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PLAGUE STUDIES IN CALIFORNIA — THE ROLES OF VARIOUS SPECIES OF SYLVATIC RODENTS IN PLAGUE ECOLOGY IN CALIFORNIA

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ABSTRACT: The status of our knowledge of the roles of various sylvatic rodents in plague ecology in California is reviewed. Two theories, Pavlovsky's doctrine of focality of zoonotic diseases and Baltazard's proposal that plague is maintained in nature in resistant rodent species, form the framework for our understanding of the occurrence and persistence of plague. The concepts of resistance, reservoir species, susceptibility, and recipient species are defined and discussed. The ecological attributes that appear to enhance the role of certain rodent species as reservoirs are proposed, and the ecological features that appear to produce epizootics are briefly outlined. Based on current information, the roles of individual species of rodents, rabbits, and some insectivores are presented and discussed in relation to epizootic potential and the epidemiology of human infection. Man's role in plague ecology leading to greater exposure to sylvatic plague is emphasized.

Plague, caused by the bacterium Yersinia pestis, is an infectious disease found primarily in wild (sylvatic) rodents. Other mammals which become infected secondarily with plague include those (e.g., carnivores) that feed on sick or dead infected rodents, and those (e.g., rabbits, shrews, and moles) that share common habitats with sylvatic rodents and are more likely to encounter infected rodent fleas. Humans may become infected when they enter or live in an area where an outbreak (epizootic) is occurring in sylvatic rodents or rabbits. Even more serious to humans is an outbreak of plague in commensal rodents in urbanized areas, where humans and rodents are closely associated and where this association may lead to epidemics. The fear of epidemic situations has led the international health community to mandate the continuous surveillance and suppression of plague wherever it is indigenous. Plague is indigenous in California; it is firmly entrenched in populations of sylvatic rodents.

The major routes of transmission among rodents and other mammals are: (1) the vector route (bite of infective fleas), (.2) the oral route (ingestion of infected specimens by cannibalism or predation), and (3) the pneumonic route (droplet inhalation, such as during stereotyped greeting behavior). Transmission to humans by fleas and among humans by the pneumonic route is well-known. It is not widely-known that humans can become infected by the oral route (ingestion of undercooked, infected meat, such as rabbit) and by direct contamination (inoculation of bacteria into wounds and abrasions on the hands during such activities as skinning infected carcasses or preparing them as food).

Plague activity has increased and become widespread in California in the last decade. Since 1970, there have been thirteen human cases with five deaths (Table 1). At least three of the fatalities developed secondary pneumonia. During the same period, epizootics occurred in a variety of locales: wilderness areas, ranches and other private properties, recreational areas (including national parks, campgrounds, and vacation communities), and urban-suburban fringes of the expanding cities in southern California. These outbreaks have caused concern among public health personnel and the people who live in and frequent these areas. A comprehension of plague ecology is necessary to develop effective educational and control programs that reduce the potential for human infection.

This report reviews the status of our knowledge of plague ecology in California. The report is based on current data and is interpreted within the framework of established theories in ecology and the epidemiology of zoonotic diseases (diseases of animals transmissible to man). The topics discussed are (1) theories of how plague is maintained in nature, (2) roles of various species of sylvatic rodents in plague ecology, and (3) man's role in plague ecology.

THEORIES OF PLAGUE OCCURRENCE AND PERSISTENCE

Two theories are presented to account for the persistence and occurrence of plague. The first is the doctrine of natural nidality of transmissible diseases (Pavlovsky 1966) or, as it is also known, the landscape theory of epidemiology in reference to arthropod-borne diseases, the theory of natural foci of diseases, or the localization of diseases (Audy 1958). Pavlovsky first formalized this doctrine in 1939, although the concepts underlying his doctrine were recognized earlier by several workers. Use of the doctrine has led to greater understanding of zoonotic diseases by reducing the bewildering complexity of these diseases to a common denominator (Olsen 1970) and by directing research to unravel this complexity (Audy 1958).

Pavlovsky proposed that zoonotic diseases exist in nature in discrete foci. The natural focus is that portion of a territory with a definite geographic character in which there has evolved a definite interspecies set of relationships between (1) the disease agent, its vectors, the animal donors (reservoirs) and (2) the animal recipients of the agents and its vectors, where the external environment favors the circulation of the disease agent. Natural foci continue to exist as long as the interspecies set of relationships, called biocenoses or communities, remain intact. Foci may become extinct through natural or man-made changes, and foci may be created through human activity. The biocenose within the focus is viewed as a superorganism; therefore, the concept is holistic as well as dynamic. Kartman (1960) declared that the focal theory of disease constitutes an ecological precept having fruitful application both to academic and practical investigation.

Table 1. The human cases of plague in California in the 1970s with the probable sylvatic rodent source of each infection.

Case	Year	Sex	Age	Probable Animal Source and Site of Infection	Location of Exposure	Location of Diagnosis	Outcome
1.	1970	M	8	California Ground Squirrel, Recreational Area.	Shasta Co.	Alameda Co.	Recovered
2.	1970	M	45	Chipmunk, Home Area.	Plumas Co.	Plumas Co.	Recovered
3.	1970	F	10	California Ground Squirrel, Recreational Area.	Kern Co.	Kern Co.	Recovered
4.	1975	F	1 1/2	California Ground Squirrel, Home Area.	Ventura Co.	Ventura Co.	Fatal
5.	1975	M	14	Rock Squirrel, Home Area.	New Mexico	San Francisco	Fatal
6.	1976	M	45	California Ground Squirrel, Home Area.	Kern Co.	Kern Co.	Fatal
7.	1976	F	6	Chipmunk, Recreational Area	Plumas Co.	San Francisco	Recovered
8.	1977	F	3	Golden-mantled Ground Squirrel or Chipmunk, Recreational Area.	Placer or Sierra Co.	San Diego	Fatal
9.	1977	M	55	Unknown (probably a pet), Work Related.	Monterey Co.	Santa Clara Co.	Fatal
10.	1977	F	48	California Ground Squirrel, Recreational Area.	Kern Co.	Kern Co.	Recovered
11.	1978	F	57	California Ground Squirrel, Home Area.	Siskiyou Co.	Siskiyou Co.	Receoverd
12.	1979	M	55	California Ground Squirrel, Home Area.	Los Angeles Co.	Los Angeles Co.	Recovered
13.	1979	M	15	California Ground Squirrel, Recreational Area.	Riverside Co.	Ventura Co.	Recovered

Most workers agree on the focal distribution of sylvatic plague (e.g., Meyer 1942, Macchiavello 1954, Audy 1958, Kartman 1960, Kucheruk 1965, Olsen 1970). Meyer (1942) noted its focal occurrence and discontinuous distribution. Kartman (.1960) stated that each focus constitutes an independent phenomenon and must be investigated as a unique epidemiologic situation. Macchiavello (1954) emphasized the uniqueness of each focus, each with its local enzootic phenomenon dependent on its own environmental ecology and rodent population dynamics. Differences of opinion exist over what constitutes a focus (Olsen 1970), and what is the size of a focus. The reason for the differing opinions is that usually only the recipient components of a focus are in evidence during plague epizootics; the reservoir components remain inapparent. Therefore, plague activity is observed over broad geographic areas in which may be found one or more true foci. Even on this broad scale, a discontinuous pattern of centers of sylvatic plague activity is evident.

The second theory specifically addresses the role of the reservoir components in the development and maintenance of the focus. Baltazard et al. (1952) proposed the idea that highly resistant species were the reservoirs of sylvatic plague. They stated that any species exterminated by a disease cannot be the reservoir of the disease; therefore, the true reservoir must be sought not among the most susceptible species, but among those whose natural resistance shows them to be the best adapted to the disease. The highly resistant rodent species are the donor or reservoir species in sylvatic plague foci, whereas the susceptible rodent species are the recipient species that undergo epizootics and become victims of the disease.

Resistant species, when infected with plague, develop a transient bacteremia but show few or no symptoms with little mortality. Bacteremias allow fleas feeding on these rodents to become infected and to pass the infection to other hosts, thus perpetuating the cycle of infection. Development of antibody, which can be tested for by serologic methods, gives evidence of prior infection with plague. Susceptible species become infected, develop a bacteremia and symptoms, and usually die. Resistance or susceptibility is not an absolute characteristic of any rodent species. Each species or population within a species may demonstrate various degrees of heterogeneity for resistance and susceptibility. Reservoir species have populations within foci that show a high degree of resistance that may approach the absolute. Even among the most susceptible rodent species, individuals are known to survive infections and demonstrate antibody titers. In summary, plague persists in resistant rodents in a latent state, whereas it is manifested in susceptible rodents.

In their study area in Kurdistan, Baltazard et al. (1952, 1953) found that two species of *Meriones* (gerbils) showed a high degree of resistance to plague, whereas two other species were susceptible and sustained epizootics. This evidence formed the basis for their theory of the role of resistant rodents in maintenance of plague foci. In California, Kartman and his associates in a series of papers (e.g., Hudson et al. 1964, Hudson and Kartman 1967) discovered a focus on San Bruno Mountain, San Mateo County, and gathered evidence that supported the theory of Baltazard and his co-workers. In several successive years, Kartman's group found that the vole, *Microtus californicus*, and the deer mouse, *Peromyscus maniculatus*. showed a high degree of resistance to plague; 60 to 100% of *M. Californicus* and up to 45% of *P. maniculatus* had antibody titers. The presence of positive sera in samples collected from these two rodent species over a period of nearly 30 years, demonstrates again the focal nature of plague and the role of resistant rodents in the plague focus.

The picture of plague persistence on San Bruno Mountain has been used as a model in the search for other foci. Search has centered either on species of *Microtus* and closely related genera or on *P. maniculatus* (Cavanaugh et al. 1965, Hudson and Kartman 1967). In central Washington, the sagebrush vole, *Lagurus curtatus* was implicated as a reservoir before a serologic test was developed and before Baltazard et al. proposed their theory (Clanton et al. 1971). The search for other foci in California has not been fruitful, although limited evidence suggests certain suspect species and sites, e.g., *M. montanus* in Mono County (Murray 1971). Currently, San Bruno Mountain is the only proven focus with long-term documentation.

Because of certain genetic and ecological characteristics, *M. californicus* and *P. maniculatus* are excellent reservoir hosts. Hubbert and Goldenberg (1970) demonstrated in *M. californicus* that the inheritance of natural resistance to plague is multigenic and is linked to dominance. Selection would favor an increasing percentage of the genetically dominant resistant individuals in this population. Genetic data for *P. maniculatus* and its inheritance of natural resistance are not available; however, the evidence of immunity to plague suggests that a genetic mechanism is operating.

In the ecological language of MacArthur and Wilson (1967), species of *Microtus* are extreme "r strategists," i.e., opportunistic species that live in short-lived, unstable habitats; maintain unstable population levels by rapidly breeding during favorable years and by crashing during unfavorable years; produce multiple litters and generations each year; and are short-lived. Wilson (1975) stated that species of Peromyscus are *r* strategists, but are closer to the "*K* strategist" end of the scale. "*K* strategists" live in stable habitats; maintain relatively stable population levels by reproducing more slowly; produce one, or at most two, litters each year; and are longer-lived. Examples of *K* strategists are chipmunks, ground squirrels, and woodrats.

Rapid reproduction in *r* strategists enhances the development and perpetuation of plague within a focus by producing a frequent supply of new individuals into the rodent-flea-rodent chain of infection. Transmission among a population of highly susceptible rodents results in high mortality to the point that transmission of the epizootic ceases. In the populations of highly resistant rodents, immunity also removes individuals from the transmission cycle. This will also lead to cessation of transmission, unless non-immunes are continuously introduced into the transmission cycle. Rapid reproduction with multiple births ensures continuity of transmission; therefore, among genetically resistant *r* strategists are found the reservoir rodent components in plague foci.

The propensity for species of *Microtus* and their allies to undergo violent population crashes is an apparent liability for continuity of transmission in the focus. The extent of the crash would lead to the extinction of the focus, if the focus is based upon one reservoir species. I propose the hypothesis that a plague focus is maintained by the combination of at least two resistant rodent species whose ecological strategies complement one another: one species is an extreme *r* strategist and the other is near the *K* end of the spectrum, or even may be a *K* strategist. This combination of species with contrasting strategies should ensure the continuity of a focus through the combined attributes of productivity and stability.

Transfer of plague from resistant reservoir species to susceptible recipient species probably occurs during commingling of hosts and their fleas within or adjacent to the focus. Epizootics among the recipient species spread outward from the focus as long as the density and continuity of susceptible populations are sufficient to maintain epizootics. What determines the rapidity of the spread of epizootics is not fully understood, but it is perhaps the densities of various rodents and their fleas and environmental conditions that influence transmission. After epizootics among recipient species have run their course, plague activity ceases except among the reservoir hosts within the focus until the densities of recipient species are again sufficient to initiate and maintain new epizootics. This accounts for the periodic fluctuations and sometimes regular cycles observed in plague outbreaks.

These theories form the framework for our current understanding of plague ecology. In California, most available data support these theories. However, our data describe mainly the roles of rodent species as data on various vector flea species are minimal or lacking. As data accumulate, particularly on the role of flea species, our concepts on plague ecology may have to be modified.

THE ROLE OF SYLVATIC RODENTS

The degree of known involvement of the various sylvatic species of rodents, lagomorphs, and some insectivores in California is summarized in Tables 2 through 4. These tables are based on data collected and compiled by the Vector Biology and Control Section, California Department of Health Services and from the literature on plague in California.

Table 2. Species and genera of rodents and rabbits from which laboratory-confirmed evidence of Yersinia pestis has not been detected in California. Those followed by a single asterisk (*) have been extensively sampled; those with two asterisks (**) occur in special habitats or in "plague-free" areas and have rarely been sampled; and those without asterisks have been never, rarely, or inadequately sampled.

Ochotona princeps
Castor canadensis**
Aplodontia rufa
Sciurus griseus*
Ammospermophilus nelsoni
Spermophilus mohavensis
Spermophilus tereticaudus**
Eutamias alpinus
Eutamias panamintinus
Eutamias sonomae
Perognathus spp.*
Microdipodops spp.
Dipodomys spp. (except ordii)*
Zapus spp.
Phenacomys spp. (=Arborimus)
Clethrionomys occidentalis
Lagurus curtatus
Microtus longicaudus*
Microtus oregoni**
Microtus townsendii**
Neotoma albigula**
Sigmodon hispidus**
Ondatra zibethicus**
Onychomys spp.
Peromyscus eremicus
Erethizon dorsatum

Table 3. Species of small mammals from which laboratory-confirmed evidence of Yersinia pestis has been found, but whose roles in plague ecology are considered to be fortuitous, limited owing to their restricted distribution in California, or uncertain owing to the little data available for each species.

Fortuitous	Limited	Uncertain
Sorex sp.	Spermophilus townsendii	Ammospermophilus leucurus
Scapanus latimanus	Eutamias umbrinus	Sciurus niger
Thomomys spp.		Eutamias minimus
		Glaucomys sabrinus
		Dipodomys ordii
		Neotoma lepida
		Peromyscus boylii
		Peromyscus californicus
		Peromyscus crinitus
		Reithrodontomys megalotis

Insectivora.– Few shrews and moles have been found positive for plague. Hudson et al. (1964) obtained two positive pools of Sorex vagrans tissues taken from seven animals in 1963. Three moles, Scapanus latimanus, (two from Plumas County and one from Calaveras County) were found positive in 1976. Because of the few isolates and the high degree of specificity exhibited by their fleas, the role of insectivores is considered to be fortuitous.

Lagomorpha.--Kartman (1960) and Von Reyn et al. (1976) reported on human cases of plague in the western U.S. associated with contact of infected rabbit tissues; no such cases have been acquired in California. Although most cases are associated with cottontails (Sylvilagus spp.), isolations of plague from Lepus spp. are also recorded. There have been few isolates of plague from rabbits of either genera in California. Most records come from the 1930s and 1940s from Monterey, San Luis Obispo, and Ventura Counties, but a positive cottontail was found during a rodent epizootic in a new suburban development in Los Angeles County in 1978.

Table 4. Species and genera of rodents and rabbits from which laboratory-confirmed evidence of *Yersinia pestis* has been detected repeatedly in California. Those with an asterisk (*) or their fleas have been associated with human cases in California.

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*Marmota flaviventris**

*Spermophilus beecheyi**

Spermophilus beldingi

*Spermophilus lateralis**

*Eutamias amoenus**

Eutamias merriami

Eutamias quadrimaculatus

*Eutamias speciosus**

*Eutamias townsendii**

Tamiasciurus douglasii

Neotoma cinerea

*Neotoma fuscipes**

Peromyscus maniculatus

Peromyscus truei

Microtus californicus

Microtus montanus

Sylvilagus spp.

Lepus spp.

Rabbits are thought to acquire plague infections through associations with infected rodents; most records of rabbit plague in California are concurrent with epizootics in rodents. The extent of plague activity in rabbit populations is unknown because systematic surveys of rabbits have not been undertaken. Their associations with rodents in shared habitats may enhance transmission. The danger to man is to those that hunt, skin, and prepare rabbit as food.

We do not know the role of pikas, *Ochotona princeps*, in plague ecology, for only two or three specimens have ever been examined in California. Pikas in Russia and Mongolia are known to undergo epizootics. The disjunct, insular distribution patterns of *O. princeps* at higher elevations precludes its role as a frequent source of infection to man. Nevertheless, pikas occur within the broad outlines of known foci and may play an amplifying role in epizootics among rodents using lava rim and talus habitats.

Rodentia.-- The two important families of sylvatic rodents in plague ecology are the Cricetidae, which contain both reservoir species and recipient species, and Sciuridae, which contain important recipient species. Plague has never been isolated from Aplodontidae (mountain beaver), Erethizonidae (porcupines) and Zapodidae (jumping mice) in California. The habits and habitats of beavers (Castoridae) and muskrats (Cricetidae) appear to preclude any role in plague ecology; isolates have never been taken from these rodents. The status of Geomyidae and Heteromyidae will be briefly discussed, although evidence of plague is rare in these rodents.

Geomyidae.--Two records of plague isolations from gophers exist from California: Meyer (1947) reported plague in *Thomomys bottae* from San Luis Obispo County in 1942, and Murray (1971) reported a positive gopher from Fresno County in 1966. The habits of gophers relegate them to a fortuitous role in plague ecology. Because of their lack of involvement in any known zoonotic disease cycle, their inclusion for control for health purposes in the California Health and Safety Code is unjustified and unwarranted.

Heteromyidae.-- This family contains three genera in California: *Dipodomys* (kangaroo rats), *Microdipodops* (kangaroo mice), and *Perognathus* (pocket mice). Species of *Microdipodops* have limited distributions along the eastern border of California, whereas *Dipodomys* and *Perognathus* are widely distributed and are relatively abundant wherever they occur. In spite of extensive sampling, one seropositive *D. ordii* taken in Lassen County in 1973 is the sole evidence of plague for this family in California.

Bacon and Drake in Washington (1958) and Holdenried and Quan in New Mexico (1956) demonstrated experimentally that two species of *Perognathus* were highly susceptible to plague infections. The latter authors, however, found two species of *Dipodomys* refractory to plague. Meyer (1947) reported that carcasses of *D. californicus* were found in the same area where an epizootic among Belding ground squirrels was occurring, but no specimens were tested. We have not observed carcasses or evidence of die-offs or declines among any population of *Dipodomys* living in areas where epizootics were in progress. We have no information concerning the influence of epizootics on populations of *Perognathus*. The roles of members of this family are unknown and at best an enigma.

Cricetidae.-- Kucheruk (1965) declared that the Cricetidae are of great significance in maintaining natural foci of plague. He stated that in this family the plague organism underwent its evolution and that the family has been of primary importance in the formation of the distribution of plague and of most natural foci.

No information is available in California for certain genera of this family, namely *Arborimus*, *Clethrionomys*, *Lagurus*, *Onychomys*, *Phenacomys*, and *Sigmodon*. Plague has been found in species of *Onychomys* elsewhere. Their carnivorous habits suggest a potentially active role in epizootics. Furthermore, experimental data from New Mexico indicate that *Onychomys* has a moderate degree of resistance (Holdenried and Quan 1956), suggesting an indicator status in plague detection. The remaining genera are rare or have limited distributions in California. Clanton et al. (1971) have gathered strong evidence in favor of reservoir status for *Lagurus* in Washington, and the Russians report an active role for species of *Ciethrionomys* in their foci.

Microtus.—-Five species of *Microtus* occur in California: *M. californicus*, *M. longicaudus*, *M. montanus*, *M. oregoni*, and *M. townsendii*. The latter two species have restricted distributions and have not been examined. *Microtus longicaudus* is widely distributed in California, but plague has not been detected from this vole. *Microtus montanus* has not yet been proven to be a reservoir species; however, persistent evidence of plague in carnivores that feed on this species in Tulelake Basin of northeastern California and in the valleys of Siskiyou County suggest this status. Murray (1971) claimed that evidence from Mono County supported its potential reservoir status there. Bacon and Drake (1958) presented experimental evidence of resistance for some populations of *M. montanus* and suggested a possible maintenance role for this species in Washington.

Neotoma.—Four species of Neotoma are found in California, with *N. albigula* occurring solely in the "plague-free" southeastern corner of the State. The other three species (*N. cinerea*, *N. fuscipes*, and *N. lepida*) are widely distributed and may play a major role in plague epizootics (Murray 1971). The available evidence of plague from *N. lepida* is one isolate from Kern County; however, records of plague in rodents identified as *Neotoma* sp. and "woodrats" before 1954 undoubtedly include specimens of *N. lepida*. Although local die-offs of *N. lepida* have been reported, other evidence suggests non-involvement in epizootics. For example, populations of *N. lepida* remained abundant in eastern Los Angeles County in 1978 and 1979 during extensive die-offs among California Ground Squirrels. Population levels were determined by trapping; no serologic or bacterial evidence of plague was found in *N. lepida*.

Neotoma cinerea is known to be highly susceptible to plague. Nelson and Smith (1976) have extensively investigated epizootics among this species at Lava Bed National Monument. We have developed objective and subjective criteria to assess population abundance of this woodrat in reference to detection of plague activity. We have proposed its status as an indicator, or sentinel, species in the sagebrush-juniper steppes and in areas dominated by lava formations.

Murray (1971) proposed a singular role for *N. fuscipes* in the movement, amplification, and maintenance of plague epizootics. He further indicated that by visual examination of material in their easily accessible huts the level of activity and abandonment could be determined. Abandonment was attributed to plague activity. For nearly 15 years, surveys of woodrat huts was the major effort toward plague detection in California. Evidence has not supported this singular role for *N. fuscipes*. Trapping results did not verify conclusions based solely on visual observations. Furthermore, other studies showed that each woodrat controls three or four huts, so apparent abandonment of greater than 50 percent of huts did not mean a decrease in population.

Evidence has accumulated that *N. fuscipes* is moderately resistant and does not, except maybe locally, undergo extensive die-offs. The most crucial evidence against Murray's hypothesis was the repeated observation of non-involvement during documented epizootics in sciurids commingling with *N. fuscipes*. Currently, we are reassessing the role of this woodrat in plague ecology.

Peromyscus.—-Of the six species of *Peromyscus* that occur in California, nothing is known of the role of *P. eremicus* in plague ecology. The roles of *P. boylii*, *P. californicus* and *P. crinitus* are based on little data and the data show resistant and susceptible individuals. *Peromyscus truei* also shows evidence of resistance and susceptibility, but this evidence is on a population level.

The role of *P. maniculatus* has been documented above. Based upon the evidence of its status on San Bruno Mountain, the consistency of antibody titers taken from this species elsewhere in the western U.S., and the extensive distribution of this rodent, Hudson and Kartman (1967) proposed that *P. maniculatus* could be used as a serologic indicator species in epidemiological studies. This approach has not been fruitful in certain areas in California (Smith et al., in preparation). Populations have been found to differ greatly in their degree of resistance and susceptibility. The heterogeneity to resistance exhibited by each species of *Peromyscus* may indicate possible reservoir status for each of them in certain foci.

Reithrodontomys.--Based on experimental data and field observation on San Bruno Mountain (Holdenried and Quan 1958, Hudson et al. 1967), *Reithrodontomys megalotis* is moderately to highly susceptible to plague.

Sciuridae.--This is the most important group of recipient species in plague outbreaks in California. Most human cases from sylvatic sources are associated with members of this family and their fleas (Table 1).

Sciurus.--*Sciurus griseus*, the Western grey squirrel, has yet to be found with evidence of plague, although this species has been examined extensively. Epizootics that have occurred among these squirrels have been caused by mites (mange) and probably by undescribed viruses.

Plague has been isolated once from the introduced fox squirrel, *S. niger*, from Palo Alto in Santa Clara County. A human case in Denver, Colorado, was acquired from an urban epizootic among fox squirrels in 1968 (Hudson et al. 1971). This species should be carefully monitored in urban areas with a history of plague.

Marmota.--Marmots in California appear to be highly susceptible and undergo intense local die-offs. Two human cases were acquired in northeastern California in the 1940s in persons handling sick or dead marmots.

Glaucomys.--Flying squirrels appear to be susceptible to plague based on the few carcasses that have been found infected. Antibody titers to plague have not been detected among the few sampled.

Tamiasciurus.--The chickaree, or pine squirrel, *T douglasii*, appears to be a moderately resistant host that has all the attributes to be an excellent sentinel species (Smith et al., in preparation).

Eutamias.--Of the ten species of chipmunks in California, seven have been found with evidence of plague. None has been found from *E. alpinus*, *E. panamintinus*, and *E. sonomae*, and one isolate is known from *E. umbrinus* from the high Sierra Nevada. Two specimens of *E. merriami* have been found positive from Riverside County, but the role of *E. merriami* has been difficult to assess, for this chipmunk is difficult to capture in live traps. Furthermore, their numbers have not decreased during epizootics among ground squirrels in Los Angeles and Riverside Counties. This species may be important in the ecology of plague in southern California.

The few *E. minimus* examined have been seropositive, demonstrating resistance. Their role in the sagebrush steppe remains unknown, but warrants further investigation.

Eutamias amoenus, *E. quadrimaculatus*, *E. speciosus*, and *E. townsendii* show heterogeneity for resistance and susceptibility among their populations. In a series of papers in preparation (e.g., Smith et al.), we document their resistance in certain areas and demonstrate their use as excellent sentinel animals in an integrated surveillance program. In the coniferous forest community, these species of chipmunks and *Spermophlus lateralis* have been associated with human cases in recreational areas (Table 1).

Ammospermophilus.—Only one (*A. leucurus*) of the two species of antelope ground squirrels has been shown to be naturally infected with plague. This susceptible species occupies desert habitats and may be an important recipient species in the low deserts.

Spermophilus.--Three species (*S. beecheyi*, *S. beldingi*, and *S. lateralis*) are important rodents in plague ecology and in the epidemiology of human plague in sylvatic areas.

Spermophilus beldingi has undergone extensive violent epizootics in the northeastern quadrant of California during the 1930s and 1940s. Although a few specimens in recent years have been shown to be plague-positive, no extensive die-offs have been reported in the last few decades. It is not known if the ecology of plague has changed in this area or if poisoning campaigns against Belding ground squirrels have masked or obliterated plague activity among these rodents. Local outbreaks of plague among these ground squirrels have been reported and documented from the high country of the Tahoe area, Yosemite National Park, and Mono County. A population in Mono County appears to have developed some resistance as antibody titers have been detected in several individuals.

Spermophilus lateralis is a highly susceptible species in the coniferous forest. This species adapts well to campground and other recreational sites, where populations may become very dense. Plague epizootics with high mortality and human cases have been associated with the golden-mantled ground squirrel. The population in Mono County shows some degree of resistance, as indicated by numerous titers in specimens tested.

The California ground squirrel, *Spermophilus beecheyi*, is the most important sylvatic rodent in plague epidemiology. Most human cases from sylvatic sources are associated with this rodent and its fleas. This species is usually highly susceptible to plague; violent rapid epizootics with high mortality are characteristic of this species when it lives in colonies, such as along the southern coastal area, the Kern Plateau, the San Gabriel Mountains, and the valleys of Siskiyou County. In the Sierra Nevada, this species lives in family groups and does not undergo extensive mortality. Local die-offs of small groups sometimes occur, but non-involvement in epizootics is also noted. Also, in the Sierra Nevada, we are picking up individual specimens of California ground squirrels with antibodies, indicating that resistance has been developing. The population in the San Jacinto Mountains has developed a high level of resistance; this study will be discussed in a subsequent paper.

THE ROLE OF MAN IN SYLVATIC PLAGUE ECOLOGY

It has become apparent that man is playing an increasing role in sylvatic plague ecology in California. During the 1970s, there was an increase in rodent epizootics and in the number of human cases. The increase is related to the increased use of recreational sites, development of new towns and cities, and the expansion of our major cities by encroachment.

In recreational sites, land use practices, increased availability of food, and protection from predators has produced favorable habitats that have allowed populations of susceptible rodents to Increase to very dense levels. Former summer home communities and recreational-oriented towns that now have become urbanized have retained the natural flora and fauna including dense populations of susceptible rodent species. This situation has allowed the development of periodomesticity in sylvatic rodents. New housing developments and communities have been built in plague endemic areas. Encroachment of our large cities also has invaded plague endemic areas and has created a mosaic of residential areas, green belts, and open natural areas. This mosaic pattern has allowed the commingling of people, pets, and wild rodents in which plague is currently circulating. As the landscaped vegetation in the residential areas matures, the eventual introduction of domestic rodents into this ecosystem increases the intimacy and risk of human infection.

Man has now created and modified habitats that have allowed increased intimacy with sylvatic rodents and plague in recreational sites and in his home environment. Because of the now greater risks of man's contacts with plague and other zoonotic diseases of rodents, it is imperative that high priority be given to research and development of effective integrated pest management programs against sylvatic rodent species to reduce this intimacy and risk.

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