Anaplasma phagocytophilum in California. J Med Entomol. In press.

6. Foley JE, Kramer VL, Weber D. Experimental ehrlichiosis in dusky-footed woodrats (Neotoma fuscipes). J Wildl Dis. 2002;38:194–8.

7. California Department of Health Service. Vector-borne diseases in California. 2004 annual report. Sacramento (CA): The Department; 2006.

8. Foley J, Clucit S, Brown RN. Differential exposure to Anaplasma phagocytophilum in rodent species in northern California. Vector Borne Zoonotic Dis. 2008;8:49–55. DOI: 10.1089/vbz.2007.0175

9. Nieto NC, Foley P, Calder L, Dabritz H, Adjemian J, Conrad PA, et al. Ectoparasite diversity and exposure to vector-borne disease agents in wild rodents in central coastal California. J Med Entomol. 2007;44:328–35. DOI: 10.1603/0022-2585(2007)44[328:EDAETV]2.0.CO;2

10. Zeidner NS, Burket TR, Massung R, Nicholson WL, Dolan MC, Rutherford JS, et al. Transmission of the agent of human granulocytic ehrlichiosis by Ixodes spinipalpis ticks: evidence of an enzootic cycle of dual infection with Borrelia burgdorferi in Northern Colorado. J Infect Dis. 2000;182:616–9. DOI: 10.1086/315715

11. Nicholson WL, Muir S, Sumner JW, Childs JE. Serologic evidence of infection with Ehrlichia spp. in wild rodents (Muridae: Sigmodontinae) in the United States. J Clin Microbiol. 1998;36:695–700.

12. Levin ML, Nicholson WL, Massung RF, Sumner JW, Fish D. Comparison of the reservoir competence of medium-sized mammals and Peromyscus leucopus for Anaplasma phagocytophilum in Connecticut. Vector Borne Zoonotic Dis. 2002;2:125–36. DOI: 10.1089/15303660260613693

13. Walls JJ, Greig B, Neitzel D, Dumler J. Natural infection of small mammal species in Minnesota with the agent of human granulocytic ehrlichiosis. J Clin Microbiol. 1997;35:853–5.

14. Foley JE, Queen E, Sacks B, Foley P. GIS-facilitated spatial epidemiology of tick-borne diseases in coyotes (Canis latrans) in northern and coastal California. Comp Immunol Microbiol Infect Dis. 2005;28:197–212. DOI: 10.1016/j.cimid.2005.01.006

15. Peavey CA, Lane RS, Damrow T. Vector competence of Ixodes angustus (Acari: Ixodidae) for Borrelia burgdorferi sensu stricto. Exp Appl Acarol. 2000;24:77–84. DOI: 10.1023/A:1006331311070

16. Brown RN, Peot MA, Lane RS. Sylvic maintenance of Borrelia burgdorferi (Spirochaetes) in Northern California: untangling the web of transmission. J Med Entomol. 2006;43:743–51. DOI: 10.1603/0022-2585(2006)43[743:SMOBBS]2.0.CO;2

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Technical Appendix

Table 1. Study sites evaluated for granulocytic anaplasmosis in wild rodents, northern and central coastal California

| Study site                      | Dominant vegetation                                           | Region                     | Latitude and longitude (decimal degrees) | Elevation (m) | Distance to coast (km) |
|--------------------------------|-----------------------------------------------------------------|----------------------------|------------------------------------------|---------------|------------------------|
| Big Basin State Park           | Redwood, live oak, tanoak, madrone, chaparral (1 site only)    | Central coast range        | 37.10.621; 122.12.328                    | 368           | 21                     |
| Humboldt Redwoods State Park   | Redwood, Douglas fir, tanoak, madrone, live oak                | Northern coast range       | 40.17.770; 123.59.178                    | 610           | 26                     |
| Hoopa Valley Indian Reservation| Douglas fir, tanoak, madrone                                   | Northern coast range       | 41.10.333; 123.56.520                    | 109–1200      | 26                     |
| King Range National            | Douglas fir, tanoak, madrone, redwood (pockets), live oak,     | Northern coast range       | 40.08.059; 124.07.404                    | 61–610        | 3.9                    |
| Conservation Area              | Douglas fir, poplars, madrone                                  |                            |                                          |               |                        |
| Mendocino                      | per-urban, live oak, Douglas fir                               | Northern coast range       | 39.40.050; 123.30.296                    | 555           | 41                     |
| Morro Bay                      | Live oak, Monterey pine, eucalyptus                            | Central coast range        | 35.22.088; 120.49.464                    | 61            | 1.6                    |
| Placerville                    | Douglas fir, Jeffrey pine, incense cedar                      | Sierra Nevada foothills   | 38.45.899; 120.49.464                    | 1189          | 206                    |
| Quincy                         | Jeffrey pine, Douglas fir, incense cedar                      | Sierra Nevada              | 39.53.408; 120.51.312                    | 1400          | 265                    |
| Sutter Buttes State Park       | Blue oak, live oak, pine, eucalyptus                          | Central valley butte       | 39.12.805; 121.48.167                    | 247           | 151                    |
| Sagehen Research Station       | Jeffrey pine, pine, red fir, white fir                       | Sierra Nevada              | 39.12.805; 121.48.167                    | 247           | 151                    |
| Siskiyou                       | Douglas fir, tanoak, madrone                                  | Klamath                    | 41.18.077; 123.32.296                    | 198           | 48                     |
| Sonoma                         | Live oak                                                       | Northern coast range       | 38.19.169; 122.36.711                    | 274           | 34                     |
| Samuel P. Taylor State Park    | Redwood, live oak, tanoak, madrone                            | Northern coast range       | 38.01.232; 122.40.774                    | 134           | 11                     |
| Trinity                        | Douglas fir, tanoak, madrone                                  | Klamath                    | 40.44.286; 123.03.222                    | 488           | 131                    |
| Sacramento Valley              | Douglas fir, tanoak, madrone                                  | Central valley             | 38.33.481; 121.25.369                    | 9             | 130                    |
| Willow Creek                   | per-urban, Douglas fir, madrone                               | Northern coast range       | 40.56.302; 123.37.615                    | 229           | 41                     |
| Yolo                           | Live oak, blue oak, foothill pine                             | Northern coast range       | 38.49.382; 122.12.250                    | 137           | 121                    |
### Table 2. Risk factors for *Anaplasma phagocytophilum* seropositivity with statistically significant odds ratios*

| Risk factor                  | Odds ratio | 95% CI lower | 95% CI upper | p value       |
|------------------------------|------------|--------------|--------------|---------------|
| *Sciurus carolinensis*       | 14.01      | 3.15         | 62.40        | 5.0 × 10⁻⁴    |
| *Sciurus griseus*            | 23.43      | 6.19         | 88.66        | 3.5 × 10⁻⁶    |
| *Neotoma fuscipes*           | 10.38      | 3.11         | 34.65        | 1.4 × 10⁻⁴    |
| *Peromyscus californicus*    | 0.07       | 0.01         | 0.43         | 4.2 × 10⁻³    |
| *Tamiasciurus douglasi*      | 6.89       | 1.43         | 33.18        | 3.5 × 10⁻⁴    |
| *Tamias ochrogenys*          | 3.92       | 1.11         | 13.81        | 0.016         |
| Humboldt Redwoods            | 3.16       | 1.55         | 6.42         | 1.4 × 10⁻³    |
| Hoopa Valley                 | 3.25       | 1.77         | 5.97         | 1.5 × 10⁻⁴    |
| Hendy Woods                  | 4.37       | 2.28         | 8.36         | 8.3 × 10⁻⁶    |
| Morro Bay                    | 0.19       | 0.07         | 0.54         | 1.7 × 10⁻³    |
| Quincy                       | 29.64      | 2.53         | 347.50       | 6.9 × 10⁻³    |
| Samuel P. Taylor             | 0.28       | 0.08         | 0.98         | 0.047         |
| Trinity                      | 15.17      | 1.98         | 115.99       | 8.8 × 10⁻³    |
| Willow Creek                 | 7.06       | 1.58         | 31.52        | 0.01          |

*CI, confidence interval.

### Table 3. Proportion of all hosts collected from sites in northern and central California represented by *Sciurus* spp. and *Neotoma* spp.

| Location                          | Animals tested | Tree squirrels tested | Proportion of animals that were squirrels | Woodrats tested | Proportion of animals that were woodrats |
|-----------------------------------|----------------|-----------------------|------------------------------------------|-----------------|------------------------------------------|
| Big Basin State Park              | 254            | 21                    | 8.3                                      | 25              | 9.8                                      |
| Humboldt Redwoods State Park      | 142            | 5                     | 3.5                                      | 8               | 5.6                                      |
| Hoopa Valley Indian Reservation   | 478            | 12                    | 2.5                                      | 273             | 56.1                                     |
| Hendy Woods State Park            | 191            | 8                     | 4.2                                      | 20              | 10.5                                     |
| King Range National Conservation Area | 29      | 1                     | 3.4                                      | 0               | 0                                        |
| Mendocino County (roadside only)  | 1              | 1                     | 100.0                                    | 0               | 0                                        |
| Morro Bay regional communities    | 407            | 0                     | 0                                        | 40              | 9.8                                      |
| Placerville City region (roadside only) | 1      | 1                     | 100.0                                    | 0               | 0                                        |
| Quincy City region (roadside only)| 6              | 3                     | 50.0                                     | 0               | 0                                        |
| Sutter Buttes State Park          | 40             | 0                     | 0                                        | 1               | 2.5                                      |
| Sagehen Research Station          | 221            | 0                     | 0                                        | 1               | 0.4                                      |
| Siskiyou County (roadside only):  | 4              | 4                     | 100.0                                    | 0               | 0                                        |
| Sonoma                            | 1              | 0                     | 0                                        | 1               | 100.0                                    |
| Samuel P. Taylor State Park       | 171            | 1                     | 0.6                                      | 21              | 12.3                                     |
| Trinity                           | 5              | 5                     | 100.0                                    | 0               | 0                                        |
| Sacramento Valley                 | 3              | 3                     | 100.0                                    | 0               | 0                                        |
| Willow Creek                      | 10             | 4                     | 40.0                                     | 0               | 0                                        |
| Yolo                              | 15             | 2                     | 13.3                                     | 13              | 86.7                                     |

*CI, confidence interval.
Table 4. Tick species and stage recovered from rodents throughout California*

| Host Species | Dermacentor sp. | D. occidentalis | Ixodes sp. | I. angustus | I. ochotonae | I. pacificus | I. spinipalpis | I. woodi |
|--------------|-----------------|-----------------|------------|-------------|--------------|--------------|---------------|---------|
|              | A    | N    | L    | A    | N    | L    | A    | N    | L    | A    | N    | L    | A    | N    | L    | A    | N    | L    |
| C. californicus | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    |
| G. subulinus  | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 2    | 0    | 0    | 0    | 0    | 0    |
| M. californicus | 0    | 0    | 0    | 13   | 8    | 0    | 0    | 2    | 4    | 0    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    |
| M. musculus   | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 3    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| N. fuscipes   | 0    | 1    | 0    | 0    | 3    | 1    | 3    | 1    | 11   | 0    | 10   | 1    | 1    | 2    | 3    | 9    | 2    | 1    |
| P. boylii     | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 0    | 1    | 0    |
| P. californicus | 0   | 0    | 0    | 1    | 3    | 1    | 2    | 0    | 1    | 25   | 7    | 0    | 0    | 0    | 2    | 4    | 0    | 2    |
| P. maniculatus | 0   | 2    | 1    | 0    | 1    | 7    | 10   | 0    | 1    | 3    | 31   | 5    | 6    | 0    | 7    | 3    | 20   | 0    | 4    |
| P. truei      | 0    | 0    | 0    | 0    | 0    | 0    | 1    | 1    | 0    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    |
| R. ratus      | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| R. megalotis  | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| S. carolinensis | 0   | 0    | 0    | 0    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 2    | 0    | 0    | 0    | 0    |
| S. griseus    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 6    | 19   | 0    | 3    |
| Sp. beechey   | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 2    | 0    | 0    | 1    | 0    | 0    |
| T. merriami   | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| T. ochrogenys | 0    | 1    | 1    | 0    | 0    | 1    | 1    | 1    | 2    | 12   | 3    | 6    | 0    | 0    | 8    | 85   | 0    | 1    |
| T. sonomae    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| Tamiasciurus douglasii | 0 | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| Sorex sp.     | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 4    | 0    | 0    | 0    | 0    | 0    |
| Total         | 0    | 5    | 2    | 0    | 18   | 19   | 15   | 4    | 4    | 17   | 92   | 19   | 16   | 1    | 1    | 10   | 22   | 139  | 9    |

*Data not shown: 1 I. hefle adult was observed on a northern flying squirrel; 3 adult I. jellisoni on deer mice. A = adult; N = nymph; L = larva.

Table 5. Ticks collected on rodents from 8 different study areas in California*

| Study areas                  | Dermacentor sp. | D. occidentalis | Ixodes sp. | I. angustus | I. ochotonae | I. pacificus | I. spinipalpis |
|------------------------------|-----------------|-----------------|------------|-------------|--------------|--------------|---------------|
|                             | A    | N    | L    | A    | N    | L    | A    | N    | L    | A    | N    | L    | A    | N    | L    | A    | N    | L    |
| Big Basin State Park        | 0    | 0    | 0    | 2    | 0    | 1    | 0    | 4    | 1    | 1    | 1    | 0    | 6    | 0    | 1    | 0    | 0    | 0    |
| Rural Yolo County            | 0    | 0    | 0    | 0    | 0    | 0    | 3    | 1    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| Humboldt                     | 0    | 0    | 0    | 4    | 0    | 0    | 1    | 13   | 0    | 0    | 0    | 1    | 3    | 12   | 0    | 2    | 0    | 17   |
| Redwoods State Park          | 0    | 3    | 1    | 0    | 0    | 0    | 4    | 3    | 0    | 2    | 19   | 3    | 5    | 0    | 0    | 1    | 10   | 97   |
| Hendy Woods                  | 0    | 0    | 0    | 0    | 0    | 0    | 3    | 0    | 0    | 0    | 1    | 2    | 0    | 0    | 0    | 0    | 0    | 0    |
| State Park                   | 0    | 0    | 0    | 0    | 0    | 0    | 3    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| King Range National          | 0    | 0    | 0    | 0    | 0    | 0    | 3    | 0    | 0    | 0    | 1    | 2    | 0    | 0    | 0    | 0    | 0    | 0    |
| Conservation Area            | 0    | 0    | 0    | 0    | 0    | 0    | 3    | 0    | 0    | 0    | 1    | 2    | 0    | 0    | 0    | 0    | 0    | 0    |
| Morro Bay regional communities | 0    | 0    | 0    | 16   | 16   | 0    | 0    | 0    | 13   | 49   | 10   | 0    | 0    | 0    | 0    | 3    | 3    | 1    |
| Samuel P. Taylor State Park  | 0    | 2    | 1    | 0    | 0    | 5    | 0    | 1    | 0    | 13   | 2    | 1    | 0    | 0    | 3    | 2    | 8    | 0    |
| Sutter Buttes State Park     | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 1    |

*Data not shown: 3 I. jellisoni adults were recovered from Samuel P. Taylor State Park; adult I. woodi were collected from Big Basin State Park (3), Humboldt Redwoods State Park (2), Hendy Woods State Park (2), and Samuel P. Taylor State Park (4). A = adult; N = nymph; L = larva.