Host-Parasite-Disease Relationships in a Mammalian Community in the Central Coast Range of California

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A contribution from the George Williams Hooper Foundation, University of California, San Francisco, California.

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INTRODUCTION

Man's relation to and dependence upon other forms of life are nowhere illustrated more vividly than in the field of his health. He has known for some time that certain of his most devastating diseases are transmitted to him by mosquitoes, fleas, lice, ticks, and various vertebrates. He is beginning to realize that in many cases these vectors obtain their initial infections from other vertebrate animals which are the natural hosts of the disease organisms. But although he is aware that many members of the animal kingdom thus form a tremendous disease reservoir which may serve as a continuing source of human infection (Meyer 1931), he is as yet largely ignorant of the complex epidemiological interrelationships which this fact implies. For a number of years the George Williams Hooper Foundation has directed research into various aspects of this problem. Part of the Foundation's program has been an investigation of the host-parasite-disease relationships existing in a natural mammalian community. The following report describes this investigation. No such study pretends to be complete or to do more than scratch the surface of this field of inquiry. However, in reporting on the ectoparasites obtained over six years from the mammals of a restricted area, we have tried to indicate some of the potentialities that such a community provides for the maintenance and spread of disease organisms dependent upon arthropod transmission.

Throughout this study, attention was focused primarily on the California ground squirrel, *Citellus beecheyi*, which has long been known as a factor in the epidemiology of plague (Wherry 1908). This squirrel is one of the commonest rodents in California and is usually an important member of any natural community in which it is found; in many areas of the state it is a serious agricultural pest. It was accordingly selected for intensive study to determine its role as a reservoir of disease.

In the choice of a site for this investigation, therefore, important considerations were an abundance of ground squirrels, an absence of human activity which would disturb natural conditions, and accessibility throughout the year. These prerequisites were provided by the environs of the Calaveras Dam, in the Livermore Hills of the central Coast Range, eight miles south of Sunol, Alameda County, California. The terrain is rugged there; some hills reach an elevation of 2000 feet, and the bottoms of some canyons are no more than 500 feet above sea level. Grassland predominates, with trees and brush growing chiefly on the northern exposures and in ravines. The climate of the region is somewhat arid. May, June, July, August, and September are largely rainless, and most of the precipitation occurs in November, December, January, and February. Rainfall in this latter period of the study varied from 17.4 to 25.2 inches per year. Conditions are influenced by the moderate weather prevailing on the coast. High morning fogs are frequent in early summer, and a heavy dew accumulates on the low vegetation nearly every night in April and May. The minimum and maximum temperatures recorded were 19° and 109° F. respectively. Mean monthly temperatures of 65°

or above occur regularly in July and August but are sometimes reached in June and may continue through September. The months of December, January and February average 52° or below. Continuous temperature records for the study area are not available, but mean monthly temperatures based on daily maximum-minimum records from the San Francisco Water Department station at Sunol have been combined with precipitation data gathered at the Dam to provide the accompanying hythergraph (Fig. 1).

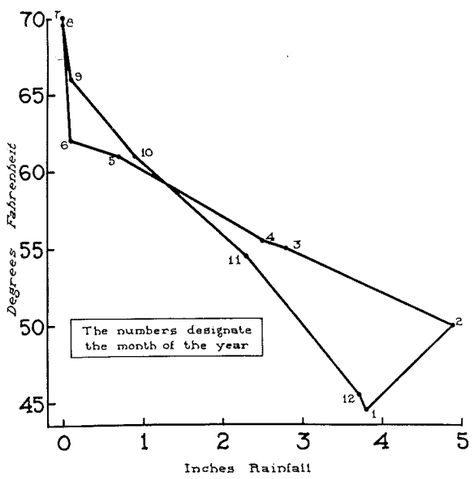

FIG. 1. Hythergraph of weather data for the environs of the Calaveras Dam, Alameda County, California, 1940-45.

The investigation covered about 100 acres on the north and east of the Calaveras Reservoir, adjacent to the Alameda-Santa Clara County line. Intensive work was restricted to an area of approximately 13 acres, of which a more detailed description has been published elsewhere (Evans & Holdenried 1943). The region appeared to be representative of much larger sections of the Upper Sonoran life zone in the central Coast Range. In addition to its ground squirrel population, it supported a considerable mammalian fauna, of which the majority of species came under observation. In view of the many opportunities for the inter-specific exchange of ectoparasites which might be involved in the transmission of disease, the study was broadened to include an examination of as many mammalian hosts and their parasites as possible.

A large-scale program of live-trapping was developed primarily to study the ground squirrels, but many other host species were frequently taken in the traps. Most of them were carefully examined for ectoparasites; the latter were removed and the hosts released after being given suitable permanent identification marks. The various mammals were lightly anesthetized with chloroform before fleas were combed from them into a pan (illustrated in Storer, Evans & Palmer 1944: 172); ticks, lice and mites were removed singly with forceps. A few dead animals that had been shot or killed by traps or automobiles were also examined.

Field work at the Calaveras Dam began in the spring of 1940 and continued into the fall of 1945. In the first two years the project was not in operation during the winter months, but from January 1943 through August 1944 field observations were made in every month except November 1943 and January 1944. During this time, collections were made from 28 species of native mammals, representing 23 genera, 15 families and 7 orders, as well as from several domestic mammals, five species of birds and three of lizards. Wherever possible, the burrows, roosts or resting places of hosts were examined as well. These sources, which included 2700 mammal examinations, yielded approximately 72,000 ectoparasites. Ectoparasites collected from squirrels especially for plague investigation are not included in this figure. Represented in this ectoparasite fauna were at least 23 species of fleas (Siphonaptera), 12 species of sucking lice (Anoplura), 6 species of biting lice (Mallophaga), 2 species of flies (Diptera), 3 species of true bugs (Hemiptera), 12 species of ticks (Ixodoidea), and 9 species of mites (other Acarina).

To detect the presence of disease organisms in these ectoparasites, it was necessary to triturate many of them in normal saline and to inoculate them into experimental animals (guinea pigs), so that not all of them were identified or permanently preserved. This was particularly true of the ground squirrel parasites. However, a preliminary study of ground squirrel fleas from the Calaveras Dam (Stewart & Evans 1941) had shown that all but a fraction of one per cent belonged to two species, which could be readily distinguished with the aid of a dissecting microscope without being permanently mounted. Most of the subsequent ground squirrel fleas were thus identified by one of us (R.H.). Doubtful specimens, and the fleas of all other hosts, were referred to authorities for identification. Similar experience with the ticks indicated that the majority of them belonged to species which could be recognized in the field while alive or when preserved in normal saline; those that required closer study were permanently preserved in alcohol, and immature forms were sometimes reared to the adult stage. Specimens of all the ectoparasite species recorded were submitted to specialists for determination or verification. An annotated host list of the different species of ectoparasites is given in the Appendix.

This entire six-year project was made possible by the willing cooperation of many individuals. In such a study it is extremely difficult to make categorical separation of the several activities and responsibilities involved. The program was initiated and directed by F. C. Evans until 1941 and the basic outline laid down at that time was, with minor changes, used to complete the study. Subsequent direction was provided by R. Holdenried, who throughout the project did much of the field work and was largely responsible for getting the ectoparasites determined and for compiling the data collected. D. S. Longanecker took over the collection of specimens in the summer of 1942 and continued with the major part of this work until its completion. Preparation of this report has been accomplished jointly by all three of us. Assistance from many other sources, however, has been the real key to the success of this work. We are particularly indebted to the following authorities for their determinations of the various ectoparasite species: J. M. Brennan (Trombidiidae); A. L. Burroughs (Siphonaptera); R. A. Cooley (Ixodoidea); O. Cope (Anoplura, Mallophaga, Acarina other than Ixodoidea); K. C. Emerson (Mallophaga); D. P. Furman (Laelaptidae); G. P. Holland (Siphonaptera); W. L. Jellison (Siphonaptera, Diptera Anoplura, Mallophaga, Acarina other than Ixodoidea); G. M. Kohls (Ixodoidea); F. M. Prince (Siphonaptera); M. A. Stewart (Siphonaptera); P. Q. Tomich (Siphonaptera); R. Traub (Siphonaptera); R. L. Usinger (Hemiptera); R. L. Wenzel (Diptera); S. F. Wood (Hemiptera). Identification of the less familiar mammal hosts was kindly done by E. R. Hall. For assistance in collecting we are grateful to J. De Lopez of the San Francisco Water Department and to A. L. Burroughs, A. S. Loukashkin, R. Rudd, K. E. Stager and P. Q. Tomich, then associated with the Hooper Foundation. We wish also to thank the San Francisco Water Department for permission to work at the Calaveras Dam. The program has been supported by the George Williams Hooper Foundation, under the able and stimulating direction of K. F. Meyer.

THE GROUND SQUIRREL POPULATION AND ITS ECTOPARASITES

Observations of the population dynamics of California ground squirrels at the Calaveras Dam have already been published (Evans & Holdenried 1943). This species is diurnal, passing the night in its burrows and engaging in foraging and other activities throughout most of the day. When active it stays relatively close to the ground surface and rarely climbs into trees or bushes. It tends to be gregarious, often digging extensive burrow systems. At the Calaveras Dam there was evidence of both estivation and hibernation for varying periods, but not all of the squirrels were inactive at the same time. Breeding took place in the early spring; young were born in April and early May, and nearly all had emerged from their burrows by mid-June. There was normally only one litter a year, which probably averaged six or seven young. As the young squirrels matured, some of them moved away from the areas of the parental burrows; August and September were the months of greatest dispersal. Once established as adult squirrels, many of them spent most of their remaining lives within ranges of less than 150 yards in greatest diameter, with occasional transfers of range to nearby territory. Thus they appeared to have a relatively fixed habitat and a restricted range. Very few squirrels evidently survived more than two years in this area.

FLEAS

Systematic collections of ground squirrel fleas were made in 42 of the 67 months covered in this study. A total of 63,907 fleas were obtained from 2321 squirrel examinations and additional collections were made from their burrows. A preliminary study of approximately 7500 of the fleas (Stewart & Evans 1941) showed that all but about a dozen belonged to two species, *Diamanus montanus* and *Hoplopsyllus anomalus*. The collections of subsequent years bore out this observation. These two species have also been found to comprise the bulk of fleas from ground squirrels in other parts of the host range (Evans, Wheeler & Douglas 1943, Linsdale 1946). One individual of *Anomiopsyllus falsicalifornicus* and a few specimens each of *Pulex irritans, Opisodasys nesiotus,* and *Orchopeas sexdentatus* were found on squirrels at various times of the year, but never more than one specimen at a time. Two other species, *Atyphloceras multidentatus* and *Monopsyllus wagneri*, were represented by single specimens collected in the burrows and were not taken from the squirrels themselves. Other than *D. montanus* and *H. anomalus,* none of these is truly a ground squirrel flea, and they obviously played an insignificant role in the ground squirrel flea fauna.

The preliminary flea survey (Stewart & Evans 1941) also demonstrated that *H. anomalus* was the most abundant species in the flea fauna of ground squirrels during the summer months, while *D. montanus* was predominant at other times. This phenomenon has been found to be true of ground squirrel flea populations on the Hastings Reservation, Monterey County, California (Linsdale 1946). A similar shift in the species composition prevailed among the ground squirrel fleas at the Calaveras Dam in each of the six years studied (Figs. 2, 3). During the winter months *H. anomalus* virtually disappeared from the ground squirrels; the highest monthly average (the average number of fleas per squirrel capture, based on all captures for a given month) from January through March was 1.3 fleas per squirrel, obtained in January 1943. In April *Hoplopsyllus* began to increase from the winter low, but it was not until July that it definitely and consistently outnumbered *Diamanus*. Through the hottest and driest season of the year (July, August and September) *H. anomalus* usually averaged 20 or more fleas per squirrel; the maximum monthly average occurred in August 1942, with 32 fleas per squirrel. There was some variation from year to year in the averages for a given month, but the phenomenon of rising to a marked peak in the summer and declining to a low in winter was constant. *D. montanus,* on the other hand, reached its peak of population density in the winter months. From April to October, when the mean monthly temperatures were 55° F. or above, the monthly average number of *D. montanus* per squirrel ranged from 5 to 17. In October, as the days became definitely cooler and the first rainstorms occurred, the number of Diamanus appearing on individual squirrels increased. From October through March the monthly averages ranged from 10 to 58

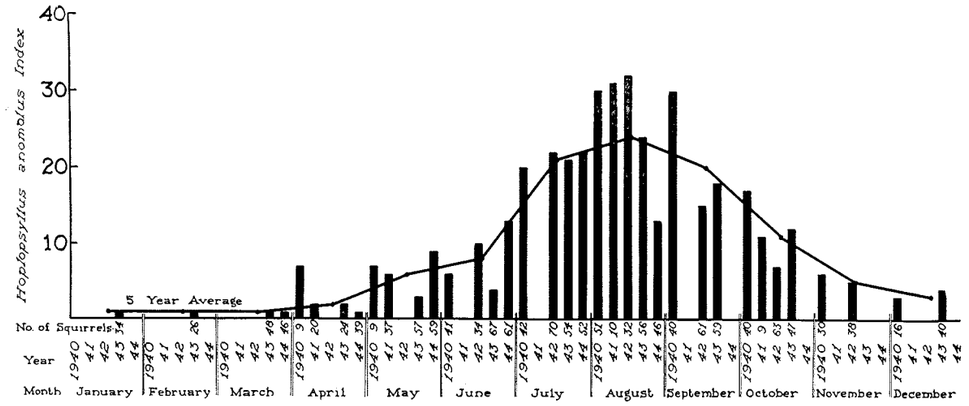

FIG. 2. Average numbers of *Hoplopsyllus anomalus* per squirrel for each month of the investigation, Calaveras Dam, 1940-44.

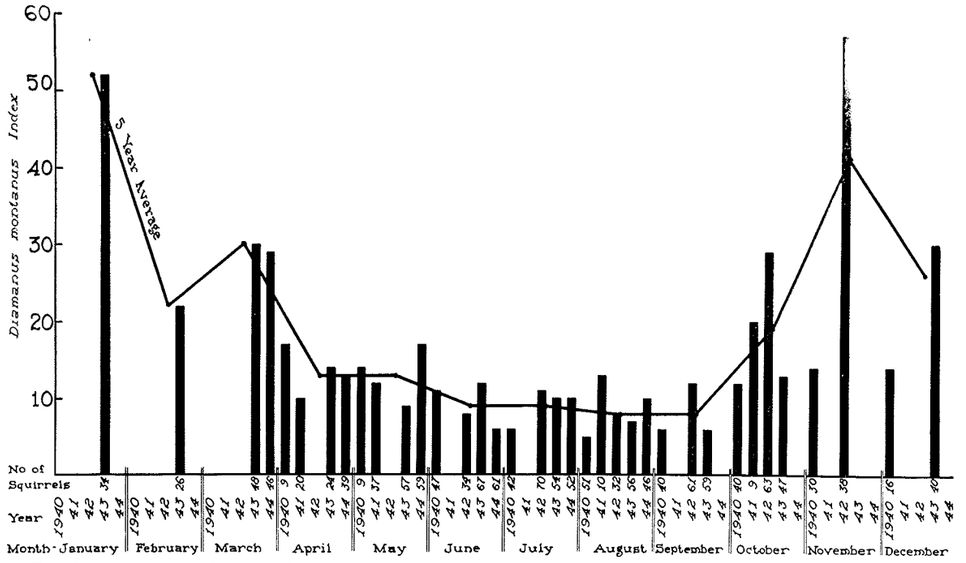

FIG. 3. Average numbers of *Diamanus montanus* per squirrel for each month of the investigation, Calaveras Dam, 1940-44.

fleas per squirrel. The peak of Diamanus density was usually reached by December. In addition to reaching its peak at a different time of year, the *D. montanus* population attained a higher maximum than that of *H. anomalus* and did not fall to as low a minimum. The two species evidently have different environmental requirements and seem to react to conditions of the environment independently of one another.

Both *D. montanus* and *H. anomalus* are capable of transmitting plague, although the former is considered to have a higher transmission potential (Wheeler & Douglas 1941). Since the chances of transmission are presumably greater with a higher flea density, the combined flea index may be of interest (Fig. 4). Fewest fleas per squirrel were found in April, May, and June. This is the transition period between the cool rainy winter months and the hot dry summer; it is also the time when the young squirrels are born and the period in which they are restricted to the nest. This low point in total flea density is the result of a decline in *D. montanus* without any compensating rise in *H. anomalus*. An increase in the latter species during the summer brings about a rise in total flea density so that by August, when the young squirrels are actively dispersing, the

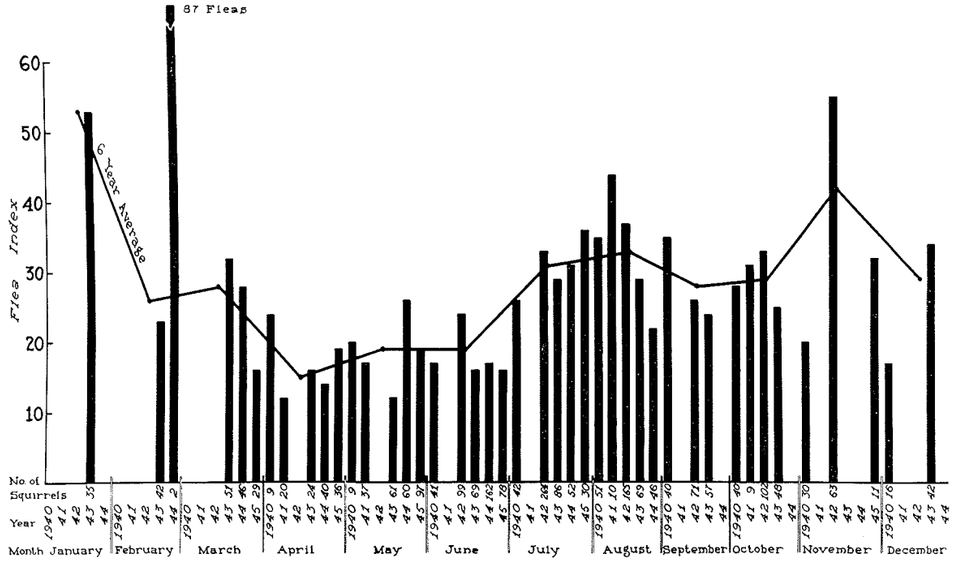

FIG. 4. Average number of fleas per squirrel for each month of the investigation, Calaveras Dam, 1940-45.

number of fleas per squirrel shows a marked increase over that of the spring. Little change in total flea density is seen in the autumn, for the decrease of *H. anomalus* is compensated for by an increase in *D. montanus*. The higher flea densities of the winter were due to Diamanus and occurred at that time of year when the squirrels spent more time in their burrows and less time outside. This high density continued into February, at which time most, if not all, of the squirrels were presumably active and had emerged from hibernation. The coincidence of a high flea density and a period of increased host activity would seem to privide conditions suitable for the outbreak of a flea-borne epizootic. Other factors are evidently also involved, for there were no apparent plague outbreaks at the Calaveras Dam during the time of our study.

A factor possibly affecting the density of parasites is any variation which may occur in the number of available hosts. The ground squirrel population at Calaveras Dam experiences a sharp annual increase in the spring, through the more or less simultaneous birth of the young squirrels. The marked summer increase in the flea index began soon after the young had emerged from the burrows. However, the squirrel population then declined continuously from its late spring peak until the following season of birth, but a corresponding decrease was not observed in either the total flea index (Fig. 4) or in the separate indices for Hoplopsyllus and Diamanus (Figs. 2, 3). Thus there was no clear correlation of the host population with that of its flea parasites.

Variations in the sex and age structure of the host population might have some effect upon the density of parasites. The combined flea index for each sex of young and adult squirrels is shown in Figure 5. In March the adult females averaged 23 fleas each, but in April the number was only 7. The average infestation of the adult males, which apparently did not occupy the nests used by the adult females with young, showed a similar decrease but remained somewhat higher than that of the adult females. Young males also had a higher average infestation than that of young females. This was evident even in June, when both sexes of young were inhabiting a single burrow and presumably shared the same nest. The slightly smaller size of the females may have correspondingly limited their flea-carrying capacity, but this is unlikely. Skin and hair conditions of the male ground squirrel may be more favorable for flea feeding, so that the parasites would remain longer on this sex than on the female and thus larger numbers would accumulate. It is also possible that after family groups have broken up and the various individuals have taken up separate burrows and nests the ecological conditions surrounding the males might favor larger flea numbers. Greater mobility on the part of males, which was observed in the young squirrels but not in the adults (Evans & Holdenried 1943), would also facilitate the acquisition of larger numbers of fleas.

Extreme age of the host did not tend to favor an undue increase in its flea fauna. At the Calaveras Dam, a four-year-old squirrel was rare and much beyond the average age of the adult population. Three squirrels of this age were examined for fleas, and none was found to have unusually large numbers.

It is commonly believed that sick or otherwise abnormal animals are particularly susceptible to parasite infestation. Ailing or under-developed squirrels

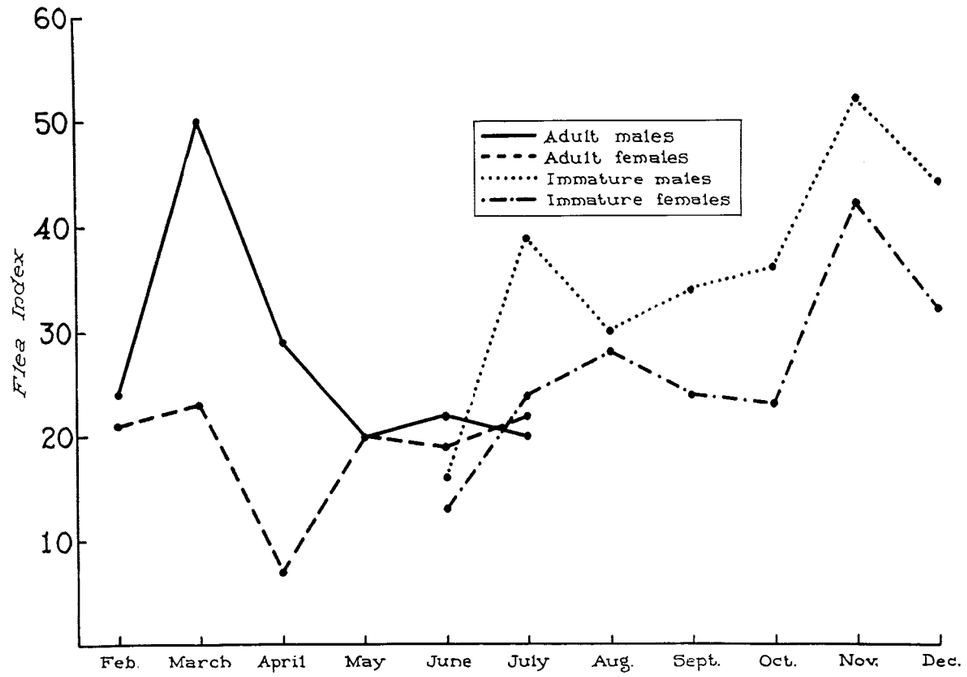

FIG. 5. The combined flea index for young and adult squirrels of each sex, Calaveras Dam, 1940-45.

sometimes had unusually high numbers of fleas. For example, an immature female that weighed only 225 grams in August, when the average weight for that age and sex was between 350 and 400 grams, was found to be harboring 276 fleas. However, an adult female which proved to be suffering from the pneumonic form of tularemia had only 10 fleas. Three immature squirrels, also infected with tularemia, had 33, 50, and 180 fleas respectively. Many of the extremely high counts, exceeding 100 fleas per animal, were obtained from apparently healthy normal squirrels. There was no indication that the flea count of a squirrel was related to its health.

Since each squirrel was given a distinctive identification mark, it was possible to keep track of the numbers of fleas taken from individual hosts. Such case histories indicated considerable fluctuations from day to day and gave some suggestion of the rate of re-infestation. During each flea-sampling period, all fleas were removed each time a squirrel was captured, but this did not seem to affect consistently the number of fleas present at succeeding captures, as illustrated by the following squirrel history, that of an immature male:

Date of capture	*No. of fleas*	*Date of capture*	*No. of fleas*
1942		1942	
June 26	22	30	22
July 10	35	November 1	28
13	21	20	115
14	7	21	130
28	55	22	42
29	47	23	42
30	28	25	31
August 6	27	1943	
7	39	January 6	131
8	28	7	177
12	20	8	147
21	21	9	85
September 15	20	February 3	28
29	64	March 16	38
October 1 (a.m.)	13	18	111
1 (p.m.)	10	19	61
2	93	20	13
27	24	April 29	13
28	30	May 1	17

In the above illustration, 1835 fleas were taken in 37 collections from a single squirrel over a ten-month period. It is evident that squirrels may be readily re-infested with fleas within very short periods of time. This phenomenon had been demonstrated some years prior to the present study by rodent investigations in the Sierra Nevada (Meyer 1938). Since these fleas normally leave their hosts for varying lengths of time, it is possible that this degree of re-infestation is a fair measure of the natural rate of flea movements. If this is so, the exposure of an individual squirrel to such a large number of parasites in a limited time must be a factor of considerable importance in the epidemiology of flea-borne ground squirrel infections.

The variations in flea counts revealed by repeated observations of the same and of different squirrels probably reflect variations in the flea populations inhabiting the squirrel nests. We did not excavate any nests which were in active use by the squirrels, for we wanted to keep conditions in the community as natural as possible. However, the preliminary survey of 1940 provided a comparison of the numbers of fleas on squirrels with those in the entrances of squirrel burrows (Stewart and Evans 1941). Flea counts from burrow entrances were much lower than those from the squirrels; they generally averaged less than 4 per entrance, and the largest number recorded from a single burrow entrance was 107, taken July 14, 1942. However, these entrance samples correlated well with those from the squirrels, for they showed a similar predominance of both *H. anomalus* and *D. montanus* and a similar seasonal shift in the relative abundance of these two species. Since these fleas are known to breed in the squirrel nests which are situated underground, changes in the subterranean environment may be the controlling factor influencing the development of the flea populations. Although microclimatic conditions in the burrows tend to be more uniform than those above ground and thus probably provide a more favorable breeding habitat for the fleas, little is known of the variations in microclimate existing there. The position of the squirrel nest in relation to the ground surface is important in this connection; some nests have been found only six inches below the surface, where temperature and humidity are probably more variable than in nests at greater depths. The age and status of the burrow system should also be considered, for old systems and nests sometimes contain large amounts of decaying feces and nest material that may be favorable to flea development, while newly constructed nests would harbor few adult fleas for some days. An investigation of the breeding habitat is necessary to further understanding of the growth of flea populations.

TICKS

Tick collecting was relatively limited in 1940, when only 29 were secured from squirrels. In 1941, approximately thirty squirrels per month were examined for ticks from April through November (except for July), and 121 ticks were taken. In 1942 similar examinations were made in late March, late May and at intervals from July 6 to November 30, in which time 629 squirrel examinations were made and 2432 ticks obtained. In 1943, collecting was accomplished in every month except November; 598 squirrel examinations were made and 979 ticks taken. Less extensive work was undertaken in 1944, but from February through August 567 ticks were secured from 305 squirrel examinations. A total of 977 ticks were taken from 284 squirrels in the period from March through July and in November, 1945.

In the first two years of the study not all of the ticks were identified, but from 1942 on all specimens were determined at least to genus. Three genera, Dermacentor, Ixodes and Haemaphysalis, were encountered on the squirrels, represented by the following species: *D. occidentalis, I. pacificus, I. sculptus* and *H. leporis-palustris*. The one record of the latter appeared to be a case of accidental parasitism; *I. sculptus* proved to be host specific for ground squirrels in this area, while *I. pacificus* and *D. occidentalis* occurred on many other hosts. *Ornithodoros turicata* was found in all stages of development in the squirrel burrows but never on a host animal; this species was obtained by scraping out the burrow as far back as three feet from the entrance and sifting the scratchings from the bottom of the burrow where it was slightly moist.

Figures showing the percentage of squirrels infested with ticks of all species (Fig. 6) and the num-

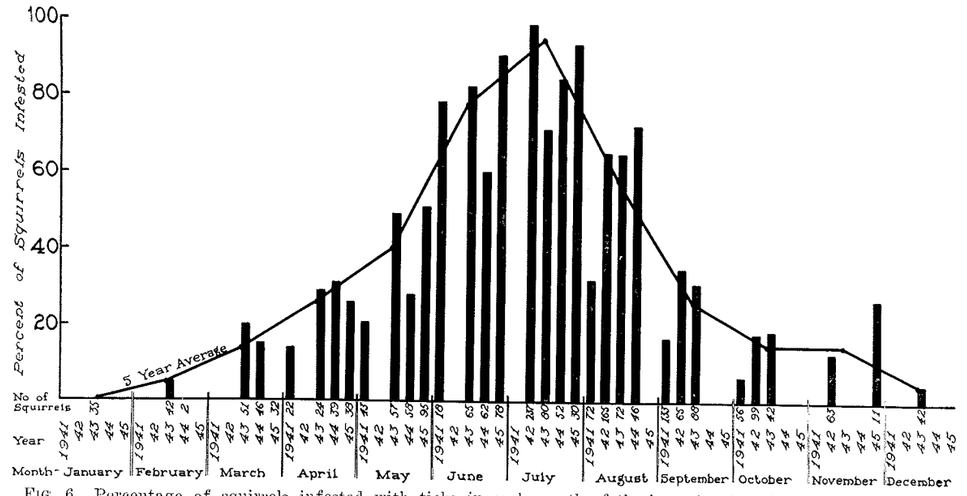

FIG. 6. Percentage of squirrels infested with ticks in each month of the investigation, Calaveras Dam, 1941-45.

bers of ticks found per every 10 hosts (Fig. 7) indicate a marked seasonal occurrence of these ectoparasites on the squirrels. Very few were encountered in the winter months, and it was not until March that they began to be taken with appreciable frequency. The degree of infestation then rose steadily and reached its peak in mid-summer, generally July, when from 82 to 98% of the squirrels had ticks. From this peak point, decline was equally steady and by November not more than 20% were ever infested. This tick "season" clearly reflects the rhythmic life history cycle of these arthropods. It suggests that tick-borne diseases may run a rather different epizootic course from that of diseases carried by fleas.

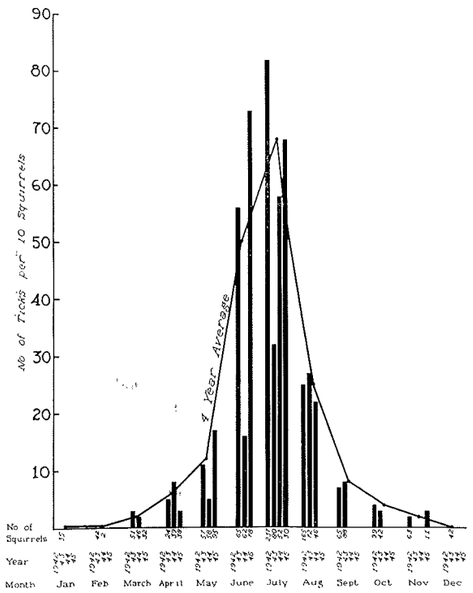

FIG. 7. Numbers of ticks per every 10 squirrels in each month of the investigation, Calaveras Dam, 1942-45.

During the peak of the tick season there seemed to be a continual supply of hungry ticks waiting for suitable hosts, to which they usually attached on the head, neck, shoulder, under the foreleg, or occasionally on a foot or near the anus. Although as many as 67 ticks were sometimes taken from a single squirrel, the number per host was usually much smaller, most frequently less than six (Table 1). Even at the height of the tick season, when nearly all of the squirrels were infested, the maximum average number of ticks per squirrel was only 8.2. This is in contrast to the large numbers sometimes occurring on other host species; in Minnesota the varying hare *(Lepus americanus)* has been found to harbor as many as 16,000 ticks *(Haemaphysalis leporis-palustris)* on a single hare and in some months to average as many as 4000 ticks per host (Green, Evans, and Larson 1943). It has been suggested that in years of heavy infestation all of the tick-feeding space on the hare is occupied (Green, Evans, Bell, Larson, and Mather 1937). No such extreme utilization of the host was found with the Calaveras Dam ground squirrels.

TABLE 1. Tick collection from California ground squirrels by month and the degree of infestation per squirrel, Calaveras Dam, 1942-45.

Month	Number of squirrels examined	Number of ticks taken	Percent of Squirrels Infested With Ticks					
			Number of ticks					
			0	1-5	6-10	11-15	16-20	over 20
January	35	0	100					
February	44	2	96	4				
March	129	22	86	14				
April	101	59	71	26	3	1		
May	210	258	56	38	5			
June	205	1022	22	50	15	7	4	2
July	399	2697	6	48	27	12	3	4
August	283	706	35	54	8	0	0	1
September	153	116	67	31	1	1		
October	141	55	82	17	1			
November	74	16	85	15				
December	42	2	95	5				
Total	1816	4955						

Laboratory studies have shown that various animals, when first infested with large numbers of larval ticks, acquire a resistance which prevents subsequent batches of larvae from engorging on them (Trager 1939, Gregson 1942). There was no evidence of such acquired resistance among the ground squirrels at Calaveras Dam. Comparison of the number of ticks found on young and adult squirrels failed to show any significant difference, as illustrated by the following figures for July 1942:

No. of ticks per squirrel	*Per cent of squirrels infested*	
	Young	*Adults*
0	1	6
1- 5	42	38
6-10	30	30
11-15	13	22
16-20	6	0
over 20	8	4

It is possible that some resistance may have been acquired by the young squirrels before they left their nests after the weaning period.

Like fleas, the ticks showed considerable ability to re-infest hosts from whom these ectoparasites had been removed. Squirrels often regained as many or more ticks within a day or so of being de-ticked:

Date of capture	*No. of Ticks*
Squirrel No. 1	
July 16	23
17	23
24	19
Squirrel No. 2	
July 6	8
8	22
10	20

The rate of re-infestation was at times quite rapid. Some squirrels were examined at intervals of less than one half-day, and their ticks removed at each capture. These individuals sometimes acquired more ticks within a few hours, as indicated by the following examples:

Date of capture	*No. of ticks*	
	A.M.	*P.M.*
July 22	4	8
July 30	4	7
October 1	3	1

Data on the occurrence of the different tick species are presented in Table 2. *Dermacentor occidentalis* appeared to be the most abundant species on the squirrels and occurred in greater numbers than any other tick. It was taken most frequently in June and July, but practically disappeared from these hosts in September. Nymphs were taken much more frequently than larvae, even at the beginning of the tick season when the earlier life stage forms must actually have been present in greater numbers. In the laboratory, larvae completely engorged in from 3 to 5 days, while nymphs required from 5 to 8 days; thus nymphs, by remaining on the host about twice as long as larvae, had about twice the chance of being collected. Size of host also has a bearing on the life stage collected; adults were not found on any rodents and were taken only from larger hosts such as raccoon *(Procyon lotor)*, gray fox *(Urocyon cinereoargenteus)*, and black-tailed deer *(Odocoileus hemionus)*, while larvae were much more abundant than nymphs on the smaller rodents such as the deer-mouse *(Peromyscus maniculatus)*. Similar distribution of nymphs and larvae of *D. occidentalis* has been found to occur elsewhere (Kohls 1937). The need for intermediate hosts makes this tick, and others with similar requirements, particularly significant as a potential agent of disease transfer.

Ixodes sculptus was the second most abundant tick on ground squirrels. This species infested squirrels most heavily from April through August but continued to be taken in small numbers in all the winter months except January. Nymphs comprised 68% of the total and were collected from March through December, while larvae, representing only 2%, were taken from May to September. The remaining 30% of the 864 *I. sculptus* taken from ground squirrels were adults. With the exception of a single male, which was not attached for feeding, all adults found on the squirrels were females; three additional males were found in squirrel burrows. Nuttall (1911) pointed out that adult male ticks of species that parasitize hosts with a more or less fixed habitat are rarely found on the hosts and that mating of these ectoparasites takes place in the host's nest. At the Calaveras Dam, this species was recorded only from *Citellus beecheyi*, except for single specimens found on a gray fox and a spotted skunk *(Spilogale gracilis)* respectively.

Ixodes pacificus was taken on squirrels much less frequently than either of the two species just discussed, and their occurrence on these hosts was apparently limited to the months from March through July. Only 42 specimens were collected from squirrels, but they were also found on a wide variety of other hosts, including several species each of birds and lizards. Adult *I. pacificus* were not taken on ground squirrels but, like those of *D. occidentalis*, were restricted to larger hosts such as deer, horse, and dog.

TABLE 2. Monthly averages by species of the number of ticks per every 10 California ground squirrels, Calaveras Dam, 1942-44.

Month and year	*I. sculptus*	*I. pacificus*	*D. occidentalis*	*Total*
January				
1943	0	0	0	0
February				
1943	*	0	..	*
1944	0	0	0	0
March				
1943	2	1	0	3
1944	1	1	0	2
April				
1943	2	1	3	6
1944	7	*	0	7
May				
1943	1	1	8	10
1944	1	*	1	3
June				
1943	15	3	36	54
1944	6	*	10	16
July				
1942	18	0	63	81
1943	(no ticks were identified this month)			32
1944	6	1	48	55
August				
1942	15	0	15	30
1943	14	0	13	27
1944	12	0	12	24
September				
1942	9	0	1	10
1943	6	0	1	7
October				
1942	1	0	0	1
1943	2	0	0	2
November				
1942	*	0	0	*
December				
1943	*	0	0	*

*Indicates that the species was present but in numbers of less than one tick per 10 squirrels.

LICE

Sucking lice, *Neohaematopinus laeviusculus*, were found on the squirrels throughout the year. They were most abundant on young squirrels just out of the nest. Although as many as 300 were found on a single host, they were most frequently present in numbers of less than 100. *Enderleinellus osborni* was collected only once, in July 1945, but because of its small size it may have been previously overlooked. Both of these species of louse are common parasites of *Citellus beecheyi* and other kinds of ground squirrels.

HEMIPTERA

A single cone-nosed bug, *Triatoma protracta*, was found in a trap with a squirrel in the summer of 1940. This species was also taken several times in association with desert and dusky-footed wood rats. It is possibly of epidemiological significance, because

it is known to transmit the trypanosomes of Chagas' disease.

THE ROLE OF GROUND SQUIRRELS IN COMMUNITY HOST-PARASITE RELATIONSHIPS

This population of California ground squirrels and their burrows yielded a total of sixteen ectoparasite species, including two sucking lice, one cone-nosed bug, eight fleas, and five ticks. These were separable into four main groups on the basis of their host occurrence. The first group includes those which were either entirely restricted to *C. beecheyi* or found singly on one or two other hosts:

Neohaematopinus laeviusculus
Enderleinellus osborni
Ixodes sculptus
Ornithodoros turicata

A second group was formed by species also largely specific for ground squirrels but taken occasionally on a good many other hosts:

Diamanus montanus
Hoplopsyllus anomalus

Group three was made up of those species which did not seem especially characteristic of Citellus and which occurred as frequently on a wide variety of other hosts:

Dermacentor occidentalis
Ixodes pacificus

The fourth and largest group was comprised of those ectoparasites which were only accidentally or casually associated with ground squirrels and which were more frequently taken from other hosts:

Triatoma protracta
Atyphloceras multidentatus
Monopsyllus wagneri
Opisodasys nesiotus
Orchopeas sexdentatus
Anomiopsyllus falsicalifornicus
Pulex irritans
Haemophysalis leporis-palustris

Twenty species of mammals which were natural members of the community were brought into the relationship of having one or more of these ectoparasites in common with the ground squirrel. Thus included were all of the mammal species examined, except the bats, shrews, and the pocket gopher *(Thomomys bottae)*. To this list may be added man, dog, and horse, three species of birds and three of lizards. It is of some interest to consider briefly the organization of the mammalian community from the standpoint of the ground squirrels and to examine the channels by which ectoparasites might be transferred from one host species to another.

A number of the smaller mammals, when released after capture, frequently disappeared into the ground squirrel burrows. Grass cuttings left by the meadow vole *(Microtus californicus)* were found a number of times at the mouths of squirrel burrows, where the voles apparently felt sheltered and could consume their food with more leisure. It seems probable that the pocket mouse *(Perognathus californicus)*, harvest mouse *(Reithrodontomys megalotis)*, and the various species of Peromyscus *(P. maniculatus, P. truei,* and *P. californicus)* also made use of the burrows as temporary or permanent shelters. Squirrel trails through both green and dry vegetation were used by all of these rodents. Among these common denizens of the burrows and trails, parasite transfer could be effected directly from host to host or, more commonly, indirectly from nest material, burrow walls and entrances, and the trail surfaces, where the parasites are left by one individual to be picked up subsequently by another. The ground squirrels seemed to be particularly effective in seeding their habitat with parasites, especially with fleas, with which other animals might come in contact. The evidence suggested that passage from ground squirrels to smaller mammals occurred more frequently than passage in the opposite direction.

Predation on the ground squirrels is also a factor permitting transfer of parasites from prey to predator. Mammals of the area which may be classified as actual or potential predators include the long-tailed weasel *(Mustela frenata)*, gray fox, coyote *(Canis latrans)*, raccoon, badger *(Taxidea taxus)*, and bobcat *(Lynx rufus)*. Such cases of transfer are often examples of accidental parasitism but may also include instances of normal progress from intermediate to final host.

A related but distinct category seemed to apply to other mammals such as the opossum *(Didelphis virginiana)*, the striped skunk *(Mephitis mephitis)*, and the spotted skunk, which frequently excavated the ground squirrel burrows. Their purpose in doing so did not seem to be to molest the squirrels themselves, but rather to search for smaller prey or often to enlarge the burrows for their own use.

The activity of the squirrels above ground carried them into habitats occupied by a number of other mammals and provided further possibility for contact between species. In rocky piles they were often associated with desert woodrats *(Neotoma lepida)*, deermice *(Peromyscus maniculatus)*, and piñon-mice *(Peromyscus truei)*, in areas of brush and trees with dusky-footed woodrats *(Neotoma fuscipes)*, gray squirrels *(Sciurus griseus)*, chaparral-mice *(Peromyscus californicus)*, and brush rabbits *(Sylvilagus bachmani)*, and in open grassy places with cottontails *(Sylvilagus audubonii)*, jackrabbits *(Lepus californicus)*, black-tailed deer, and others of the smaller mammals previously mentioned.

These community host-parasite relationships have been postulated on the basis of ectoparasite species common to the ground squirrel and one or more other mammalian hosts. A similar picture could be developed from the standpoint of each of the other host species. The intricate web of interrelationships that would result from a composite treatment of the community would be too complex for adequate representation. Host records for the various ectoparasites are given at length in the Appendix. The distribution of the several host species according to the number of parasite species recorded for each is indicated as follows:

	Number of parasite species per mammal host species			
	1-3	4-6	7-9	10-12
Number of mammal host species	11	8	6	3
Percentage of total mammal host species	39.3	28.6	21.4	10.7

Of the 28 species of free-living, non-domestic mammals examined, 17 had from four to twelve species of ectoparasites. Six host species yielded only one kind of ectoparasite in each case, but this was probably due to the infrequency of examination rather than to actual freedom from parasitism. During the period of this investigation no conditions were observed which might have led to an unusual concentration of ectoparasites, and there is no reason to believe that this degree of parasitism is not shared by other mammal faunas of similar structure.

In such a parasitological survey, the extent of specificity of host selection is of considerable interest. The distribution of the several parasite species according to the number of mammalian host species recorded for each is shown as follows:

	Number of mammal host species per parasite species				
	1-3	4-6	7-9	10-12	13-15
Number of parasite species	51	5	3	1	1
Percentage of total parasite species from mammal hosts	83.7	8.2	4.9	1.6	1.6

Of the 65 ectoparasite species with definite mammal host records, 40 were taken from single host species. As suggested above, the infrequency with which some of the hosts were examined may account for some of this apparently high degree of host specificity. Nevertheless, 17 species of ectoparasites were almost certainly host-specific in the Calaveras Dam area, as follows:

Trichodectes octomaculatus
Trichodectes mustelae
Trichodectes quadraticeps
Geomydoecus geomydis
Neohaematopinus laeviusculus
Neohaematopinus neotomae
Fahrenholzia tribulosa
Enderleinellus osborni
Polyplax abscisa
Hoplopleura acanthopus
Hoplopleura sciuricola
Solenopotes ferrisi
Cimex pilosella
Lipoptena depressa
Trichobius corynorhini
Myodopsylla gentilis
Ixodes sculptus

Thirteen species were probably restricted to small groups of closely related host species, as for example the louse *Trichodectes mephitidis* found on both striped and spotted skunks. Others in this category include the following:

Haemodipsus sp. nov.
Polyplax auricularis
Hoplopleura hesperomydis
Linognathus setosus
Foxella ignota
Histrichopsylla gigas
Odontopsylla dentatus
Cediopsylla inaequalis
Crnithodoros sp. undet.
Ixodes jellisoni
Spincturnix sp. undet.
Notoedres cati

From the standpoint of disease transfer, the ectoparasites with the least host specificity would seem to be of greatest significance. Six fleas *(P. irritans, H. anomalus, D. montanus, M. telchinum, O. sexdentatus, O. nesiotus)* and two ticks *(D. occidentalis, I. pacificus)* were the most widely dispersed species, being found on from 6 to 17 different species of hosts. All of these ectoparasites have been found naturally infected with, or have been experimentally proved capable of transmitting, such disease organisms as those of plague and tularemia. All of these species were taken by us from ground squirrels, which thus appeared to be unusually exposed to the possibility of arthropod-borne infection.

ECTOPARASITES ENCOUNTERED ON MAN

Field workers on this project were subject to occasional infestation by the various species of ectoparasites. Only five species were actually encountered on the men or their clothing. *Pulex irritans* was taken at almost every summer examination of deer beds, where this species was present in large numbers. The fleas quickly crawled up trouser legs and many attempted to obtain blood meals immediately; as many as 60 fleas were removed from one man after less than a minute's contact with the beds. *Hoplopsyllus anomalus* was also found on bodies or clothes on several occasions and was twice noted as drawing blood. The other abundant squirrel flea, *Diamanus montanus,* did not appear to infest man. In August 1944, after probing a squirrel burrow by hand, one worker found several larval *Ornithodoros turicata* on his arm; some of them were already partially engorged by the time they were detected. *Dermacentor occidentalis* was collected from man rather frequently; adults were taken in February, March, May, June, July and November, and immatures in June and July. *Ixodes pacificus* was recorded twice from workers, an adult female in April and a nymph in June. All of these records were accidental and, considering the magnitude of the project, surprisingly few. Nevertheless, it is by such accidents as these that the causative agents of many diseases are transmitted from their natural host reservoirs to human populations where, once established, they may break out in epidemic form.

ECTOPARASITE-TRANSMITTED DISEASES

PLAGUE

In November 1933 a ground squirrel shot at the Calaveras Dam by the California State Department of Public Health proved to be plague-infected. Subsequent routine surveys failed to show further evidence of this disease organism *(Pasteurella pestis)* in this area until the summer of 1942, when it was again isolated from squirrel organs and fleas (Meyer, Holdenried, Burroughs, & Jawetz 1943). Although during the six years of our study there was no indication of epizootic plague, it was evidently latent within the community.

Both of the squirrel fleas, *D. montanus* and *H. anomalus,* were also found plague-infected at the

Calaveras Dam in the summer of 1942 (Meyer, et al. 1943). No plague-infected ticks were found in our study area, but the State Department of Public Health reported 13 pools of infected ticks from ground squirrels, jack rabbits and cottontails in California from 1941 through 1943. In view of the large number of host species parasitized by some ticks and the fact that individual ticks may require several different hosts, the extent to which ticks are involved in the transmission of plague should be investigated.

Routine laboratory testing of the organs of other rodent species was initiated in 1943, but none was found positive for plague. Most of these rodents have been proved naturally plague-infected at various times elsewhere in California. Recent observations (Meyer and Holdenried 1949) indicate that plague may be spread from wild to domestic rodents; on a ranch where plague infection was demonstrated in both ground squirrels and rats *(Rattus norvegicus* and *R. rattus),* infected squirrel fleas, *D. montanus* and *H. anomalus,* were obtained from rats, while rat fleas, *Nosopsyllus fasciatus* and *Leptopsylla segnis,* were entirely absent from ground squirrels.

TULAREMIA

In 1943 and 1944, tularemia *(Pasteurella tularense)* was isolated from the organs of six ground squirrels, two pools of ticks removed from ground squirrels, the organs of two meadow voles, and a pool of fleas from the meadow voles, all collected at the Calaveras Dam. No tularemia epizootic was observed on the study area in the six years covered by this investigation. Although an estimated 93,000 ectoparasites were inoculated into guinea pigs, *P. tularense* was detected only 10 times. Like plague, tularemia appeared to be in enzootic form among the ground squirrels during this study. Evidence that fleas may not play an important part in the spread of this disease has been reported in a study of a tularemia epizootic near San Francisco (Burroughs, Holdenried, Longanecker, & Meyer 1945). Ticks are generally considered to be the most important vectors. The tularemia-infected ticks from the Calaveras Dam were not identified, but the following species found there have been reported naturally infected: *Haemaphysalis leporis-palustris* by Parker & Spencer (1927), *Dermacentor occidentalis* by Parker, Brooks, & Marsh (1929), and *Ixodes pacificus* by Davis & Kohls (1937).

TRYPANOSOMIASIS

Several young squirrels, brought to the laboratory in July and August 1940, lost weight while they were held under observation. They showed a marked anemia, and blood films revealed trypanosomes, approximately one in every twenty fields. Mrs. B. S. Davis in the Zoology Department of the University of California at Berkeley has kindly determined that they resemble *Trypanosoma otospermophili* (Wellman & Wherry) and are in the *lewisi* group of trypanosomes rather than the *cruzi* group as originally stated by Meyer et al. (1943). The life history of this species has not been studied, but other species in the group pass through a development cycle in fleas, passing out with the feces in the infective stage. One or both of the squirrel fleas, *D. montanus* and *H. anomalus,* probably serve as intermediate hosts and vectors for the trypanosomes.

RELAPSING FEVER

The spirochetes of relapsing fever, *Borrelia turicatae* (Brumpt), were recovered from three of five pools of *Ornithodoros turicata* which had been collected from squirrel burrows (Burroughs & Holdenried 1944). This tick has been reared in the laboratory for five generations with relapsing fever spirochetes passing from generation to generation by ovarian transmission (Davis 1943). Pavlovsky & Skrynnik (1945) report that naturally infected females of *Ornithodoros papillipes,* kept in the laboratory for as long as 13 years, have been able to transmit relapsing fever spirochetes to guinea pigs throughout that time. If this occurs in nature, the tick vector may be a more efficient spirochetal reservoir than the mammalian host.

SUMMARY

A field study of the California ground squirrel and associated mammals in a natural community at the Calaveras Reservoir and Dam in Alameda and Santa Clara Counties, California, from 1940 to 1945 included the collection and identification of approximately 72,000 ectoparasites, and the inoculation of many of them into laboratory test animals for the detection of disease organisms. The 65 species of ectoparasites, taken from one or more of the 28 mammalian host species, included 22 species of fleas, 12 of sucking lice, 5 of biting lice, 2 of flies, 2 of true bugs, 13 of ticks and 9 of mites. Particular emphasis was placed on the fleas and ticks of the ground squirrels.

The flea population from ground squirrels consisted almost entirely of two species, *Diamanus montanus* and *Hoplopsyllus anomalus.* The latter was most abundant and predominated in the flea fauna during the summer months, the former from October through March. A combined index of flea density indicated a low density in late spring, when the young squirrels are born and confined to their burrows, and a high density throughout the winter and until the time of increased squirrel activity and the mating period in early spring. Squirrels were often quite heavily re-infested with fleas soon after their previous ectoparasites had been removed. Male squirrels harbored a greater number of fleas than females.

The ground squirrel tick population showed a marked seasonal fluctuation, reflecting the development of the ticks; they occurred in greatest numbers during the summer, and only a few squirrels were found infested in the winter months. Like the fleas, the ticks readily re-infested squirrels previously relieved of ectoparasites. Both adult and immature *Ixodes sculpus* occurred on the squirrels, but only nymphs and larvae of *I. pacificus* and *Dermacentor occidentalis.* The seasonal occurrence of ticks suggests that tick-borne diseases run a rather different course from that of flea-borne infections.

The various ectoparasites collected from ground squirrels showed differing degrees of host specificity. Twenty other mammals had one or more ectoparasites in common with the ground squirrel. Some of these mammals apparently occupied the ground squirrel burrows, some were actual or potential predators of the squirrels or of the other mammals living with them, and some were associated with the ground squirrels because they occupied habitats entered by the latter during their daily activities. These various relationships illustrate the means by which ectoparasites may be transferred from one host to another and the extent to which the mammalian community may be linked together by parasitism.

Five species of ectoparasites were encountered at various times on the field workers engaged in this study. These accidental occurrences demonstrate the manner in which man may acquire ectoparasite-borne diseases.

Plague, tularemia, trypanosomiasis, and relapsing fever were isolated from the mammal hosts or their ectoparasites. No epizooties were observed in the area, and both plague and tularemia were evidently latent during the period of this study.

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APPENDIX

Annotated Ectoparasite-Host List from Calaveras Dam, Alameda Co., California

(Initials in parentheses indicate name of determiner, given in full in the Introduction.)

Class INSECTA

Order MALLOPHAGA

Family Trichodectidae

Trichodectes octomaculatus Paine
Host: Raccoon, *Procyon lotor*
Date: July 23, 1940—several. (O. C.).

Trichodectes mustelae Schrank
Host: Long-tailed weasel, *Mustela frenata*
Date: May 6, 1941—several. (O. C.).

Trichodectes mephitidis Packard
Host: Striped skunk, *Mephitis mephitis*
Date: June 16, 1940—several. (O. C.).
Host: Spotted skunk, *Spilogale gracilis*
Date: July 23, 1944—several. (W. L. J.).

Trichodectes quadraticeps Chapman
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 21 and 25, 1941—several thousand from each of three pups examined; also taken in large numbers from an adult. (O. C.).

Geomydoecus geomydis (Osborn)
Host: Pocket gopher, *Thomomys bottae*
Date: March 16, 1943—moderate numbers on 1 individual (W. L. J.).
April 4, 1945—well over 100 on a gopher. (R. H.).

Family Menoponidae

Myrsidea latifrons (Carriker)
Host: Nests of cliff swallow, *Petrochelidon pyrrhonota*
Date: July 20, 1945—several. (K. E. M.).

Order ANOPLURA

Family Haematopinidae

Neohaematopinus laeviusculus (Grube)
Host: California ground squirrel, *Citellus beecheyi*
Date: Present throughout the year. Most frequently found on young squirrels. June 4, 1941; June 14, 1941 (O. C.); Dec. 20, 1943; June 8, 1944 (W. L. J.).

Neohaematopinus neotomae Ferris
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: August 20, 1942—1. (W. L. J.). A number of other wood rats were examined, but this louse was obtained only once.

Fahrenholzia tribulosa Ferris
Host: California pocket mouse, *Perognathus californicus*
Date: November 13 and 19, 1941. (One mouse harbored over 100 lice.) Obtained on three different mice. (O. C.).

Enderleinellus osborni K. & F.
Host: California ground squirrel, *Citellus beecheyi*
Date: July 10, 1945—5. (W. L. J.).

Polyplax auricularis Kellogg
Host: Chaparral mouse, *Peromyscus californicus*
Date: September, 1943 (day not recorded). (W. L. J.).

Polyplax abscisa Fahrenholz
Host: California meadow vole, *Microtus californicus*
Date: Nov. 12, 1941—10. (W. L. J.); March 22, 1945. (D. P. F.).

Hoplopleura acanthopus (Burmeister)
Host: California meadow vole, *Microtus californicus*
Date: March 22, 1945—7. (W. L. J.). Either this species or *P. abscisa* or both present throughout the year. Recorded as early as March and as late as November. Heavy infestations, up to several hundred, on some mice, particularly old males. Young hairless mice found in nests also had lice.

Hoplopleura hesperomydis (Osborn)
Host: Deer-mouse, *Peromyscus maniculatus*
Date: April 13, 1945—3. (W. L. J.).

Hoplopleura sciuricola Ferris
Host: Western gray squirrel, *Sciurus griseus*
Date: July 10, 1945—6. (W. L. J.).

Linognathus setosus (Olfers)
Host: Brush rabbit, *Sylvilagus bachmani*
Date: May 10, 1944—1. (W. L. J.).

Solenopotes ferrisi (Fahrenholz)
Host: Black-tailed deer, *Odocoileus hemionus*
Date: October 6, 1943—50 collected; more were present. (W. L. J.).

Haemodipsus sp. nov.
Host: Brush rabbit, *Sylvilagus bachmani*
Date: May 10, 1944—1. (W. L. J.)
Host: Cottontail, *Sylvilagus audubonii*
Date: March 22, 1945—5; July 12, 1945—11. (W. L. J.).

Order HEMIPTERA

Family Reduviidae

Triatoma protracta (Uhler)
Host: Taken in trap with California ground squirrel, *Citellus beecheyi*
Date: Summer, 1940—1. (R. L. U.).
Host: Taken in traps with desert woodrat, *Neotoma lepida.*
Date: Summer, 1940—several. (S. F. W.).
Resting place: Found only in one or two of about 8 dusky-footed woodrat houses (*Neotoma fuscipes*).
Date: Spring, 1941—several. (R. H.).

Family Cimicidae

Cimex pilosellus (Horvath)
Host: Yuma bat, *Myotis yumanensis.*
Date: June 13, 1943—9 collected from 8 adult and 32 immature bats which left their roost beneath a tile roof in the unusually hot afternoon. May 8, 1944—obtained again from bats flying at night. November 30, 1944—11 collected at a roost of this host. (R. L. U.).

Oeciacus vicarius Horvath
Host: Cliff swallow, *Petrochelidon pyrrhonota.*
Date: July 19 and 20, 1945—over 100 bed bugs in some nests. (R. L. U.).

Order DIPTERA

Family Hippoboscidae

Lipoptena depressa (Say)
Host: Black-tailed deer, *Odocoileus hemionus.*
Date: October 6, 1943—about 30. June 2, 1945—12 from a dead fawn. (W. L. J.).

Family Streblidae

Trichobius corynorhini Cockerell
Host: Long-eared bat, *Corynorhinus rafinesquii.*
Date: March 15, 1945—2 (R. L. W.).

Order SIPHONAPTERA

(Families according to Jellison and Good, 1942)

Family Ischnopsyllidae

Myodopsylla gentilis Jordan and Rothschild
Host: Yuma bat, *Myotis yumanensis*
Date: June 16, Aug. 10, 1943; September 28 and 30, 1943—several; Aug. 26, 1944—28; Aug. 24, 1944—20. (P. Q. T.).

Eptescopsylla vancouverensis (Wagner)
Host: Long-eared bat, *Corynorhinus rafinesquii*
Date: March 10, 1946—2 ♀ ♀. (P. Q. T.).

Family Hystrichopsyllidae

Atyphloceras multidentatus (Fox)
Host: Burrow of California ground squirrel, *Citellus beecheyi*
Date: April 29, 1940—1 ♂. (M. A. S.).

Hystrichopsylla gigas (Kirby)
Host: California meadow vole, *Microtus californicus*
Date: March 22, 1945—3. (A. L. B.).

Peromyscopsylla hemispherum Stewart
Host: California pocket mouse, *Perognathus californicus*
Date: December 9, 1940— 1 ♀. (R. T.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: October 24, 25, 26 and 29, 1941—10 from 4 mice. (R. T.).
Host: Deer-mouse, *Peromyscus maniculatus,* and piñon mouse, *P. truei.*

Date: Taken on occasion from both species, usually in the fall. (R. T.).

Carteretta carteri Fox
Host: California pocket mouse, *Perognathus californicus*
Date: Taken in May, June, September, October and November. Of 32 pocket mice examined, 13 were flea-infested, 12 of them with *C. carteri.* Never more than one or two on one host. (W. L. J.).
Host: Deer-mouse, *Peromyscus maniculatus.*
Date: December 5, 1940—1 ♂. (W. L. J.); April 3, 1942—2. (A. L. B.).

Meringis cummingi (Fox)
Host: California meadow vole, *Microtus californicus*
Date: July 8, 1944—1. (F. M. P.).

Ceratophyllus petrochelidoni Wagner
Resting place: Nests of cliff swallow, *Petrochelidon pyrrhonota*
Date: July 19 and 20, 1945—13 ♂♂ and 18 ♀♀. (G. P. H.).
Dr. Holland in a recent publication (1949) states "*C. petrochelidoni* appears to be rare. The writer has examined many nests of cliff swallows (which are almost undoubtedly the true hosts) for further specimens, but without success. There are no additional Canadian records at this time.
Recently Mr. P. Quentin Tomich of the University of California at Berkeley submitted a series of fleas from Calaveras Dam, Alameda Co., California, ex nests of *Petrochelidon albifrons.* These proved to be *Ceratophyllus petrochelidoni,* ———."

Dasypsyllus gallinulae (Dale)
Host: Cottontail, *Sylvilagus audubonii*
Date: June 10, 1944—1. (G. P. H.).

Diamanus montanus (Baker)
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 21, 1941—1 ♂, 2 ♀♀; May 28, 1941—1 ♀. (W. L. J.) July 31, 1944—1. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: Taken in variable abundance throughout the year on hosts and in their burrows. (M. A. S., W. L. J., and R. H.).
Host: California pocket mouse, *Perognathus californicus*
Date: May 9, 1940—1 ♂ (W. L. J.).
Host: Desert woodrat, *Neotoma lepida*
Date: November 12, 1940—1 ♀. (W. L. J.).
Host: Dusky-footed woodrat, *Neotma fuscipes*
Date: May 3, 1940—1 ♂. (W. L. J.).
Host: Cottontail, *Sylvilagus audubonii*
Date: June 16, 1943—1; May 8, 1944—1. (A. L. B.).

Foxella ignota (Baker)
Host: Long-tailed weasel, *Mustela frenata*
Date: May 6, 1941—3 ♂♂, 4 ♀♀; June 9, 1941—1 ♂. (W. L. J.).

Malaraeus telchinum (Roths.)
Host: Western harvest mouse *Reithrodontomys megalotis*
Date: November 14, 1941—1; July 9, 1943—1. (A. L. B.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: October 29, 1940—3 ♂♂, 3 ♀♀. (W. L. J.).
July 30, 1942—1. (A. L. B.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: October 24, 1940—1 ♀; December 7, 1940—1 ♀; September 16, 1941—1 ♀; September 24, 1941—1 ♂. (W. L. J.); Nov. 19, 1941—1; Nov. 21, 1941; March 1943—4; Dec. 22, 1943—1; March 21, 1944—4. (A. L. B.).
Host: Piñon mouse, *Peromyscus truei*
Date: September 23, 1940—1 ♂; May 1, 1941—1 ♀. (W. L. J.); July 30, 1942—3. (A. L. B.).
Host: Desert woodrat, *Neotoma lepida*
Date: October 27, 1940—1 ♂ (W. L. J.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: May 30, 1940—1 ♀. (W. L. J.).

Monopsyllus wagneri (Baker)
Host: California pocket mouse, *Perognathus californicus*
Date: December 9, 1940—1 ♂. (W. L. J.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: December, 1940—1 ♂, 2 ♀♀. (W. L. J.).
Resting place: Burrow of ground squirrel, *Citellus beecheyi*
Date: July 1, 1940—1 ♂. (M. A. S.).

Odontopsyllus dentatus (Baker)
Host: Cottontail, *Sylvilagus audubonii*
Date: May 8, 1944—1. (A. L. B.).

Opisodasys nesiotus Augustson
Host: Striped skunk, *Mephitis mephitis*
Date: May 28, 1943—1. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: July 19, 1940—1 ♀; one or two others on various occasions. (M. A. S.).
Host: California pocket mouse, *Perognathus californicus*
Date: September 23, 1940—1 ♀. (W. L. J.).
Host: Western harvest mouse, *Reithrodontomys megalotis*
Date: November 14, 1941—2. (A. L. B.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: October 24, 1940—1 ♀. (W. L. J.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: Taken in every month except January, when no hosts of this species were examined. (W. L. J. and A. L. B.).
Host: Piñon mouse, *Peromyscus truei*
Date: November 13, 1941—2; July 30, 1942—1. (A. L. B.).
Host: Desert woodrat, *Neotoma lepida*
Date: May 6, 1941—1 ♀. (W. L. J.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: July 17, 1942—1; March, 1943—1. (A. L. B.).
Host: California meadow vole, *Microtus californicus*
Date: Nov. 12, 1941—1. (A. L. B.).

Orchopeas sexdentatus (Baker)
Host: Long-tailed weasel, *Mustela frenata*
Date: May 6, 1941—1 ♀. (W. L. J.).
Host: Spotted skunk, *Spilogale gracilis*
Date: September 30, 1940—1 ♀. (W. L. J.).
Host: California ground squirrel, *Citellus beecheyi*
Date: May 31, 1940—1 ♀; one or two others on several occasions (M. A. S.).
Host: Desert woodrat, *Neotoma lepida*
Date: Taken in every month in which these hosts were examined (May through December). (W. L. J.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: Taken in every month in which these hosts were examined (March through November). (W. L. J. and A. L. B.).
Host: California meadow vole, *Microtus californicus*
Date: May 25, 1941—1 ♀. (W. L. J.).

Anomiopsyllus falsicalifornicus Fox
Host: California ground squirrel, *Citellus beecheyi*
Date: July 29, 1944—1. (F. M. P.).

Family Pulicidae

Cediopsylla inaequalis (Baker)
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 28, 1941—2♀♀. (W. L. J.).

Ctenocephalides felis (Bouché)
Host: Opossum, *Didelphis virginiana*
Date: July —, 1942—5. (A. L. B.).
Host: Dog, *Canis familiaris*
Date: Sept. 29, 1943—72 (P. Q. T.).

Hoplopsyllus anomalus (Baker)
Host: Spotted skunk, *Spilogale gracilis*
Date: September 30, 1940—1♂, 7♀♀; October 2, 1940—2♀♀ (W. L. J.); July 23, 1944—6. (A. L. B.).
Host: Striped skunk, *Mephitis mephitis*
Date: May, 1942—1. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: Taken in variable abundance throughout the year on hosts and in their burrows. (M. A. S., W. L. J., and R. H.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: July 30, 1942—1. (A. L. B.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: August 1, 1942—7. (A. L. B.).
Host: California meadow vole, *Microtus californicus*
Date: June 3, 1941—1♀. (W. L. J.); July 22, 1942—2. (A. L. B.).
Host: Cottontail, *Sylvilagus audubonii*
Date: June 16, 1943—2. (A. L. B.).

Hoplopsyllus foxi Ewing
Host: California jackrabbit, *Lepus californicus*
Date: June 17, 1944—1. (A. L. B.).
Host: Cottontail, *Sylvilagus audubonii*
Date: May 8, 1944—2; June 10, 1944—2. (A. L. B.).

Pulex irritans Linnaeus
Host: Opossum, *Didelphis virginiana*
Date: July 24, 1940—1♀. (W. L. J.).
Host: Raccoon, *Procyon lotor*
Date: July 23, 1940—2♀♀; July 27, 1940—1♂, 4♀♀. (W. L. J.); July 28, 1944—3. (A. L. B.).
Host: Spotted skunk, *Spilogale gracilis*
Date: September 30, 1940—6♂♂, 11♀♀; October 2, 1940—12♂♂, 15♀♀. (W. L. J.); July 23, 1944—7. (A. L. B.).
Host: Striped skunk, *Mephitis mephitis*
Date: June 16, 1940—1♀. (W. L. J.).
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 21, 25 and 28, 1941—19♂♂, 34♀♀; June 21, 1941—1♂, 3♀♀. (W. L. J.); July 31, 1944—4♂♂, 8♀♀. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: August 3, 1940—1♀; August 22, 1940—1♂; single specimens on several occasions in September and October, single specimens also recorded several times from burrows. (M. A. S.).
Host: Desert woodrat, *Neotoma lepida*
Date: May 25, 1941—1♀. (W. L. J.).
Host: Black-tailed deer, *Odocoileus hemionus*
Date: June 2, 1945—2. (R. H.); present in deer beds in August, September and October. (A. L. B. and R. H.).

Family Tungidae

Echidnophaga gallinacea (Westwood)
Host: Opossum, *Didelphis virginiana*
Date: June 4, 1941—3♀♀. (W. L. J.).
Host: Long-tailed weasel, *Mustela frenata*
Date: June 15, 1944—1. (A. L. B.).

Class ARACHNOIDEA

Order ACARINA

Family Argasidae

Argas reflexus (Fabricius)
Resting place: Roost of bat in an abandoned cabin.
Date: November 30, 1944—6. (R. A. C., part by R. H.).

Argas sp.
Host: California quail, *Lophortyx californicus*
Date: December, 1942—1 larva. (R. A. C.).

Ornithodoros coriaceus Koch
Host: Black-tailed deer, *Odocoileus hemionus*
Date: September 24, 1942—13 larvae; October 6, 1943—14 larvae and nymphs from a dead fawn. Nymphs were also taken on several occasions from April through June 1940 and in June and August 1941 on the ground. (R. A. C. and R. H.).

Ornithodoros turicata (Dugès)
Resting place: Burrow of California ground squirrel, *Citellus beecheyi*
Date: May, July, August and September—adults, nymphs and larvae. (R. A. C. and R. H.).

Ornithodoros sp. undet.
Host: Yuma bat, *Myotis yumanensis*
Date: September 28 and 30, 1943—3 larvae. (R. A. C.).

Family Ixodidae

Dermacentor occidentalis Marx
Host: Raccoon, *Procyon lotor*
Date: June 8, 1943—1 adult♀; July 28, 1944—2 nymphs. (R. H.).
Host: Spotted skunk, *Spilogale gracilis*
Date: July 23, 1944—4 larvae, 44 nymphs. (R. H.).
Host: Striped skunk, *Mephitis mephitis*
Date: June 16, 1940—1 nymph. (R. A. C.).
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 21, 1941—1 adult♀. (R. A. C.); July 31, 1944—1 larva, 2 nymphs. (R. H.).
Host: California ground squirrel, *Citellus beecheyi*
Date: Taken abundantly from May through August on host as well as from their burrows; nymphs and larvae only. (R. A. C.).
Resting Place: Ground surface or low vegetation.
Date: Adults and nymphs on several occasions from May through August.
Host: Western gray squirrel, *Sciurus griseus*
Date: July 10, 1945—4 nymphs. (R. H.).
Host: California pocket mouse, *Perognathus californicus*
Date: June 20, 1941—4 nymphs; June 27, 1941—15 nymphs. (R. A. C.); July 10, 28, 30; August 22, 1941—a total of 28 nymphs; July 26, 1944—8 nymphs. (R. H.).
Host: Western harvest mouse, *Reithrodontomys megalotis*
Date: July 9, 1943—2 larvae, 1 nymph. (R. H.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: August 22, 1941—3 nymphs; September 24, 1941—3 nymphs; July —, 1943—55 larvae, 18 nymphs; May 17, 1944—39 larvae; July 18 and 19, 1944—9 larvae, 3 nymphs; September 6, 1944—1 nymph. (R. H.).
Host: Piñon mouse, *Peromyscus truei*
Date: August 21, 1941—1 nymph. Also taken on other occasions. (R. A. C.).

Host: Desert woodrat, *Neotoma lepida*
Date: June 10, 1940—2 nymphs; June 12 and 18, 1941—3 nymphs. (R. A. C.); July 6 and 10, 1942—8 nymphs; May 27 and 28, 1943—3 larvae and 4 nymphs. (R. H.). March through August—nymphs.
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: May, July, August and November—larvae and nymphs. (R. A. C. and R. H.).
Host: California meadow vole, *Microtus californicus*
Date: April, July and August—nymphs and larvae. (R. H.).
Host: Cottontail, *Sylvilagus audubonii*
Date: June 10, 1944—1 nymph. (R. H.).
Host: Black-tailed deer, *Odocoileus hemionus*
Date: September 24, 1942—26 adults; October 6, 1943—1 nymph, 24♀♀ and 28♂♂; June 2, 1945—7♀♀ and 7♂♂. (R. H.).
Host: Horse, *Equus caballus*
Date: June 9, 1943—11 adults of both sexes. Adults taken again in October and November, 1943. (R. H.).

Dermacentor albipictus Packard
Host: Black-tailed deer, *Odocoileus hemionus*
Date: September 24, 1942—1 nymph. (R. A. C.); October 6, 1934—23 nymphs and adults. (R. H.).
Host: Horse, *Equus caballus*
Date: November 13, 1941—50 nymphs and adults. (R. A. C.); October 1, 1943—1♀; October 2, 1943—1 nymph, 4♀♀; November 12, 1943—2♀♀; November 24, 1943—47 adults, 2 nymphs. (R. H.).

Ixodes angustus Neumann
Host: Piñon mouse, *Peromyscus truei*
Date: June 19, 1941—1 adult♀. (R. A. C.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: November 5, 1943—2 adult♀♀; November 23, 1944—16 nymphs; November 25, 1944—1 adult♀. (R. H.).
Host: California meadow vole, *Microtus californicus*
Date: April 13, 1945—1 adult♀. (R. H.).

Ixodes jellisoni Cooley and Kohls
Host: California pocket mouse, *Perognathus californicus*
Date: October through December—adults of both sexes. (R. A. C.).

Ixodes neotomae Cooley
Host: Desert woodrat, *Neotoma lepida*
Date: October 16, 1940—2 adult♀♀, 12 nymphs. (R. A. C.).

Ixodes pacificus Cooley and Kohls
Host: Broad-footed mole, *Scapanus latimanus*
Date: June 21, 1944—2 larvae (R. A. C.).
Host: Opossum, *Didelphis virginiana*
Date: June 4, 1941—6 nymphs. (R. A. C.).
Host: Raccoon, *Procyon lotor*
Date: June 8, 1943—1 nymph. (R. A. C.).
Host: California ground squirrel, *Citellus beecheyi*
Date: March through July—nymphs only. (R. A. C. and R. H.).
Host: California pocket mouse, *Perognathus californicus*
Date: June through August—nymphs only. (R. A. C.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: May 1, 1943—1 nymph. (R. H.).
Host: Western gray squirrel, *Sciurus griseus*
Date: July 10, 1945, 1 nymph (R. H.).
Host: Desert woodrat, *Neotoma lepida*
Date: March 15, 1945—1 larva, 1 adult♀. (R. A. C.).
Host: Black-tailed deer, *Odocoileus hemionus*
Date: December 5, 1943—16 adults of both sexes. (R. H.).
Host: Horse, *Equus caballus*
Date: June 9, 1943—1 adult♀. (R. H.).
Host: Dog, *Canis familiaris*
Date: November 18 and 23, 1942—16 adults of both sexes; November 1, 1943—10 adults of both sexes. (R. H.).
Host: California jay, *Aphelocoma californica*
Date: June 6, 1943—9 nymphs. (R. A. C.); June 22, 1944—2 nymphs. (R. H.).
Host: Rufous-crowned sparrow, *Aimophila ruficeps*
Date: March 31, 1945—3 larvae (R. A. C.).
Host: Golden-crowned sparrow, *Zonotrichia coronata*
Date: April 21, 1944—3 larvae; April 21, 1944—2 nymphs. (R. A. C.).
Host: Whip-tailed lizard, *Cnemidophorus tessellatus*
Date: June 8, 1941—1 nymph. (R. A. C.).
Host: Alligator lizard, *Gerrhonotus multi-carinatus*
Date: May 21, 1941—1 nymph; May 15, 1943—16 larvae, 39 nymphs from one host. (R. A. C.).
Host: Fence lizard, *Sceloporus occidentalis*
Date: April 9, 1943—9 larvae, 13 nymphs from one host (R. H.).

Ixodes rugosus Bishopp
Host: Spotted skunk, *Spilogale gracilis*
Date: September 29, 1940—1 adult♀. (R. A. C.).
Host: Long-tailed weasel, *Mustela frenata*
Date: June 9, 1941—25 nymphs. (R. A. C. determination in question.).

Ixodes sculptus Neumann
Host: Spotted skunk, *Spilogale gracilis*
Date: July 23, 1944—1 adult♀. (R. H.).
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 25, 1941—1 adult♀. (R. A. C.).
Host: California ground squirrel, *Citellus beecheyi*
Date: Taken in abundance from hosts and burrows. Adults (almost all were♀♀) in every month except January. Larvae from May through September. Nymphs from March through December. (R. A. C.).

Ixodes sp.
Host: Adorned shrew, *Sorex ornatus*
Date: November 12, 1941—1 larva. (R. A. C.).
Host: Trowbridge shrew, *Sorex trowbridgii*
Date: March 20, 1943—6 larvae. (R. H.). (not *I. soricis*).
Host: Spotted skunk, *Spilogale gracilis*
Date: September 30, 1940—4 nymphs. (R. A. C.).
Host: California pocket mouse, *Perognathus californicus*
Date: May 12, 1941—3 larvae. (R. A. C.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: October 28, 1940—1 larva. (R. A. C.).
Host: Deer-mouse, *Peromyscus maniculatus* and piñon mouse, *P. truei*
Date: February through May—larvae and nymphs. (R. A. C. and R. H.).
Host: Desert woodrat, *Neotoma lepida*
Date: May 25, 1943 and 1944—larvae; November 25, 1942—1 nymph. (R. H.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: May to November—nymphs. (R. A. C.).
Host: California meadow vole, *Microtus californicus*
Date: August 9, 1941—1 nymph. (R. A. C.).
Host: House mouse, *Mus musculus*
Date: May 15, 1944—3 larvae. (R. H.).

Haemaphysalis leporis-palustris (Packard)
Host: California ground squirrel, *Citellus beecheyi*

Date: May 28, 1941—1 ♂ and 1 nymph. (R. H.)
Host: California jackrabbit, *Lepus californicus*
Date: June 17, 1944—2 adult ♂ ♂, 23 larvae. (R. H.).
Host: Cottontail, *Sylvilagus audubonii*
Date: July 6, 1942—1 adult ♀, 3 adult ♂ ♂, 1 nymph; June 10, 1944—23 adult ♀ ♀, 39 adult ♂ ♂, 52 nymphs, 150 larvae. (R. H.).
Host: Brush rabbit, *Sylvilagus bachmani*
Date: May 23, 1941—about 30 adults, 30 nymphs and 10 larvae. (R. A. C.); May 10, 1943—6 ♀ ♀ and 7 ♂ ♂. (R. H.).
Host: California jay, *Aphelocoma californica.*
Date: June 6 and 9, 1943—13 nymphs, 1 larva; July 15, 1944—15 larvae. (R. H.).

Family Spinturnicidae

Spinturnix sp. undet.
Host: Yuma bat, *Myotis yumanensis*
Date: June 16, 1943—several; also found free on the roosts at various times. (W. L. J.).

Family Laelaptidae

Euhaemogamasus liponyssoides (Ewing)
Host: Broad-footed mole, *Scapanus latimanus*
Date: June 21, 1944—3. (D. P. F.).
Host: California meadow vole, *Microtus californicus*
Date: March 22, 1945. (D. P. F.).

Euhaemogamasus ambulans (Thorell)
Host: California meadow vole, *Microtus californicus*
Date: March 22, 1945. (D. P. F.).

Euhaemogamasus sp.
Host: California pocket mouse, *Perognathus californicus*
Date: November 3, 1943—1. (W. L. J.).

Haemalaelaps glasgowi (Ewing)
Host: California meadow vole, *Microtus californicus*
Date: From 2 mice March 22, 1945 (D. P. F.).

Laelaps kochi (Koch)
Host: California meadow vole, *Microtus californicus*
Date: Nov. 12, 1941—2. (D. P. F.).

Family Trombidiidae

Trombicula sp.
Host: California pocket mouse, *Perognathus californicus*
Date: November 3, 1943—6. (W. L. J.).

Trombicula californica Ewing
Host: California meadow vole, *Microtus californicus*
Date: Nov. 12, 1941—1. (J. M. B.).

Family Dermanyssidae

Genus not determined
Host: Deer-mouse, *Peromyscus maniculatus*
Date: September 16, 1941—and on several other occasions. (O. C.).
Host: California meadow vole, *Microtus californicus*
Date: September 25, 1941 and on several other occasions. Also found in mouse nests where they sometimes numbered in the thousands. (O. C.).

Family Sarcoptidae

Notoedres cati (Hering)
Host: Bobcat: *Lynx rufus*
Date: July 27, 1945—50+ (D. P. F.).

Family Macrochelidae

Macrocheles sp. nov.
Host: California meadow vole, *Microtus californicus*
Date: March 22, 1945—1. (D. P. F.).