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Henry S. Fitch

Fish and Wildlife Service, U.S.D.I., Leesville, La.

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INTRODUCTION

The impact of rodent use on the fluctuating crop of annual vegetation in the foothill ranges of California entails vast losses to the livestock industry to which these areas are mainly devoted. Recognition of this loss led to the conception of the present cooperative study as an integrated part of the larger problem—the development of the most economical management practices for the foothill ranges.

Of the many rodent species which compete with livestock for range forage in the foothill belt, the majority are of minor importance because of small size, low populations, or food preferences different from those of stock, with perhaps even some beneficial bearing. Much of the damage to the ranges is caused by a few species, and perhaps paramount among these is the California Ground Squirrel (*Citellus beecheyi*), the subject of this report. Throughout the far western states ground squirrels of the *Citellus beecheyi* complex are among the most destructive of native rodents. In most parts of California control measures have long been vigorously practiced wherever the squirrels threatened the existence of cultivated crops, with the result that these rodents have been held in check or locally exterminated. But on range lands the mar-

gin of profit to be gained by their elimination is much smaller and control is more difficult; in some situations it is unprofitable.

The present study was limited to one locality, the San Joaquin Experimental Range 23 miles northeast of Madera in oak-digger pine woods of the lower foothills on the west flank of the Sierra Nevada. The locality is fairly typical of the entire foothill belt almost encircling the Great Valley of California. The present findings should in general apply throughout this belt, but minor differences resulting from variations in altitude, soil and plant types, and natural histories of the several geographic races of squirrels might be expected.

The objectives of this ground squirrel study were to determine the kinds and amounts of food taken by the squirrels from a forage crop of which the quantity and composition were accurately known through measurements; to measure the populations of squirrels and to trace their changes throughout the year and over periods of years; to determine the factors limiting or influencing the population, including the roles of the several squirrel predators; to find out as much as possible concerning the habits and natural history of the squirrels.

An extensive literature already exists regarding the classification, distribution, habits, and means of control of this and related species of ground squirrels. An especially important paper is that of Grinnell and Dixon, 1918, *Natural History of the Ground Squirrels of California,* in which much detailed information concerning the ecology of this and other ground squirrels is set forth. Howell (1938) in his *Revision of the North American Ground Squirrels* brought the classification up to date, redefining the ranges of the several geographic representatives of this species.

More recently several intensive ecological studies have been made on this species of ground squirrel in different parts of its range. Storer, Evans and Palmer (1944) in a study at Bass Lake, California, only 20 miles from the Experimental Range but at a higher altitude under different ecological conditions, live-trapped and marked ground squirrels and other rodents in 1938 and 1939 on a four acre area. The numbers of squirrels dealt with were small but the findings, particularly in regard to seasonal dormancy, are of significance in affording sharp contrast with data from the Experimental Range for the same two years. Another important paper is that of Evans and Holdenreid (1943), *A Population Study of the Beechey Ground Squirrel in Central California.* The population dealt with was of the race *beecheyi* subspecifically distinct from *C. b. fisheri* of the present report, and the locality is Calaveras Reservoir, about 120 miles west and a little north of the Experimental Range. This latter study was pursued primarily from the viewpoint of plague relationships, but also touched upon the feeding habits. Live-trapping and field observations were carried on in 1940, 1941, and early 1942, but for only part of each year. Some of the findings set forth are at variance with those of the present study.

The most detailed field study of this, or perhaps any mammal, is that of Linsdale (1946), *The California Ground Squirrel.* It is based mainly on narrative field notes of 21 different observers over an eight year period at the

Hastings Wildlife Reservation, about 115 miles southwest of the Experimental Range. Mannerisms and behavior are particularly stressed, and the molts, reproductive physiology, anatomy and parasites are most thoroughly dealt with. However, but little effort was made to determine the effect of the squirrels on the vegetation. Comparatively few data were obtained on predation, and live-trapping was on a smaller scale than in the present study.

Figures and statements in Linsdale's paper in many instances indicate or suggest important ecological differences between the population studied by him and that of the Experimental Range in such matters as feeding, season and extent of dormancy, and critically limiting factors which determine numbers and local distribution. Differences are to be expected since distinct geographic races in contrasting environments are involved. An understanding of such geographic variation is essential in dealing with this rodent successfully over its entire range.

The present study was planned and carried out under the direction of Everett E. Horn of the U. S. Fish and Wildlife Service, to whom the writer wishes to express appreciation for help in many ways. The work was done in cooperation with the U. S. Forest Service, California Forest and Range Experiment Station. Thanks are due members of the Experimental Range staff: Dr. Harold H. Biswell and Jay Bentley especially rendered valuable assistance and advice from time to time in connection with problems involving the forage. Howard Twining, Daniel F. Tillotson, and John E. Chattin identified material in pellets of raptors and "scats" of predators. Many persons helped from time to time with the field work, and of these Freeman Swenson and Frank Hagarty are due especial mention for their continued interest and initiative.

A detailed account of the economy and ecology of the general area has already been set forth, describing the topography and soil (Talbot, Nelson and Storie, 1942), vegetation, livestock relationships (Wagnon, Guilbert and Hart, 1942), and wildlife (Horn and Fitch, 1942). The area is in rolling, wooded foothills, characterized by shallow, rocky soil with granite outcrops, and small areas of grassland interspersed with brush, Digger pine, blue oak, and interior live-oak.

HISTORY AND METHODS

The rodent enclosures, from which data concerning the amount of vegetation destroyed by squirrels were obtained, were installed at the San Joaquin Experimental Range in 1935. Other field work was begun the last week of March, 1938. Relatively few squirrels for the population study were trapped in 1938, as only a few miscellaneous traps of ineffectual types were then available. For part of 1939, trapping was carried on with make-shift traps which were not wholly satisfactory, and the 80 acres was first covered by May 1939. In 1940, traps were available in quantity, and field assistance for this and other projects was rendered by several helpers, Freeman Swenson, Frank Hagarty, Bernard Mitchell, Jack Ramley, and Raymond Sharp. In 1941, during the writer's absence, from March through September, trapping was carried on successively by Freeman Swenson, Henry Hjersman, and

Lowell Adams. In 1942, after the writer had left for military service early in February, trapping was continued through May by Frank Hagarty. In 1946 the area was trapped by the writer during the period January 13 to April 13. Data are thus available for three full years, 1939, 1940, and 1941, with two more years' data, 1942 and 1946, for the late winter and spring period of maximum ground squirrel activity and more meager data for 1938. During the course of this study, on the 80 acre area where live-trapping was carried on, 1,552 squirrels were captured a total of 15,936 times. Records of captures were distributed as follows: 1938—377, 1939—2874, 1940—5289, 1941—5072, 1942—1620, 1946—704. Numbers of animals caught each year were as follows: 1938—182, 1939—572, 1940—643, 1941—625, 1942—353, 1946—226.

No record was kept of the number of "trap days" involved, but usually around 200 traps were set several times a week. Usually only half the area was trapped at one time, in alternate, bi-weekly intervals. During each trapping period one or several traps were readily accessible to every animal on the area. Trapping success depended less on the actual number of traps used than on their careful placement at points where the animals were constantly tempted, their adjustment and mechanical efficiency, and the amount of disturbance by cattle, birds, ants, and other animals that might steal the bait or trip the traps. Placement at random or spaced in a grid system over the area would have caught very few squirrels, as it was observed that these animals were shy of traps encountered afield during their foraging, and usually gave them only passing notice. Traps set on burrow mounds or at loafing places where squirrels habitually spent their time, were most apt to be successful, but often a capture was preceded by hours of maneuvering on the part of the squirrel, too cautious to enter immediately. While some individuals were readily trapped, others were so shy that they avoided capture for long periods though traps were almost constantly available to them. Several are unrepresented in the records for an entire calendar year though trapped at the same burrow system in both the year preceding and the one following the lapse. The maximum number of captures recorded for any one squirrel were 117, these extending over a 20 month period. This was a male squirrel, and several other males were each caught more than 100 times, but 80 captures was the maximum recorded for any female. A few crippled individuals, evidently handicapped so that they could not forage normally, became unusually persistent repeaters. One adult female, which had broken its leg, was caught 19 times during a month.

The 80 acre area where live trapping was carried on was grazed by cattle from January through August and was stocked at the rate of one head per ten acres. Utilization was classed as moderate to close. The area was rectangular, about half a mile long, and a quarter mile wide.

The box traps used were constructed of half inch mesh galvanized wire, open at one end, and tripped by means of a pendulous trigger (Horn and Fitch 1946:222). Bait was a mixture of wheat and milo maize, which was scattered in a trail from the outside into the trap beneath and behind the trigger. In the winter, traps were set in the open on burrow mounds, and were baited in the morning before the squirrels began to feed. In summer, sets

were made in the shade of rocks, trees or bushes in spots where the squirrels were accustomed to stay, and traps were protected from the sun by covering with strips of wood and bark, or "cow chips." They were usually sprung during the heat of the day and were set and baited during the early morning and late afternoon for the two daily foraging periods of squirrels at that season.

In 1938 the squirrels trapped were marked with numbered aluminum tags and colored celluloid disks in each ear, but so many of these were lost that the system was abandoned, and marking was accomplished by toe clipping. On each animal two toes always on different feet, were amputated, and 121 different toe combinations were possible (the rudimentary thumbs were not used). These series of toe formulas were used repeatedly in combination with different key ear marks, eleven in all.

At each capture the identification formula, date, sex, weight, breeding condition, and location of the animal were recorded. Location was estimated in terms of distance in feet, and direction of the nearest landmark, usually a tree, bush, rock, or post. These named landmarks were well distributed over the area so that usually any point to be recorded was within 100 feet of one.

Study of the feeding habits was commenced in March 1938 and continued throughout the duration of field work, but few observations were made in 1946. The bulk of feeding records were obtained from field observation of a few individual squirrels which could be closely observed, but these were well distributed in different types of situations in various parts of the Range. Miscellaneous feeding records were gathered as opportunities arose, from stomach or cheek pouch examinations, or from direct observation on feeding.

Most feeding records were obtained from relatively tame squirrels conditioned to the presence of humans, and observed either for an entire day at a time, or through a main foraging period. Under the most favorable conditions every item taken during a feeding period could be recorded, for instance when a squirrel was feeding at close range, mainly on one kind of fairly large food item, such as acorn, or fruits of filaree or tarweed. At other times, when the food included a variety of minute items, it was impossible to determine just what was taken, even by close range observation.

Census methods.—Counting the squirrels on any extensive acreage was found to be difficult, mainly because of the uncertainty as to how many were underground at any one time. Much time was spent in making counts of the numbers seen per minute while walking across different pastures of the Range. Through use of comparable counts made on the 80 acre trapping area with its approximately known population, census of the entire Range was attempted. There was no consistency in the counts obtained, and it appears that a very large sample would be required for a statistically accurate census. Counts were made only on days which were favorable to squirrel activity, and only during parts of the day when they were thought to be out in maximum numbers. Differences in terrain posed the most serious obstacle in obtaining comparable counts between different areas. Where brush, trees, rocks, and irregularities in the ground surface obscured the view, fewer squirrels could be seen than in open areas. The trapping area was relatively open compared with the

Range as a whole, and since its population was used as a standard of comparison the numbers computed from counts on other areas are apt to be erroneously low.

On each of the pastures where counts were made, squirrels were unevenly distributed. Concentrations occurred at few places with much sparser populations intervening. In the mile or half-mile walk across a pasture, often several squirrels were seen within a few seconds and these might be the only ones seen.

In this locality February and March are the best months for making counts; then there is no dormancy, and squirrel foraging is concentrated within a few hours during the middle of the day, so that the whole population is apt to be active at the same time. The vegetation is still low so that the animals can be readily seen at this time of year. In summer counts the number per minute is consistently lower even though the actual population is much greater, having been increased by the annual crop of young. Variation among individuals in time of activity during the increased hours of daylight, high vegetation obstructing view of the counter, and tendency of the squirrels to stay in sheltered places, and to forage in trees, are all factors which prevent one from seeing so large a percentage of the number present. These same factors are variables which introduce a margin of error in comparing the counts from any two areas.

In an attempt to sample rapidly squirrel populations of relatively large areas several hundred counts of numbers seen per mile were made from an automobile, driving at constant speed of 20 miles per hour over various roads in Madera County range lands. Examination of these data indicates that the samples are inadequate. A road ran diagonally for the length of the trapping area a distance of .54 miles, and a total of 74 counts were made on this road, all in the breeding season when the entire population was active, and all at times of day when squirrel activity was judged to be at its maximum. The number of squirrels per count averaged 11.6 but varied from 3 to 27. Though the counts were made in 5 different years, change in the squirrel population itself was not an important cause of the differences; trapping records indicate that the active population was at all times either between 250 and 300, or near these extremes. Counts were made in nine different months and the number of counts per month varied from 4 to 18. To summarize these records, the average of four counts was 18.2 squirrels; of five counts, 9.2; of six counts, 15.2; of eight counts, 16.2; of fifteen counts, 10.9; of eighteen counts, 10.1.

These figures suggest that for this distance and population density at least 10 counts would be necessary to obtain a reliable average. As this stretch of road was .54 miles, the average 11.6 squirrels seen represent 21.5 per mile where a population density of two to three per acre was present. On this basis one squirrel per acre would be represented by a count of about eight or nine per mile—other things being equal. On the trapping area there were occasional oak trees and rock outcrops but for the most part the view was unobstructed, and squirrels were often counted at a distance of 100 yards or more. In rocky or brushy or wooded terrain, or with high vegetation obscuring the view, the ratio of number seen to those actually present would be lower.

In an attempt to check the population of the trapping area as determined by total numbers trapped, use was made of the familiar "Lincoln Index", based upon recapture of marked animals—the ratio among animals taken during a given period, of recaptures from a previous period:

$$\frac{\text{Total population}}{\text{Number caught in first period}} = \frac{\text{Number caught in second period}}{\text{Number caught in both first and second periods.}}$$

Deaths or movements off the area between periods would affect the figure obtained, but would not be an important source of error in month to month computations. However, two peculiarities of the squirrel population studied rendered this standard census method almost worthless by distorting the ratios obtained. Varying appetite for bait among individuals, and differences in wariness to the traps caused some to repeat frequently while others persistently evaded capture, tending to give an erroneously low population figure. Retirement into, and emergence from dormancy, occurring in varying degrees through most of the year, likewise produces a false ratio of repeaters to the entire population for any given sample period. The margins of error caused by these several factors cannot well be evaluated or separated, but their effect is apparent in the erratic fluctuations of the figures obtained. When a two months period was used as the census time, the resulting figure averaged 129 per cent of that obtained with a one month census, the difference being due to movement and dormancy. Separate computations were also made for different sex and age groups. The figures in Table 1 are based on a one month census period immediately followed by a month post-census. In many cases the figure is almost certainly below the actual number, due mainly to the error caused by individual difference in tendency to enter traps or to avoid capture. Inclusion of this table is intended to show limitations of this census method where varying wariness, trap experience and bait addiction, and habits of different individual animals are involved.

TABLE 1.—Distorted census figures obtained from trap ratio of repeaters to others on 80 acres.

	1939	*1940*	*1941*	*1942*
January	262	277	245	282
February	217	279	225	262
March	221	203	197	190
April	793 (249 adults)	387 (191 adults)	308 (165 adults)	135
May	535	462	375	
June	479	399	388	
July	474	304	304	
August	289	423	234	
September	236	301	227	
October	223	258	197	
November	181	220	163	

Young squirrels newly emerged above ground do not enter traps as readily as adults and may be little attracted by the grain bait, as they seem to prefer

natural foods of succulent kinds. It has long been recognized by those engaged in control operations that poisoning just after the young emerge is apt to yield poor results. Therefore the young are not represented in their true proportions in the April and May catches, and the census figures obtained for those months are correspondingly low.

The actual numbers of squirrels present during the breeding season are perhaps best indicated by the number of individuals actually trapped during the period January, February, March and April, when the whole adult population is active and the situation is not complicated by presence of small young. Even in the figures obtained at this season there is some margin of error for certain individuals which are missed even during intensive trapping, and there is movement to the study area of new individuals, in the constant gradual shifting that occurs. Also, some are trapped within the boundaries of the area, which range mainly outside it. These last two factors tend to make the numbers trapped erroneously high for a representation of the true population present. At other times of year, varying dormancy of part of the population, and the rapidly changing numbers of young still further obscure the true population density. It can only be estimated from the relative numbers of different sex and age groups, and from the percentage of the breeding adult population represented. Allowance must be made for expected normal mortality as indicated by reduction from one year to the next of any given group of individuals.

Even direct counts probably do not give a true ratio of young to adults, since the young are less conspicuous and after first emerging sometimes retire into the burrows again for periods of days. Several attempts to determine dispersal and causes of loss, in newly emerged litters failed because the young seen and counted at a burrow on one day usually could not be located there on later dates, and must have come above ground only occasionally during the first week or two after emergence.

FEEDING

Quantities consumed.—In the past the feeding has been less thoroughly studied in its quantitative aspects than it has qualitatively. The kinds of food taken differ according to season and locality, while the amount required to maintain an animal is doubtless fairly constant over any long period, though subject to variation due to the age, sex, and physiological state of the individual, and the palatability and nutritive value of the kinds of food used.

Linsdale (1946:222) stated "In evaluating the effects of squirrels on forage crops it is not enough to determine that certain kinds of plants are eaten. Nor can the effects be computed correctly by determining the amount of food contained in the stomach at any one time or taken in one day. These are not suitable bases for computation, partly because they change continuously and irregularly."

The variation mentioned by Linsdale was also apparent in the present study and it is evident that no precision measurement of squirrel damage to the forage crop can be made. The forage crop is affected by so many other variables that it is difficult to identify the effect of ground squirrels. Never-

theless, it is believed that in general the extent of damage to the forage can be determined by use of experimentally controlled plots, direct observation of the quantity and kind of vegetation used by feeding squirrels at different seasons, and the determination of the squirrel population.

Grinnell and Dixon (1918:629-630) stated that in feeding experiments in captivity: "Fifty grams . . . of green alfilaria was found to be the average daily ration for an average-sized squirrel. In cases where all food had been withheld from the squirrels the previous day, the greatest amount of succulent alfilaria, the favorite food of the squirrel, consumed in one day was 80 grams . . ."

"It is believed by us that two ounces of green forage or one-half ounce of dry grain is an average stomach-full for an average sized California Ground Squirrel and that two stomach-fulls represent a day's ration."

Storer, Evans, and Palmer (1944:189-190) obtained somewhat similar figures for the food consumption of the ground squirrel from purely theoretical calculations. Quoting Kleiber that the food requirement of a mammal is proportional to the ¾ power of its body weight or the "metabolic body size", they estimate the metabolic body size of a ground squirrel: Average weight .5 kg.; metabolic body weight = $.5^{3/4}$ kg. = .6 kg. As standards they quote Smith that 161 gram laboratory rats ate 14 to 15 grams of stock ration (dry weight 13 grams) daily, and Ranson that 30 gram *Microtus agrestis* daily ate 19 grams of combined herbage, roots, and cereal (dry weight 5.7 grams). The laboratory rat and *Microtus* were calculated to consume respectively 52 and 81 grams per kilogram of metabolic body size. On the same basis ground squirrels were computed to consume either 31 or 49 grams daily of air dry food weight (depending whether the *Microtus* standard, or the rat standard was used). The authors state that the higher figure may more nearly approximate the natural "average rodent diet"; "but both diets probably are below average in quantity because animals in captivity are thought to expend less energy than those free in nature". It is of interest that the lower figure of 31 grams per squirrel per day closely approximates Grinnell's and Dixon's estimate of one ounce (= 28.35 grams—"two half-ounce stomach-fulls) of dry grain per squirrel per day.

Field observations and laboratory feeding in the present study have indicated, however, that these estimates are too high. To consume an ounce, or about 30 grams dry weight per day (the approximate figure accepted by Grinnell and Dixon, and less than the lower figure mentioned by Storer, Evans and Palmer) a squirrel feeding on new succulent vegetation of high moisture content, 80 per cent or more, would have to consume at least 150 grams of actual food. Probably this amount is rarely, if ever, taken in a day.

In the summer of 1946, feeding experiments with dry wheat were made with nine different squirrels of both sexes—adults, and young of the year which had already attained the size of small adults. For 90 squirrel days of feeding, an average of 22.5 grams per squirrel per day was taken, but for different animals the average daily consumption varied from 31.1 to 12.4 grams. These tests were made in mid-summer when the long daylight hours promoted maximum intake of food.

Two other squirrels in confinement were fed entirely on natural foods of the same kinds being used by those in the wild. The amount taken each day was determined by weighing the uneaten residue and subtracting this from the amount offered; control samples were kept to check any weight loss by evaporation, and corrections of a few percent were applied to the amount decreased, to obtain a more accurate figure of the amount actually eaten. Ordinarily on each day only one kind of food was offered, thus relative positions of different foods on the scale of preference were checked. The records extended over the period March 14 to May 8, 1941. During this time weights of the two animals were recorded at the beginning and ending of each day's feeding and fluctuated between 445 and 576 grams, but with no consistent downward or upward trends. For 53 days' feeding the kinds and amounts taken were as recorded below:

TABLE 2.—Quantities of natural foods eaten by ground squirrels.

Kind of food	Number of meals	Average weight of meal	Estimated percentage of water	Estimated dry weight
Broadleaf filaree ..heads	20	66.95 gm	86 %	9.4
Broadleaf filaree ..leaves	8	44.2 gm	87 %	6.3
Ground lupine ....plants	8	67.8 gm	85 %	10.2
Layia ....flowers	4	63.2 gm	75 %	15.8
Goldfields ....flowers	2	100.0 gm	75 %	25.0
Birdseye gilia ....flowers	2	46.3 gm	75 %	11.5
Slender oat ....florets	2	33.5 gm	71 %	9.7
Blue-dicks ....flowers	2	23.5 gm	75 %	5.9
Popcorn flower ....plants	2	32.9 gm	85 %	4.9
Spanish clover ....plants	1	38.3 gm	80 %	7.7
Acorn	2	10.0 gm	41 %	5.9

Though all the foods listed above are extensively used by squirrels under natural conditions, several were taken sparingly by these caged individuals. When mature heads of soft chess were offered, both squirrels ignored them and fasted till the following day when other food was made available. For the better liked kinds of food, heads of filaree and plants of lupine, the amount recorded as eaten daily (average 67 grams) probably approximates the quantity taken under natural conditions.

When squirrels are feeding upon succulent green stuff, sixty to seventy grams ordinarily makes up the amount consumed in a day's foraging, though occasionally this may be exceeded. During the winter, when such material comprises the diet, only one daily foraging period is the rule; little feeding is done before mid-morning, and most squirrels have retired for the day by mid-afternoons. Forty-six stomachs collected in the latter half of January 1941, when segregated according to hours of collection, showed progressively increasing weights for each successive hour.

Most of the squirrels in the 2-3 p. m. group had not yet completed their foraging day when collected.

TABLE 3.—Average weights of stomach contents at different hours of the day.

Hour	Number of stomachs	Stomach contents weight in grams (Average and extremes)
9–10 a.m.	4	7.0 (4.5–9)
10–11 a.m.	10	10.5 (7–17)
11–12 m.	10	14.7 (7–25)
12:50–2 p.m.	14	25.9 (19.5–40.6)
2–3 p.m.	8	45.9 (37.5–64)

In spring, as days grow longer and warmer, the foraging periods are less sharply circumscribed and lengthen until in summer there are two daily feeding periods with a resting period intervening. Amounts of food taken per squirrel are correspondingly increased. By late afternoon part of the morning meal is digested and the stomach is again filled to capacity. Since most of the squirrels during late spring and early summer are young or half-grown, having smaller stomach capacity than adults, the amount per squirrel per day eaten at this season may not much exceed the winter figure.

Direct observation of squirrels foraging under natural conditions and taking items of which weight and number could be accurately recorded, also showed that the amount taken in a day of feeding was variable. For several complete days of feeding, the items taken and their weights, as determined from duplicate samples collected on the spot, are shown below. The examples here presented are selected from a large number of all-day records, and are those for which weights can be most accurately estimated because relatively few kinds of items were taken and these were of relatively constant size. For each of the "squirrel days" recorded below, length of active day and periods of actual foraging are shown in Figure 11.

TABLE 4.—Kinds and amounts of food taken by foraging ground squirrels.

A. Young adult female, December 8, 1939

Kind of food	Number of items	Weight per item in grams	Gross weight in grams	Dry weight in grams
Red-stem filaree plants (rosette stage)	58	.26	15.08	2.05
Red-stem filaree leaves	1	.08	.08	.01
Broadleaf filaree plants (rosette stage)	71	.336	23.85	3.10
Broadleaf filaree leaves	107	.102	10.91	1.42
Popcorn flower leaves	22	.08	1.76	.26
Red brome plant	1	.10	.10	.01
Oat leaves	1	.01	.01	.....
Buckthorn weed leaves	1	.08	.08	.....
Fescue leaves	1	.002	.002	.....
Total food weight for the day			51.87	6.85

TABLE 4.—(*Continued.*)

B. Adult female nursing litter, April 21, 1939

Kind of food	Number of items	Weight per item in grams	Gross weight in grams	Dry weight in grams
Broadleaf filaree seeds	1521	.067	101.91	14.12
Ground lupine pods	112	.0955	10.70	8.03
Ground lupine entire plant	3	.44	1.32	.99
Popcorn flower nutlets	12	.086	1.03	.52
Clover leaves	1	?	trace	
Brodiaea leaves	several	?	trace	
Total food weight for the day			114.96	23.66

C. Adult male, June 30, 1939

Kind of food	Number of items	Weight per item in grams	Gross weight in grams	Dry weight in grams
Acorns	91	.21	19.11	11.36
Redberry berries	88	.14	11.29	5.65
Wedgeleaf ceanothus fruits	8	.25	2.00	1.00
Ripgut brome seeds	2	.0142	.03	—
Total food weight for the day			32.43	18.01

D. Same adult male, August 14, 1939

Kind of food	Number of items	Weight per item in grams	Gross weight in grams	Dry weight in grams
Acorns	13	3.8	49.4	29.3

E. Same adult male, September 14, 1939

Kind of food	Number of items	Weight per item in grams	Gross weight in grams	Dry weight in grams
Acorns	7	3.8	26.6	15.8

TABLE 4.—(*Continued.*)

F. Adult female, October 11, 1938

Kind of food	Number of items	Weight per item in grams	Gross weight in grams	Dry weight in grams
Yellow tarweed seed heads	901	.0375	33.79	8.55
Acorns (liveoak)	26	.5	13.00	9.00
Droppings of squirrel and rabbit	10	.3	3.00	3.00
Ripgut brome seeds	59	.0142	.84	.84
Total food weight for the day			50.63	21.39

Remarkable difference between individuals in amount of food taken is indicated. Sex and age differences and seasonal activity are evident factors. The adult male which was observed for the June, August and September records, was fat and sluggish, and did not wander far from his burrow, showing little inclination to feed. The female squirrel which took almost 115 grams of green stuff during one day in April may be typical of those lactating, which were observed to forage more persistently and voraciously than others. The young adult female which took nearly 52 grams of succulence in the course of a December day's feeding is thought to be representative of the entire population at that time of year.

If the figure of 70 grams of green feed per day per squirrel is accepted as the average requirement, then each animal would take approximately 4.7 pounds per month. The breeding population of the study area, calculated at 2.3 squirrels per acre (5 year average), would consume approximately 10.8 pounds per acre each month during the late winter and spring when most direct competition with livestock occurs. For the less accurately measured population over the Range, if the 1939-1940 calculation of 1.51 squirrels per acre in the breeding population is used, then 7.0 pounds per acre would be taken monthly.

For other times of year estimates of the food consumption are complicated by the presence of young in fluctuating numbers. The spring squirrel population is increased more than four-fold within a few weeks as the females give birth to litters. By the time the young are weaned, their numbers already have been much reduced, and by the time they have grown large enough to consume quantities comparable to those taken by adults, many more have been eliminated. The maximum rate of food consumption, occurring in early summer, may amount to nearly three times the monthly poundage consumed by the breeding population in early spring. But amounts consumed taper off rapidly through the summer and fall months, as death and retirement into dormancy reduce the active population.

The amount of vegetation eaten by squirrels, even if it could be determined with precision, would not be indicative of the full extent of damage to the forage crop, because there is further destruction by trampling, by cutting of stalks which are discarded or used only in part, and by stunting of the vege-

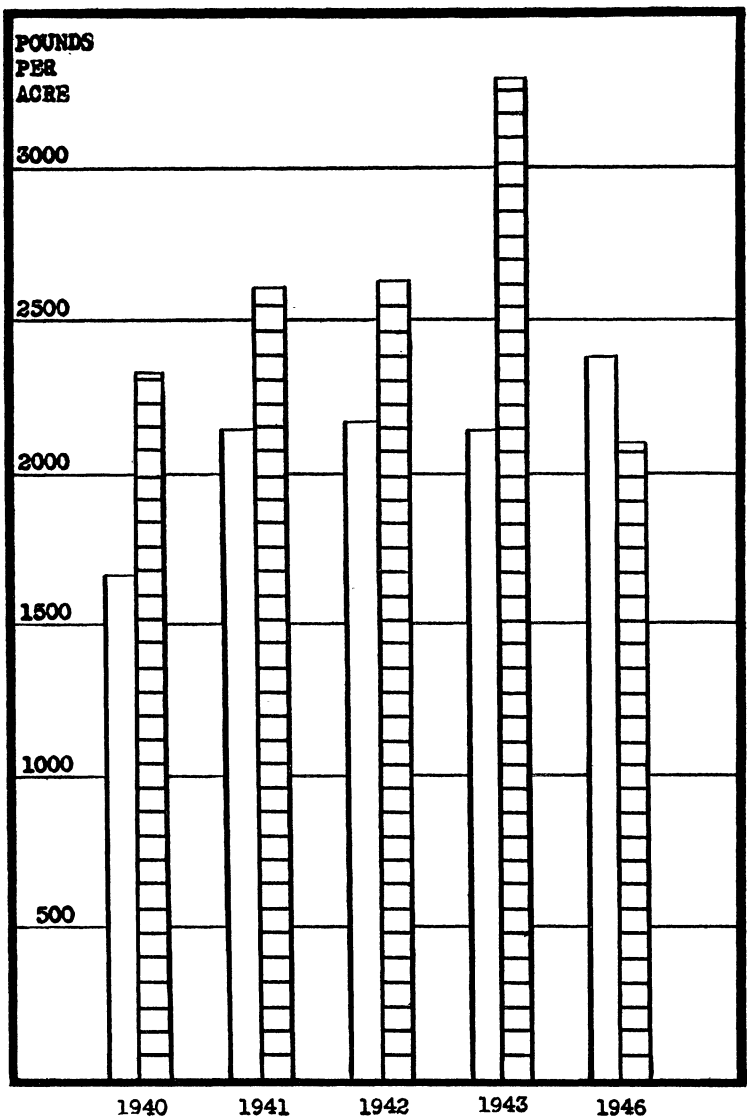

Figure 1.—Pounds per acre (air dry weight) of forage yield at height of growing season in a squirrel enclosure stocked at 12 squirrels per acre (left hand open column of each pair), and a control enclosure with no animal use (right hand, cross-hatched column of each pair). In 1946 the squirrels were removed, and the relatively greater yield of the squirrel enclosure that year indicates the amounts of forage destroyed by them other years.

tation which is eaten back during the early stages of growth. Data from the enclosures indicate that the use of vegetation by the squirrels reduces the yield by an amount considerably greater than the animals could have eaten, even allowing the maximum amount for each animal.

Effect on vegetation in enclosures.—Further data on the amount of vegetation destroyed by squirrels was provided by the half-acre enclosure where six were kept. At the height of the growing season in 1936, 1937, 1938, 1939 and 1940, visual estimates of the total density and the percentage of each forage species were made on 100 square-foot quadrats in the squirrel enclosure and the control. Hardly any significant trends in the differences between the two areas could be discerned. In the squirrel enclosure, however, broadleaf filaree, the favorite year-round food of the squirrels, was consistently less abundant than in the control. Its relative scarcity was compensated mainly by a greater abundance of soft-chess, little used by the squirrels except in the earliest stages of growth. Ground lupine, one of the less common forage species and a specially preferred squirrel food, comprised each year in the squirrel enclosure only a small fraction of its density in the control. These and other less well defined differences were not cumulative or progressive. Each year, both within the enclosures and outside, the amount and composition of the vegetation fluctuated widely under the influence of weather, and various factors other than squirrel use. With no animal use other than by the squirrels, utilization of the forage crop was extremely light, and competition between plant species was intensified. Each year at the beginning of the growing season after fall rains began, the accumulation of dead vegetation was raked up and removed from each enclosure to avoid the piling up of old growth choking out most of the broadleaf species and the transition to rank grasses which would have occurred otherwise. This artificial treatment further obscured the effect of the squirrels themselves.

In 1937, 1938, 1939, 1940, 1941 and 1942, the residue of dry forage on squirrel and control plots was measured at the end of the dry season (by weights of clippings from 100 square-foot random samples). In each of these years there was much less vegetation remaining on the squirrel enclosure than on the control, varying from 65.1 per cent to 83.3 per cent, and averaging 75.5 percent (figure 2).

In 1940, 1941, 1942 and 1943 the enclosures were further sampled by clipping of the green vegetation at the height of the growing season (100 square-foot quadrats) and weighing the air dry clippings (figure 1). The yield of the squirrel enclosure varied from 66.1 per cent to 82.3 per cent of that of the control, and averaged 75.4 per cent. In 1946 another sampling of yield was made with both enclosures virtually free from rodent use (a single surviving squirrel was trapped and removed from the squirrel enclosure in January). In 1946 the yield of the squirrel enclosure was 113.3* per cent of

* The approximate correctness of this percentage was borne out by a similar calibration sampling by the Experiment Station in 1947, when the control plot yielded 2054 pounds per acre and the squirrel plot, under protection, yielded 2386 pounds per acre, or 116.2 per cent.

the control. Using this 1946 figure as a standard of comparison, it appears that the squirrels destroyed on the average each year during the growing season an amount equivalent to 37.9 per cent of the yield produced by the control enclosure. The yield of the squirrel enclosure was reduced by an amount varying from 801 to 1629 pounds per acre (average 1058) in the four years that green clippings were made.

It is immediately apparent that these quantities greatly exceed the amounts

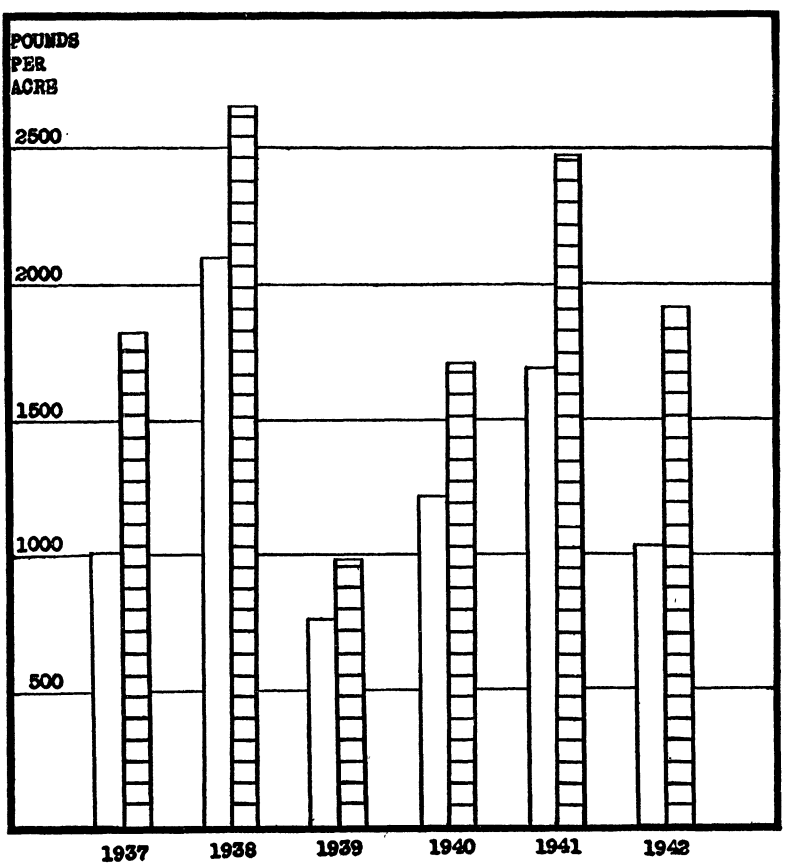

Figure 2.—Pounds per acre of dry forage remaining in September in squirrel enclosure (left hand, open column of each pair) and in control. Note reduced poundage in both enclosures as compared with Figure 1, the relatively greater difference, and the year-to-year fluctuations.

that could have been eaten by the squirrels. In the 210 days representing the average span of the growing season, twelve squirrels eating probably not more than 70 grams apiece daily of green stuff would consume a total of 389 pounds. At least seventy-five per cent of the weight is moisture. The air dry weight represented—97.5 pounds—is less than one-tenth of the average quantity apparently destroyed by squirrel activity in the enclosure. Much of this discrepancy must be due to the stunting effect that results from cropping of small plants in their early stages of growth. Cutting of plants which are not eaten, and trampling could account for further loss.

The enclosure data show the potential destructiveness of the squirrels, but do not show how much they destroy on the open range. In the enclosure, with a greater quantity of vegetation present, the amount cut and trampled per squirrel is probably greater, and destruction tends to be magnified. On the range, with stock and other animals competing for the vegetation, the destruction per squirrel is doubtless less. Maximum destruction in poundage per squirrel might be expected in those years when the forage crop is heaviest. The composition of the forage crop also would be a factor determining the amount destroyed.

The measurements of squirrel damage in the enclosure are subject to some margin of error from other causes. Mortality was fairly frequent and deaths were not always discovered immediately, so, at times, the area was understocked. Too frequent trapping in the plot to check the number of squirrels would have resulted in further disturbance and trampling of the vegetation. Being limited in their movements, the enclosed squirrels were less able to find succulence or free water than were those of the unconfined population. Apparently as a result of this deficiency, they always became emaciated in summer. One oak tree grew inside the enclosure, and use of the varying acorn crop partially diverted the squirrels from the forage crop, especially in summer and fall.

The conclusions indicated by the enclosure data are that squirrel use in the population density of 12 per acre does not harmfully alter the composition of the forage crop, which shows only light utilization; that the annual forage yield under this degree of use is decreased, apparently in the neighborhood of one thousand pounds per acre; and that the quantity actually eaten by the squirrels is much less than that otherwise eliminated by them.

Kinds of food eaten.—In their feeding ground squirrels take mainly the more nutritious kinds of plant food available. Many plant species are entirely ignored by them, and others are utilized only to the extent of one particular part or organ. In general, high content of crude protein and essential minerals, and comparatively low content of crude fiber and cellulose characterize most of the types of vegetation selected as food. Composition (in percentages of dry weights) of some of the favorite foods at different seasons are shown below. The figures are from those published by Gordon and Sampson (1939).

TABLE 5.—Composition of forage plants.

LEAF

Kind of plant	Month	Contents: Calcium	Phosphorus	Crude Protein	Fiber
Soft chess	February	.86	.49	22.50	24.60
Red brome	March	.57	.24	26.63	——
Broadleaf filaree	December	1.79	.40	26.70	10.94
Redstem filaree	January	2.02	.51	29.29	9.38
Yellow tarweed	June	1.39	.20	7.62	20.72
Ground lupine	March	1.57	.46	27.43	18.53
Popcorn flower	February	2.01	.76	28.20	12.60

SEED

Kind of plant	Month	Contents: Calcium	Phosphorus	Crude Protein	Fiber
Ripgut brome	June	.14	.34	10.68	6.14
Broadleaf filaree	August	1.34	1.54	29.99	18.15
Yellow tarweed	June	.31	.67	22.79	19.19
Layia	August	.67	.82	20.89	19.21
Popcorn flower	August	1.34	.84	30.93	——
Blue oak	November	.08	.11	5.01	6.31
Wedgeleaf ceanothus	June	.35	.31	22.43	——

The above figures, show that certain summer and fall foods, as acorns, and ripgut brome seeds, are deficient both in protein and in mineral content, as compared with the diet at other times of year. The behavior of squirrels feeding upon tarweed and acorns indicated clearly that these were foods low on their scale of preference, and were taken only in the absence of the foods which better supply nutrition and succulence at other seasons. Use of tarweed seeds stopped as soon as new green growth was available in the fall. Blue oak acorn meats were discarded in part, after nibbling, more often than they were eaten entire, and were often carried about in the cheek pouches for hours before being used at all. Even in the dry season, however, the diet is relatively high in essential food elements as compared with the forage crop as a whole. Summer composition of the common range plants is very low in protein. For instance, in September, soft chess contains: calcium .241 per cent; phosphorus .164 per cent; crude fiber 38.32 per cent; crude protein 3.76 per cent. In June broadleaf filaree contains: calcium 2.444 per cent; phosphorus .169 per cent; crude fiber 28.70 per cent; crude protein 3.36 per cent. In the dry season these two species are important, though nutritionally deficient, stock foods, but are not used at all by the squirrels. Most of the other common herbaceous species show similar trends in the high percentage of fiber and low percentage of protein after drying at the end of the growing season.

Leaves are an important food source, and 40 kinds were recorded used, principally in winter and early spring. Hardly any dry leaf material is taken, and tarweed is about the only kind used during the dry season. August is the only month of the year during which no use of foliage was observed. Foliage of herbs such as filaree and popcorn flower was used mostly in the rosette stage before the plants had produced heads.

Flowers of 34 kinds were utilized and they constitute a major food source, from January through September. During March, April and May the many kinds of flowers taken seem to include some of the most preferred foods, and may be an important cause of the rapid weight gain during late spring. Mature seeds were taken from 18 different kinds of plants, and seed material comprises most of the food from the height of the growing season until the fall rains set in. In late spring the varied diet includes many kinds of seeds whereas throughout late summer and fall a few species make up most of the food—principally acorn, tarweed, turkey mullein, and ripgut grass. Fruits, capsules, or berries, (consisting mainly of the fleshy encasing wall rather than the enclosed seed material) were eaten from 12 species. Stem material is a minor part of the diet, and was used from only 7 kinds of plants. It is taken mostly in early spring while still tender and succulent, and its use is mainly incidental at times when the squirrels are feeding on foliage of the same species. Occasionally during the dry season old stems of filaree or popcorn flower are nibbled, but do not make up an appreciable part of the food. At times small plants are dug or pulled out and eaten entire. Filaree and ground lupine are those that serve importantly in this way, but 11 kinds have been recorded used. Subterranean portions of plants were recorded eaten from only four kinds, not including certain fungi and toadstools which were seen used on several occasions but were not identified.

Seasonal changes in the parts of plants used as food are shown in the following table. It is seen that leaf and stem material make up most of the diet during the early stages of growth in winter and decrease abruptly in spring when many kinds of flowers and seeds, ripe but still succulent, are preferred. Leaf and stem material (tarweed) again increase in importance in the dry season, apparently as a source of succulence. Flowers are eaten in nine months of the year, but mainly in late spring and early summer. Seeds other than acorns are eaten through most of the year but make up highest percentages of the food in late spring. In the table, acorn is included in the "seed" column but also is shown separately.

TABLE 6.—Monthly percentages of plant parts in the ground squirrel diet.

	Leaf and Stem	*Flower*	*Seed*	
			Total	Acorn
January	97.3	1.8	.9	(.9)
February	80.0	1.2	18.8	(18.8)
March	45.5	1.0	53.5	(10.5)
April	17.4	8.5	74.1	(1.6)

TABLE 6.—(*Continued.*)

	Leaf and Stem	*Flower*	*Seed*	
			Total	Acorn
May	.8	9.2	90.0	—
June	17.1	12.1	70.8	(13.7)
July	27.5	20.7	51.8	(23.1)
August	3.9	7.9	88.2	(63.9)
September	—	6.0	94.0	(62.5)
October	.2	—	98.8	(62.7)
November	16.9	—	83.1	(83.1)
December	98.0	—	2.0	(2.0)

The following list summarizes the kinds of plants seen eaten, the months of the year during which each was used, and the part of each taken. For parts of plants the following abbreviations are used: L = leaf, F = flower, S = seed, Fr = fruit, St = stem, Pl = entire plant, R = root, B = bulb or corm. Months are indicated by number; 1 = January, etc. For the sake of brevity species are recorded in only a few instances in which the genera involved are among the more important foods, and the species differ importantly.

In many instances the season of squirrel use in any one year of a certain plant species and part is ordinarily shorter than indicated; the spread is due to its later or earlier development under the influence of varying weather, in the successive years of observation. A relatively few kinds of food make up the bulk of the diet, and most of the kinds of food here listed each made up only a fraction of one per cent of the total. For most kinds use was recorded regularly at about the same season each year, but some kinds were recorded in only one or two years. For example use of loosestrife was recorded many times during the early summer of 1938, but other years it was much scarcer and was not seen eaten.

The list is based on the 51,755 separate food items which squirrels were observed to eat in the course of monthly observations from April 1938 to January 1942. Samples of each kind were collected and weighed, and the monthly food composition by weight was calculated. In the list, those items marked with an asterisk made up more than one per cent of the monthly diet, while those marked with a double asterisk comprised more than ten per cent of the food for the month.

List of ground squirrel food plants on the San Joaquin Experimental Range, showing parts eaten and months of use.

Aesculus, Buckeye (L-9; F-6*; S-10*)

Amsinckia, Buckthorn weed (L-1, 2, 3, 4, 5)

Agoseris, Dandelion (L-3; F-4, 5*)

Arctostaphylos, Manzanita (F-1*, 2, 3; Fr.-4*, 6**, 7*)

Astragalus, Locoweed (L-2)

Avena, Oat (S-4, 5, 6)

Baeria, Goldfields (F-3, 4*)

Brodiaea, Blue-dicks (L-3, 4, 5; F-4, 5*; Fr-5; B-4)

Bromus mollis, Soft chess (L-1, 2*, 3, 4, 10, 11*, 12; S-5, 6)

Bromus rigidus, Ripgut brome L-5, 6, 10; S-5**, 6, 7, 8*, 9)

Bromus rubens, Red brome (L-1, 2, 3, 12)

Calandrinia, Red maids

(L and St-1*, 2*, 3*, 4, 5, 6, 11*, 12; F-3; Pl-1)

Ceanothus, Wedgeleaf ceanothus (Fr-6)

Centaurea, Star thistle (L-3*; S-6)

Cerastium, Mouse-ear chickweed (L-4)

Dodecatheon, Shooting star (L-3)

Echinocystis, Man-root (L-4)

Eremocarpus, Turkey mullein (F-7*, 8, 9; S-8, 9*)

Eriogonum, Eriogonum (L-7; F-6*, 7**, 8**, 9*; St-7, 8)

Erodium botrys, Broadleaf filaree (L-1**, 2**, 3**, 4**, 5, 6, 10, 11*, 12**; F-3*; Fr-3*, 4**, 5, 6; S-5**, 6**, 7**, 8, 9; St-3, 4, 5, 6; Pl-1, 2, 3, 11, 12; R-5, 7)

Erodium cicutarium, Red-stem filaree L-1, 2, 3, 4, 12; F-3; Fr-3, 4, 5; Pl-1, 2; R-1, 12)

Erysmium, Wall flower (L-2)

Eschscholtzia, California poppy (L and F-3, 4)

Festuca, Fescue (L-1, 2, 3, 11, 12*; Pl-12)

Gilia, Gilia (F-4,5)

Gnaphalium, Everlasting (F-6, 7)

Godetia, Godetia (F-5, 6; Pl-6)

Hemizonia virgata, Yellow tarweed (L and St-2*, 3*, 4, 6*, 7*; S-6, 7**, 8**, 9**, 10)

Hemizonia wrightii, Wright's tarweed (L-2*, 3; F-5, 6, 7; S-5, 6)

Hordeum, Wild barley (L-1, 2, 3, 11, 12; S-5, 6; Pl-3; R-5)

Hypochoeris, Rush (L-1, 4)

Juncus, Rush (L-3, 6; S-5)

Layia, Layia (F-4)

Lessingia, Lessingia (L and St and Pl-2)

Lotus americanus, Spanish clover (L-4, 5, 6, 7; Fr-1)

Lotus strigosus, Hairy lotus (L-2, 3; F-4; Fr-4, 5)

Lotus subpinnatus, Fine-leaf lotus (L-6)

Lupinus benthami, Lupine (F and Fr-4)

Lupinus bicolor, Ground lupine (L-2, 3**, 4*; Pl and St-3, 4; Fr-3, 4, 5)

Lupinus formosus, Lupine (L and F-4, 5*; Fr-5)

Lythrum, Loosestrife (L and S and Pl-6)

Madia, Tarweed (F-7*)

Mimulus, Snapdragon (F-4)

Navarettia, Navarettia (F-6, 7)

Nemophila, Baby blue-eyes (L-1, 2, 3)

Oenothera, Evening primrose (F-3)

Orthocarpus, Owl's clover (L and Fr-3)

Pectocarya, Pectocarya (F-3)

Phacelia, Phacelia (L-3, 4*; F-4)

Pinus, Digger pine (S-1, 2, 3, 8, 11)

Plagiobothrys, Popcorn flower (L-1*, 2*, 3*, 4, 10, 11*, 12*; S-3, 4*, 5; St-7)

Pterostegia, Pterostegia (L-3)

Quercus douglasii, Blue oak (S-2**, 3**, 4*, 6*, 7**, 8**, 9**, 10**, 11**)

Quercus wislizenii, Interior live-oak (S-1, 2**, 3*, 6**, 7**, 8**, 9**, 10**, 11**, 12*)

Rhamnus, Redberry (Fr-6*, 7)

Scrophularia, Figwort (F-4)

Silene, Windmill Pink (L-3; S-5, 6, 7)

Stellaria, Chickweed (L-2, 3)

Thysanocarpus, Fringe-pod (F-4)

Tillea, Tillea (Pl-2*)

Trifolium, Clover (L-3, 4*, 5; F-4*, 5*, 6; Pl-6)

Tropidocarpum, Tropidocarpum (L and F-2, 3)

All those plants species were eaten which usually comprised as much as one per cent by volume of the forage crop in years when the vegetation was measured. Common plant species make up nearly all of the food and availability is an important factor in determining what is taken. Some moderately common plants apparently are avoided. Listed below are 53 kinds not observed to be eaten by squirrels. Specific names are included only when there is present on the area some other species of the same genus which *is* utilized by the squirrels.

List of plants on San Joaquin Experimental Range not observed eaten by ground squirrels

Allocarya	*Eriodictyon*	*Plantago*
Amsinckia (intermedia)	*Eriophyllum*	*Poa*
Asclepias	*Eschscholtzia*	*Pogogyne*
Brickellia	*(californica)*	*Polypogon*
Briza	*Euphorbia*	*Pellea*
Capsella	*Filago*	*Ranunculus*
Ceanothus (divaricatus)	*Galium*	*Rumex*
Cephalanthus	*Gymnogramme*	*Salix*
Calycadenia	*Heliotropum*	*Saxifraga*
Chorizanthe	*Hugelia*	*Scutellaria*
Clarkia	*Limnanthus*	*Sidalcea*
Collinsia	*Linanthus*	*Solanum*
Cynodon	*Lithophragma*	*Stachys*
Cyperus	*Matricaria*	*Stipa*
Daucus	*Mimetanthe*	*Streptanthus*
Delphinium	*Micropus*	*Trichostema*
Eleocharis	*Molluga*	*Uropappus*
Erigeron	*Nicotiana*	*Xanthium*

In addition to the plants of this list, there were 45 other uncommon or rare genera which were not seen used by the squirrels.

In summer and fall but little economic damage to the forage crop results from the actual feeding of squirrels since the acorns, tarweed foliage and seeds, eriogonum, turkey mullein seeds and staminate flowers, cast seeds of ripgut grass and cast seeds of filaree used then are not available or palatable to cattle. Squirrel damage to the forage crop in summer must be due largely to trampling.

In winter squirrels are using for food the same herbaceous green material grazed by cattle. Their feeding is then in direct competition with livestock except to the extent that they are still using acorns stored by them in the fall. As the growing season progresses, the squirrels become gradually more selective in their feeding and begin to take flower and seed material some of which is little used by stock. In general most of the damage to the forage is done during the period of green growth in late fall, winter, and early spring.

The amount of forage destroyed by a squirrel in the course of its daily feeding hence varies according to the season. The loss is greatest in spring at about the height of the growing season, when, occasionally, entire mature plants such as wild oats are cut in order to secure the relatively small portion desired as food. In hay fields such cutting of stalks may almost completely destroy the crop on the area where a squirrel forages. In utilizing filaree seeds not yet cast from the plants, the squirrels pluck the entire fruits the exteriors of which are discarded after removal of the relatively small seeds. In a sample of filaree fruits similar to those used by squirrels, the parts habitually discarded—receptacle, sepals, styles and carpel walls—comprised 79.1 per cent by weight.

As might be expected feeding is determined largely by availability of food species where the animal occurs. Though there is rapid change in food during the season, there are usually several kinds of plants at stages of development

at which they are acceptable as food at any one time, and of these the most readily obtainable will be taken in largest quantities. Composition of the plant community varies greatly on different pastures of the Range and also varies within small areas, so that no two squirrels living at different places have exactly the same amounts or kinds of food available. In watching the feeding of squirrels, the observer is constantly impressed with their selectivity, especially so in the later stages of plant growth, when they use only certain species and certain parts of the plants. Actually their foraging is directed at only a small percentage by bulk of the total forage crop at such times. Certain species such as windmill pink, ground lupine, and loosestrife, which make up only insignificant parts of the forage crop, are, at times, sought so persistently that they constitute important parts of the diet. They are least selective during the early stages of green growth, and at times seem to graze indiscriminately off the surface mat of vegetation.

The preponderance of two kinds of plants among the many comprising the diet is illustrated by the following table of their computed percentages by weight in the total food observed taken. It is shown that filaree makes up the bulk of the food throughout the winter and spring and gradually diminishes to an insignificant proportion at the end of the dry season; that acorn during the same period gradually increases from a small percentage in early spring to more than three-fourths of the total in fall. Grass is taken throughout most of the year but in relatively small quantities. Acorn and filaree combined outweigh all other foods except in June and July; in these months tarweed and eriogonum are of major importance.

TABLE 7.—Percentage by weights of filaree, acorn, and grass in ground squirrel diet.

	Filaree	*Acorn*	*Grass*	*Other*
January	90.2	.9	1.5	7.4
February	53.8	18.8	3.1	24.3
March	49.4	10.5	1.1	39.0
April	72.8	1.6	.1	25.5
May	70.6	—	14.2	15.2
June	33.8	13.7	.1	52.4
July	22.0	23.1	—	54.9
August	2.0	63.9	2.6	31.5
September	.7	62.5	1.0	35.8
October	—	62.7	.2	37.1
November	11.2	83.1	2.9	2.8
December	92.2	2.0	2.8	3.0

Filaree is the most important food source in this locality, and in one stage or another it is used throughout most of the year. Foliage is used from the time its growth starts in the fall until it dries out in late spring, entire plants are taken during the early rosette stage in the winter, flowers and fruits during the later stages of growth, and seeds both before and after they are cast, and to a diminishing extent throughout the summer. The establishment of this alien plant in the range of the California ground squirrel must have profoundly

affected the animal's ecology, and doubtless permits its existence in higher population densities than could otherwise find sustenance. Red-stem filaree apparently is preferred, but broadleaf, being more abundant on the Range, is more used there.

The plants are eaten entire mostly when the leaf expanse of the rosette is an inch or two in diameter. Heaviest utilization was observed at times in early winter when the soil was dry, following a rainless period. A squirrel would scratch away the dirt at the base and grasp the plant beneath the rosette with its incisors to uproot it. Occasionally the attenuate terminal portion of the root was discarded, but the fleshy basal portion was eaten with relish. At times when the soil was moist, squirrels feeding on young filaree plants snipped off separate leaves rather than uprooting entire plants. As the turgid petioles were cut, distinct snaps were audible to an observer within several yards, rendering it easy to count the leaves eaten. Small undeveloped leaves near the center of the rosette and large basal leaves lying against the ground usually are not taken. In filaree plants grown past the rosette stage, the leaves are used much less. The flowers and immature fruits are occasionally eaten, when the squirrels are foraging mainly for the leaves. Sometimes only the style or "stork's bill" portion of an immature fruit is cut off and eaten.

When the fruits have begun to mature they are no longer eaten entire, but are plucked, stripped of their seeds and discarded. For many weeks during

Figure 3.—Finishing root of a Filaree plant, rosette of leaves already eaten.

the spring filaree seeds continue to be a principal food source of the squirrel population, and in this period rapid gain in weight is made. The foraging squirrel reaches for each fruit with its forefeet, catches it between the incisors, and plucks it with a sudden sideways jerk. Then, holding the elongate "stork's bill" of the combined styles between the forepaws, and twirling it with a rapid rotary motion, it gouges out the seeds from beneath the sepals with its lower incisors.

In late spring when the forage crop has mainly dried out, squirrels occasionally take fleshy joints of filaree stems in which succulence still remains. Just after seed-casting, filaree seeds can be procured in quantity in certain places where heaps of the long coiled styles, with carpels still attached, accumulate. Gathering of these minute items is accomplished with great rapidity as the squirrel grasps the seeds one after another, between its incisors and snips off the dry styles, sometimes at the rate of several in a second. After a few weeks, the remaining seeds have become less accessible. The barbed carpels enclosing the seeds have bored into the ground, aided by the spring mechanism of the attached hygroscopic styles, and, as a result of trampling and wind, most of the brittle styles have been broken off. In getting the seeds, a squirrel employs its forepaws to advantage for manipulating the styles to guide the attached carpels to its mouth. On two occasions squirrels feeding entirely on cast filaree seeds which they were gathering from the ground were seen to pause and eat small quantities which they had pouched, but pouching of such minute seeds occurs only exceptionally. Soon after the beginning of fall rains in October, the germinating seeds of filaree are extensively used.

Use of acorns has been recorded for every month except May. In the latter part of June, with the forage crop already mostly dried and high temperatures often preventing extensive foraging expeditions in the open, the squirrels begin to climb through oak trees in search of the small green acorns, which are used in large numbers because of their minute size. Trees which are bearing heavily are discovered and returned to regularly, until the squirrels have largely shifted their activities to oaks, where they spend most of their time climbing or loafing in the shade. By the end of July a substantial portion of the acorn crop may have been used. Meanwhile the remaining acorns have been growing rapidly.

In climbing through the outer branches of trees to gather acorns, the squirrels clumsily knock off more than they themselves secure. Also, many acorns are intentionally dropped by them, some after having been hulled out and briefly nibbled. The abundance of acorns and their monotony as a steady diet cause the squirrels to leave more than they eat. The meats hulled out by them are made available to various other acorn eating wildlife species. Most of the acorn mast taken by Valley quail at this locality is that discarded by squirrels (Glading, Biswell and Smith, 1940:138). In August and September pouching of acorns is commonly observed as the squirrels gather heavy loads and carry them back to feeding places. Large and ripe acorns are nearly always carried to the ground before being eaten. When fallen acorns accumulate it

becomes profitable for the squirrels to forage beneath the trees. Ordinarily the supply of acorns is greatly in excess of the squirrels immediate need. Often the meats are shelled out, nibbled, and then dropped or pouched. While loafing or foraging the squirrels are often carrying pouched acorns which may be nibbled from time to time.

In October when acorns are present in greatest abundance and have ripened, squirrel activity is to a large extent devoted to laying up caches. So far as observed, acorns are the only natural food regularly cached in this region. Caches are made mainly in the afternoon after the main feeding period for the day is over, and fallen acorns are used. In gathering them squirrels display unusually sustained activity, searching over the ground surface with short hurried movements, nosing though debris and rapidly pouching those found. When the small, elongate acorns of live-oak are gathered, a dozen or more often are carried in the cheek pouches, which are greatly distended by them. At close range a faint rattling is audible when the squirrel moves, as the pouched acorns shake together. Most frequently caches are made at distances of 100 feet or more from the places where acorns are gathered. Having filled its pouches to capacity, the squirrel suddenly ceases to search and usually following some beaten path runs from the foraging place to its caching area. There, moving slowly, it examines the ground minutely for a few seconds selecting a place for the cache. In a few seconds a pit, commonly about three inches in depth, is dug with rapid strokes of the forefeet, and the squirrel

Figure 4.—Caching pouched grain.

leans forward, with its head in the pit to eject part or all of its load of acorns by movements of its tongue and cheek muscles (figure 4). Then it rapidly scratches loose dirt back over the acorns and finishes the process by forward tamping movements with the soles of its forefeet (figure 5), leaving no discernible trace. Usually a pouch full of acorns serves to fill several caches. Often a squirrel abandons a pit when it is only partly dug, and searches for another site. No notice was taken by squirrels, conditioned to the presence of humans, of persons following closely and digging out each cache as the squirrel left it. The animal would dig unconcernedly a few yards away and deposit another cache.

That the caches are not separately remembered and returned to by a squirrel is suggested by the haphazard and hurried manner in which they are made, often after several false starts, and by the fact that the animal after completing a cache seemingly fails to take careful note of its location before moving on. In preparing to make a cache the squirrel may move several feet, sniffing and occasionally scratching at the ground immediately in front of it before finally digging the pit and depositing its load. It fills the pit and moves on with no more than a momentary pause and with no apparent attention to nearby landmarks which might aid in relocating the cache on some subsequent occasion. In any case a squirrel would scarcely be able to remember the separate locations of the several hundred caches made by it during the acorn season. In January 1940, after the fall crop of acorns had disappeared, a squirrel

Figure 5.—Covering over a cache.

was observed recovering acorns from caches in sandy soil near a creek bed. It was feeding in part on new green vegetation, but the stored acorns seemed to make up the greater part of its food. Much of its foraging time, several hours daily, was spent digging more or less aimlessly in the general area where caches had been made, but it was evident that the caches were not separately remembered. It seemed to be aided to some degree by scent when the acorn sought was near at hand.

In January 1939, weeks after the fall acorn crop had disappeared, an adult female was seen making numerous trips into her home burrow, emerging each time with pouches full of live-oak acorns, which were then stored in typical surface caches in the vicinity. Some of these acorns had sprouts several inches long which protruded from the squirrel's mouth as she carried them. The nearest live-oak was more than 100 yards distant from the home burrow of this squirrel, and beyond its usual foraging range. On several other occasions in winter and early spring squirrels were observed to emerge from their burrows with pouched acorns which had evidently been stored there in fall. Grinnell and Dixon (1918:629) cite several instances of finding food stores in burrows. Extensive excavation was not possible in the present study, but it is believed

Figure 6.—Eating leaves of Tarweed in July.

that such storing is not a common habit locally else it would have been seen oftener during the many hundred hours spent watching squirrels.

Yellow tarweed is one of the important food plants for squirrels in the region of the Experimental Range. During winter and early spring the tender new leaves are used along with the foliage of many other plant species but as the squirrels become more selective in their feeding, and take mostly flower and seed material, tarweed is hardly used. In June, after drying out of the main forage crop tarweed is one of the few succulent herbs remaining, and the squirrels again turn to it as an important food source (figure 6). At this time of year only the leaves and the more tender terminal portions of stems are taken; the coarse pithy stalks are not attacked. Plants which have been grazed back by cattle, and have stooled out with a dense growth of succulent leaves are favored. Since only a small percentage of the squirrel population lives within reach of watering places during the dry season, the succulence available in

Figure 7.—Eating seeds of Tarweed in September.

tarweed may be a vital factor in providing them with the necessary amount of moisture. Utilization continues through July and early August. Usually in August or September, as tarweed passes the height of its flowering season, the squirrels commence to utilize its seeds. For several weeks these seeds continue to be heavily used and, with acorns, comprise most of the squirrels' food. At this season daytime temperatures in the open still are apt to be uncomfortably high for the squirrels, so that much of their foraging is done in shade of trees and bushes. During morning and evening foraging periods when temperature is more moderate, they venture into the open to obtain the seeds, moving about rapidly, standing on their hind legs and reaching up for the slender fruiting branchlets with their forepaws and dragging the flowers down to their mouths (figure 7). Tarweed seeds may be preferred to acorns, as the latter are taken mainly when the tarweed is unavailable due to excessive sunshine temperatures.

The less common Wright's tarweed is utilized to a limited extent, in situa-

Figure 8.—Eating nutlets of Popcorn Flower.

tions where it occurs, during early spring. In May the seeds of this early-flowering species are occasionally eaten by squirrels.

Grass amounted to only a small fraction of the diet (14.2 per cent in May; 3 per cent or less in other months). In late fall and early winter all the common annual species were grazed along with other new growth, but broad-leaved herbs were taken in much greater quantity, either because they were more easily secured, or because they were actually preferred. No use in any form of the several perennial grasses was recorded.

Grass seeds are taken mostly in late spring when they are maturing and "in the milk" but are still attached to the plants. Heads of ripgut brome are easily reached from the ground, but stalks of tall wild oat are more apt to be cut at the base. On several occasions squirrels seen to cut the long stalks left most of the head unused, possibly because it could not be sampled beforehand to determine whether it had attained the proper stage of ripeness. Only those grass species with relatively large seeds are used to any important extent. Red brome seeds, similar to those of ripgut except for size, have never been observed used by the squirrels, nor have the small seeds of the abundant fescue. Seeds of soft chess and of Australian chess are rarely sampled though they are common and readily available, indicating that they must be low on the scale of preference as squirrel foods.

Popcorn flower is much used in winter and spring. Under primitive conditions before filaree became established it may have been the most important winter food. In the early rosette stage, the plants like those of filaree, are sometimes dug out and eaten entire. The foliage is less used after the onset of rapid spring growth. For a short time when the plants have matured, and before the seeds are cast, squirrels take the ripe nutlets by drawing the stems crosswise through their mouths with rapid movements of the forepaws removing each nutlet with the tongue and lower incisors. Seeds of phacelia and buckthorn weed are stripped from the stems in much the same manner, but are taken sparingly, and their hairy stems may be a deterrent.

During winter and early spring Red maids is avidly sought perhaps because of its tender and succulent quality. Often a squirrel will spend many minutes on an area of a few square inches feeding greedily from the dense mat formed by this plant. Flowers are preferred to the foliage. In May the crop has largely dried out and utilization is discontinued.

For a brief interval during spring, flowers of birds-eye gilia are much used but apparently the foliage and stems are distasteful. Gilia never makes up more than a small percentage of the composition but these flowers are conspicuously colored and of fairly uniform height, rendering it easy for a squirrel to gather it in quantity, catching the stems and directing the flowers to its mouth with quick movements of its forepaws.

Of the many kinds of food eaten only a few, the larger seeds, berries and fruits, are pouched. No pouching of flower, leaf or stem material has been observed, for these are eaten on the spot as they are gathered. Most kinds of seeds used are likewise eaten where they are found. Pouching shortens periods of active foraging by eliminating the time required for actual eating of the

food in an exposed situation away from shelter or above ground in trees or bushes where footing is precarious and there is danger of being caught helpless. Ordinarily it serves as a means of transporting food from such foraging places to nearby feeding places where it can be eaten in relative safety and comfort. At times when the sunshine temperature is near the maximum that can be endured by the squirrels, brief periods of hurried foraging alternate with longer intervals in which the squirrel retires to a shaded spot to lounge and eat at leisure (figure 9). The small seeds of Windmill Pink constitute an important food source in late spring, when sunshine temperatures usually are uncomfortably high in the exposed places where the plant grows. At the same season seed capsules of Godetia are similarly pouched in quantity and carried to feeding places by the squirrels. Ripe fruits of the shrub Wedgeleaf Ceanothus, where they are available, are moderately used by squirrels, and usually are pouched and carried to the ground before being eaten (figure 10).

Predatory habits.—Much has been written regarding the occasional meat-eating habits of various sciurids. Like most others the California ground squirrel sometimes takes animal food. Many instances of egg eating have been recorded on the Range. On one occasion a clutch of gopher snake eggs was found littered over a squirrel burrow mound, and the shells were broken open with their contents removed. Most of the bird nests involved were those of quail (Glading, 1938). On one occasion a squirrel was seen to dig out a quail egg from sand in the creek bed where evidently it had been cached. Bird eggs are often carried back to burrows to be eaten. Several instances of predation on nests of killdeer and mourning doves likewise have been recorded. Some of the dove nests destroyed were in low trees, others were on the ground. On one occasion a pair of brown towhees was seen fluttering at a squirrel and driving it along a horizontal live-oak limb toward the trunk of the tree. Investigation

Figure 9.—Eating seeds from pouched capsules of Windmill Pink, in shade of manzanita bush.

disclosed that the towhees' nest containing four young birds was situated in the outer twigs of the limb. No actual instances of squirrel predation on live birds have been observed. Foraging squirrels have been seen to make sudden dashes or lunges at mourning doves on the ground nearby. The doves invariably escaped untouched. Possibly such squirrels were merely driving away potential competitors. Small birds attracted to the traps by the bait—crowned sparrows, juncos, and occasional lark sparrows—are sometimes caught along with a squirrel. In such instances the bird is usually found dead and partly eaten. Once a squirrel was caught in a large wire funnel trap with several white-crowned sparrows. As it dashed about eluding attempts to remove it, one of the sparrows fluttered within reach; instantly the squirrel seized the bird in its forepaws and killed it, with a quick bite, then dropped it. On August 5, 1938, an adult squirrel foraging through a rock outcrop where a pair of adult California quail with their brood of small young were resting caused the hen quail to give high alarm notes, and instantly the young scattered and hid. The cock quail also gave alarm notes and threateningly strutted toward the squirrel, which cowered back under twigs of a protecting oak limb and sat there motionless. The two adult quail ran about fifty feet away to a thick live-oak where they hesitated and walked about nervously, uttering clucking sounds. The squirrel soon resumed foraging, nosing about over the ground still within the area where the young quail were hiding, but either it

Figure 10.—Climbing for ripe fruits of Wedgeleaf Ceanothus.

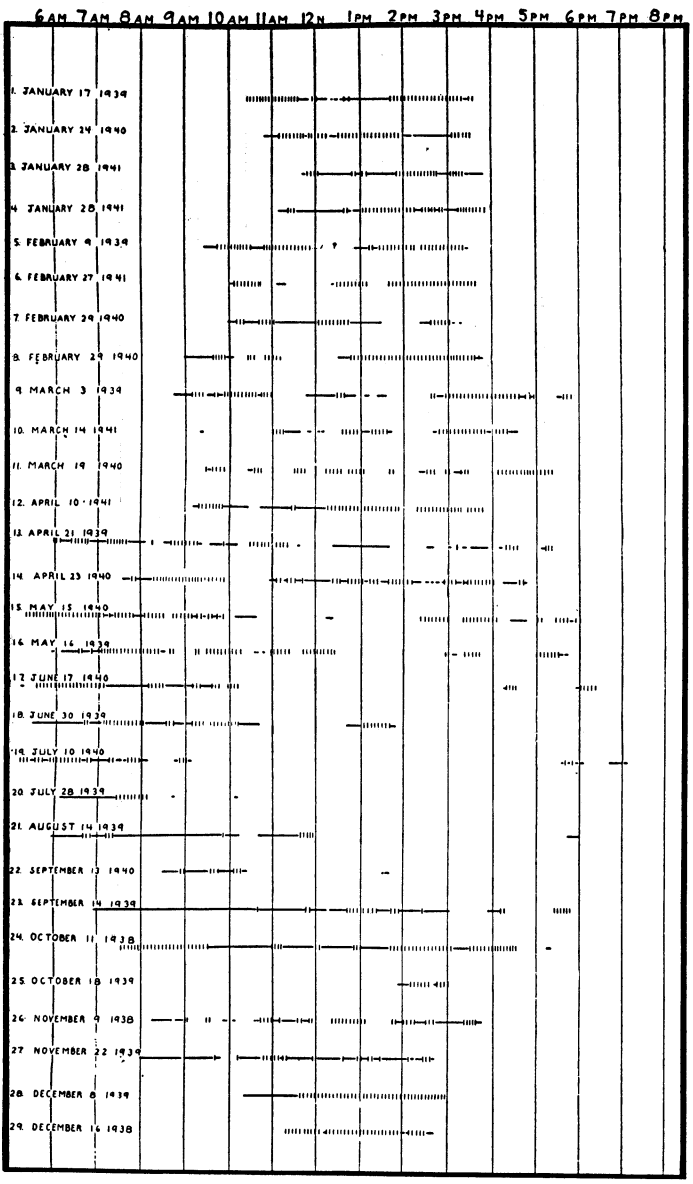

Figure 11.—Diagram showing time spent above ground by individual squirrels on 29 full days of observation. Vertically parallel lines represent active foraging, horizontal lines represent time spent otherwise (as in loafing, caching, or exploring). Note short active days with concentrated mid-day foraging in winter, and relatively longer days with early morning foraging during summer.

did not find any, or it was not interested in them. After five minutes the young quail began to emerge from hiding, gave high peeping rallying notes, and several ran together into a compact group. The squirrel was only a few feet away, within sight and hearing of the unprotected brood, but it paid no attention to them, and moved away to another rock outcrop. After a few seconds the cock quail ran down toward the brood, uttering warning notes which hushed their calls to a subdued peeping. This incident shows that the squirrels do not invariably prey upon birds when opportunities arise.

Grasshoppers seem to comprise the most often used source of animal food taken by the squirrels. Foraging squirrels have been seen to dash after flying grasshoppers flushed at their approach. In most observed cases the grasshopper flew too far for the squirrel to follow, or lit where it could not be found. In open situations such as paved roads, the squirrels' pursuit is more apt to be successful. One will make a series of quick runs and sharp turns persistently following a flying insect, which is finally pounced upon as it lands. On summer days when the temperature is not too high squirrels are commonly seen foraging for grasshoppers in the road and eating in quantity those crushed by passing automobiles.

Squirrels have been seen carrying or eating young cottontails which they had evidently taken from the nests. Once an adult cottontail was seen chasing a squirrel around the side of a bush, possibly in an attempt to defend its nest.

A squirrel was seen carrying a large adult pocket gopher which was still warm, limp, and bleeding, and was found to have a puncture through the back of the skull, evidently made by the squirrel's incisors. This gopher may have been taken by surprise away from its burrow. Another time a squirrel was seen eating a young gopher. On other occasions squirrels have been seen to display only mild interest in gophers digging or emerging to feed in the vicinity, with no special attempt to stalk or catch them. Squirrels have also been seen carrying or eating remains of kangaroo rats, which may possibly have been caught in the burrows, or may have been found dead.

Squirrels are not averse to feeding upon members of their own species when opportunities arise, and individuals which die from disease or accident near burrows are apt to be partly devoured by others. The carcasses are handled in characteristic fashion; the side of the cranium is gnawed away and the brains are eaten out. The skin is torn back and the flesh gnawed away from the limb bones. One afternoon a few hours after poison had been distributed over a pasture, several dead squirrels were found near their burrows and one had the side of its face and an eye eaten away. Dissection of another squirrel found a few feet away disclosed the missing parts in its stomach. Squirrels run over on roads by passing automobiles are often fed upon by others.

These observations clearly indicate a tendency to seek meat or other animal food occasionally, and such food may be an essential part of the diet. Yet animal food, by bulk, must comprise an extremely small proportion of the diet. During the periods of intensive observations on feeding squirrels, the few small animal items consumed never made up appreciable percentages of the daily food.

BEHAVIOR

Foraging habits.—Detailed knowledge of the behavior, and the daily schedule of activity of squirrels is of practical value in the application of control measures. The time of activity during the day varies greatly according to temperature and other conditions. On mid-winter days dry and warm enough to favor squirrel activity, the animals are to be seen above ground, mostly between the hours of 10 or 11 a.m. and 4 p.m., and mainly within the period 11 a.m. to 3 p.m., (figure 11). In contrast, during the hotter part of the summer, hours of most pronounced activity are between 5 and 9 a.m. with another active period in late afternoon between 4 p.m. and dusk. During the mid-day hours when heat is intense, few are to be seen above ground and these limit their activity to shady spots, seldom venturing into the open. On cloudy or unseasonably cool days in late spring or summer, the squirrels are freed from the limitations imposed on them by intense heat, and are conspicuously

Figure 12.—Standing at attention in response to alarm chirp of another squirrel.

active during the mid-day hours. In winter there is some activity nearly every day unless rain is continuous, but wind, cold fog, and rain limit activity and cause foraging periods to be short and hurried. On a warm clear winter day following several cold and stormy ones, squirrel activity is at a peak, each animal foraging ravenously after the period of fasting.

During the course of normal foraging a squirrel grazes intently for usually only five or ten seconds, then pauses and looks about keenly for an instant, as it masticates the food secured. At intervals of a few minutes there are usually longer pauses during which the squirrel sits at attention and looks about for any sign of possible danger. Foraging squirrels are alert to the warning chirps of others, even though these may be hundreds of yards away. Upon hearing a chirp, the one foraging may sit up at attention (figure 12) or may hurry back to a more sheltered spot, or mount a rock or stump to obtain a better view.

In winter much of the feeding is done within the area of the burrow mounds where the squirrels live. New growth of herbaceous species acceptable as food is abundant almost everywhere, and feeding is limited more by the weather than by the actual supply of food. At this season squirrels are apt to emerge from their burrows about mid-morning and spend an hour or two sitting on boulders with hair fluffed out, sunning themselves and waiting for dew to dry off the vegetation before beginning to forage around noon. Fog closing in often sends them back underground for the day.

In making more extended foraging expeditions, a squirrel often heads for some outlying escape burrow which will serve as a refuge in any emergency, or it may visit a neighboring occupied burrow system. After satisfying its appetite, it may spend hours loafing in the vicinity, exploring the holes, or digging to enlarge them. At any sudden alarm, the natural tendency of a squirrel is to bolt for its home burrow. Sometimes one taken by surprise dashes straight toward the observer from a distance of 100 feet or more in order to reach its burrow. Or it may duck into any burrow which happens to be convenient for temporary refuge. Often, one which has resorted to such an emergency refuge reappears after a moment, for a homeward dash, but may duck back or into another convenient refuge with startled chirps, if it finds danger unexpectedly near. After the spring period of rapid forage growth, squirrels tend to extend their activities in correlation with their increasing selectivity of foods. Vegetation has become high enough to impede their movements, but it also affords effective concealment. Individuals taken by surprise often crouch motionless, or "freeze," and escape notice until at a favorable moment they run for their burrows.

After the beginning of the dry season, the vicinity of the burrow mounds no longer provides preferred foods and the animals habitually travel back and forth from them, visiting swales for remaining succulence, and trees and bushes for their acorns and berries, or merely for shade. Well beaten runways through the vegetation soon appear indicating the routes of travel.

Most intensive foraging periods are on short winter days, when a squirrel may feed for two or three hours with only brief pauses. As days become

warmer and longer in spring, periods of foraging become longer and more interrupted. Short expeditions into the open, or climbing above ground in trees and bushes may alternate with much longer periods of basking, loafing, dust bathing and occasional nibbling of pouched material. In hot summer weather, oak trees bcome the favorite resort of the squirrels, both as a source of food, and as protective shade. Burrows situated in exposed locations may be deserted, as the animals take over old ones beneath the trees, or dig new ones there. Foraging becomes mainly arboreal, and a squirrel may spend hours daily climbing through the trees. A small percentage of the squirrels even transfer their habitations to the trees and make straw nests in hollow trunks or limbs. These squirrels are clumsy climbers. When proceeding among the smaller branches and twigs, they may sprawl in ungainly fashion, with one or two legs hanging unable to find a foothold. Even when ascending or descending a sloping trunk, they usually move slowly with none of the grace of a tree squirrel. But on a few occasions individuals have shown agility and surefootedness in crossing on small twigs and branchlets from one tree to another along an apparently familiar course.

Individuality.—While reactions to certain situations and stimuli appear stereotyped, the existence of individual variation in temperament was one of the most striking traits of the squirrel population studied. This was impressively illustrated by the varying responses of different squirrels to the presence of humans. After nearly four years of baiting, live-trapping, and handling of those on the 80 acres where this study was concentrated, the population there was not conspicuously either tamer or wilder than squirrels on remote parts of the Range subject to little or no disturbances from humans. On any one area all degrees of wildness could be observed in different individual squirrels. Many were so wild that they would duck for shelter upon sighting a person 100 yards or more away, and would remain underground for a long time. Others were so tame that, even at a first encounter, they would permit a person to approach within 20 or 30 feet, and would continue to feed unconcernedly. The bulk of the population was somewhat intermediate with respect to degree of wildness and few would knowingly allow a person to approach within 100 feet, except perhaps when sitting alertly at a burrow entrance ready to duck underground.

Several unusually tame individuals were frequently followed and observed for the purpose of obtaining data on their feeding, and other habits. Such squirrels gradually become conditioned to the presence of humans, and would permit a person to come within three feet without displaying any uneasiness. All such animals appeared to be in good condition and, in so far as could be determined, were normal in every respect other than in their reactions to humans. Of nine such animals which were extensively observed over periods of months, seven were females and only two were males. One male and one female were apparently young of the year though of nearly adult size when discovered, the other seven were all old adults. Some of these tame squirrels were known for as much as two years, and their survival expectancy seemed fully as good as that of wilder ones. They were just as wary of traps as others,

and likewise seemed exceedingly watchful for their natural enemies. In each, as it was observed at close range, the constant alertness to detect snakes and other ground lurking enemies was impressive. In moving through thick vegetation, or around rocks or brush where its view was obstructed, such a squirrel was observed to proceed with the greatest caution. It would advance tensely, examining the ground around it carefully at each step, and often flinching nervously at the snapping of a stem or straw. Especial caution was displayed while going into a burrow entrance. In pausing to peer ahead, straining forward, the squirrel would flick its tail from side to side jerkily, in the same manner as one actually watching a snake. This behavior was most noticeable in warm weather when snakes were apt to be encountered.

In less tame squirrels, attempts to detect and avoid snakes could not be so well seen but may have been equally well developed. Those frightened to their burrows usually slowed down to a walk and entered cautiously if not too closely pressed. Others seen foraging in the distance moved about with the same tense, stalking gait.

Usually, tame squirrels seemed to ignore the presence of an observer but their behavior may have been somewhat influenced by his presence. After moving behind a bush or boulder obstructing its view, a squirrel sometimes would manuever around to its edge and peer out as if to assure itself that it was not being stalked. One too closely approached would suddenly become tense ready to dash for safety, but if the observer then waited quietly for a few seconds, it would either resume foraging as before on the spot, or bound away a few inches. Occasionally one closely approached while intent upon its foraging would suddenly notice the nearness of the observer and would sit up and eye him sharply for a few seconds, then turn away apparently satisfied as to his innocuousness. At times one displayed more active interest, and would run toward a person jerkily, a few steps at a time, until almost at his feet, then, sniffing, would look intently up at him. Traps, or other strange inanimate objects sometimes evoked the same reaction.

Social behavior.—Though ground squirrels live in close association, the general demeanor of one squirrel toward another is usually either indifference or intolerance. Individuals may happen to forage or rest within a few inches of each other with neither showing any interest in the other. Probably in these instances each has become accustomed to the other through long association, and one is most apt to be aggressive toward those with which it is not well acquainted. One venturing beyond its usual foraging range proceeds with caution and alertness, and is usually ready to retreat when threatened by another.

Often when two squirrels happen to be near together, one suddenly runs up to the other and noses it. The two animals may meet facing each other and touch noses, or nose each other vigorously about the mouths and cheeks. The action usually lasts only a second or two but may be quickly repeated. Linsdale (1946) records numerous instances of such behavior under differing circumstances which seem to indicate that age or sex are not determining factors.

Rather this behavior seems to be a stereotyped "meeting reaction" by which an individual asserts itself socially toward another and perhaps tests its reactions or its identity. Often such a meeting ends in a show of hostility. The approached squirrel may nip at the other but usually turns away and stands with tail arched as the other makes advances. If the nosing continues, the approached squirrel often gives its tail a violent flick, repulsing the other, and bounds away a few feet. This reaction—turning away and standing tense—seems to be an act of appeasement which discourages hostilities on the part of the one approaching. If the approached squirrel is inclined to resist, it faces and nips at the other with ears laid back and tail fluffed out. If neither is inclined to yield ground, they close in with slow, cat-like movements, and crowd each other, pushing with their inward-turned hindquarters. Occasionally one springs several inches off the ground. Most often such fights last only a few seconds and but little damage is done. Sometimes the fights are sufficiently violent and prolonged so that the combatants suffer serious injury. They may interlock and roll on the ground biting each other. Growls and high squeals are given during the fighting. Occasionally individuals are seen which have deep wounds, and sometimes these become seriously infected. Death may result in some cases, but probably squirrels are seldom or never killed outright in fights.

No evidence of territorialism in the usual sense was found in the course of the present study. Evans and Holdenreid (1943:258) attempt to establish from their obseravtions "that adult males maintained individual territories, which they defended against invasion by other males. . . ." In the present study it was often observed that five or more males occupied the same burrow system during the breeding season, while adjacent areas were unoccupied. The fighting which occurs constantly, cannot be considered truly territorial, but results from the naturally hostile tendency of each squirrel toward others, the aggressiveness associated with sexual behavior, and defense of food or feeding spot from use by others.

In instances where several adult males lived in close proximity, fights and pursuits were frequent, but there was no evident intent to exclude a rival from any definite territory. At times two such animals might forage for long periods within a few yards of each other, and of their burrows, with no show of hostility, or they might merely stalk around each other menacingly when they happened to meet. In the half acre enclosure where six male squirrels were kept, there was some indication of a scale of dominance and of subordination. Certain smaller animals seemed to be pursued and attacked much more frequently than the others.

Though fights are most frequent and conspicuous during the late winter and spring breeding season, they may occur at any time of year. A summer encounter between two large squirrels, probably males, was observed August 17, 1938, when snarling sounds attracted the observer's attention to one pursuing another over a boulder. It overtook the pursued one with a flying tackle, and they clinched and rolled about on the ground biting each other, their tails thrashing. One broke away and ran slowly and heavily for a few yards, then

paused. When it started again, the other pursued and overtook it, and a second time they interlocked rolling about on the ground. After several such clinches and breaks, the pursuing squirrel ran back in the direction from which it had come. The pursued stopped in a hunched position with its head resting on the ground, apparently injured in the fight.

In squirrels observed at close range, a habit commonly noticed was rubbing of the back against various objects such as bases or low branches of shrubs, and rocks of convenient height. The actions of such a squirrel resembled those of a friendly cat being stroked; it would rear up and turn sideways to press the object across its shoulders. The back rubbing was preceded and followed by a good deal of sniffing at the spot selected. This was a prominent phase of behavior in adult males loafing in the vicinity of their home burrows, and was even more noticeable in those exploring or visiting nearby burrow systems. It was interpreted as the leaving of scent, to advertise presence in, and occupancy of, a vicinity to other squirrels.

Since the above paragraph was written, Linsdale (1946:108-114) has described in detail the dorsal skin glands involved in the behavior just recorded. A glandular area of skin just behind the shoulders bears about 30 enlarged and modified sudoriparous glands which produce a musky scent. His accompanying table indicates that these glands are generally more numerous and better developed in males than in females. He mentions instances of animals rubbing the glandular area in loose earth, on a twig and the edge of a board, and states that sometimes a squirrel noses the side of another "as if to identify it." Also, he states: "The position of the glands indicates a possible use to discourage capture by a carnivore." This latter use seems improbable. Ground squirrels locally are a favorite prey species of all those bird, mammal and reptile predators large enough to obtain them. In numerous squirrel remains found left by various predators after making a meal, no tendency to avoid the glandular area in question was ever observed. Therefore, it appears most likely that a purely social function is subserved by the scent produced.

Late in September 1938, several days were spent in observation from a blind at a watering place which had become a focal point of squirrel activity. Many of the animals using it had been marked with colored celluloid ear disks for individual identification. Several were permanently resident in the area, others came distances of 100 to 200 yards beyond their usual foraging range to obtain water. The spot had been baited with grain and squirrels had formed the habit of loitering in the vicinity after drinking. Because of this unusual concentration, of more than thirty squirrels, quarreling was frequent. It was noticed that individuals which habitually frequented the area were most aggressive, while those which came from longer distances were relatively timid, and yielded ground readily. Age, size, and sex were less important than familiarity with surroundings in determining dominance. Most severe fights were between individuals which seemed familiar with the area. At this place half-grown young squirrels were observed to behave aggressively toward much larger ones, and an old adult female long resident in this vicinity was the most frequent

aggressor. Some fights had no apparent cause other than the crowding of the animals in close proximity. But in many instances it was evident that the attacking squirrel was driving the other from the bait, even when the bait was in a set trap which the defending squirrel was too cautious to enter.

Voice.—The familiar chirp of the ground squirrel varies significantly in pitch, loudness, and inflection according to the occasion. An individual animal uses its voice infrequently and only under unusual disturbance. One may pursue its routine activities for days at a time without making any vocal sound.

Perhaps the primary function of the voice is to warn other individuals in the community of an imminent danger. A distinctive type of chirp is that given in response to the sight of a hawk or other large bird flying in the vicinity. This consists of a single short syllable of unusual loudness and carrying quality;—"*cheesk,*" or "*chisk*"—usually given as the animal bolts for shelter. Sometimes, two such notes are uttered in rapid succession. Other squirrels within hearing instantly come to attention or run for shelter, and each, in turn, repeats the alarm as it sights the object of potential danger. From these chirps, the course of a hawk may be traced along a canyon wall or over rolling hills as individual squirrels, already put on guard by others, sound the alarm, each as the bird comes within its range of vision. The red-tailed hawk is the most common source of danger evoking this type of alarm note. Hawks soaring high overhead seem not to be noticed by the squirrels as only those flying low excite alarm. Hawks perched in trees even at a fairly close range seem not to be noticed by squirrels until they fly; then instantly alarms are sounded. Horned owls are as much feared as hawks. Low-flying vultures apparently are not distinguished from large hawks and elicit the same response. On one occasion a squirrel was seen sitting near its burrow entrance alertly watching a vulture as the latter stood tearing at a dead squirrel only about 30 feet away. The squirrel's lack of fear in this instance evidently was due to the fact that the vulture was not in flight. Cooper hawks seem to be as much feared as the larger kinds. Sharp-shinned hawks have on several occasions been noted to cause squirrels to give alarm chirps but other times they have been seen to pass near without being noticed by squirrels, and they are apparently about the minimum size of birds recognized as potential enemies. California herons in several observed instances caused squirrels to give these alarm chirps. Often squirrels released from live-traps and running for shelter at close range give a single-syllabled chirp similar to the hawk warning but of more suppressed and less penetrating quality. A trapped squirrel when first approached gives a low, subdued note "*chisk!*", peculiar in its rising inflection and exclamatory quality.

A type of chirp usually distinctive is that given in response to sight of a snake. Upon seeing one, a squirrel edges up to it (figures 13 and 22) often coming within a foot or so, but always, in observed instances, keeping beyond its striking range. Straining forward tensely and sniffing, with its hind feet firmly planted, far back, and prepared to bound away, the squirrel examines the snake, and at short intervals, flicks its tail violently from side to side. It may back or sidle away, move around to another angle, and again face the snake to continue its watching at a new stance. Sometimes the whole perform-

once is carried out in silence but in most observed instances, peculiar chirps were given, "*cheet'-ik-irr-irr-irr*" distinctive in the low, vibrating quality, and the series of suppressed notes following the loud initial sharp note. These succeeding notes blend into each other producing a trilling or rolling sound which fades gradually toward its end. The sound has less carrying quality than some other chirps, as for example, the hawk warning, but nevertheless can be heard for considerable distances. On one occasion an observer located a squirrel and nearby snake, after recognizing the chirps and following up the sound from a distance of 700 yards. At a distance the trilling terminal notes usually are not audible, and the sharp initial chirp is not readily distinguishable as that of a snake warning. The most effective method of finding rattlesnakes on the Range was by listening for this "snake warning." Several field workers became familiar with the significance of this chirp and over a three year period dozens of rattlers were located by means of it. Considerable variation in the sound was noted from time to time. On some occasions when the chirp was not altogether typical, and lacked the distinctively prolonged terminal trill, investigation nevertheless disclosed that snakes were the cause of disturbance. But when the typical trilling chirps were heard, investigation nearly always yielded a snake, or at least fresh tracks in the vicinity showed that one had been there and had reached shelter before the observer arrived. One observer thought he was able to correlate variations of this chirp with the distance of the squirrel from the snake, the most typical, trilling chirps being given at close range, while sharper chirps lacking the trill and uttered at shorter intervals were given by squirrels watching a snake from a distance of several yards or more. The chirping and tail waving of squirrels which have located a snake serve to attract attention of others in the vicinity. Investigation of the characteristic chirp frequently has led an observer to a group of squirrels, as many as six, all gathered within an area of a few square yards and watching intently. Usually in such instances only one squirrel probably the original discoverer is chirping, though several may be flicking their tails. The warning value of the squirrel behavior is evident in such cases. Other squirrels foraging in the vicinity are informed of the presence and approximate location of the snake, and are often saved from coming suddenly upon it unawares and being struck. In nearly all recorded cases of "snake warning" the rattlesnake was the kind involved, it being by far the most abundant snake on the Experimental Range. However, in several instances, a gopher snake was found to be the source of disturbance; once a squirrel was found to be giving the "snake warning" as it watched a large garter snake, and another time one was found to have its attention focused upon a four-foot long California racer. In one exceptional instance when a typical "snake warning" chirp was investigated it was found that eight or ten squirrels were near the source of the disturbance perched on rocks and on branches of a live-oak all within 25 feet and watching intently, a centrally situated object. They did not disperse until the observers had come within a few yards. The squirrel which was chirping was five feet above the ground in a rock crevice, looking down upon a horned owl, which was sitting on the ground directly below it, and holding in its claws a freshly killed pocket gopher.

A chirp several times heard given by squirrels when a dog or coyote came into the vicinity, and frequently on other occasions in response to disturbance by humans, often consists of three syllables—*"chwee-chu-chuk!"* The first syllable is loud and sharp with the carrying quality of the "hawk warning." The second syllable is suppressed and the terminal syllable is loud and emphatic, with an exclamatory quality. The low middle syllable may be entirely omitted —*"chwee-chuk'!"*—or it may be double—*"chwee-chu-chu-chuk!"* This chirp typically is given only once at an alarm, immediately after the source of danger is sighted and usually while the squirrel is sitting at attention; following it a series of less sharp chirps of one or two syllables may be given at intervals of a few seconds. These sharp chirps serve to forewarn other squirrels of the approach of a prowling predator while it is still distant.

A similar chirp is given on occasions of comparatively mild alarm such as when suddenly sighting in the middle distance a person or large animal which might or might not be a source of danger to the squirrel. This chirp might be written as *"cheesk'-isk-isk-isk-isk"*—with the first note loud and sharp and the following series of notes rapidly uttered varying in number blending into each other and becoming successively fainter. The terminal notes of this call are produced so rapidly that it is difficult to count them. The expulsion of air from the lungs by which each chirp is produced is accompanied by violent contractions of the diaphragm and muscles of the thorax and throat. Often the tail is given a quick flick as the initial sharp note of a chirp is sounded.

Mother squirrels warning their young of approach of a person or some other potential but comparatively mild danger have been heard to give a low melodious note—*"chwërt"*—uttered at intervals of two or three seconds over periods of minutes. It expresses uneasiness and distrust rather than an actual alarm. Litters of young playing around burrow entrances usually come to

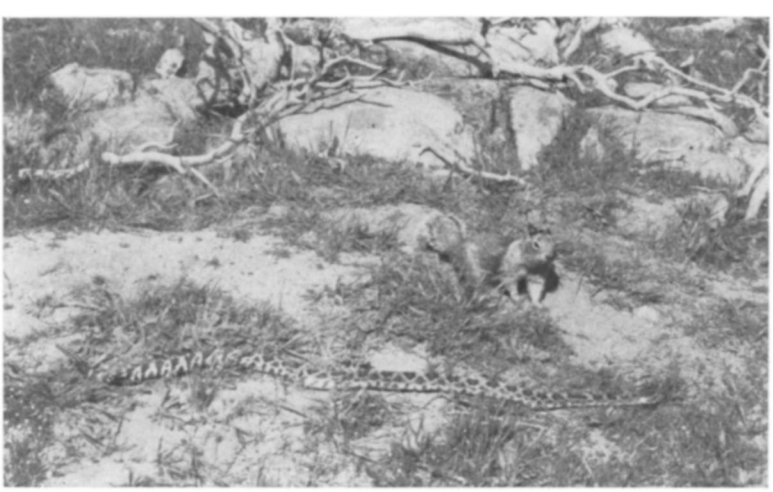

Figure 13.—Nervously watching a rattlesnake near burrows.

attention at the sound but do not retreat underground unless there is some further indication of danger. Squirrels which have uttered the alarm note described in the preceding paragraphs at sight of a predator have been heard to give series of these notes during the period of recovery before foraging was resumed.

Severity and kind of alarm rather than any stereotyped reaction to a specific predator as such, are the factors which determine the types of chirps given. Thus, the short, sharp "hawk warning" is generally given while the squirrel is frantically sprinting to its burrow. The "predator warning" is usually given as the squirrel sits in comparative safety within easy reach of some shelter, and utters the multiple notes of this chirp, with their distinctly scolding quality. The "snake warning" likewise is a scolding chirp uttered by an animal in no immediate danger, but keyed to a state of high nervous tension in the presence of its dreaded natural enemy. Foraging squirrels, under observation at the instant that snake warnings were given by individuals distant but within hearing, usually reacted by sitting at attention and looking about alert-

Figure 14.—On look-out in dead brush.

ly. If these squirrels had recognized the true significance of the warning chirps, they might have been expected to ignore the sound, since the discovery of rattlesnakes beyond the limits of their own small foraging areas would have no immediate importance to them.

All of the sounds so far described are modifications of the same basic chirp, but under unusual stress several other kinds of sounds are also produced. One of these is a low growl or snarl which principally seems to express defiance. It is given by squirrels caught in steel traps. Occasional individuals caught in box traps also growl with accompanying aggressive behavior; they may lunge against the side of the trap in an attempt to get at the observer. Such behavior is exceptional, and usually the trapped squirrel lies silent and motionless as the trapper approaches. On one occasion a squirrel, which was watched from a blind as it entered a large live-trap, began dashing about within the trap with low growls as soon as it discovered that it was confined. Several other squirrels in the vicinity but outside the trap paid no heed to it and continued to pick up bait. Growling is most often given during encounters between one squirrel and another, usually underground. Such encounters occur when a squirrel is forced to take refuge in the burrow of another at some sudden alarm, or during the breeding season, when pursuit and fighting is a prominent phase of squirrel behavior. The snarling sound consists of short syllables *"churr-churr-churr"* sometimes uttered continuously for periods of minutes, variable in loudness, inflection, and length, depending on the circumstances. An observer who saw a pair of copulating squirrels at close range, said that both male and female made snarling sounds during the process.

Under stress of extreme pain or fear, squirrels give a sharp squeal. On frequent occasions in the field, squirrels have been heard to give this note at the instant of being struck by a rattlesnake. Squirrels caught in wire snares set in their surface runways gave similar squeals, sometimes several in succession. The distress squeals produced strong reactions in all other squirrels that were within hearing; they would sit up at attention and some would give alarm chirps, others would mount rocks or similar lookouts to determine the cause and direction of the disturbance.

A more subdued squeal, of high pitch and ending in a trill, is given by squirrels pursued by others. The pursued squirrel may give the note at the instant when both animals are pausing momentarily a few feet apart before the chase is renewed. In observed instances the sound had no noticeable effect on the pursuing squirrel.

Each of the chirps and calls described above is subject to much variation in different individuals and on different occasions. Calls heard in the field are not always typical of those described above, but are often more or less intermediate in character. No combination of letters can adequately represent the sound made by a squirrel. For different renditions and interpretations of some of the calls here described, see Linsdale (1946:97-103).

SEASONAL RESPONSES

Dormancy.—In the foothill habitat with its mild climate and varied food supply, conditions are favorable for year long activity above ground, and periods of dormancy are shorter and less regular than in populations of this species in other regions. At all times of year at the Experimental Range squirrel activity is conspicuous. Not all members of any one age or sex group are dormant at any one time. Individuals differ greatly in their time of dormancy, and some remain active throughout the entire year.

Records of dormancy of individual squirrels are fragmentary, as few were tame enough so that direct observations of their activity from day to day could be made, and they could not be trapped with sufficient regularity to establish proof of presence or absence. But in many instances individuals caught frequently over periods of weeks were sometimes noted to have disappeared. Then suddenly they would reappear after absences of weeks or months. Especially in January and early February of each year many old females not seen since early the preceding summer reappeared. In one instance, an adult female which had been observed daily in the fall of 1938, had disappeared on November 29, and was absent for 50 days thereafter. On January 17 it emerged from hibernation and was active for the remainder of the winter. In late August 1940, an old adult female which had been a frequent repeater disappeared, having first become fat. For three months thereafter it was not seen, and when finally recaptured late in November in its usual location, it was emaciated, having undergone reduction to just over half its August weight. Most adult females seemed to spend an even longer time in dormancy, as few are seen or trapped from June until the following January.

To illustrate seasonal dormancy, the records of a female squirrel first trapped as a half-grown young on May 3, 1939 are recorded below. It was recaptured at intervals through the summer and fall of its first year, but as an adult in 1940, 1941, and 1942 it disappeared throughout the summer and fall months and emerged from dormancy during late winter in thin or even emaciated condition.

TABLE 8.—Records of dates trapped and monthly weight of a female ground squirrel, indicating intervening dormancies.

	Dates of capture	(Average weight in grams for the month)
1939	May 3, 18, 19	313
	June 8, 10	380
	July (no records, possibly dormant)	
	August 10	360
	Sept. 26, 27	465
	Oct. 5, 13, 17, 18, 19	469
	Nov. and Dec. (no records, probably dormant)	
1940	Jan. 27	480
	Feb. 9, 13, 15, 26	457
	March 27, 29	505

TABLE 8.—(*Continued.*)

	Dates of capture	(Average weight in grams for the month)
	April 1, 9, 11, 19, 22, 23, 25	530
	May 1, 7, 8, 11, 16, 17, 21, 22, 23	699
	June 7	800
	July through Nov. (No records, dormancy)	
	Dec. 17, 19, 20	400
1941	Jan. 14, 15, 16, 18, 31	462
	Feb. 5, 6, 7, 17, 18, 19, 20, 21, 22	486
	March 5, 6, 7, 11, 17, 18, 19, 20, 21	462
	April 2, 16	535
	May 7, 28	715
	June through Dec. (No records, dormancy)	
1942	Jan. 8, 21	485
	Feb. 11	550
	March 6	537
	May 13, 18	630

Most other adult females followed the same general pattern in their seasonal occurrence as repeats in the trapping records, and in their weight fluctuations. Some emerged from dormancy in December, but others apparently spent most or all of January in dormancy before finally emerging. Even for

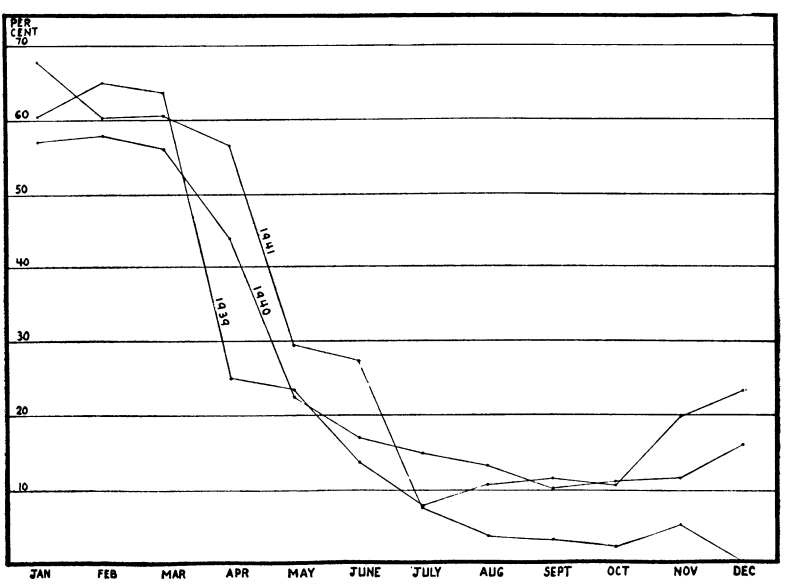

Figure 15.—Percentage of adult females in month to month trapping records for three different years. The females are in the majority during the breeding season, January and February, but are much outnumbered by young during the spring months, and undergo further decrease in summer and fall as some retire into dormancy. In 1941 the adult females comprising two-thirds of the January population had disappeared entirely by the following December.

squirrels which were active, long periods sometimes elapsed between captures, and hence from trapping records alone it cannot be definitely stated just when any individual was dormant.

Old adult females certainly spend more time in dormancy than other age and sex groups, but the entire population is active throughout the breeding season, and only at that time of year can an accurate idea of the population composition as to sex and age groups be obtained. For the fall, winter and spring of 1941-1942, the following changing age and sex ratio was obtained from the total number of captures.

TABLE 9.—Monthly percentage of ground squirrel age and sex groups in fall, winter and spring trapping records.

	Percentage of old females	Percentage of old males	Percentage of young adult females	Percentage of young adult males
October	3.16	18.7	28.0	50.0
November	.53	20.9	26.8	51.8
December	.99	23.3	21.8	54.0
January	15.7	21.3	24.5	38.5
February	21.8	13.6	30.2	35.6
March	18.5	17.9	21.0	42.6
April	21.9	19.2	23.3	35.6
May	9.3	18 6	36.1	36.1

Though adult females certainly spend more time in dormancy than males or younger females, it is probable that some old males and young of both sexes become dormant at least for short intervals. Young adults, especially females, are more abundant during the breeding season, late winter and spring, than they are during the fall months preceding. Irregular fluctuations in numbers of young from month to month in the summer, as censused by the ratio of marked to unmarked individuals, evidently are caused by a changing proportion undergoing dormancy. In September 1940 the young, then mostly approaching adult size, were 40 per cent more abundant than in August and almost as abundant as they had been in June. The apparently extensive aestivation of young in the summer of 1940 is correlated with the fact that they were in excellent condition and already early in the summer were well matured. Additional evidence of dormancy in young is provided by the fact that those recaptured after intervals of many weeks showed less weight gain than those trapped regularly over the same length of time. For a group of 14 males and 8 females trapped in July and September 1940 but not in August, average weight gains were 84 and 66 grams respectively, while in a larger group of individuals each captured in all three months, the weight gains for just the same length of time were 118 grams for males and 76 grams for females. The ratio of young males to young females trapped is high each year through the summer and fall months, and swings back in favor of the females just before and during the breeding season, demonstrating that in young as in adults the females have more tendency to become dormant than the males. Dormancy periods of young seem to be much shorter than those of adults.

It is fairly certain that there is some dormancy in adult males, though they

were never known to disappear for long periods of months as did adult females. In 1941 feeding conditions were so favorable that both males and females were unusually fat through the late spring and summer, and both sexes of old squirrels became so scarce, as compared with young that it is fairly certain each month of late summer and fall was passed in dormancy by

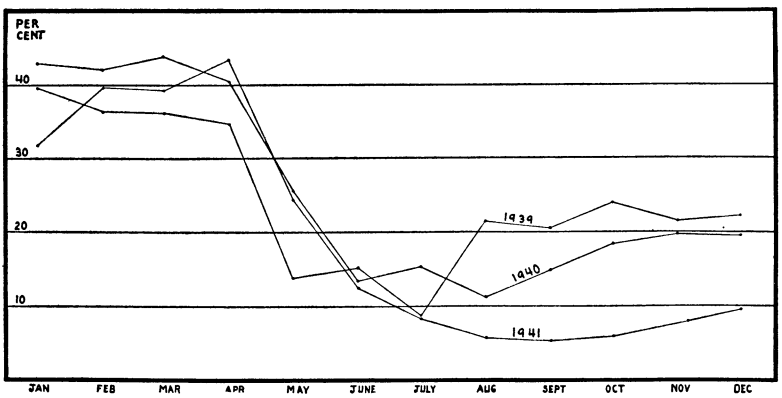

Figure 16.—Percentage of adult males in entire population in month-to-month trapping record. Trend is similar to that of females but seasonal change is less marked because a smaller proportion retire into dormancy.

part of the old male population. In 1939 and 1940 several old males were noticed to be fat and sluggish during late summer and fall, spending but little time above ground daily, and not showing much interest in feeding.

An idea of the extent of dormancy in one sex or age group as compared with another may be obtained by tracing back from the breeding season the records of groups of individuals known to have been on the trapping area a long time. For any one month absence of an individual from the records is due either to its avoidance of traps or its dormancy at the time. Avoidance of traps is not correlated with age or sex, so the differences shown demonstrate varying dormancy. In the following table, only individuals known to have been within the trapping area during most of the months involved, are included. "Number in group during breeding season," thus, does not represent the entire population, but is a selected sample of it (See Table 10).

These figures demonstrate that adult females have, in summer and fall, a consistently higher incidence of dormancy than have adult males, that the young of either sex have less dormancy than adults. It shows that dormancy was much more extensive in the summer and fall of 1941 than in 1940, and that differences between age and sex groups were accentuated in 1941 as compared with 1940. Similar data tracing the 1940 breeding population back through 1939 indicate that dormancy that year was less extensive than in either 1941 or 1940, (but are not strictly comparable since the entire area was not trapped each month in 1939).

No general conclusions as to dormancy can be drawn, beyond the fact that

TABLE 10.—Relative numbers of males and females and of yearling and old adult squirrels active during different months of the year.

	Number in group during breeding season	Percentage of breeding season group trapped in each month of year preceding											
		Dec.	Nov.	Oct.	Sep.	Aug.	Jul.	Jun.	May	Apr.	Mar.	Feb.	Jan.
Old males in 1941	50	58.0	58.0	56.0	40.0	24.0	28.0	30.0	56.0	54.0	54.0	68.0	48.0
Old males in 1942	18	38.8	50.0	33.3	27.7	33.3	44.4	61.1	72.2	33.3	61.1	72.2	55.5
Old females in 1941	78	23.1	16.6	17.9	17.9	17.9	23.1	32.1	39.8	42.3	56.4	75.6	46.2
Old females in 1942	68	0	8.8	2.9	2.9	4.4	11.7	39.7	44.1	26.5	64.7	66.2	60.3
Young adult males in 1941	92	54.4	59.7	70.6	58.7	36.9	35.9	39.1	22.8	2.2	not yet emerged		
Young adult males in 1942	78	62.8	83.3	82.1	61.5	62.9	57.5	26.9	16.6	not yet emerged			
Young adult females in 1941	80	63.7	66.2	65.0	57.5	36.2	36.2	41.2	46.2	6.3	not yet emerged		
Young adult females in 1942	69	37.7	59.4	62.3	62.3	62.3	59.4	63.8	49.2	40.6	not yet emerged		

throughout the summer and fall many and sometimes nearly all of the old females are inactive, that some dormancy apparently occurs in adult males and young of both sexes, and that there are great differences from year to year in amount of dormancy, apparently correlated with feeding conditions and the weight attained during early summer.

Within a few miles of the Experimental Range notable differences in seasonal schedules occur in other ground squirrel populations. At considerably higher elevations in the Sierra Nevada and its foothills, a long hibernation is enforced by the severe winter climate, and aestivation probably does not occur. The sparse woods which is a feature of the terrain at the Range gives way to open rolling land within three or four miles to the west and south. Ground squirrels occur in this open land though in much lower numbers. The absence of the oaks and other trees which on the Range provide so much of the summer food and critically needed shade, must profoundly alter squirrel ecology. Casual observations suggest that aestivation occurs much more extensively.

In a study of ground squirrels of this species in the vicinity of Bass Lake, less than 20 miles away but at higher altitude, 4500 feet as against 1100 feet at the Range, Storer, Evans, and Palmer (1944) found a different seasonal schedule, with general hibernation, lasting from about November 1 to April 1. They record that "Females apparently went into hibernation before the males, since only 2 females were caught after September 25 and at least 7 males were active in mid-October. Breeding apparently occurred in the latter part of April," that is shortly after emergence from hibernation, and some three months later than it occurs at the Experimental Range. Emergence of young recorded by them was correspondingly later, as indicated below. Populations

First date of emergence of young in:	Experimental Range	Bass Lake
1938	May 3	July 18
1939	March 23	July 7

at higher elevations are evidently more regular in their seasonal schedules than are those at the Range, which vary individually in their response to weather conditions, and apparently change from year to year in their time and duration of dormancy, according to changes in the weather.

Weights.—Definite seasonal trends in weight can be traced, but some individuals do not conform closely to these. There are notable weight differences between individuals. Even within the same age and sex group, and in the same situation some may be more than twice as heavy as others. Most rapid change in weight occurs in spring, as the squirrels gain steadily through April, and May. In late May or early June they reach a peak, having gained, on the average, around 30 per cent in the course of a few weeks. During this period of gain, a varied and nutritious diet is taken, including much flower and seed material. After drying out of the forage crop, weight begins to decline. The decrease is much more abrupt if the crop of some of the favorite summer foods are short, but in favorable years the weight may be maintained at a high level through the summer. Rarely, adult males may attain a maximum weight of more than 1300 grams.

The percentage of the population undergoing aestivation probably depends upon feeding conditions and the extent to which they are able to lay up a store of fat. All squirrels known to have entered dormancy were fat and in good condition at the time of disappearance. The majority of adult females disappeared for the summer and fall, but the percentage remaining active was much higher in 1939 when they were not so fat and food was relatively scarce. In 1941 squirrels gained more weight than in 1940, and aestivation was correspondingly more complete.

Male and female weight fluctuations parallel each other through most of the year, but their trends deviate in the breeding season. Male weights are then reduced, probably as a result of continual fighting, pursuing of prospective mates, and consequent injuries and loss of foraging time. During the same period developing embryos in many of the females added to their weights. The increase due to pregnancy is not striking, as the young are relatively small at birth, and a full term litter of foetuses weighs hardly more than the stomach of an adult filled to capacity.

The following table, based on the 1942 breeding season, shows the average weights of the different age and sex groups in successive months. Numbers in parentheses indicate sizes of the samples which were of necessity small for the older groups with relatively few survivors.

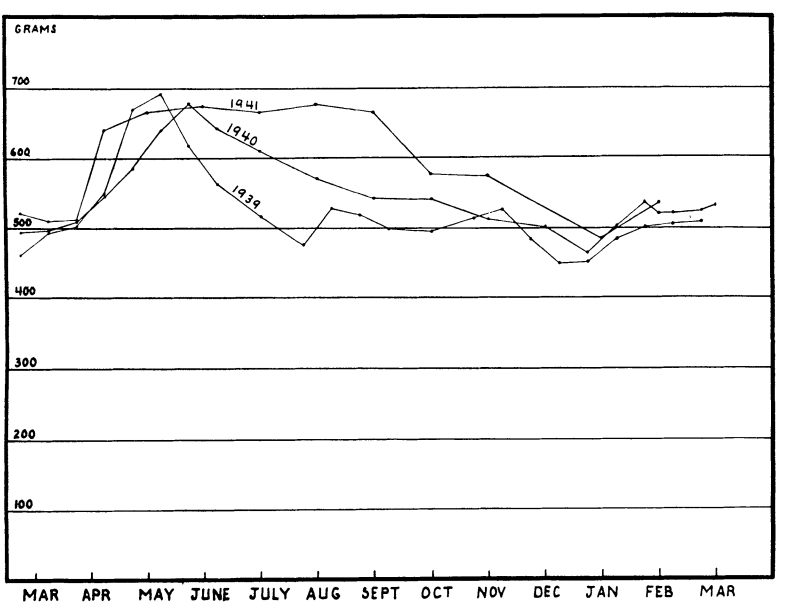

Figure 17.—Average weights of adult female squirrels trapped in three different years, showing rapid gain in late spring, and wide variation from year to year depending on weather conditions. Due to extensive dormancy in late summer and fall, samples for those seasons are small.

TABLE 11.—Average weight in grams of age and sex groups in 1942.

	January	February	March
1938 ♂♂	764.8 (6)	722.6 (5)	560.0 (5)
1939 ♂♂	668.3 (6)	603.0 (4)	595.6 (5)
1940 ♂♂	750.4 (40)	714.4 (21)	648.6 (20)
1941 ♂♂	647.4 (63)	634.3 (58)	586.1 (21)
1938 ♀♀	483.8 (10)	492.9 (8)	526.4 (8)
1939 ♀♀	511.2 (17)	552.5 (13)	527.3 (12)
1940 ♀♀	494.4 (17)	542.6 (26)	542.7 (16)
1941 ♀♀	495.5 (56)	502.9 (58)	483.6 (36)

The time of emergence of young squirrels, and their size at emergence has differed from year to year. Ability of the females to continue providing sufficient milk for their large litters of well grown young may depend largely on the forage crop. The average weights of lactating females recorded after first emergence of young varied a good deal from year to year.

In 1939 and 1946 the young were relatively small at the time of their first appearance, and may have been forced to shift for themselves at an earlier age because mothers were in poorer condition. At any rate newly emerged young were much easier to trap in 1939 and 1946 than in other years, for instance 1940, when special effort was made to catch them with but little success.

Growth rate and condition of young from year to year varies according to the food supply. The first few weeks of their activity above ground corresponds with the season when preferred foods are most abundant and when adults are gaining weight. During this time their growth is exceedingly rapid. After drying out of the forage, subsequent growth depends on the available supply of acorns, tarweed, and other summer foods. If these are scarce, as in 1939, the young may make little or no growth for the remainder of the dry season. But if conditions are favorable, with good crops of acorn, tarweed, and some late succulence remaining, the young continue to make rapid growth and many of them are already nearing adult size early in the summer.

Breeding cycle.—In the fall, testes of the male squirrels enlarge, and in late October and November most appear to be in breeding condition. Enlargement of the testes may be correlated with the change in diet from dry seed material to green newly sprouting annual plants soon after the first fall rains. At least the enlargement was observed to follow closely on this change in diet, both in old animals and in young of the year. Despite this change, males show little evidence of sexual behavior during the fall months.

None of the females appeared to be in breeding condition before the first of January. In fall and winter females have the vaginal canal sealed off from the exterior by a layer of skin, both in old adults which have survived previous breeding seasons and in young adults which have not yet bred. In the females coming in heat the genital region becomes noticeably swollen and the skin becomes somewhat discolored. In the course of a few days the vaginal canal

opens, and its lips become thickened, protruding, and turgid, and at this stage breeding occurs. Actual copulation has not been seen by the writer and must take place underground in most instances. Chasing of females by males was observed constantly during the breeding season. Yearlings breeding for the first time, seem to lag somewhat behind the old adults, as indicated by the following figures showing percentage of those appearing to be in breeding condition (with genitalia swollen and vaginal canal open) at different stages during the 1940 season.

	Jan. 1-15	Jan. 16-31	Feb. 1-15	Feb. 16-29	Mar. 1-15
Old adults	28%	54%	54%	15%	0
Young adults	10%	29%	44%	21%	0

By March, in 1940, apparently all mating activity for this season had ceased, and most adult females either were gravid or already had given birth to young.

In 1946 the breeding season was later; females were first found in breeding condition on January 22 and the last one which had not attained breeding condition was taken 49 days later on March 12. In pregnancy the swelling of the external genitalia subsides. After birth of young the lips of the vaginal orifice shrivel and adhere closely along a longitudinal slit. Before the birth of young, the nipples are minute especially in females which are breeding for the first time. In those which have suckled young during previous seasons, the nipples are more prominent, about 1 mm in length. Early in lactation the nipples are small and flesh-colored but later become enlarged, dark, and roughened. After the young are weaned, the nipples shrivel to horny knobs, and eventually the outer layer of dark, wrinkled, thickened skin is sloughed off.

Though the actual breeding season lasts nearly two months the peak is confined to a much shorter period. From year to year the time of the breeding season varied according to weather conditions. In 1938 young did not appear above ground until May 3, whereas in 1939 they were first recorded on March 23, in 1940, April 17, in 1941, April 16, in 1942, April 28, and in 1946, April 7.

In their mating activities squirrels probably are promiscuous. Each individual generally keeps to itself in its home life underground though at times two or more may use the same burrow entrance. Encounters between individuals are usually characterized by a show of either hostility or indifference; but little sociability is displayed.

Linsdale (1946:459) states: "Long periods of watching ground squirrels through the early spring seemed to show that a temporary pairing of male and female took place each spring, sometime between the end of January and the middle of March. After a pair had occupied common ground for a period, possibly as long as two weeks, the male would move to a new location. The female would then select a burrow in some inconspicuous site and prepare it for the litter of young." However, no definite evidence of this "pairing" is set forth in the same author's ten-page narrative field notes of reproductive be-

havior (*op. cit.*: 326-335). Occupancy of common ground or even use of the same burrow entrance cannot be considered as indication of pairing in view of the usually hostile demeanor of the individuals involved in such associations. Breeding males undoubtedly do move about to visit neighboring burrow warrens or even shift their headquarters under the stimulus of sexual urge, but that they direct their movements with reference to any one female except at the moment of sexual pursuit is unlikely. In the present study squirrels of both sexes were intensively observed in the breeding season, and in no case was a recognized "mate" in evidence though the individuals in question might participate in a sexual pursuit with any squirrel of the opposite sex which happened to be in the vicinity.

During the breeding season males frequently chase other squirrels of either sex, and fights are frequent. Underground encounters occur often, and are brought to the attention of a quietly approaching observer by snarling and thumping as if from a struggle. As a result of this activity squirrels lose patches of hair and suffer skin and flesh wounds. In early March almost every squirrel is badly scarred from fighting during the course of the breeding season. Females usually sustain injuries on the back and rump where they are bitten by pursuing males. Sometimes patches of hair are pulled out leaving areas of bare skin, but usually the skin is broken, leaving ugly sores as much as an inch in diameter. None of the females examined appeared to be in critical condition from the injuries. Males usually are more severely scarred than females, and facial injuries are most frequent. As a result of frontal attacks, the cheeks, lips, and supraorbital ridges of males often sustain deep wounds which are apt to be infected. The consequent inflammation and swelling makes eating difficult and painful to some of the injured animals. The sores are sometimes malodorous and trapped squirrels are attended by buzzing swarms of blow flies, which deposit eggs in the pelage around the open wounds. Some individuals known to have been in excellent condition through the early part of the winter were gaunt and emaciated with ragged pelage at the end of the breeding season, as a result of their injuries. The most seriously afflicted ones were the younger animals. This is well illustrated by a young adult caught regularly through the winter of 1940-41, weights of which on various dates were as follows: Sept. 16—540 gms. Oct. 16—550 gms., Nov. 8—660 gms., Dec. 9—650 gms., Jan. 13—650 gms., Feb. 5—640 gms., March 6—420 gms. When captured in early March this squirrel had numerous bites, some infected. It ran slowly and heavily when released, showing that it was in weakened condition from its wounds.

Occasionally at this time of year males are found so weakened that they are hardly able to escape to their burrows, and can be caught by hand. Some have even been found in dying condition. Mortality resulting directly and indirectly from fighting must be one of the factors which bring about reduction of the males, especially where the population is high. Almost every individual probably suffers some weight loss because of this activity. In April breeding activity and most of the fighting is ended. The wounds heal rapidly and become covered with a growth of new hair, and weight losses are regained.

The large scrotal testes undergo a decrease in size more gradual than their enlargement and descent in fall.

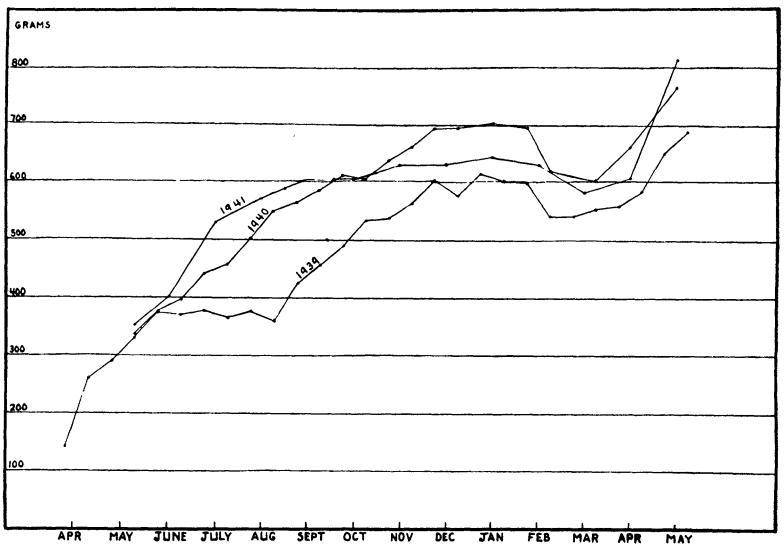

Figure 18.—Average weights of all young male squirrels trapped in three different years. Note rapid early growth, cessation of growth during critically dry summer of 1939, and loss of weight during breeding season each year.

MOVEMENTS

Effective application of control measures involves knowledge of the extent of daily movements, foraging ranges, and migratory tendencies of the species. In the present study many full days were devoted to direct observation of the movements of individual squirrels, and thousands of movement records were obtained from live-trapping. The movements shown by the trapping records are of various types which cannot be distinguished readily. These records are of most value for showing long-time movements, and are judged unsuited to demonstrate the extent of home range. Detailed direct observations on the movements of a number of relatively tame squirrels provide a better basis for showing home ranges. Figure 19 shows the ranges of several individuals of different sexes and ages, as mapped from hundreds of hours of observation. From these maps it will be seen that the range is small, only 100 to 150 yards in greatest diameter, and that most of the activity is restricted to an even smaller area in the central portion. Foraging out to the peripheral portion of the home range is relatively infrequent. Occasionally some preferred food source induces a squirrel to make unusually long foraging expeditions from its home base, beyond the limits of the usual home range. No definite or sharply defined boundaries limit an individual squirrel's sphere of activities. It usually stays at certain spots or within small areas (only a small fraction of the home

ranges shown), but at any time it may venture out farther than usual. The tendency of each to explore new territory is limited by the tendency to keep where the home burrow or other safe and familiar shelter is easily accessible. Much of the activity may be confined to the area encompassed by the burrow mounds, when food is plentiful there. Most foraging is done within a few yards of the home burrow system, or from outlying burrows used as secondary bases. As the squirrel works out from these it becomes increasingly uneasy and alert. Unusually long trips to points where food or water attract it may be made daily at certain seasons. In these instances the same route is habitually used, and travel is hurried and purposeful.

In trapping, often many captures of a squirrel were made at the same spot. The chances of one being caught were somewhat proportional to the nearness of a trap to its center of activity. The capture of a squirrel was often preceded by long and hesitant maneuvering of the animal in the vicinity, until its desire for the bait overcame its instinctive caution toward the trap. Traps encountered in outlying portions of the range were apt to be left and forgotten as the animal continued its foraging after a period of reconnoitering.

Evans and Holdenreid (1943) are of the opinion that adult male squirrels have smaller home ranges than females or young. No such tendency was found in the present study. On the contrary females were found to make less extensive movements than males of the same age group.

Being only a half mile long and a quarter mile wide, the trapping area was not well adapted to show unusually long movements, which may have often taken squirrels far beyond its boundaries where they would not have been

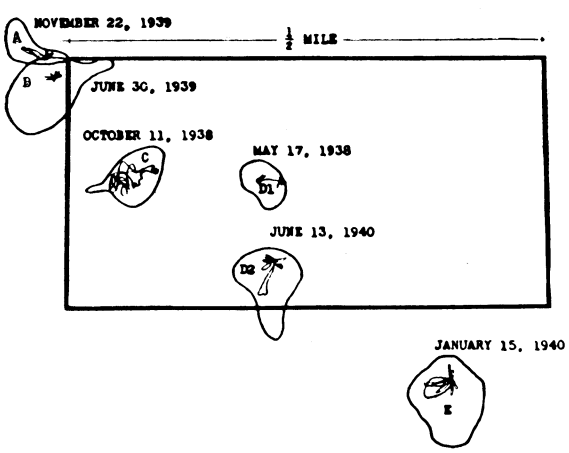

Figure 19.—Diagram showing extent of daily movement in relation to entire foraging range of several different squirrels. Records for A extended from November 22, 1939 to March 3, 1940; for B from June 6, 1939 to January 1, 1941; for C from September 13, 1938 to February 4, 1940; for D1 from May 4, 1938 to November 9, 1938, for D2, the same squirrel as preceding, after it had moved, from December 16, 1938 to August 12, 1940; for E from December 12, 1939 to August 19, 1940. Ranges of all but E shown in relation to 80 acre trapping area.

recorded. But the squirrels proved to be sufficiently localized so that their movements could generally be followed. A peripheral strip about 100 yards wide was trapped from time to time, recording many of the animals that had shifted across the borders of the study area itself.

The extent of movement recorded for any one squirrel was of course determined partly by the frequency with which it was captured, and the length of time over which the records extended. One thousand and forty-three squirrels had records extending over periods of months as follows: 1 to 2 months—10.71%; 2 to 3 months—8.72%; 3 to 4 months—5.56%; 4 to 5 months—5.94%; 5 to 6 months—4.41%; 6 to 7 months—4.79%; 7 to 8 months—4.79%; 8 to 9 months—5.93%; 9 to 10 months—4.79%; 10 to 11 months—5.66%; 11 to 12 months—5.26%; 12 to 15 months—7.35%; 15 to 18 months—5.26%; 18 to 21 months—6.71%; 21 to 24 months—5.84%; 24 to 36 months—5.66%; 36 to 48 months—1.82%.

TABLE 12.—Movements of 1043 ground squirrels, according to distance and sex.

Distance in feet	Percentage of total squirrels	Female-male percentage in sample
Less than 100	8.94	65.9 to 34.1
100 to 200	16.27	53.8 to 46.2
200 to 300	16.56	56.9 to 43.1
300 to 400	14.18	57.0 to 43.0
400 to 500	12.08	44.9 to 55.1
500 to 600	8.57	40.0 to 60.0
600 to 700	5.23	40.9 to 59.1
700 to 800	3.61	39.5 to 60.5
800 to 900	4.38	26.1 to 73.9
900 to 1000	2.28	29.2 to 70.8
1000 to 2000	7.04	21.7 to 88.3
More than 2000	.86	none to 100.0

For nearly half, the distances recorded were between 100 and 400 feet, within the probable foraging radii of the animals, and so may have involved no actual shift in headquarters. For distances over 400 feet the numbers taper off, and it is evident that the longer movements occur comparatively seldom.

Females are distinctly more sedentary than males. Among those squirrels with recorded distances of less than 400 feet, females comprised the majority, while among those making the longest movements males predominated. Young squirrels in their first year move about more than do adults. The maximum distance that each young male was trapped from its original home burrow tended to increase gradually from month to month. For 30 recaptured at intervals of 6 to 10 months the average distance moved was 971 feet, and 93.4 per cent had moved more than 300 feet. In contrast, in a group of 89 young females recaptured after 4 to 10 months the average distance moved was 177 feet, and only 12.4 per cent had moved more than 300 feet. Movements of more than 300 or 400 feet are apt to represent shifts to home ranges entire-

TABLE 13.—Average monthly movements of 826 ground squirrels.

	Adult Males		*Adult Females*		*Young Males*		*Young Females*	
	Number of movements	Average movement in feet	Number of movements	Average movement in feet	Number of movements	Average movement in feet	Number of movements	Average movement in feet
March to April, or April to May	81	187	70	105	10	268	19	109
May to June, or June to July	47	169	36	105	96	287	63	260
July to August, or August to September	30	178	26	177	106	359	70	254
September to October, or October to November	31	189	17	128	78	263	46	162

ly distinct from those originally used. From these figures and from general observations, it appears that young females have comparatively slight tendency to wander from their original home ranges, and that young males have a tendency to disperse by gradual stages, so that by the following breeding season nearly all of them have shifted to new home ranges. Often several different ranges are occupied at different times over periods of months. Movement was sufficiently extensive so that a large proportion of the young males marked on the trapping area would have moved away from it and others would have replaced them by the following year.

Squirrels were poisoned annually in early summer on the area of the Range headquarters, and for the remainder of the year few were present. But in late May, June, and July there was influx of half-grown young which occupied rock outcrops, board piles and sheds and were much in evidence until removed. For the population as a whole, shifts are more frequent in summer and fall, when limited food supply and moisture provide motivation for wandering. In winter and early spring, abundant green foliage is always available.

BURROWS

Numbers and arrangement of burrows.—Much of the squirrels' time is spent underground, and burrow systems excavated are extensive. Permanently occupied burrows usually have from ten to fifty separate holes within an area perhaps fifty feet square. Only the centrally located ones are interconnected underground; peripheral holes usually end blindly or connect with only one or two others. The larger burrow systems are nearly always situated about rock outcrops, and tunnel beneath the rocks. Digging predators such as badgers or coyotes and erosion during heavy storms, enlarge many burrow entrances to a foot or more in diameter. Nest cavities are situated within the central interconnecting maze of tunnels. Surface runways radiate from the most used burrow entrances to feeding places. At intervals along these runways are isolated holes which serve in emergency when a squirrel is taken by surprise at a distance from its home burrow. Such isolated holes have tunnels usually only two or three feet long, ending blindly with no terminal enlargement, but outwardly they have the appearance of being well used. During the course of its daily foraging a squirrel tends to loiter in the vicinity of such escape burrows, clearing out the entrances, and digging and wallowing in the mounds of earth in front of them. When the young have dispersed, many dig new small burrow systems of their own. These are apt to be situated where conditions are not favorable at all seasons, and are deserted later, but the main, well-established burrow systems are constantly in use, being occupied by successive generations of squirrels. The actual nests are usually at depths of two feet or more, in globular chambers a foot or more in diameter, and completely filled with stems and roots of fine dry grass. One, which probably belonged to an adult female squirrel, was 14 inches in horizontal diameter and 8 inches in vertical diameter, and its roof was 16 inches beneath the soil surface.

In one burrow system, probably fairly typical, there were 20 open holes of which only 8 were interconnected. The other 12 ended blindly at distances

Figure 20.—Tearing out mouthful of dry grass for nesting material.

Figure 21.—Old male squirrel carrying dry grass back to nest.

varying from 14 inches to twelve feet. Six were simple, others had one, two or three side branches. Summer nests in hollow oak trunks, usually are situated where they can be easily approached from the ground by way of horizontal limbs. In tree nests the squirrels are safe from certain natural enemies, notably rattlesnakes and badgers, and may be freer from fleas than are those which live in burrows.

In the 80 acre trapping area in March 1940, there were 3485 open holes 2786 of which were units of large, permanently occupied colonial burrow systems. The remaining 699 were outlying burrows, some separate and isolated, others in clusters of several within a few square yards, but probably not connected underground. There were 144 extensive burrow systems with an average of 19.4 holes per system. There were, on the average, 17.2 open holes and .71 burrow systems to each squirrel. Holes averaged 43.6 to the acre. Though tending to be concentrated on certain parts of the area, the holes were so distributed that it probably would have been impossible to find an area as large as an acre on which there was none.

In March 1946, all large burrow systems, and even many of the outlying escape burrows were the same ones present in 1940, but the total number of holes had undergone reduction, to 3265, with 40.8 per acre and 20.0 per squirrel. The burrow system most extensive in 1940 had 93 separate entrances. These were scattered over an area of more than 100 feet in longest diameter, and probably the majority of them were not interconnected underground. This large burrow system was situated on an open, east-facing slope at a distance from any extensive rock outcrops, though there was one centrally situated large sunken boulder. Thirteen squirrels (9 males and 4 females) lived in the vicinity. Six years later in March 1946 this same burrow system was even more extensive, having 121 open holes, but only five squirrels (2 males and three females) were known to stay in the vicinity.

The varying number of animals at such a burrow system, not closely correlated with the population density of larger areas, nor with the number of holes, rather, reflects concentration by short shifts in response to location of food sources, which vary greatly in relative abundance from year to year. In years when the crop of blue oak acorns is heavy, burrow systems located at or near productive trees are enlarged and extensively occupied, but in other years when this crop fails, the same burrow systems may fall into disuse as the animals transfer to quarters from which live-oak acorns or other foods are accessible.

Burrow associates.—A long list of terrestrial animals inhabiting the range occasionally or habitually use ground squirrel burrows for shelter. In the severe summer climate of this region many animals retreat underground to depths where moderate temperatures prevail; squirrel burrows are the most common and convenient retreats, and nearly all digging mammals of the region take advantage of them to some extent. Predators, including the coyote, badger, striped skunk and possibly the gray fox sometimes use enlarged squirrel burrows for their dens. Cottontails depend partly on squirrel burrows for shelter

and in spring when the soil is soft and easily dug, often enlarge them to a convenient size. Pocket gophers, though not at all dependent upon squirrel burrows, often dig around and through the mounds where the fertile soil may promote growth of favorite food plants. Commonly, squirrel burrow entrances are seen plugged with fresh gopher mounds, and the tunnels of the gophers often join those of squirrels. The more spacious and deep squirrel burrows when disused may be favorite locations for the nest chambers of the gophers. Kangaroo rats commonly use squirrel burrow entrances and being relatively weak diggers, take advantage of the deep and extensive excavations and merely dig their own side passages well inside them. The large burrow entrances of the squirrels are advantageous in allowing the rats to enter at high speed in times of emergency. The white-footed mouse has habitat preferences similar to the ground squirrel on the Range, and often seems to depend on squirrel burrows for shelter. Pocket mice, rock mice, and brush mice use squirrel burrows only occasionally. Woodrats occasionally take over old squirrel burrows when these are situated at bases of rock outcrops or bushes.

The burrowing owl in this region depends on squirrel burrows for its homes and was the only bird seen to use them. It is rare on the Range but common a few miles farther west in the treeless belt of the lower foothills.

Most of the local reptile species utilize squirrel burrows. The presence of these holes in sufficient numbers to provide ample shelter may be one of the critical factors which determine rattlesnake abundance. While occupancy of squirrel burrows by most of the animals heretofore mentioned has little evident effect on the squirrels, and constitutes one-sided relationships of more or less incidental significance in squirrel ecology, presence of rattlesnakes in the burrows is a matter of vital concern to the rightful owners. Gopher snakes also prefer the shelter of squirrel burrows underground. On many occasions recently killed young gopher snakes, badly mangled and lacerated, have been found on squirrel burrow mounds, where evidently they had been dropped by squirrels after being fatally bitten in underground encounters. Squirrels finding small snakes in the open have been seen to approach menacingly, as if about to attack, while scolding them. To test this reaction further a small gopher snake was placed in a cage with a tame adult female squirrel. The squirrel, with hair fluffed out, moved around it with slow, tense steps. As the snake started to crawl away, she closed in and bit it sharply on the tail, but bounded back as the snake drew up on the defensive. When the snake started away again, she closed in for another quick bite, which was delivered on the posterior part of the body, seriously injuring the snake, and causing it to coil, writhing and thrashing. The squirrel grew bolder, and moved up watching for an opening, then seized the snake's body in her forepaws, severed its spinal cord with a quick bite through the back, and again dropped it. This was repeated time after time and each successive bite was placed farther up on the snake's body toward its head, until the reptile was almost entirely immobilized and helpless, then the squirrel picked it up in her forepaws and bit it through the head and neck. After being thoroughly mangled the snake was dropped and none of it was eaten by the squirrel. When discarded its injuries resembled those of snakes found dead on burrow mounds, which almost certainly had been killed

in similar encounters. Of the snakes found killed in this way all but one were less than 18 inches in length, and half-grown or adult ones would be fully able to cope with the squirrels. On a few occasions large lizards, skinks and whiptails, were also found dead and similarly bitten on the burrow mounds. The king snake and the striped racer use the burrows but probably do not molest the squirrels under ordinary circumstances. The whiptail and brown-shouldered lizard characteristically rely on squirrel burrows for shelter.

Several amphibian species, the tree-toad, spadefoot toad, California toad, and tiger salamander are dependent largely on rodent burrows including those of squirrels for protection from desiccation during the dry season.

Of invertebrates, tarantulas (*Eurypelma*), Jerusalem crickets (*Stenopelmatus*), large beetles (*Eleodes*) and many smaller kinds habitually resort to the squirrel burrows, but nothing has been learned of their relationship to the squirrels themselves.

EARLY DEVELOPMENT

At birth the young are remarkably small in proportion to the adults. During the period March 5-15, 1940, six litters were born in captivity by

Figure 22.—Scolding a small gopher snake on a burrow mound.

females live-trapped a few days before. In each of four of these litters there were seven young; another litter had eight and still another had six. This whole lot of young averaged 8.9 grams at birth. For the different litters average weights in grams of newborn young were as follows: 8.9, 7.6, 7.2, 11.7, 9.8, 8.5. The newborn young were foetus-like in appearance, had disproportionately large heads, with eyelids and ear openings sealed (figure 23). The skin was loose and wrinkled, pale flesh color, and semi-transparent, so that the pigmented eyeball, and some of the visceral organs could be faintly seen through it. These young were naked except for downy vibrissae and minute hairs on the chin. In one that was measured, the tail was about 20 mm., hind foot 8 mm., ear 1½ mm. These newborn young were capable of slow, writhing movements. Remarkable powers of resistance in the young were shown when the mother of a day-old litter escaped from the cage. Two days later several of the deserted young still survived although they had crawled out of the nest and had ben exposed and chilled. Young one week old (figure 24) had increased in weight by 66 per cent. Though still feeble and helpless they were noticeably larger and stronger than at birth and were better able to crawl about. The dorsal surface of the heads, bodies and tails were partly suffused with dark pigment, but the ventral surfaces were still pale flesh color. Fine, dark hair was beginning to appear on the dorsal surfaces. The mystacial, genial,

Figure 23.—Litter of newborn squirrels, blind, naked, and helpless.

and supraciliary vibrissae had become prominent, and the longest were about 4 mm. in length.

At the age of two weeks the young on the average had increased to 268 per cent of their weight at birth. They were beginning to take on a squirrel-like appearance, and had a covering of fine dark colored fuzzy hair dorsally. The vibrissae were about 6 mm. in length. At 18 days they had more than tripled in weight. The vibrissae had grown to about 12 mm.; the hair on the head was beginning to show the characteristic variegated pattern, and fine hair was noticeable on the ventral surface.

At 4 weeks weight had increased to five times that at birth and measurements were as follows: total length—148 mm., tail—50 mm., hind foot—25½ mm., ear—10 mm., longest vibrissa—17 mm., hair on body—4 mm. The tails were becoming fluffy, with hairs about 4 mm. in length. At 32 days some of the young had their eyes partly open. The measurements were: total length—177 mm., tail—53 mm., hind foot—29½ mm., ear—11½ mm., longest vibrissa—20 mm. At 34 days all had their eyes open. At 43 days the squirrels had increased in weight more than seven-fold, and their measurements were as follows: tail—61 mm., hind foot—33 mm., ear—15 mm., vibrissa—27 mm., hairs on tail—16 mm.

Throughout the period of suckling in the litter of young kept, the mother was in good condition, and was little disturbed by the handling and observing of the young. She was fed on the same kind of green vegetation which made up most of the natural food of squirrels in the wild during the same period. It is probable that the suckling young made approximately normal growth up to the time of weaning.

Figure 24.—Litter of squirrels one week old; still foetus-like but much larger and stronger than at birth, with hair beginning to appear.

At 55 days the young were alert and active, able to run about, and were about the minimum size of young commonly seen above ground (figure 26). They had recently acquired short molariform teeth and were beginning to feed on succulent green material, supplementing the milk diet. They attempted to bite when handled. A few days later this litter was separated from the mother, and subsequently failed to make normal growth, though some survived to an age of several months. Development after the beginning of active life above ground is best studied from records of young live-trapped in the field on successive occasions, though these records are not very complete for any one animal.

Young squirrels at the time of their first appearance above ground usually weighed somewhat more than 100 grams. But age and degree of development at the time of first emergence vary. The smallest young found above ground weighed about 70 grams. Such individuals obviously had emerged prematurely and were as yet inadequately prepared to cope with the dangers of life in the open; their gait in running was slow and unsteady, and they were easily caught by hand except when burrows were immediately available to them as shelter. None of these unusually small squirrels was known to have survived. Other young are much farther developed at the time of first emergence. In the spring of 1940 on the 80-acre trapping area, after the first appearance of a litter the area was carefully examined with binoculars almost daily for other newly emerging litters. It was found that usually several members of a litter emerge about the same time, and usually a group may be seen gathered within radius of a few feet, near burrow entrances. Some of these young were remarkably large when they first appeared, and many weighed over 200 grams

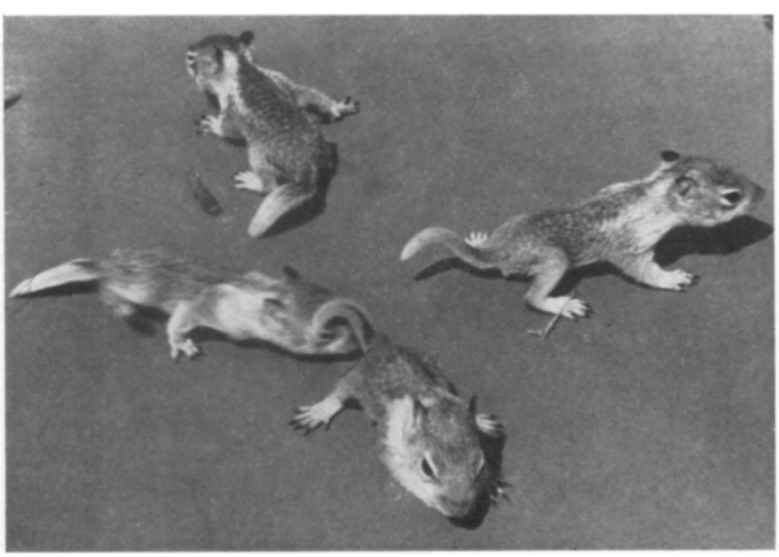

Figure 25.—Squirrels 36 days old; now able to crawl about actively, but not sufficiently developed to come above ground.

when trapped within a few days after emergence. Among the factors which may hasten or delay emergence, the weather is most important, but inadequate supply of milk by the mother, or heavy infestations by fleas and other ectoparasites in the nest might conceivably hasten the departure of the young squirrels.

At first the young tend to stay within a few feet of holes of the home burrow system and confine their activities to the area within which the holes are distributed. They are playful and curious, chasing each other, and frisking about, or sitting at attention intently observing objects in the vicinity. At this stage of their development the young are on the average considerably less wary than adults. They are already capable of giving the stereotyped reactions of adults to various stimuli. At first sight of a snake or a hawk, for instance, the young will give the characteristic "snake warning" or the "hawk warning" appropriate to the occasion. The mother of a litter often may be seen with or near the group and it is probable that her reactions to various visual and auditory stimuli influence their subsequent behavior. Young put on the aleart by the mother's alarm note were wilder on subsequent occasions, and through the behavior of the mother evidently had learned to recognize potential danger in the presence of humans. The young are able to feed upon succulent vegetation from the time of their first appearance above ground. At this season foods of nutritious kinds are abundant and adults are gaining weight rapidly. From the start the young seem to take the same kinds of vegetation as do the adults and no different preferences have been noted. Seeds of popcorn flower and

Figure 26.—Squirrel 54 days old, about the size of those first emerging from parental burrows, and sufficiently developed to shift for itself above ground. Has increased in weight ten-fold since birth, but still weighs only one-fifth as much as an adult.

filaree are preferred foods at this season, and the young appear to be as dexterous as the adults in handling them. Suckling must continue for at least a week or so after the young begin to take plant food, but gradually they become more independent, wander farther from the home burrow in their foraging, and are no longer seen clustered in groups, although several may dash for the same burrow from different directions when danger threatens.

By the time the young have attained a weight of 300 grams they are fully independent and may have left the home burrow to settle down in some new location.

POPULATION

Density and composition.—Among the objectives of the present study were determining how many squirrels were present on selected areas, following their population changes at different seasons, and their trend over periods of years, and the finding of means to estimate population density of extensive areas. The extent of squirrel damage on any area is more or less proportional to the population density, which changes continually, both seasonally, and from year to year, subject to the interaction of innumerable environmental factors.

Live-trapping and marking of squirrels on the 80 acre area provided as a basis of comparison with other areas, an approximately known population density. In late winter and spring, the time of maximum activity, binocular counts were made which tended to verify the trapping records but this counting was time consuming and hardly practical where terrain was irregular. Each year in 1939, 1940, 1941, and 1942, virtually every squirrel of the adult population was trapped during late winter and spring, as shown by the fact that scarcely any new unmarked ones were caught in the latter part of the breeding season. The numbers caught reveal approximately the actual breeding population. In 1946 the area was less intensively trapped, and 221 were recorded but some still remained uncaught. The proportion of those remaining uncaught may be estimated from the ratio of new ones to others in the last two weeks of spring trapping. The actual breeding populations recorded on the area in 1939 to 1942, and the estimated population for 1946 were:

1939	251	(114 males, 137 females)
1940	304	(132 males, 172 females)
1941	296	(124 males, 172 females)
1942	283	(139 males, 144 females)
1946	245	(109 males, 136 females)

These figures, of course, do not provide a direct indication of the population density, because the factor of individual movement remains to be considered. From the ranging of those individuals intensively observed, and the trends of movement records in marked squirrels recaptured, it appears that home ranges of about 400 feet diameter may be most typical. The squirrels trapped on the study area represent not only the 80 acres within its boundaries, but also a peripheral strip of probably half a "home range" in width. If the figure of 400 feet is accepted as the typical home range diameter, then

the peripheral strip to be included would be 200 feet wide, and would amount to approximately 40 acres. The squirrels trapped on the 80 acres, accordingly, would represent the population of 120 acres. The five year average of the breeding population—275.8 squirrels—thus represents a population density of 2.3 per acre.

In view of the rapid rate of population replacement from year to year, this population was fairly stable, more so than the forage crop which provided its food. During the period of the study no sudden or extensive reduction by disease occurred, and the population showed no marked fluctuations, except in its annual cycle with the sudden appearance and subsequent gradual elimination of each year's crop of young. Nevertheless, casual observers of the local squirrel population were often heard to remark at different times during the course of the study that squirrels were "way up" or "way down." Impressions are apt to be deceptive, and especially so unless the seasonal factors of dormancy, change in foraging habits according to temperature and food supply, and the sudden rapid increment of the population by the annual crop of young, and subsequent reduction are all taken into account.

Many of the factors which tend to reduce squirrel populations act much more drastically upon the small young than upon the adults. Most of the young squirrels trapped were already at least half-grown and had survived the stages of highest mortality. But even these half-grown young were eliminated more rapidly than the adults. The actual number of young trapped each year and the percentage remaining on the area and surviving to become breeding adults were as follows:

	Number trapped	Percentage surviving to following year
1939	321	36.1
1940	339	51.6
1941	329	44.6

For the three years females comprised 45.6% of the remaining survivors that attained maturity and 40.9% of all the females survived, whereas only 31.1% of all young males survived, to be caught as breeding adults. The difference is evidently due to extensive movement of young males off the area rather than actual mortality.

The relatively low rate of survival in 1939 is clearly a result of the scarcity of food during the dry season of that year, when conditions were critical, and young squirrels made hardly any growth. The high survival in 1940 is likewise correlated with abundant food sources that year. The numbers trapped are not at all indicative of relative sizes of the successive annual crops, since fewer traps were available in the spring of 1939. Actually, young squirrels appeared to be far more abundant that year. Of adult squirrels comprising the breeding population, each year slightly less than half usually are young born the preceding year; the majority are survivors two or more years of age. The percentage of these old survivors in different years were as follows:

	Percentage of old survivors among breeding males	Percentage of old survivors among breeding females
1940	56.9	58.1
1941	45.4	48.3
1942	40.2	54.7

The 1942 population was mostly assignable to known age groups, since records had then been kept for a period of more than three years. The percentages comprised by each age group of each sex were as shown in Table 14.

TABLE 14.—Percentages of survivors from 1938, 1939, 1940, and 1941 in the 1942 ground squirrel population.

	Percentage of 1942 breeding females	Percentage of 1942 breeding males
Young of 1938, or earlier years	11.5	5.0
Young of 1939	16.5	4.3
Young of 1940	25.2	31.0
Young of 1941	46.8	59.7
Total	100.0	100.0

In each instance the "young of 1938 or earlier years" probably included some survivors from 1937, and possibly even from 1936, but these could not be definitely allocated as to age group because they were all marked after the 1938 young had attained adult size.

Of the 221 adult squirrels trapped on the area in the spring of 1946, eleven, or approximately five per cent, were marked survivors of the pre-war study. Of these, five were 1942 young (relatively few young, only 75 were marked that year), five were of the 1941 crop, and one was a survivor from 1940, hence was six years old. It is likely that there were other survivors which escaped capture because they had shifted across the boundaries of the area. Evans and Holdenreid discuss longevity on the basis of their three years study; they state that the life expectancy of these squirrels is more than two years, and quote Grinnell and Dixon, 1918, in stating that "the lifetime of a squirrel, if it dies of old age, has been estimated as five years." In the present study, the single six-year-old squirrel captured showed no signs of senility and appeared to be in excellent condition, except for blindness in one eye, an injury sustained during its first year. Therefore, the potential longevity is at least six years, and probably longer.

At times of year other than the breeding season, the factor of dormancy, differing in sex and age groups, obscures the true composition of the population. From the latter part of January through February, March, April, and most or all of May, the whole population (except for small young in the nests) is active above ground daily. It is then evident that females outnumber males. For the five years of trapping at this season males comprised from 41.9

to 49.1 per cent of the adult population trapped, and averaged 44.9 per cent. Later, through the summer and fall, all adults become scarcer, and of those remaining the males are considerably more numerous than females, more of the latter having entered dormancy. In the following table, percentage of adult males to the total adult population trapped is shown for each month of three different years. Deviations from the trends are due in part to unrepresentative or too small samples. The same months in successive years are not always strictly comparable, for instance the 1939 season was several weeks ahead of 1940 and 1941 in plant growth, and drying out of the forage crop, and changes in the squirrel population were correspondingly early that year.

During the same three years, relative numbers of adults and young among squirrels trapped showed even greater irregularity from month to month and differences between years, subject to the size of the annual crop of young, and the extent of dormancy in the adult population.

The relatively low percentages of adults in the fall months of 1941 indicate more extensive dormancy that year. In 1939 there was much less dormancy and evidently it began earlier in correlation with the early maturing and drying out of the forage.

The disappearance from the area of any squirrel might be due either to its death or to its movement elsewhere. Because of the poorly known factor of emigration from the trapping area, mortality there could not be measured accurately. On the basis of measured movements, deaths were known to be more important than shifts elsewhere, in the disappearance of a large part of the population in the course of a year. Survival on the area, until the following year, of squirrels trapped occurred in the following percentages of different sex and age groups caught in 1940 and 1941.

All adults	(597)	36.0%
All young	(662)	48.2%
Old males	(253)	26.9%
Old females	(344)	42.7%
Young adult males	(414)	41.0%
Young adult females	(248)	60.0%

Most of the young were caught in summer or fall when already well-grown, while the adults were caught mainly in the breeding season before young appeared. The apparently higher percentages of survival in the young are due to the relative shortness of the period involved. Females of both young and adults are shown to have a higher survival expectancy than males, hence the preponderance of females during the breeding season. Greater tendency of the males to make movements away from the area also accounts for part of the difference. Among the adults there was no consistent difference in survival expectancy between one-, two-, and three-year-olds.

Though the total number of squirrels on the trapping area showed only minor changes from year to year, the number occupying any one small area or burrow warren changed a great deal. Thirty-eight subdivisions of various sizes, of the 80 acres showed the following numbers in different years of trapping during the breeding season (numbers incomplete for 1946):

TABLE 15.—Proportion of males in monthly samples of adult ground squirrel population trapped.

	1939		1940		1941		Three-year Average
	Number of Adults	Percentage of males	Number of Adults	Percentage of males	Number of Adults	Percentage of males	Percentage of males
January	43	39.5	140	42.9	164	31.7	38.0
February	66	36.4	218	42.1	164	39.7	39.4
March	69	36.2	155	44.0	163	39.3	39.8
April	49	59.0	102	48.0	69	43.0	50.0
May	51	37.0	103	53.0	110	45.0	47.6
June	36	47.0	61	44.0	77	31.0	40.7
July	15	53.0	49	51.0	32	53.0	52.3
August	43	67.0	37	46.0	14	64.0	59.0
September	48	65.0	45	60.0	6	100.0	75.0
October	43	70.0	57	63.0	12	75.0	69.3
November	48	52.0	52	63.0	18	61.0	58.6
December	49	49.0	58	55.0	9	100.0	68.0

TABLE 16.—Proportion of adults in monthly samples of ground squirrels trapped.

	1939		1940		1941		Three-year Average
	Total Catch	Percentage of Adults	Total Catch	Percentage of Adults	Total Catch	Percentage of Adults	Percentage of Adults
May	136	37.8	214	48.1	205	53.7	46.5
June	125	28.8	203	30.0	194	39.7	32.8
July	92	16.5	163	30.1	210	15.2	20.6
August	134	32.0	151	24.5	158	8.9	21.8
September	151	31.8	182	24.6	131	4.6	20.3
October	125	34.4	195	29.3	152	7.9	23.8
November	116	41.4	168	31.0	139	12.9	28.4
December	108	45.3	164	35.4	95	9.5	30.1

TABLE 17.—Yearly variation in ground squirrel numbers on small areas.

	1939		1940		1941		1942		1946	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Area 1	6	5	6	8	5	7	5	7	6	6
Area 2	7	10	6	10	6	7	3	7	5	9
Area 3	1	1	2	4	5	5	6	2	2	1
Area 4	4	2	2	6	3	3	4	2	4	4
Area 5	1	3	1	0	2	3	5	3	0	5
Area 6	1	2	2	5	1	2	0	2	1	2
Area 7	0	2	3	3	1	4	0	3	4	6
Area 8	2	1	2	2	2	5	1	3	2	4
Area 9	1	1	0	2	0	1	2	0	2	3
Area 10	4	7	3	3	5	3	2	3	3	5
Area 11	4	4	5	8	5	9	4	13	1	4
Area 12	5	6	10	6	8	10	6	8	1	4
Area 13	2	5	8	6	4	13	9	5	6	7
Area 14	3	3	2	3	2	1	2	1	6	3
Area 15	6	5	3	9	12	11	7	8	4	9
Area 16	0	1	3	5	1	2	1	3	2	1
Area 17	6	3	5	3	3	7	8	6	5	6
Area 18	2	7	6	7	3	2	4	2	0	3
Area 19	2	5	3	8	2	5	3	1	6	6
Area 20	3	3	5	3	3	3	6	2	4	4
Area 21	3	3	1	1	2	3	3	2	3	1
Area 22	1	1	9	4	4	5	1	7	2	3
Area 23	3	1	5	5	5	4	3	2	1	2
Area 24	2	3	4	6	2	6	8	2	3	2
Area 25	1	2					3	0	3	3
Area 26	5	6	3	3	2	3	7	3	1	1
Area 27	2	1	2	4	4	3	1	0	0	0
Area 28	0	0	1	1	2	2	4	1	0	0
Area 29	8	9	8	10	5	14	8	8	6	4
Area 30	0	0	1	5	2	3	0	2	1	2
Area 31	2	4	0	0	1	0	2	2	0	1
Area 32	5	5	4	2	0	2	2	2	0	0
Area 33	2	4	4	4	1	2	1	1	2	1
Area 34	1	2	1	5	1	4	2	3	6	3
Area 35	0	0	0	2	1	1	2	2	0	0
Area 36	3	8	3	8	8	7	4	4	3	2
Area 37	3	5	2	3	3	1	3	5	4	4
Area 38	0	0	1	0	0	0	1	0	0	0

Over the Range as a whole, squirrel populations were found to be very unevenly distributed, in correlation with abundance and variety of food supply, and presence of adequate shelter. Greatest concentrations were along the larger swales, especially where there were nearby oak trees, and rock outcrops, providing a combination of good feeding grounds and protected burrow sites. Open oak woods with numerous rock piles or outcrops also provided favorable habitat. Dry, steep slopes, canyon walls, and extensive stretches of thick chaparral, or of open grassland with shallow soil, are habitats little used by the squirrels. Degree of utilization of the forage crop by cattle appeared to be unimportant as a factor determining the abundance and distribution of the squirrel population. The "Natural Area" protected from grazing over a period

of years had one of the lowest population densities of the entire Range, but part of it was poisoned annually, and the remainder was brushy. Very close grazing, by sheep for instance, might be expected to bring about a reduction of squirrels by reducing the quantity and variety of their food supply. But the "close" and "moderate to close" utilization of the more heavily grazed pastures (1 and 3) apparently favored their abundance, as these areas were the most densely populated. Increase of filaree and other broad-leafed herbs at the expense of grass species, which occurs under heavy grazing, would favor the increase of squirrels. Favorable distribution of oak trees, rocks, soil and slope, have probably been more important factors in affecting the squirrel populations.

For several pastures of the Range where counts of adults were made in the winter and spring of 1939 and 1940, and again in early 1946, the averages shown in Table 18 were obtained.

TABLE 18.—Ground squirrel numbers on different pastures of the San Joaquin Experimental Range.

Area	1939-1940		1946	
	Number of squirrels	Squirrels per acre	Number of squirrels	Squirrels per acre
80 acre study area and 40 acre border	278	2.3	245	2.0
Pasture 2	406	1.8	243	1.1
Pasture 3	365	2.4	98	.6
Pasture 4	364	.6	107	.4
Pasture 5	294	1.2	82	.3
Pasture 6	469	1.5	103	.3
Pasture 8N	147	1.6	39	.4
Pasture 8S	137	1.4	49	.5
Pasture 9N	85	.9	26	.3
Pasture 9S	87	.9	16	.2
Pasture 10N	115	1.3	19	.2
Pasture 10S	164	1.8	45	.5
Total	2911 (1.51 per acre)		1072 (.55 per acre)	

The number of squirrels for each pasture was calculated from the average per minute recorded in strip counts made by walking across the areas, and compared with the average per minute recorded on the 80 acre study area, where the number was known from live-trapping. The 1946 figures are based on much fewer counts than those of 1939-1940. But the indication that population density in many pastures had undergone sharp reduction was borne out by general impression in driving through them. In the absence of observations throughout most of this interval, there seems no plausible reason why the population of a large portion of the Range should have been reduced to about 37 per cent of its 1939-40 density, and why during the same period, the trapping area underwent only slight reduction.

The annual peak in numbers of squirrels comes in late February and March when most or all of the females have given birth to litters averaging seven, presumably almost quintupling the population. No definite instances of non-breeding females were recorded. The average population of just over 1½ per acre as estimated for the Range in 1939 and 1940, would be increased to nearly 7½ per acre. Many of the small young must perish before they are old enough to come above ground. Evans and Holdenreid (1943) suggest that still-births may be an important factor. On several occasions remains of young too small to leave their nests were found on burrow mounds dead and partially eaten, perhaps by adult squirrels. Unfavorable weather and disease may be important causes of early mortality, but with the data now available it is impossible even to estimate the proportion of young which die before they are old enough to come above ground.

The most vulnerable stage in the squirrel life cycle is probably the period after first emergence from the nest burrow. General emergence of young takes place within a period of a few weeks. They usually first appear at many different burrows on the same day, and for weeks thereafter the numbers steadily increase. These inexperienced young are easy prey for predatory birds and mammals, of which the food requirements are much increased at that season due to the fact that they are providing food for their young as well as for themselves. The proportion comprised by squirrels in the diet of several predator species increases sharply at the time the young squirrels emerge.

Effects of predation.—The red-tailed hawk is by far the most important raptor species in its effect on ground squirrels in this locality. In a study of red-tailed hawks on the Experimental Range (Fitch, Swenson and Tillotson, 1946) it was found that the ground squirrel was the favorite food species; of 4036 pellet prey occurrences 1049 were squirrel and of 625 nest prey items 380 were squirrel. It was calculated that ground squirrels comprised over 50 per cent by weight of the year round diet, and that a pair of hawks in their 320 acre territory would annually eliminate about 144 squirrels, or .45 per acre. As virtually the whole Range falls within the territories of paired adult hawks, and there is an additional but variable population of wandering adults and unpaired young, the figure is thought to be conservative. It amounts to only 7.7 per cent of the annual increase calculated for the 1939-40 population.

In this particular region, the rattlesnake is the most important of all ground squirrel predators. Attempt was made to determine numbers of rattlesnakes by marking and releasing many of those found; 679 were released and 156 of these were recaptured a total of 203 times. From the ratio of marked snakes recaptured to others on a 160 acre sample area, making due allowance for movement, it appeared that the population density was slightly more than one rattlesnake per acre.

Among 19 prey species identified from scat and stomach examinations of rattlesnakes, ground squirrels were by far the most freqently represented, and comprised 116 of the 285 items. While mice and lizards made up most of the food of the smaller snakes, ground squirrels and occasional young rabbits

comprised nearly all the food of the large ones. On the basis of weight, ground squirrels were computed to be 68.8 per cent of the total food taken.

Frequency of feeding in rattlesnakes is not well known. Storer and Wilson (1932:169-173) present figures on the food consumption of three in confinement, for a combined total of 7 years of feeding. These snakes took a total of 65 rats and mice, average 9.29 per snake per season, with an average weight of 99.5 grams per meal. Only one snake weight is given and this individual consumed an annual average food weight 2.63 times its own original body weight, but no record of its growth is given. At the Experimental Range, three adults taken soon after their emergence from hibernation in 1946 were kept confined in an outdoor concrete pit for a year, and were fed mainly on pocket gophers and kangaroo rats. Food was weighed before being offered and weight of each snake was also recorded at the beginning and end of the season, and several times between. Attempt was made to simulate natural conditions in the pit, which was provided with an insulated box where the snakes took refuge at times when temperature was high. The experiment was not entirely satisfactory, as one snake was known to have fed before it was captured in the spring, and neither of the two females produced young. The data obtained seem to indicate that an adult rattlesnake requires a prey weight of at least twice its own body weight to maintain itself in good condition throughout the growing season. The average weight of a large series collected in spring was about 200 grams; their average food requirement thus might be around 400 grams apiece or 440 grams per acre with the population density indicated for this place. If the diet consists of 68.8 per cent squirrel, as indicated by the sample

Figure 27.—Remains of squirrel partly eaten by Red-tailed Hawk.

obtained, then it might be concluded that rattlesnake predation annually eliminates about one or two young squirrels per acre.

However, during the dry season, mid-June to October, hardly any rattlesnake feeding records were obtained. Practically all the records of predation on ground squirrels were in spring and pertained to small young squirrels. Presumably the snakes continue to feed throughout the summer, but by midsummer most young squirrels have grown so that they would be too large for all but the largest rattlesnakes to swallow. In the second half of the growing season predation on ground squirrels must be much reduced.

On the other hand field observations have shown that frequently squirrels are bitten and killed but not eaten by the rattlesnakes. The young as well as the adult snakes occupy squirrel burrows and are always ready to strike any squirrel which comes within reach, and even the smallest rattlesnakes have enough venom to kill adult squirrels. Sudden close-quarter encounters with rattlesnakes lying in the burrows must often occur. In such underground encounters, squirrels must be at a tremendous disadvantage in detecting and avoiding snakes in the dark. It was often noticed that squirrels released from live traps at dusk had difficulty finding their way about. In moving through their burrows they must be guided largely by tactile sense, using their elongate vibrissae. Rattlesnakes have eyes adaptable to low light intensities, and are able to detect approach of a rodent by the temperature-sensitive pit, even in complete darkness. Rodents struck by hunting rattlesnakes are ordinarily released, and tracked down after death. In many instances, the victim wanders too far to be found or dies in an inaccessible place. Presumably in such cases the snake continues to prowl until other prey has been obtained.

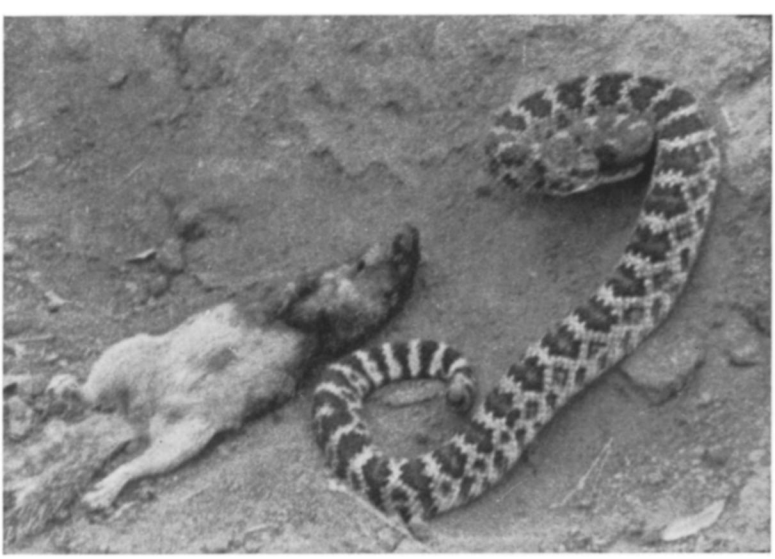

Figure 28.—Rattlesnake and adult squirrel partly swallowed and disgorged by it.

Several mammalian predators, the coyote, gray fox, badger, and bobcat, are all fairly common on the Experimental Range, and each includes a substantial proportion of ground squirrel in its food. Coyotes have been subject to control on the Range since 1936, when 35 were caught in 30 days trapping. Numbers recorded taken other years were as follows: 1937-1938, "about 30"; 1938-1939, "about 30"; 1939-1940, 13; 1940-1941, 13; 1942, 7; 1943, 5; 1944, 8; 1945, 1. Greater numbers were trapped and poisoned on adjoining ranches. In 1173 coyote scats there were 1924 occurrences of vertebrate prey, 254 arthropod occurrences, 30 occurrences of carrion of large mammals, and 42 occurrences of plant food. Many of the arthropods were of kinds found on carrion and were probably taken accidentally, but the Jerusalem cricket occurred 116 times. The ground squirrel was the most frequently occurring of all scat items, with 414 representations. Assuming that each prey occurrence represented one individual animal, and estimating percentage weight of the total food comprised by each kind of prey, on the basis of average weight of each, ground squirrel comprised 31.2 per cent, and was second only to rabbit. As each coyote consumes the equivalent of one large ground squirrel daily, and nearly one-third of this food actually consists of ground squirrel, it appears that a coyote must eliminate approximately 120 ground squirrels in the course of a year. In each of the years 1939-1940 and 1940-1941 when 13 coyotes were removed from the Range, the total population from spring until removal the following winter must have been between 15 and 20 animals. Accepting the lower figure, there might have been, on the 4600 acre area of the whole Range, one coyote to about 300 acres, and coyote predation would have eliminated .4 squirrels per acre annually.

Gray foxes were probably as numerous as coyotes. In June 1938 a fox den with seven half-grown young was located in a deep crevice of a rock outcrop on a brushy slope. Scattered remnants of prey in the vicinity included tufts of rabbit fur, quail feathers, and especially ground squirrel remains, characteristically the tail tip only. In a small collection of fox scats made in 1940, there were 102 vertebrate prey items of which 89 were rodent and rabbit, 10 were birds and 3 were reptile. Plant food, arthropods and birds all made up larger percentages of the fox's food than they comprised in that of the coyote. Ground squirrels were computed to make up 24.3 per cent by weight of the vertebrate prey items taken, excluding from the computations 101 occurrences of arthropods, carrion, and plant food of which the weight could not be accurately estimated though it probably made up only a few per cent of the total.

Nearly every old and large squirrel burrow system had holes with entrances greatly enlarged by badger digging. The fresh diggings were noticed almost daily in winter and spring. Several times ends of squirrel tails, dropped by a badger that had finished its meal, were found on the freshly excavated mounds. Squirrels cornered in shallow, blind-ending escape burrows seemingly would be easy prey for a badger, but those in main burrow systems with many connecting passages could usually escape. Even in burrows around rock outcrops signs of badgers having dug out squirrels have been observed. Some squirrels

may be dug out while dormant, and perhaps others are cornered in blind ending crevices in the rocks. The badger is probably one of the most important squirrel predators locally, but nothing is known of its population density or the actual percentage of squirrels in its food. Bobcats are fairly common locally perhaps outnumbering foxes or coyotes, but they tend to stay in the more brushy and rocky areas where the squirrel population is lowest, and are more apt to hunt rabbits, woodrats, or pocket gophers.

Several other predators are known to take their toll from the squirrel population, but singly or combined they are of only minor importance. The golden eagle, ferruginous rough-legged hawk, prairie falcon, and marsh hawk are all known to hunt on the Range occasionally but the total number of squirrels killed by them must be small. Among 41 prey items recorded in two Cooper hawk nests, only one was a squirrel. Among 1471 vertebrate prey items in horned owl pellets only 13 were squirrel, though predation on them is more severe when the owls are nesting, as in 1939 ground squirrels comprised 11 of 67 prey items from four different nests, and were recorded from three of the four nests (Fitch, 1940). Gopher snakes are less common than rattlesnakes on the Range, and were found in a ratio of one to 3.7, probably a little less than one to three acres. Among 72 gopher snake prey items of 12 kinds, there were 5 ground squirrels, which were calculated to make up 28 per cent of the food weight. If the gopher snake's food requirement is similar to that of the rattlesnake, a prey weight of 400 grams to a snake would be taken, and this would amount to 120 grams per acre. The 28 per cent of this weight comprised by ground squirrel would constitute about one young squirrel to six acres. Among 116 barn owl pellet prey items there were no squirrels, nor are the raccoons, skunks, weasels, opossums, and king snakes that occur in this locality known to prey upon them.

To sum up predation data, the breeding population of about 1.51 squirrels per acre (with more than 55 per cent females) in 1939 and 1940, had a potential annual increase of about 5.8 per acre, of which known predation factors could have accounted for the following numbers:

TABLE 19.—Numbers of ground squirrels eliminated by predators.

Kind of predator	*Number of squirrels per acre annually eliminated*
Rattlesnake	2.00
Red-tailed hawk	.45
Coyote	.4
Gray fox	unknown
Badger	unknown
Gopher snake	.17

Data on the numbers and feeding habits of two important squirrel predators, the badger and gray fox, are insufficient even to estimate the number of ground squirrels destroyed by them. It is fairly certain that neither eliminates more than one per acre annually. Major predation factors, as here crudely

measured or estimated, appear to account for a little more than half the annual increase. Other predators combined (including the horned owl and Cooper hawk) could not be expected to take more than a fraction of one per acre.

Other causes of death are obscure. Several times particularly after periods of unusually cold and wet weather in winter and spring, dead or dying squirrels have been found, with no external injuries or other apparent causes. One sent to the Fish and Wildlife Service Disease Research Laboratory at Los Angeles was found to have extensive pneumonia, which presumably was the cause of death. Wetting and chilling in the nests and loss of feeding periods may be contributing causes to deaths resulting from unfavorable weather and disease induced by it. At all times of year, dried and partly decomposed carcasses of squirrels often appear on burrow mounds, cast out by other occupants after the animal has died underground. Occasional squirrels have been found in weakened and greatly emaciated condition, while other normally healthy ones lived in the same or adjacent burrow systems. As one example, a large adult male trapped on July 12, 1940, weighed 650 grams and appeared in normal health, but 36 days later it was found so weak and emaciated that it was easily caught by hand as it feebly attempted to reach its burrow; it then weighed 390 grams. Series of squirrels collected on the Range and examined each year by the California State Department of Health have not revealed the presence of tularemia or sylvatic plague.

SUMMARY

California ground squirrels were studied at the San Joaquin Experimental Range in 1938, 1939, 1940, 1941 and the early part of 1942, with a small amount of supplementary field work in 1946. During this time, on an 80 acre intensive study area, 1552 squirrels were marked, and captured a total of 15,936 times; census counts, feeding records and general observations were recorded from this same area and from many other parts of the Range.

The quantity of food consumed by an individual squirrel was found to vary greatly according to conditions. Squirrels in confinement, fed upon dry wheat in summer, took on the average about twenty-two grams daily, and some fed upon natural green foods of preferred kinds consumed from 10 to 100 grams (representing a dry weight of 6 to 25 grams). Others intensively observed in the field during entire days of feeding took amounts estimated at from 27 to 115 grams (representing dry weights of 7 to 29 grams). In a half-acre ground squirrel enclosure stocked to represent a concentration of 12 squirrels per acre, average yield of vegetation was reduced by 1058 lbs. (dry weight) per acre, annually, more than ten times the amount the squirrels might actually have eaten. Much of this loss must have been due to stunting of vegetation eaten back during early stages of growth, and to trampling and cutting of plants not actually eaten; on the open range in competition with stock, damage per squirrel would be somewhat less.

Sixty-three kinds of plants were recorded in the year-long feeding of the squirrels, but a few species, filaree, acorns, tarweed, eriogonum, popcorn

flower, and seeds of ripgut grass make up the bulk of the diet. Use of many of the foods is limited to a short season. Competition with stock is most severe during late fall, winter and spring, but is much reduced in the dry season, when feeding is diverted from forage plants to acorns, tarweed, turkey mullein and cast seeds of ripgut grass. Squirrels are highly selective in their feeding, and choose only the more nutritious foods.

In their daily activity squirrels are much influenced by temperature. In winter they are above ground only during the middle of the day, but in summer they are most active in early morning and late afternoon.

These squirrels are generally hostile toward one another. Chasing and fighting occurs frequently at all times of year and especially in the breeding season, but there is no territoriality. Home ranges are not sharply defined but are usually 100 to 150 yards in diameter. Some individuals may spend their entire lives within the same home range. Others may shift repeatedly. Males are less sedentary than females, and young of the year move about more than adults. Voice plays a prominent part in social behavior. Different kinds of warning chirps are given to indicate presence of a snake, raptorial bird, or mammalian predator.

Seasonal dormancy occurs in this region, but in only part of the population. Extent and duration of dormancy vary a good deal from year to year according to weather and feeding conditions. Aestivation-hibernation occurs in a large proportion of adult females, from early summer until December or January. Adult males and young of the year are dormant in smaller numbers and for shorter periods. Squirrels become fat before entering dormancy, and favorable feeding conditions, as in the summer of 1941, favor extensive dormancy. Squirrels emerge in thin or emaciated condition after months of dormancy.

The entire population is active during late winter and spring. Breeding occurs in the latter half of January and early February. The breeding population was between 2 and 3 per acre each year on the study area, but was lower on other parts of the Range. Young, averaging seven per litter, emerge above ground usually in April, and grow to nearly adult size during the summer. The following winter the surviving young comprise about half the breeding population. Elimination is most rapid at the time young first appear above ground. The principal natural enemies of ground squirrels in this area are the coyote, gray fox, badger, rattlesnake, and red-tailed hawk; the bobcat, gopher snake, horned owl, and Cooper hawk are less important. Attempt was made to determine the population of each of these predators, and the numbers of squirrels taken by them. No basis for estimating populations of badgers or gray foxes could be found, and the proportion of squirrels in their diet is not well known. Frequency of feeding in the rattlesnake is not well known either, and the population figure obtained is questionable. Best estimates of predation possible with the data at hand seem to account for about half the annual increase of ground squirrels. Apparently many are eliminated through other causes, of which diseases and weather may be important.

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