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# SEROLOGIC EVIDENCE OF *YERSINIA PESTIS* INFECTION IN SMALL MAMMALS AND BEARS FROM A TEMPERATE RAINFOREST OF NORTH COASTAL CALIFORNIA

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ABSTRACT: From 1983 to 1985, 463 serum samples from 11 species of mammals in Redwood National Park (RNP) (California, USA) were evaluated for antibodies to *Yersinia pestis* by the passive hemagglutination method. *Yersinia pestis* antibodies occurred in serum samples from 25 (36%) of 69 black bears (*Ursus americanus*), one (50%) of two raccoons (*Procyon lotor*), five (3%) of 170 dusky-footed woodrats (*Neotoma fuscipes*), and one (<1%) of 118 deer mice (*Peromyscus maniculatus*). Two hundred seventy-three flea pools, consisting of 14 species of fleas, were collected from small mammals and woodrat nest cups. Viable *Y. pestis* were not isolated from any of the flea pools. Significant between-year variations in the frequencies of seropositive bear or small mammal sera were not observed. A significantly higher frequency of plague antibodies was observed in bear sera taken during September collections. Frequencies of seropositive bear sera did not vary significantly by sex or age group of bears. Significant differences were not observed in the frequencies of seropositive small mammals by forest habitat type in which they were captured. This is the first report of *Y. pestis* infection in Redwood National Park, and the first detailed report of *Y. pestis* activity in a temperate rainforest.

*Key words:* Epizootiology, fleas, *Neotoma fuscipes, Peromyscus maniculatus,* plague, Redwood National Park, serologic survey, *Ursus americanus, Yersinia pestis.*

## INTRODUCTION

Bubonic plague, a flea-transmitted disease of rodents caused by the bacterium *Yersinia pestis,* has been known in California since 1900. Its early history there and in other western states is well-documented (Eskey and Haas, 1940; Meyer, 1942; Link, 1953). However, it was not known to exist in the north coastal counties of California until 1976 when a collaborative serologic survey involving the California State Department of Health Services (CDHS), U.S. Fish and Wildlife Service, and the U.S. Centers for Disease Control (CDC) found antibodies to *Y. pestis* in the sera of coyotes (*Canis latrans*) collected in Humboldt County (CDHS and CDC records). Plague antibodies subsequently were found in the sera of domestic dogs, deer mice (*Peromyscus maniculatus*), California ground squirrels (*Spermophilus beecheyi*), a striped skunk (*Mephitis mephitis*) and a bobcat (*Felis rufus*). These seropositive animals were collected in drier inland areas characterized by Douglas-fir (*Pseudotsuga menziesii*) and oak-grasslands, in the southern part of the county.

Between 1983 and 1985, black bears (*Ursus americanus*) were live-captured and radio-collared as part of a study on their movements, behavior and physiology at Redwood National Park (RNP) (Schroeder, 1987). In conjunction with these studies, serum samples were tested for the presence of plague antibodies. When it became evident that some bears had antibodies to *Y. pestis,* the serologic aspect of this study was expanded to include rodents and in-

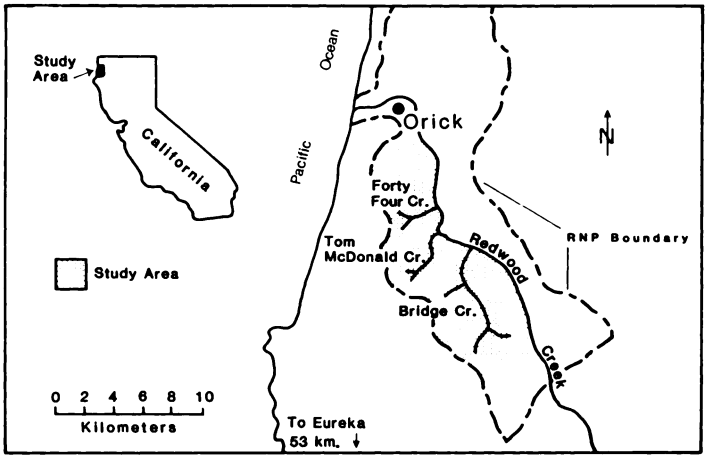


FIGURE 1. Redwood National Park study area.

sectivores. In the following report, we summarize the serologic findings for both bears and small mammals.

## STUDY AREA

Redwood National Park (41°5′ to 41°50′N, 123°52′ to 124°9′W) is a 42,900 ha tract of land in the Pacific Coastal Range, along coastal Humboldt County, California (USA; Fig. 1). Much of the park is centered on Redwood Creek, which is oriented in a north-northwesterly direction and flows into the Pacific Ocean approximately 60 km north of Humboldt Bay. The area is characterized by high relief, steep slopes, and narrow valley bottoms (Janda et al., 1975). The moderating effect of the Pacific Ocean results in mild, wet winters and cool summers, with frequent coastal fog. Annual rainfall varies from 185 to 256 cm. On an annual basis, daily temperatures range from a mean minimum of 6 C to a mean maximum of 16 C (Janda et al., 1975). Elevation ranges from sea level to 850 m.

This study was conducted on an area on the southwestern side of the Redwood Creek watershed. Logging was the dominant land use of the study area before its inclusion into RNP (Muldavin et al., 1981). Dominant tree species are redwood (*Sequoia sempervirens*), Douglas-fir and tan oak (*Lithocarpus densiflora*). Because of the progression of timber harvests, various stages of vegetative succession are represented. Several discontinuous stands of old-growth redwood still remain.

For this report, six forested habitats were considered: (1) riparian with red alder (*Alnus rubra*) and salmonberry (*Rubus spectabilis*) as dominant species; (2) moist redwood with redwood and sword fern (*Polystichum munitum*) as dominant species; (3) redwood/Douglas-fir on mesic slopes with redwood and Douglas-fir as dominant species; (4) Douglas-fir/mixed evergreen with this habitat characterized by Douglas-fir, tan oak, madrone (*Arbutus menziesii*), redwood, huckleberry (*Vaccinium* spp.), rhododendron (*Rhododendron macrophyllum*), salal (*Gaultheria shallon*) and chinquapin (*Castanopsis chrysophylla*); (5) alder/festuca in drier sites dominated by alder, and including *Festuca sabuliflora*, *F. arundinacea*, *Hierochloe occidentalis* and Douglas-fir; and (6) brush where the habitat is characterized by coyote brush (*Baccharis pilularis*), cat's ear (*Hypochoeris radicata*), blue blossom (*Ceanothus thrysiflorus*), Douglas-fir and *Whipplea modesta*. A more complete description of the area is given by Muldavin et al. (1981).

## MATERIALS AND METHODS

### Small mammals

From September 1983 to September 1985, rodents and insectivores were live-trapped (H.

B. Sherman Traps, Inc., Tallahassee, Florida 32316, USA; National Live Trap Corporation, Tomahawk, Wisconsin 54487, USA) in forest habitats of RNP. The habitat type was recorded at each specific site of capture. All animals were anesthetized with ethyl ether.

Between 0.5 and 1.0 ml of heart blood was taken by cardiac puncture from each animal. After clotting, serum was separated and frozen. Sera were shipped to the Plague Branch, CDC (Fort Collins, Colorado 80522, USA) and tested for antibodies to *Y. pestis* by the passive hemagglutination test (W.H.O. Expert Committee on Plague, 1970). A titer of $\geq$1:16 was considered diagnostic for plague. The numerator of all titers is omitted from tables for convenience.

Each animal was brushed vigorously for 1 to 2 min over a white enamel pan; all fleas collected were stored at 4 C in sterile 2% saline. After the identity of each flea was determined, flea pools were sent to CDC and tested for viable *Y. pestis* by mouse inoculation (Quan et al., 1981). Each flea pool was composed of 1 to 25 conspecific fleas taken from the same mammal species, at the same site and on the same date.

In addition, fleas were collected from nest cups of dusky-footed woodrats (*Neotoma fuscipes*) between December 1984 and November 1985. Each nest cup was placed in a Berlese-Tullgren funnel; a 60-watt bulb was used to drive the fleas to the bottom of the funnel where they were trapped in water (Southwood, 1966). Pools of conspecific fleas taken from the same site on the same date likewise were shipped to CDC and tested for viable *Y. pestis*.

Marrow samples from the long bones of animals found dead were tested at CDC for *Y. pestis* antigen by the fluorescent antibody method (Quan et al., 1981).

### Bears

Bears were captured with Aldrich spring-activated foot-snares (Alton Chittester, Clallam Bay, Washington 98326, USA) and homemade culvert traps, and on five occasions, with the aid of hounds. Two free-ranging bears also were taken by Cap-Chur® apparatus (Palmer Chemical and Supply Company, Inc., Douglasville, Georgia 30133, USA). The habitat type of each capture site was recorded.

After capture, each bear was immobilized with a 2:1 mixture of ketamine hydrochloride (Bristol Laboratory, Syracuse, New York 13201, USA; Parke-Davis Company, Morris Plains, New Jersey 07950, USA)/xylazine hydrochloride (Mobay Corporation, Animal Health Division, Shawnee, Kansas 66201, USA) administered with a jabstick syringe or Cap-Chur® dart, at a dosage of 0.91 mg ketamine hydrochloride/kg of estimated body weight (Addison and Kolenosky, 1979). Weights and measurements were recorded for each animal.

Each bear was marked with an aluminum ear tag and lip tattoo for permanent identification (Graber, 1982). A lower first premolar was extracted, and age of the bear was estimated through cementum annuli analysis by a private laboratory (Matson's Laboratory, Milltown, Montana 59851, USA). The age of each bear also was estimated by tooth wear, and head and body size (Poelker and Hartwell, 1973). Age estimates by these methods usually were in close agreement; in cases where annuli were difficult to interpret, age estimates were adjusted by the other parameters.

Blood samples were collected from the femoral vein, allowed to clot for 1 hr at ambient temperatures, and centrifuged at 3,200 rpm for 15 min. Each serum sample was stored in a plastic tube, frozen and sent to CDC for serologic testing as described above.

While immobilized, each bear was examined carefully for injuries and ectoparasites. Ectoparasites were preserved in 70% ethyl alcohol with 5% glycerin; subsequently, they were identified.

Fecal samples $\leq$7-days-old were collected and frozen. The habitat type of each collection site was recorded. The frequency of rodent remains in the bear scats was determined by methods outlined in Graber (1982).

## RESULTS

### Small mammals

Serum samples from 379 rodents and 13 insectivores from forested habitats were tested for antibodies to plague (Table 1). Six rodents, including five *N. fuscipes* and one *P. maniculatus*, were seropositive for plague (Table 1), with titers ranging from 1:32 to 1:2,048 (Table 2). Five of 360 small mammals trapped from the Bridge Creek watershed (Fig. 1) and one of 31 small mammals from Tom McDonald Creek (Fig. 1) were seropositive; one small mammal from Forty-four Creek (Fig. 1) was seronegative. Differences between the frequency of seropositive rodents among the watersheds were not significant (Chi-square test, $P > 0.05$). Two additional *P. maniculatus* from Bridge Creek (Fig. 1) had titers of 1:8.

The frequency of seropositive small mammals from the various forest habitats

TABLE 1. Mammals evaluated for plague antibodies, Redwood National Park, California, 1983 to 1985.

| | Number of sera sampled | Number seropositive (≥1:16) | % Seropositive |
|---|---|---|---|
| Rodentia | | | |
| *Neotoma fuscipes* | 170 | 5 | 3 |
| *Peromyscus truei* | 47 | 0 | 0 |
| *P. maniculatus* | 118 | 1 | <1 |
| *P. boylii* | 37 | 0 | 0 |
| *Eutamias townsendii* | 5 | 0 | 0 |
| *Clethrionomys californicus* | 1 | 0 | 0 |
| *Aplodontia rufa* | 1 | 0 | 0 |
| Subtotal | 379 | 6 | 2 |
| Insectivora | | | |
| *Sorex trowbridgii* | 10 | 0 | 0 |
| *S. pacificus* | 3 | 0 | 0 |
| Subtotal | 13 | 0 | 0 |
| Carnivora | | | |
| *Ursus americanus* | 69 | 25 | 36 |
| *Procyon lotor* | 2 | 1 | 50 |
| Subtotal | 71 | 26 | 37 |

were compared (Table 3). The differences were not significant (Chi-square test, $P > 0.05$). Also, no significant differences ($P > 0.05$) were found when the 170 *N. fuscipes* were considered alone.

With the exception of a woodrat sampled in January, all seropositive rodents were found between April and September

TABLE 3. Frequency of seropositive small mammals from various forest habitat types of Redwood National Park, California, 1983 to 1985.

| Habitat type | Number sera sampled | Number seropositive (≥1:16) | % Seropositive |
|---|---|---|---|
| Riparian | 24 | 0 | 0 |
| Moist redwood | 54 | 1 | 2 |
| Redwood/Douglas-fir | 86 | 2 | 2 |
| Douglas-fir/mixed evergreen | 64 | 1 | 2 |
| Alder/festuca | 31 | 0 | 0 |
| Brush | 133 | 2 | 2 |
| Totals | 392 | 6 | 2 |

of each year (Table 2). This also was when most of the rodents were trapped. Significant differences among seasons were not observed in the frequencies of seropositive small mammals collectively, or for *N. fuscipes* alone (Chi-square test, $P > 0.05$).

Overall, the frequency of seropositive small mammals declined (two of 30 in 1983, two of 99 in 1984, one of 41 in 1985); this difference was not significant (Chi-square test, $P > 0.05$) for all small mammals collectively, or for any of the small mammal groups individually.

Twelve species of fleas were collected from 417 live-trapped rodents and insectivores from RNP (Table 4). Over 2,100 fleas of 14 species were collected from these small mammals and from an additional 37

TABLE 2. Variation in titers by month in seropositive mammals, Redwood National Park, California, 1983 to 1985.

| | Month | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Titer | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
| 2,048 | | | | | | | | | W[a] | | | |
| 1,024 | | | | | | | | | | | B | |
| 512 | | | | B | | | | | | | | |
| 256 | | | | W | | B | | B | B | | | |
| 128 | | | | | W | BB | | B | BB | B | | |
| 64 | W | | | | M | B | BBB | B | BB | BB | | |
| 32 | | | | | | | B | | BBW | | | |
| 16 | | Ra | | | | | | B | | B | | |
| 8[b] | | Ra | | | | MM | B | | | B | | |

[a] W, Woodrat (*Neotoma fuscipes*); B, Bear (*Ursus americanus*); M, Deer mouse (*Peromyscus maniculatus*); Ra, Raccoon (*Procyon lotor*).

[b] A titer of 1:8 is suspect, but not diagnostic, of plague.

TABLE 4. Frequency of species of fleas infesting rodents and insectivores, Redwood National Park, California, 1983 to 1985.

| Flea species | *Peromyscus* spp. ($n$ = 210) infested | | *Neotoma fuscipes* ($n$ = 180) infested | | *Microtus* spp. ($n$ = 2) infested | | *Sorex trowbridgii* ($n$ = 11) infested | | *Eutamias townsendii* ($n$ = 5) infested | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Number | % | Number | % | Number | % | Number | % | Number | % |
| *Orchopeas sexdentatus cascadensis* | 10 | 5 | 148 | 82 | 0 | — | 1 | 9 | 1 | 20 |
| *Opisodasys keeni* | 108 | 52 | 6 | 3 | 0 | — | 0 | — | 0 | — |
| *Atyphloceras multidentatus* | 4 | 2 | 10 | 6 | 0 | — | 0 | — | 0 | — |
| *Catallagia scullent* | 18 | 9 | 18 | 10 | 0 | — | 0 | — | 0 | — |
| *Rhadinopsylla sectilis* | 4 | 2 | 0 | — | 0 | — | 0 | — | 0 | — |
| *Ceratophyllus ciliatus protinus* | 0 | — | 0 | — | 0 | — | 0 | — | 2 | 40 |
| *Eumolpianus orarius* | 0 | — | 0 | — | 0 | — | 0 | — | 1 | 20 |
| *Peromyscopsylla selenis* | 0 | — | 0 | — | 1 | 50 | 1 | 9 | 0 | — |
| *Hystrichopsylla occidentalis linsdalei* | 1 | <1 | 0 | — | 0 | — | 0 | — | 0 | — |
| *Corypsylla kohlsi* | 1 | <1 | 0 | — | 0 | — | 0 | — | 0 | — |
| *Malaraeus telchinus* | 0 | — | 0 | — | 1 | 50 | 0 | — | 0 | — |
| *Oropsylla montana* | 0 | — | 1 | <1 | 0 | — | 0 | — | 0 | — |
| No fleas present* | 89 | 42 | 25 | 14 | 0 | — | 10 | 91 | 1 | 20 |

* Additionally, no fleas found on one *Aplodontia rufa*, one *Clethrionomys californicus*, six *Sorex pacificus*, and one *S. obscurus*.

woodrat nest cups; 274 flea pools were evaluated for viable *Y. pestis* (Table 5). The fleas from 20 rodent specimens were lost; thus, not all fleas listed in Table 6 were included in the 274 flea pools tested. *Yersinia pestis* were not recovered from any of the flea pools.

The long bone from one *N. fuscipes* found dead in a bear den near Tom McDonald Creek was negative for *Y. pestis*. Blood was not collected from this animal.

### Bears

Twenty-five (36%) of 69 bear sera from RNP were seropositive for plague (Table 1), with titers ranging from 1:16 to 1:1,024 (Table 2). Owing to duplicate samples of

TABLE 5. Fleas from 417 small mammals and 37 woodrat nest cups, Redwood National Park, California, 1983 to 1985.

| Flea species | Numbers of fleas | | | Number of flea pools evaluated |
|---|---|---|---|---|
| | Vertebrates | Nest cups | Total | |
| *Orchopeas sexdentatus cascadensis* | 781 | 550 | 1,331 | 101 |
| *Opisodasys keeni* | 260 | 5 | 265 | 47 |
| *Atyphloceras multidentatus* | 21 | 229 | 250 | 51 |
| *Catallagia sculleni sculleni* | 40 | 121 | 161 | 47 |
| *Rhadinopsylla sectilis goodi* | 4 | 77 | 81 | 14 |
| *Malaraeus telchinus* | 2 | 3 | 5 | 3 |
| *Ceratophyllus ciliatus protinus* | 4 | 2 | 6 | 2 |
| *Eumolpianus orarius* | 1 | 0 | 1 | 1 |
| *Peromyscopsylla selenis* | 3 | 0 | 3 | 1 |
| *Hystrichopsylla occidentalis linsdalei* | 1 | 2 | 3 | 3 |
| *Corypsylla kohlsi* | 1 | 0 | 1 | 1 |
| *Corypsylla ornata* | 0 | 2 | 2 | 0 |
| *Epitedia* sp. | 0 | 3 | 3 | 2 |
| *Oropsylla montana* | 1 | 0 | 1 | 1 |
| Totals | 1,119 | 994 | 2,113 | 274 |

TABLE 6. Frequency of seropositive bear sera by sex and age group in bears sampled at Redwood National Park, California, 1983 to 1985.

| | Males | | Females | | Total | |
|---|---|---|---|---|---|---|
| Age (mo) | Number sera tested | Number positive | Number sera tested | Number positive | Number sera tested | Number positive |
| 0–12 | 6 | 1 | 2 | 0 | 8 | 1 |
| 13–47 | 13 | 7 | 10 | 4 | 23 | 11 |
| ≥48 | 15 | 5 | 23 | 12 | 38 | 17 |
| Totals | 34 | 13 | 35 | 16 | 69 | 29 |

some bears, this represented a total of 22 (40%) different seropositive bears among 55 individual bears sampled during this period. A significant difference was not observed in the annual variation of plague-positive bear sera (11 of 33 in 1983, 13 of 32 in 1984, one of four bear sera in 1985) (Chi-square test, $P > 0.05$).

Serum from bears found to be seropositive were sampled between the months of April and November (Table 2); however, this also was when most (62 of 69) bear sera were collected. It was notable that seven of 10 bears sampled during September collections had plague antibodies. To determine if this was an unusually high frequency, we estimated a binomial distribution for plague in the RNP bears from the previous three months and found that 12 (32%) of 37 bear sera from June, July and August collections were seropositive. Based on a binomial distribution (Steel and Torrie, 1960) we estimated the probability of observing seven or more seropositive bears in a sample of 10 animals if the real frequency was 32% in the population. The probability is $P = 0.0167$. Thus, the frequency in September is unexpectedly high, suggesting that the prevalence of plague antibodies is higher among RNP bears in September than it is in June, July and August.

Bears <1-yr-old appeared to have a lower frequency of exposure to *Y. pestis*, compared to older bears (Table 6). However, significant (Chi-square test, $P > 0.05$) differences were not observed in the frequency of seropositive bears by sex or age group (Table 6).

Two radio-collared bears were found dead. One bear had been tested previously and found to be seronegative for plague. The other bear had been seropositive (1:64) on 19 October 1983 and seronegative on 6 March 1984; it was found dead on 25 June 1984. Both bears were negative for *Y. pestis* in the marrow of their long bones.

Fleas were not found on any of the bears. However, lice and ticks were collected and will be reported elsewhere.

Following the methods of Moore et al. (1974), rodent hairs were found in 16 (6%) of 283 fecal samples of bears collected between April and December 1981 to 1984.

### Raccoons

Blood was collected from two raccoons found freshly dead near Bridge Creek on 26 February 1985. One animal had a titer of 1:16; the other had a titer of 1:8. One carcass was retrieved later, but there was no evidence of *Y. pestis* in the marrow of its long bone.

## DISCUSSION

### Small mammals

Rodents are the main reservoirs of plague worldwide (Kucheruk, 1965). In summarizing the importance of rodents in the enzootiology of plague in California, Nelson (1980) emphasized that plague in mammals other than rodents usually is fortuitous. Some species, such as lagomorphs and insectivores, share common habitats with sylvatic rodents and encounter infected rodent fleas, whereas carnivores commonly are infected by feeding on sick or dead rodents.

Serologic evidence for sylvatic plague was noted in both *N. fuscipes* and *P. maniculatus* at RNP. This was similar to the serologic findings of plague reported in *Neotoma cinerea* and *P. maniculatus* in Lava Beds National Monument (Nelson and Smith, 1976).

There was no evidence to suggest which species of fleas were transmitting plague among the rodents at RNP. However, at Lava Beds National Monument, Nelson and Smith (1976) reported that *Y. pestis* was isolated from a pool of *Orchopeas sexdentatus*, a flea commonly found on *N. cinerea*. This flea was common on *N. fuscipes* and in their nest cups at RNP, and also was found occasionally on *P. maniculatus* (Table 4). It was the most common flea observed during our study (Table 5). Any future plague surveillance at RNP should include collection of this species of flea.

#### Bears

Past evidence has suggested that wild carnivores and omnivores may serve as sentinels to aid in identifying the geographic and temporal distribution of sylvatic plague (Barnes, 1982). Predators and scavengers often feed on large numbers of rodents. Since many carnivores produce antibodies but show little or no clinical illness after ingesting plague-infected prey or carrion (Barnes, 1982), they are important for detecting plague in regions where its incidence is low among rodent reservoirs.

There are few studies on plague serology in bears. Studies in carnivores usually have been done in conjunction with animal damage control programs; thus, most information on plague serology in bears is incidental to more extensive studies with other carnivores (Barnes, 1982).

In California, 47 (23%) of 203 black bear sera taken from seven counties between 1974 and 1982 were seropositive for plague (Smith et al., 1984). This included five seronegative bears from Humboldt County.

Several studies have dealt with the persistence of plague antibodies in laboratory, sylvatic and domestic animals (Cavanaugh et al., 1965; Rust et al., 1971). Experimental evidence for the persistence of plague antibodies in bears is lacking. However, field evidence from recaptured bears in this study indicated that titers may persist between 2 and 7 mo. One bear had a titer of 1:64 on 11 August 1983 and a titer of 1:16 on 3 October 1983, indicating that detectable antibodies persisted for at least 2 mo. In another case, a bear was seronegative on 12 August 1983, had a titer of 1:64 on 19 October 1983, and was seronegative on 6 March 1984; this indicated that antibodies persisted <7 mo.

Rodents usually compose only a small portion of a black bear's diet (Martin et al., 1951). Grenfell and Brody (1981) found that the diet of black bears in Tahoe National Forest (California, USA) included *Tamiasciurus douglasii, Otospermophilus* sp., *Callospermophilus* sp., *Reithrodontomys* sp., *Microtus* sp., *Scapanus* sp., and *Sorex* sp. These small mammals occurred in <1% of the total fecal samples but could be seasonally important. Graber (1982) reported that rodents, including *Erthizon dorsatum* and *Spermophilus beecheyi*, were only an incidental part of the diet of black bears from Yosemite National Park (California, USA). Thus, the 6% frequency of rodents in the diets of RNP bears appears to be relatively high.

After black bears were shown to be seropositive for plague in 1983 at RNP, the testing program was expanded to include indigenous rodents and insectivores. Bear denning sites on the study area usually had woodrat nests associated within 10 m; in at least 12 cases, woodrat nest material was incorporated into bear dens. Thus, an effort was made to ensure that woodrats were adequately represented in the survey.

#### Raccoons

The role of raccoons in plague enzootiology at RNP is not clear. In limited experimental studies, responses to oral challenge with *Y. pestis* in raccoons did

not produce signs of morbidity but did produce an antibody response that became detectable in 8 to 14 days; usually this reached a peak in 20 to 30 days, and subsided to low or undetectable levels in 6 to 8 mo (Barnes, 1982).

#### Fleas

Most species of fleas are not highly host-specific and commonly occur on two or more taxonomically related or ecologically associated host species. These hosts are termed the true hosts for a given species of flea. Under certain circumstances fleas may be found incidentally on other hosts; these instances of incidental distribution are called straggling. Because plague is primarily a flea-borne disease, straggling of infective fleas promotes the spread of plague to other susceptible hosts.

Records of fleas from black bears in North America are rare. Black bears are true hosts for two fleas in western North America: *Chaetopsylla tuberculaticeps* and *C. setosa* (Hubbard, 1947; Holland, 1985). We have not found records or observed straggling of fleas to black bears. The apparent absence of fleas from bears in this study supports the thesis that bears with antibody titers obtained their infections by ingesting plague-infected rodents.

The most abundant fleas taken at RNP were *O. sexdentatus*, whose true hosts are species of *Neotoma*, and *Opisodasys keeni*, whose true hosts are species of *Peromyscus* (Table 4). Both species of fleas are known vectors of plague in rodents.

*Atyphloceras multidentatus, Catallagia sculleni sculleni, Epitedia* sp., *Hystrichopsylla occidentalis linsdalei, Peromyscopsylla selenis* and *Rhadinopsylla sectilis goodi* are nest fleas associated with species of *Neotoma*, *Peromyscus* and various microtine rodents; thus, instances of straggling among these hosts are hard to identify. Of these latter fleas, *H. occidentalis linsdalei* is a known vector of plague in rodents. *Malaraeus telchinus*, found in this study, also is a plague vector.

*Ceratophyllus* [*Amonopsyllus*] *ciliatus protinus* (previously *Monopsyllus ciliatus protinus*) was found in the nest cup of a woodrat, and is a known vector of plague to rodents and humans. One *Oropsylla* [*Diamanus*]*montana* (previously *Diamanus montanus*), whose true host is *Spermophilus beecheyi*, was found on a woodrat; this flea is the most important sylvatic vector of plague in the western United States.

#### Habitats

Past studies have shown a close association of sylvatic plague with desert, steppe and dry montane habitats (Kucheruk, 1965; Barnes, 1982). Finding an apparent plague nidus in a temperate rainforest is unusual. However, seropositive bobcats and plague-positive mountain beavers (*Aplodontia rufa*) have been found in the temperate rainforest in Washington (U.S. Public Health Service Files, Fort Collins, Colorado 80522, USA), suggesting that *Y. pestis* is more versatile in its range of habitats than previously believed.

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