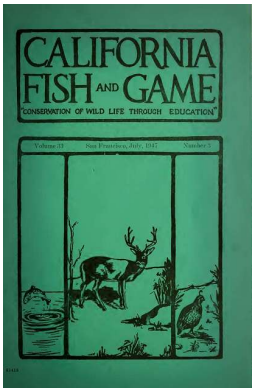
California Fish and Game 104(1): 36-59; 2018

From the archives

Ecology of a cottontail rabbit (*sylvilagus Auduboni*) population in Central California



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The cottontail rabbit of the western Sierra Nevada foothills (*Sylvilagus auduboni vallicola*) is sufficiently abundant in some areas to figure in the ecology and economy of the region in various ways—as a game animal as a reservoir of disease potentially transmissible to humans; and as a destroyer of vegetation, either cultivated crops or forage on range lands. During the course of wildlife studies at the San Joaquin Experimental Range, data were collected bearing on various phases of cottontail ecology. Especially during 1939, 1940, and 1941, many rabbits were live-trapped incidental to the trapping of ground squirrels, and information was obtained as to their numbers and activities, and various other factors, on an 80-acre area.

The experimental range is situated in, and typical of, a foothill belt used primarily for grazing of beef cattle. Interest in the rabbits in this region centers in their effect on range forage. The species is little hunted in this part of the State partly because other more popular small game species are abundant, partly because it is heavily infested with fleas, and partly because it is considered unsafe to handle since it is a carrier of tularemia. This region is mainly open woodland of oak (*Quereus douglasii* and *Quercus wislizenii*) and pine (*Pinus sabiniana*), occasional patches of chaparral and an annual type forage of broadleaf herbs and grasses; mostly it is rolling land, but there are occasional bluffs and ravines. The soil is generally shallow and rocky; outcrops and loose piles of decomposing granite rock are prominent features of the terrain. The brush patches and rock piles provide shelter for numerous wildlife species including the cottontail. The climate is one of mild winters and hot, rainless summers with temperatures over 100 degrees F. Annual precipitation averages approximately 22 inches.

This study was part of a program of wildlife investigation planned and initiated by Everett E. Horn of the U.S. Fish and Wildlife Service, in collaboration with the California Forest and Range Experiment Station, U.S. Forest Service. Lowell Adams, Freeman Swenson, Frank Hagarty and Bernard Mitchell helped with the live-trapping. Howard Twining, Daniel F. Tillotson and John E. Chattin analyzed scats and pellets in connection with the predation phase of the work. Assistance rendered by WPA Project No. 165-2-08-225 is acknowledged.

Methods

The rabbit population was intensively studied on an 80-acre area by marking for future identification and releasing all that could be live trapped. At each capture, sex, weight, catalogue number or formula, and exact location of the animal were recorded in the field.

Those taken in 1939 and 1940 were marked with serially numbered aluminum ear tags and colored celluloid disks manufactured for use by commercial rabbit breeders; those trapped in 1941 were marked by toe clipping. Food habits data were obtained on this same area by following rabbits as closely as possible recording the kind and amount of vegetation taken.

Seasonal Bait Acceptance

During 1939, 1940 and 1941, trapping effort was fairly constant year-round; on the 80 acres where population studies were made, approximately 200 traps were kept set for several days each week. Differences in the catch of rabbits reflected both actual changes in their number and changing season acceptance of the grain baits used. Throughout the growing season October through May, while green food was abundantly available, rabbits only rarely entered the traps. It is assumed that natural foods were much preferred to the grain mixture of wheat and milo maize with which the traps were baited. In summer after the main forage crop had dried out, grain was taken freely, and nearly all recorded captures of rabbits were in the dry season—summer and early fall. The total number of captures recorded each month during the three-year period in which live trapping was in progress is shown in Fig. 48. Each year the catch was highest in August at the peak of the dry season. Trends

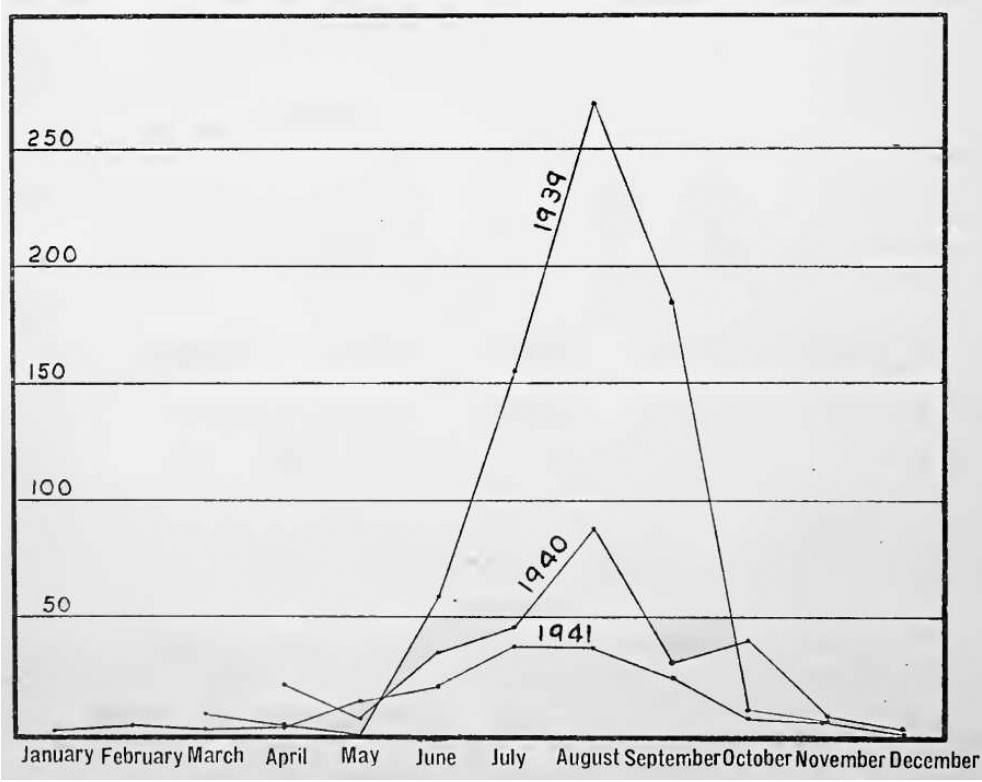

Figure 48.—Numbers of captures of cottontails from month to month on 80-acre trapping area in three different years. Trapping effort was fairly constant through the year and the fluctuating catch reflects seasonal variation in bait acceptance.

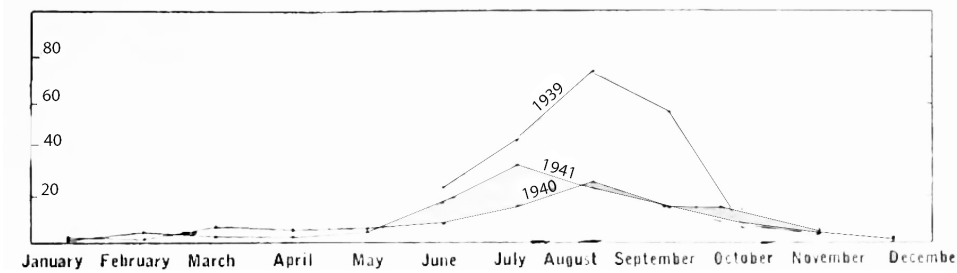

FIGURE 49.—Numbers of cottontails live-trapped on an 80-acre study area each month in 1939, 1940, and 1941. The month-to-month changes in total catch are influenced mainly by changing bait acceptance rather than by actual changes in numbers of rabbits.

were similar for all three years, but in 1939 bait was taken much more readily. During the dry season that year natural food was scarce due to the short forage crop and early drying. In 1941 the forage crop was heavier and succulence longer persisting than in 1940, and the catch of rabbits was correspondingly light. During the course of live trapping, the few rabbits caught in winter and spring were often individuals which had been trapped frequently during the preceding dry season, and had perhaps acquired a special liking for the bait used.

MOVEMENTS

During the three-year period, 228 rabbits were trapped a total of 1,159 times. The different locations of capture for an individual provided information concerning extent of foraging range, homeing propensities, and shifts in centers of activities.

Foraging Range.—Numerous captures of some individuals within a fairly short time revealed the extent of normal foraging activities or "cruising radius." As the numbers of records on individual rabbits increased, the foraging ranges plotted from them usually tended toward an oval shape. In many instances diameters of foraging ranges may be indicated by the maximum distance recorded between points of captures. When records are few, the distance is apt to be unrepresentatively short. For the 134 individuals each trapped at different locations on the area, maximum distances between points of capture, "foraging diameters," are presented in Table. 1.

TABLE 1.

	2 captures	3 to 5 captures	6 to 11 captures	11 to 21 captures	21 or more captures
Number of rabbits	27	36	39	27	5
Average of foraging diameters in feet	451	496	723	781	1,044
Extremes of foraging diameters in feet	30-1,450	50-1,200	250-2,100	250-1,700	820-1,300

If the sexes differ in extent of home range, the difference is slight. Females may move about somewhat less than males, but some of the largest home ranges, plotted for individuals having many repeat records, were those of females. The average "foraging diameter" for all females (72) captured at more than one point was 626 feet, as against 632 feet for the entire group of 124, including both sexes. If the distances between captures actually represent the extent of foraging areas, home ranges of, roughly, eight or nine acres for both sexes were indicated, but probably in most instances the areas were somewhat larger. Ingles (1941: 234) wrote of this same species studied at a locality 200 miles northwest: "The home range of a male rabbit may be as much as 15 acres since three were taken at stations 400 yards apart. The home range of a female rabbit is often less than an acre, which may be shared with as many as four other rabbits."

The difference may be due to the spotty distribution of food and of shelter—scattered clumps of blackberry thickets—where Ingles' study was made. His conclusions were based on comparatively few individuals on a small area. The open and uniform terrain on the Experimental Range would promote extensive movement.

Measured distances between points of capture are not entirely satisfactory for showing home ranges. The shorter distances represent individuals for which the records do not reveal the true extent of the areas covered while the longer distances in some instances may represent unusually long foraging trips, and in others possibly reflect shifts of headquarters over periods of time. The median of "foraging diameters" recorded, for all those with more than five captures, was 700 feet. This distance is probably roughly representative of the diameter within which most of the activities of an individual are confined.

Several opportunities arose to watch the extent of movements of unusually tame and easily recognizable individuals frequently encountered in the field. Two in particular were intensively observed and were often followed in attempts to record their feeding. One of these was an old female, the other was a young of the year slightly more than half-grown. Both were somewhat more limited in their observed movements than were other individuals whose ranges were revealed by trapping, but the observations were made principally around dusk. Though activity is pronounced at that time of day, it appears that the rabbits then tend to forage in proximity of cover, ranging more widely after dark. Individuals were often trapped at night in areas of open grassland where they were never seen to venture in the daylight, and droppings were also abundant in such places.

Small young have much smaller foraging areas than have adults. One was usually seen foraging within a few yards of some pile of rock or brush or similar shelter into which it might dash at any alarm. Young less than half-grown were trapped in small numbers; usually a larger size is reached by the time the dry season sets in rendering grain bait more attractive than natural foods. A few young did seem to acquire a taste for the bait early in the season, and these entered traps frequently, each always at about the same place near the edge of some covert. The rabbits moved a good deal more widely than the ground squirrels which were trapped on the same area.

Homing.—Ability to return within a short time to the home range with which it was familiar was demonstrated by each of three rabbits which made homing movements of 4,400 feet, 3,550 feet, and 3,150 feet respectively, after being trapped and removed from the experimental range headquarters where cottontails were often troublesome in taking bait set out to trap quail. Twenty others similarly trapped and removed to the rabbit study area slightly more than three-fourths mile away, all failed to make homing movements, apparently. Ten were never recaptured, and the remaining 10 were recaptured on the study area; several of

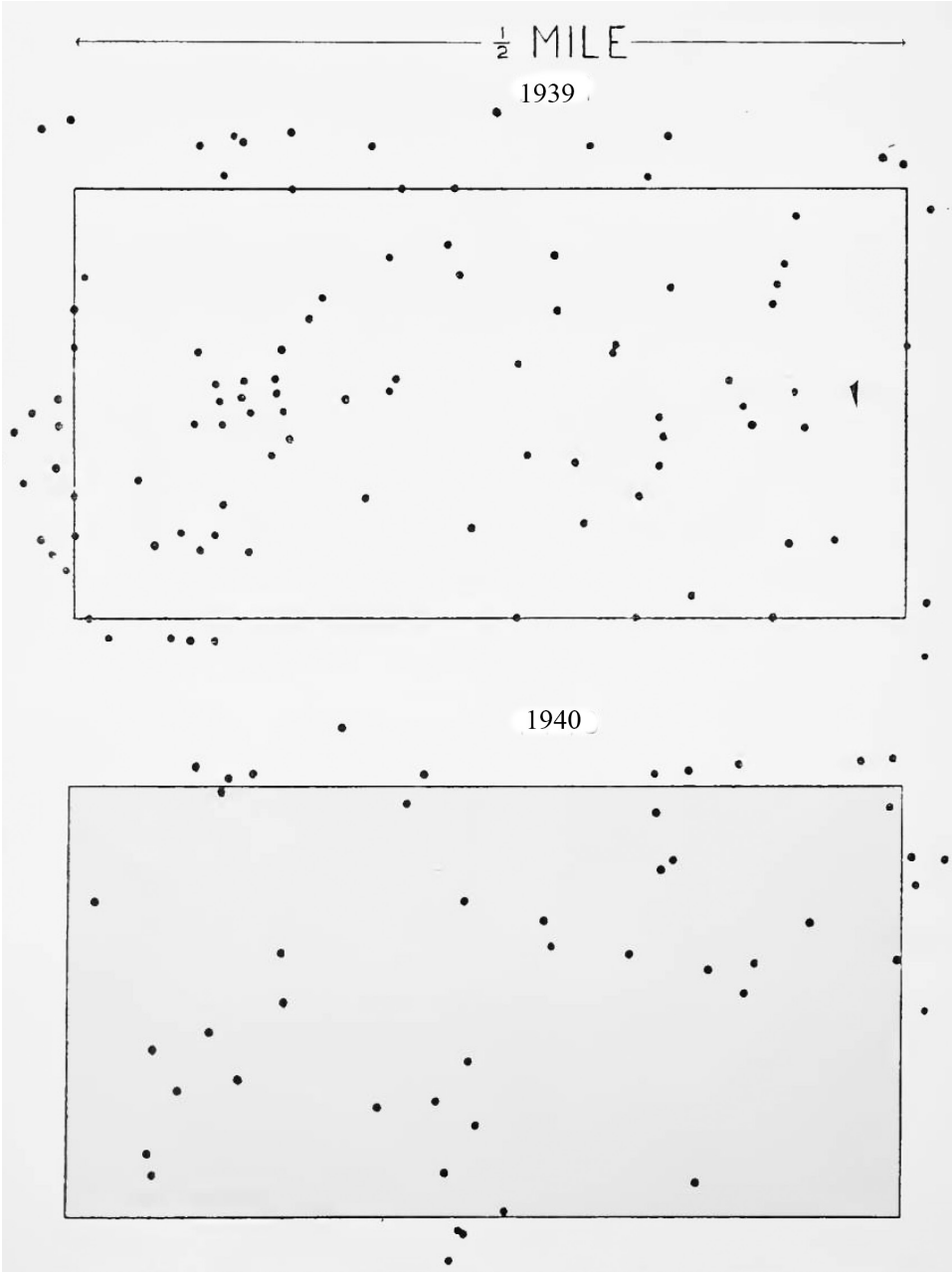

FIGURE 50.—Map showing distribution of individual cottontails live-trapped in 80-acre study area in summers of 1939, 1940. Each dot represents central point of an individual home range. Note relative abundance in 1939, and concentration near left margin of area where water was available.

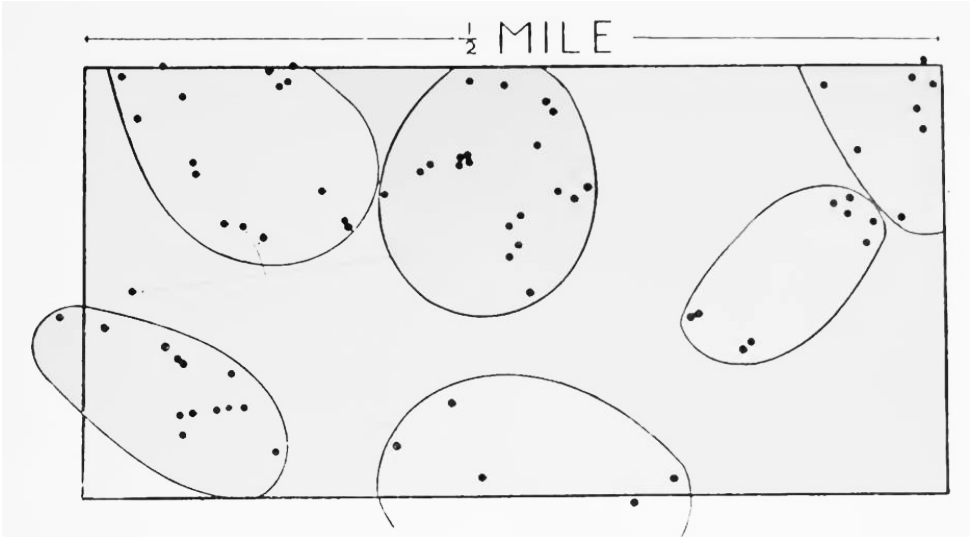

FIGURE 51.—Home ranges of sex different cottontails on 80-acre study area, as plotted for each from points of capture over periods of months. Three outlying points of capture from home range in upper center evidently resulted from trips to water supploy outside usual range.

them were taken repeatedly over long period of months indicating that they had settled down in the new location near where they were released. Distances of movement from the point of release recorded for members of this group after recapture varied from zero to 2,200 feet.

Shifts of Range.—Only one clear-cut instance of shift in range, or migration was obtained. This involved a male trapped five times within a two-week period in August, 1940, when it was less than half-grown. All these records were within an area of 450 feet diameter. The remaining record for this animal was obtained on June 2, 1941, when it was killed near the headquarters area, having made a movement of 3,300 feet.

The study area was not well adapted for the recording of long movements since it was only a little wider than the maximum diameter of a foraging area, and but twice as long. Shifts of range in most cases would have taken the rabbits beyond its boundaries where they would not have been recorded except by accident.

However, such shifts may be an important factor in affecting the population turnover which is apparent from the trapping records. Many rabbits were caught frequently over periods of weeks and then disappeared abruptly from the records even during the dry season when bait acceptance was still good. Perhaps most of these were actually eliminated by predators and other causes of natural death, but some possibly transferred their activities elsewhere.

During the dry season of 1939, forage in general, and especially succulence and water, was unusually scarce. Near one end of the study area, seepage in the dry creek bed, and a nearby stock trough, furnished watering places much used by the rabbits. Trapping records that year indicated some clustering in this part of the area, while the 1940 records were more evenly distributed.

Further evidence of shift in foraging range to include critically needed food or succulence was obtained at the headquarters area. Here, two unfenced lawns were watered regularly through the summer. These lawns were within a cleared area adjacent to

roads, buildings and a small orchard, where rabbits were rarely seen during the green season. But in the dry season, especially in 1939, the lawns were exceedingly attractive to the cottontails. Shortly before dusk they would begin to congregate, and later in the evening a person driving up in a car would often see as many as 30 dashing from the lawns to seek cover. It seemed evident that most of the individuals involved had extended or actually transferred their foraging ranges to include areas of the lawns.

Population

On the 80-acre area where live-trapping was carried on, information was obtained regarding the population density of cottontails. In computing the numbers actually present, use was made of the Lincoln Index—the ratio obtained in a given sampling period, of previously marked individuals recaptured to all those caught, including some not previously marked. The census formula used was as follows:

$$\frac{\text{Total population of 80 acres}}{\text{Number Caught January to July}} = \frac{\text{Number caught August to December}}{\text{Number caught January to July and recaptured August to December}}$$

In choosing the two sampling periods necessary for the computation, most plausible figures were obtained by division into a January to July preliminary period during which part of the population was trapped and recorded, and an August to December post-census sampling to obtain the ratio of the previously marked individuals to the population as a whole. This division of periods was made to include, in each, a part of the July-August season of maximum bait acceptance. Other divisions in which one or both periods fell within a spring or fall season of poor bait acceptance and few captures produced obviously distorted census figures. The number trapped which were used in the census, were as follows:

Year	January to July	August to December	Both Periods
1939	49	78	25
1940	22	31	13
1941	49	35	18

From these figures, census computations were made as follows:

1939 census:	x/49= 8/25	25x=3722	x=153 cottontail
1940 census:	x/22=31/13	13x= 682	x= 53 cottontail
1941 census:	x/49=35/18	18x=1766	x= 95 cottontail

In each instance the figure obtained represents the number present in early summer—a population of adults, and subadults or well-grown young of the year. Aside from the pronounced year-to-year fluctuations suggested by the above figures, the population of course, goes through an annual cycle resulting from the seasonal limitation of breeding, but the pattern of this cycle cannot be shown with present data. The population presumably undergoes rather gradual reduction throughout the dry season, until it is again augmented by the annual

crop of young, perhaps several litters for each female during the course of the breeding season. Most of these small young are rapidly eliminated during the time they are helpless in the nest and for many weeks afterward while they are extremely vulnerable to predation.

The annual Lincoln Index census probably gives a fairly accurate approximation of the numbers present on the area. Checks were obtained by the use of one-month sampling periods. From these censuses the following figures were obtained for July and August for each of the three years.

	1939	1940	1941
July	153	39	760
August	152	36	38

These are considered less accurate than the figures from the six-month sampling periods, mainly because of the smaller numbers involved. The August 1941 figures are considered particularly unreliable since they were dependent upon the small and inadequate sampling in September of that year when bait acceptance was poor.

Even assuming that the actual census figures obtained are an accurate representation of the numbers on the area, they do not indicate correctly the population density, for many of the animals trapped on the area ranged outside it in varying degrees, some perhaps merely overlapping its boundaries in the course of their wanderings. By plotting the range of each individual rabbit, on the basis of distribution of its sites of capture, attempt was made to determine what percentage of its range lay outside the study area. Those having numerous records all well inside the boundaries were assumed to forage entirely within the area. Those whose records of capture clustered along one edge were assumed to range mainly outside, the estimated percentage depending on the pattern of the location records and the known extent of typical foraging ranges in other individuals. Those for which only a single record was available near an edge, were assumed to range almost entirely outside the area. In a few instances where only one or two location records were available, the estimate was merely a guess but usually the range was roughly evident. In several samplings by live-trapping of a peripheral strip, many of the marked rabbits were recaptured and the extent and direction of their activities outside the main study area were indicated. Attempt was made to estimate to the nearest 10 percent the portion of each range falling within the trapping area, but at best these estimates are merely approximations.

For 103 rabbits trapped on the area in 1939, the sum of percentages of ranges on the area totaled 6,575; dividing by 100, there were the equivalent of nearly 66 complete "rabbit ranges" within the 80-acres area. This indicates a population density of one cottontail to 1.2 acres. For the 47 trapped in 1940 percentages of ranges totaled 3,000, representing 30 "rabbit ranges" or a population density of one per 2.6 acres. Using the data in a different manner, it appears that of the 103 present in 1939, 55 had ranges centering inside the area, 35 centered outside, and 13 centered in the immediate vicinity of the boundary, or yielded such meager data that it could not be determined on which side they centered. In 1940 comparable handling of data indicated that 32 centered inside and 15 outside the area.

It is evident that, in the vicinity of the trapping area at least, the 1939 summer population had undergone sharp reduction by the summer of 1940, but with no apparent cause. In a preliminary paper on ecology of wildlife species of the San Joaquin Experimental Range (Horn and Fitch, 1942;115) it was stated concerning the cottontail population: "***during 1939 and early 1940 their numbers remained fairly stable except for seasonal fluctuations.

During the summer of 1940 the numbers dropped to less than half of the 1939 summer populations, most of this reduction occurring over a six-weeks' period." Further study of the data suggests another interpretation. No dead or diseased rabbits were seen during the time of the supposed reduction which was based mainly on impression. But it does appear that the reduction must have involved unusually heavy mortality of adults rather than mere variation in the success of the annual crop of young. Thus of the 103 rabbits caught on the area in 1939, only 9, or 8.7 percent were recaptured in 1940. But of the 47 total caught there in 1940, 18, or 38 percent were recaptured in the 1941 season. Survival expectancy of adults was more than four times as high in the summer of 1940—other things being equal. Possibly during the critically dry conditions of 1939, the animals moved about so much more extensively that this, rather than actual mortality, was an important cause of population turnover on the 80 acres.

In the early summer of 1940 an attempt was made to determine the population density of the rabbits over the range as a whole. Road counts were made, driving in a car at 10 miles per hour after dark in the early part of the night at times apparently favorable for rabbit activity. The roads followed passed through 12 different experimental pastures totaling 1,754 acres in area. For each road count made on these various pastures a comparable road count was made on the 80-acre study area where the population was evident through live trapped data. Thus the relative abundance could be judged from the numbers seen per unit of time on any area as compared with the trapping area.

On the 80-acre trapping area, in 739 minutes of driving, there were seen 41 rabbits, or an average of one in 19.8 minutes. In 1,023 minutes of driving on roads of the other pastures, 88 were recorded—an average of one in 11.7 minutes. Thus rabbits were apparently 1.7 times as abundant on the larger area. The population of the trapping area was computed at one to 2.6 acres, or .384 per acre. Thus the population density of the 1,754 acres would amount to 1.7 x .384, or .654 rabbits per acre. This is the only available computation of the cottontail population over the experimental range as a whole, but it represents a low point in both the year-to-year fluctuations and the annual cycle. Thus, at times it may amount to several per acre, especially in areas that are unusually favorable as cottontail habitat.

The 80-acre study area appeared to be one of the less favorable places on the Experimental Range more rugged terrain with abundant granite rock piles, patches of chaparral, and fallen live-oaks with their dense protective screen of twigs, provided optimum cottontail habitat.

Feeding

The feeding of cottontails on the Experimental Range is determined by the changing seasonal availability of food plants. In this region the food consists almost entirely of annual grasses and broadleaf herbs. In late fall, winter, and early spring (the growing season) many species were suitable for food, providing succulence and high protein and mineral content. In the summer dry season feeding conditions were much less favorable; protein and mineral content of the forage crop in general had dwindled, crude fiber had increased, and only a few species retained succulence. This remaining succulence was concentrated in the larger swales, and creek beds, but in years that are more than ordinarily dry it may be largely lacking. Presence of water then becomes a critical factor.

Seasonal trends in the feeding habits are best illustrated by extracts from field notes concerning feeding behavior recorded on different dates.

In late March feeding rabbits were observed to take tips of grass blades, foxtail fescue (*Festuca megalura*) and soft chess (*Bromus mollis*), stems of popcorn flower (*Plagiobothrys nothofulvus*), and fruits of filaree (*Erodium botrys*). Throughout April the flowering heads of an abundant small composite, gold fields (*Baeria chrysostoma*) were an important food. Popcorn flower stems and soft chess heads and once a plant of everlasting (*Filago gallica*) were also observed eaten in April. A rabbit eating heads of soft chess was seen to reject those of red brome (*Bromus rubens*) after reaching up to sniff them.

In June dry heads of soft chess were an important food perhaps because of ready availability. One rabbit watched for 58 minutes took 244 heads of soft chess and nothing else. Slender-leaf rush (*Juncus oxymeris*), heads of foxtail fescue, plants of Spanish clover (*Lotus americanus*), stalks of tarweed (*Hemizonia vergata*), leaves and seed heads of Australian chess (*Bromus arenarius*), and head of clover (*Trifolium* sp.) were taken in quantity; oat (*Avena barbata*) and leaves and bark of button-willow (*Cephalanthus occidentalis*) were also seen eaten on one or more occasions.

In July several observations indicated that stalks and heads of soft chess continued to be the principal foods. Stalks and heads of fescue, lupine (*Lupinus formosus*), tarweed, turkey mullein leaves (*Eremocarpus setigerus*), dock (*Rumex* sp.) and, on one occasion, dry oak leaves were seen taken. The turkey mullein, dock, and tarweed were apparently used because of their succulence at this season when most other vegetation was dry.

In August tarweed was increasingly used. In one rabbit followed throughout a foraging period, tarweed was estimated to comprise 90 percent of the meal. In feeding on tarweed the animal usually cut the stalk and ate outward from its base, discarding the terminal parts. Soft chess heads and straws continued to be important foods. Several times rabbits were observed grazing on the surface mat of cast seeds of foxtail fescue. Rushes (*Eleocharis* and *Juncus*) already too closely cropped to be accessible to stock, continue to provide an important source of food and succulence to the rabbits. Spanish clover, turkey mullein, dock and thistle (*Cirsium* sp.) also were recorded as being eaten in August.

In September rabbit grazing on cast fescue seeds was recorded several times; also use of soft chess, toad rush, flowers of tarweed, and dry navarettia (*Navarettia* sp.)

The only October feeding record obtained was of a cottontail taking a dry turkey mullein plant.

The quantities of forage required to maintain a cottontail are not well known. In a summer feeding experiment, a 340-gram young fed for 25 days on dry wheat, with water available, ate on the average 14.5 grams daily—only 4.1 percent of its body weight. A 950-gram adult in 11 days of feeding ate an average of 23.7 grams daily—only 2.5 percent of its body weight. However, both rabbits lost some weight during the experiment, and this concentrated food is unrepresentative of their diet in the wild. Ingles (1941:239) records that two adults which he fed a mixture of green forage for a 15-hour period ate 209 grams and 171 grams, respectively. In estimating rabbit damage on the range, allowance must be made for the fact that plants cut and destroyed are often only partly eaten, that vegetation is adversely affected by trampling, on the runways and elsewhere, and that plants eaten back in the early stages of growth are stunted. The total damage therefore greatly exceeds the loss of vegetation actually consumed by the rabbits.

Weights

Weight was recorded at each capture, and was found to fluctuate widely. Adults usually weighted between 750 and 1,300 grams; those in good condition frequently weighed more than 1,000 grams. Day to day fluctuations of 40 grams or more were often recorded, apparently due mainly to differences in extent of feeding before capture. Individuals caught frequently over periods of weeks often tended to lose weight, possibly as a result of facial bruises sustained in their attempts to escape, which perhaps made eating difficult and painful. Seasonal trends in weights are somewhat obscured by this tendency to weight loss in consistent repeaters.

In late summer of 1939 there was a general downward trend in weights evidently resulting from the short forage crop with lack of early disappearance of swale succulence during the dry season. No such tendency at this time of year was apparent in 1940. Maximum weights were recorded in April and May, but few were caught at that season, as bait acceptance was poor.

For an adult female caught 21 times in nine different months over an 18-month period, average monthly weights were as follows: August, 1930—1,052 grams; September, 1939—1,012 grams; January, 1940—1,055 grams; April, 1940—1,225 grams; July, 1940—1,180 grams; August, 1940—1,110 grams; May, 1941—1,300 grams; August, 1941—1,055 grams; February, 1942—(dead in trap)—825 grams.

Unusually complete weight records were obtained for one female rabbit first trapped as a small juvenile soon after leaving its nest, and recaptured frequently during the ensuing 17 months, even during the winter season when bait acceptance was low. The weight records for this individual are shown in Figure 52.

Reproduction

Breeding is ordinarily limited to the late fall, winter, and spring months—the growing season when green forage is abundant. In rabbits trapped during the dry season, the genitalia had retrogressed so that sex was not readily determined, and it was evident that breeding activity had ceased. The reproductive physicology may be controlled by the seasonal change in diet. As an exceptional instance, a one-third grown young was seen in November, 1946, in the headquarters area. It must have been born during the dry season, but the watered lawns and gardens around the headquarters buildings may have provided green feed necessary to stimulate reproduction at a season when it does not normally occur. Orr (1940:143) stated that "The breeding season of the Audubon cottontail in California extends from December to June." On the experimental range observations suggest that it may begin and end somewhat earlier. Concerning the rate of reproduction, Orr (loc. cit.) stated: "Sufficient data are lacking to definitely state the number of litters born annually, but considering the length of the breeding season it is not improbable that in many instances this number may exceed two. The average number of young per litter based on records of 19 pregnant females, is 3.6 with extremes of two and six."

On November 9, 1940, an adult female was seen gathering dry grass for nesting material and carrying it to a burrow beneath an oak bush. After pulling up each mouthful, she would deposit it in the freshly dug burrow. Many mouthfuls of grass were gathered, all within three or four feet of the bush. This was probably near the beginning of the breeding season and the nest evidently was being prepared for a litter of young.

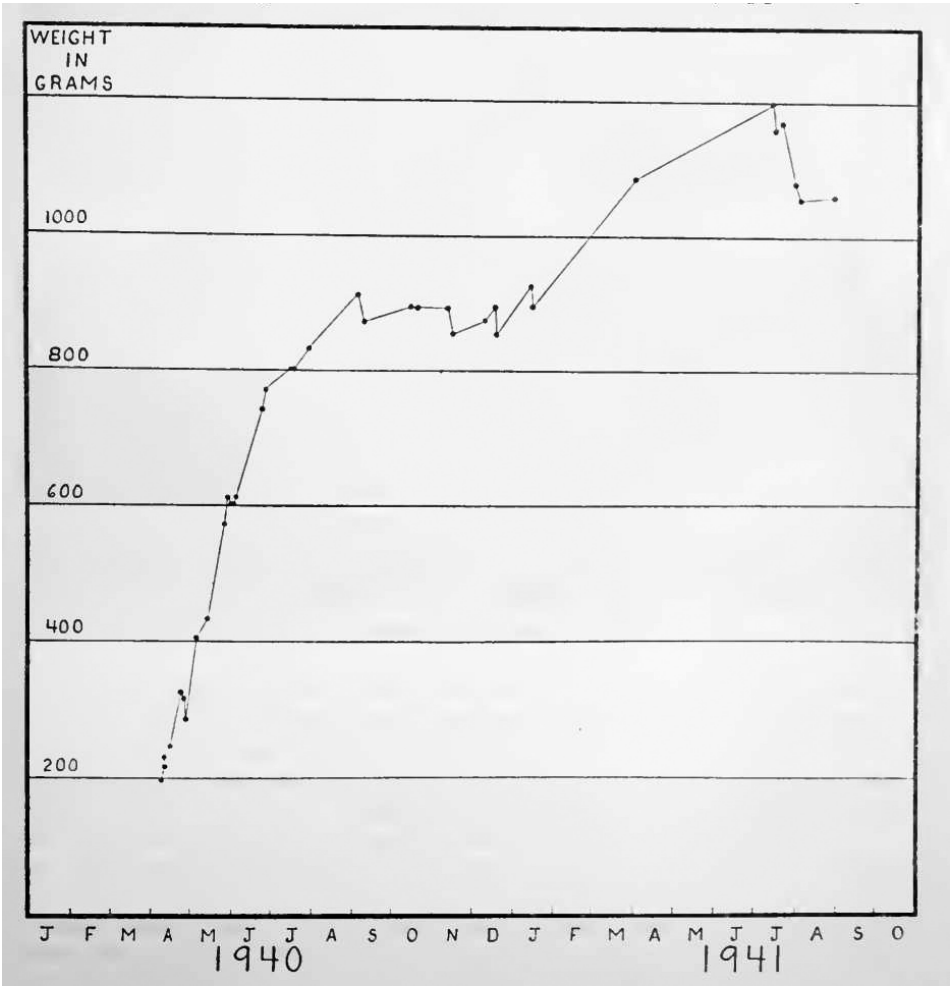

FIGURE 52.—Weights of a female cottontail on dates of capture beginning soon after leaving nest, showing rapid gain for first three months with more gradual and less regular subsequent growth.

On January 18, 1939, a nest was found on the surface of the ground in a rounded depression, well concealed by a dense covering of high grass. This was in a swale of an ungrazed area. The one young in the nest weighed 60 grams.

On the following day a destroyed nest was found where it had been dug out, in an exposed situation in sandy soil near a creek bed. The nest chamber was three inches below the soil surface, and the cavity was about eight inches long by five inches deep with a bed of dry digger pine needles, a softer interior of dry fescue and rush, and lining of rabbit fur. A fresh ground squirrel digging and feces were found about a foot from the nest suggesting the possibility that one of these rodents had robbed it.

On January 25, 1939, a nest with two small young rabbits was discovered. The nest cavity was just beneath the ground surface, and was lined with rabbit fur but had no plant material. The entrance and the cavity itself were so small that it would seem impossible for an adult cottontail to enter. The young still had their eyes closed, and had a sparse covering of hair.

On January 28, 1941, at about 10 a.m., another adult was seen making its nest. It was under a live-oak and was moving in a brisk, jerky fashion examining the ground litter minutely, and from time to time picking up dry oak leaves in it mouth. Having obtained a small mouthful of leaves, with a few straws and other debris mixed in, it entered a freshly dug hole with a mound of still moist earth in a more exposed situation on the other side of the tree. After a few seconds it backed out having deposited its load, and resumed the search. In a period of about five minutes it made 15 trips into the hole with nesting material—mostly dry oak leaves and some dry grass (probably soft chess). At 4:30 p.m. the site was located with difficulty and it was observed that the hole was plugged with loose earth and the burrow mound leveled and completely covered with a layer of dry oak leaves. Four weeks later this hole was dug out. The entrance was covered with dry oak leaves. The litter of young presumably had been destroyed early by heavy rains. The nest cavity about a foot from the entrance, contained evidence of dead young rabbits.

Ordinarily the nests are so well concealed that they are rarely found while in use, but remains of those dug out and destroyed by predators were found frequently during the winter and spring moths. Usually it was not possible to identify the predator involved. Only a few of those seen destroyed were recorded. On March 21, 1939, three such destroyed nests were recorded, and in the first week of May, 1938, several were noticed.

On April 10, 1939, a small young cottontail was seen in tall grass a few inches from the entrance of its nest burrow, into which it ran when disturbed. The burrow was dug out and was found to have a tunnel about eight inches long leading to a nest chamber five inches beneath the ground surface, which seemed barely large enough to contain an adult rabbit. It was lined with grass and a small amount of fur. Only the one young was found in it.

The nest recorded latest in the season was one discovered on May 24, 1938, when attention was attracted to it by a rattlesnake which was swallowing a very young rabbit and had three others already inside it. An adult cottontail was about 15 feet distant, and remained in the vicinity, allowing close approach. The nest was not dug out at the time of discovery but was investigated later in the day. At this time a second rattlesnake was found partly inside the nest, and it had eaten three more young cottontails evidently of the same litter. The entrance to the burrow was barely large enough to admit the snake's body, but it was partly plugged with loose dirt. The entrance led into a rounded chamber about 7 x 4 x 4 inches, with a nest of dry grass (soft chess and foxtail fescue) lined with rabbit fur.

From the foregoing accounts it is obvious that the habits of the cottontail in this locality are variable, as regards site selected for birth of litter, type of breeding burrow or lack of it, and composition of nest. Ingles (1941 :24) has shown that the female cottontail may not even enter the breeding burrow but returns to it infrequently to allow the young to suckle as she stands over the entrance. In some of the nest burrows discovered this arrangement seemed unlikely because the nest chamber was several inches from the entrance. But other nests were so small that it was difficult to see how the adult could have squeezed inside. It is probable that squirrel burrows are sometimes used as breeding places by the cottontail. Extensive squirrel burrow systems may have as many as 100 open holes, many of which are not connected underground, and only a few of the entrances are regularly used by the squirrels in going to and from their nests. One winter morning freshly dug mounds of earth heavily tracked by cottontail were often found beside such burrows, showing that the rabbits had enlarged underground portions during the night.

Several times remains of cottontail too young to have left the nest were found partly eaten on ground squirrel burrow mounds, presumably victims of the squirrels. On one oc-

casion a squirrel was seen carrying a live young cottontail in its mouth. Once a cottontail was seen chasing a squirrel around the edge of a bush, possibly in defense of its nest.

Natural Enemies

Several kinds of mammalian predators, at least four species of raptorial birds, and two of the larger species of snakes, all numerous on the experimental range and elsewhere in the general region, prey regularly upon cottontail. Many records of predation were gathered, and an attempt was made to compute the population density of each species which might be important as a rabbit predator. These data are not sufficiently complete to afford a clear picture of the role of predation in limiting the cottontail population, especially since the reproductive potential of the rabbits in this region is not well know. Some predator species take only the small young before these have left the nest. Other kinds take heavy toll from the adult populations, but it is evident that the inexperienced young are especially susceptible to predation by many natural enemies. The combined toll of the several predators comprises an impressive total, which must be a major factor if not the decisive one in limiting cottontail distribution and abundance.

Coyote.—Control of coyotes by trapping was begun on the experimental range in the winter of 1935-36. The recorded numbers eliminated each year from the 4,600-acre area were as follow: 1935-36, 35; 1936-37, no record; 1937-38, "about 30"; 1938-39, "about 30"; 1939-40, 13; 1940-41, 13; 1942, 7; 1943, 5; 1944, 8; 1945, 1. Each year an unknown number was also eliminated from adjoining ranches. It is evident that in recent years the population has been held far below its former level. In 1939 and 1940, at the time the rabbit population was studied the coyote population averaged perhaps one to 300 acres between the breeding season and the time of control operations the following winter.

In a year-round collection of 1,173 coyote seats, mostly from regular defecating places on roads and trails of the experimental range, in 1939 and 1940, 1,924 vertebrate prey items were identified. These made up most of the food, though supplemented by a few occurrences of grasses, berries, insects and some carrion. Of the 1924 items, "rabbit" (presumably cottontail but possibly pertaining to the relatively rare jack rabbit in a few instances) made up 19.6 percent (21.1 percent in 1939, 17.0 percent in 1940). A truer interpretation of the relative importance of rabbit in the coyotes' diet here may be gained by computing its percentage weight of the total. The total live-weight of recorded items was estimated by obtaining the average weight for each species, multiplying this by the number of its occurrences, then adding up these totals. Cottontail, with an average of 800 grams, was the heaviest kind of prey recorded taken by coyotes in this locality. The weight used as standard for the cottontail, and those for other prey species represent in each case that of a small adult. Many or perhaps most of the prey animals taken by coyotes may have been immature. The ratio of juveniles in various states to adult animals was perhaps roughly similar for each, but the usual adult weight affords the best standard of comparison.

Another variable is introduced by the inexact correspondence between number of scat occurrences and number of individual prey items eaten. But for squirrel- and rabbit-sized prey animals fairly close correspondence might be expected (Murie, 1946 : 275). For mouse-sized rodents, and more minute items less accurate figures on the number eaten could be obtained, but this inaccuracy would not affect the proportions of the larger and more important items to any great extent. In general, the assumption of one prey animal of the average weight of the species for each scat occurrence, is thought

to afford a rough approximation of the percentage by weight of the coyote's diet. The same assumption has been made for the other carnivores and raptors discussed below. In Table 2 prey weights by percentage were obtained from computations on this basis.

TABLE 2.—Composition of Coyote Food (Based on 1,173 scats)

Prey		Occurrence in coyote food	
Species	Average weight in grams	Number of occurrences	Computed percentage by weight of total recorded prey
Cottontail	800	377	45.4
Ground squirrel	500	414	31.2
Gopher snake	500	79	6.0
Woodrat	200	162	4.9
Pocket gopher	100	234	3.5
Kangaroo rat	60	361	3.3
Other (29 kinds)	variable	297	5.7
Totals		1,924	100.0

It is indicated that by weight cottontail made up a greater percentage of the diet than did any other kind of prey, and amounted to nearly half of the total.

Gray Fox.—At the time of the study, gray fox were probably somewhat more abundant than coyotes on the area, judging from trappings' estimates and the greater frequency with which they were seen. However, no basis for estimating their actual numbers is available. In June, 1938, a den was located with seven half-grown pups. Scattered remnants of prey in the vicinity included parts of several cottontail.

A small collection of 887 fox scats made on the experimental range contained 102 vertebrate prey items, besides a few insects, berries, and other plant material, and one occurrence of carrion. The scats were collected at different times of year but mainly represented the fall months.

The number of occurrences and computed percentages of the total prey weight for the principal prey species of the gray fox are presented in Table 3.

TABLE 3.—Composition of Gray Fox Food (Based on 87 scats)

Prey		Occurrence in gray fox food	
Species	Average weight in grams	Number of occurrences	Computed percentage by weight of total recorded prey
Cottontail	800	11	35.7
Ground squirrel	500	12	24.4
Woodrat	200	17	13.8
Bird (4 kinds)	variable	10	10.2
Pocket gopher	100	14	5.7
Kangaroo rat	60	17	4.1
Other	variable	21	6.1
Totals		102	100.0

Though this sample is too small to be relied upon, its trend seems to indicate that rabbit was the most important single prey species of the fox, and made up more than a third of the total.

Badger.—Digging of badgers was frequently seen on the study area, but no basis for estimating the population of badgers was discovered. It is unlikely that these predators are able to catch adult cottontail except under unusual circumstances, but they may be responsible for much of the predation on small young in the nest. On many occasions cottontail nests dug out and destroyed by mammalian predators were found. Though the predator involved was never definitely identified, it is probable that badgers figured in at least some instances.

A badger kept in captivity throughout one summer consumed daily one small adult cottontail or its equivalent.

Bobcat.—Judging from the occurrence of their tracks, bobcats are fairly common in the more brushy and rocky parts of the Experimental Range, but nothing was learned concerning their actual numbers, or the food taken by them. As they are known to prey extensively upon rabbits elsewhere, (Grinnell, Dixon, and Linsdate, 1937: 615, 618, 620) it is probable that they take large numbers of cottontail locally.

Red-tailed Hawk.—This large raptor was determined to occur in a permanent population of about one to 160 acres, with an additional unstable population of fledged young and migratory adults, (Fitch, Swenson and Tillotson, 1946). Many instances of predation on cottontail were recorded. On one occasion the head of an ear-tagged adult male rabbit from the study area was found beneath the perch of a hawk about a quarter mile from where the rabbit had been trapped. On January 30, 1941, a hawk was seen to catch an adult cottontail by a sudden steep swoop from its perch on a 15-foot oak snag. The rabbit must have emerged from brush at the foot of the tree to cross an open space, completely unaware of the danger. It took the hawk about two minutes to kill the rabbit.

Among 625 prey items of the hawks recorded as brought to the young in the nests, cottontail were third in abundance with 62 records (all of young ones), and on the basis of weight were computed to comprise 26.5 percent of the total. Among 4,036 prey occurrences from 2,094 red-tailed hawk pellets, the more important kinds both in numbers and percentages of total weight are presented in Table 4.

Table 4.—Composition of Red-tailed Hawk Food (Based on 2,094 pellets)

Prey		Occurrence in red-tailed hawk food	
Species	Average weight in grams	Number of occurrences	Computed percentage by weight of total recorded prey
Ground squirrel	500	1,049	49.5
Cottontail	800	322	24.2
Gopher snake	500	190	8.9
Pocket gopher	10	794	7.4
Rattlesnake	300	70	2.1
Other	variable	1,611	7.9
Totals		4,036	100.0

Cottontail was third in abundance among all prey taken by the hawks, and comprised about one-fourth of the total prey weight taken.

Cooper Hawk.—A few pair of these hawks nest on the experimental range, and in winter the population is considerably increased by migrants, but no definite figures on their numbers were obtained. In 1939, two nests were observed, and a total of 41 prey items were recorded, two of which were young cottontail (Fitch, Glading, and House, 1946 :153). The other prey items were all of smaller kinds, mainly birds and lizards, and the cottontail were estimated to comprise approximately 16 percent by weight of the recorded food.

In one instance an adult cottontail found freshly killed and partly eaten under the edge of a bush was thought to have been the victim of a Cooper hawk. These hawks are considered of secondary importance as cottontail predators because of their relatively low numbers, small size and preference for other kinds of prey.

Horned Owl.—These large and common owls feed much more extensively on rabbits than on any other kind of food. Seven times, in the fall of 1938, spring and fall of 1939, and 1940, and late winter of 1941 and 1947, counts were made of horned owls heard at different points on a 1,920-acre section of the range. These counts representing the minimum number of owls present, varied from 5 to 25. Roughly, a population of one owl to a hundred acres is indicated. A sample of 654 pellets representing approximately 1,471 individual prey items was analyzed in 1939, 1940 and 1946. For the principal prey species, number of occurrences and computed percentages of total weights were as presented in Table 5.

TABLE 5.—Composition of Horned Owl Food (Based on 654 pellets)

Prey		Occurrence in horned owl food	
Species	Average weight in grams	Number of occurrences	Computed percentage by weight of total recorded prey
Cottontail	800	205	61.1
Woodrat	200	240	17.9
Kangaroo rat	60	201	4.5
Pocket gopher	100	115	4.3
Ground squirrel	500	13	2.4
Reptile (at least 8 kinds)	variable	44	5.0
Bird (at least 12 kinds)	variable	45	2.3
Other (including many insects)	variable	608	2.5
Totals		1,471	100.0

It is indicated that cottontail made up more than half the food by weight, though taken in slightly smaller numbers than woodrats.

Barn owl.—These are much less common than horned owls on the Range, and were seen at only a few places. In a collection of 240 pellets there were 517 prey items of which 415 were pocket gopher and pocket mouse. Only four were cottontail (all young) which were computed to make up around 3 percent of the total prey weight represented by the sample.

Rattlesnake.—This reptile is probably the most common of all rodent and rabbit predators on the Range. Over a three-year period 679 were marked and released, and

the ratio of these recaptured to others seemed to indicate a population of two or three per acre, but accurate census is impracticable as the figures might be distorted by many unknown variables. Of the rattlesnakes recorded, nearly half were adults. A total of 271 prey items were identified from stomachs and droppings of the snakes. For the principal prey species, number of occurrences and computed percentages of total weights see Table 6.

Table 6.—Composition of Rattlesnake Food (Based on 271 food items)

Kind of prey	Average weight in grams	Number of occurrences	Percentage of total prey weight
Ground squirrel	206	111	70.5
Cottontail	206	24	15.2
Kangaroo rat	60	32	5.9
Gopher	67	2	2.5
Other	variable	92	5.9
Totals		271	100.0

Though this food sample is small, as compared with those obtained for carnivores and raptors, prey weights were determined with a precision not practicable for the predatory mammals and birds. Food items were palped from snake stomachs, and were actually weighed, except those in which digestion had reached an advanced stage.

From these figures it appears that cottontail make up nearly one-sixth of the snakes' food. As a result of the winter and early spring breeding season most of the young were already too large for the snakes to eat when the latter emerged from hibernation. The peak of rattlesnake activity occurs during April, May and early June and all the records of rabbits occurred during that time, involved late litters of young rabbits in the nest and large adult snakes in every instance. Squirrels and kangaroo rats were often found dead, showing evidence of rattlesnake bite, but some of the snakes involved were known to have been too small to eat the animals they had killed. Some rabbit mortality may occur also. On June 28th, an adult rattlesnake was seen to strike a cottontail in the field. Rabbits are probably less liable to be killed in this way than are burrowing rodents which often encounter the snakes underground.

Gopher Snake.—This species is much less common than the rattlesnake locally—perhaps only one-fourth as numerous. A total of 70 food items were palped from gopher snake stomachs; and an analysis of these is presented in Table 7.

Table 7.—Composition of Gopher Snake Food (Based on 70 food items)

Kind of prey	Average weight in grams	Number of occurrences	Percentage of total prey weight
Cottontail	400	3	37.1
Ground squirrel	180	5	27.9
Woodrat	200	3	18.6
Bird egg	8.5	20	5.3
Gopher	130	2	4.0
Other	variable	37	7.1
Totals		70	100.0

The high percentage of cottontail in this small sample may be unrepresentative. One giant gopher snake, nearly seven feet long, had eaten an adult cottontail which weighed as much as most of the smaller food items combined. Such incidents as this must be rare, and comparatively few gopher snakes are big enough to swallow any but nesting cottontail.

Discussion.—The data set forth above suggest that the cottontail bears the brunt of predation pressure from most of the larger species of mammal, bird, and snake predators. The breeding season is long, and adult females may soon replace lost litters, or may normally rear two or more litters in a year, thus offsetting the heavy losses to natural enemies.

The summer population of adults and well-grown young after the breeding season amounting in 1939 to one per 1.2 acres, represents a rabbit-weight of about 670 grams per acre, a figure to be born in mind in connection with measured predation factors.

Computation of the rabbit-weight per acre eliminated by predation has been attempted on the basis of the known or estimated population of each predator species, the normal daily food requirement, and the percentage of the food weight which rabbits comprise. The population of coyotes was computed at one to more than 300 acres; the fox population at possibly the same figure (or probably somewhat more), the red-tailed hawk at one to 160 acres; horned owl at one to 100 acres; rattlesnake 2.5 per acre; gopher snake, 6 per acre. Reducing these figures to population density per acre and multiplying by the food requirement, and the percentage comprised by rabbit, we obtain the data presented in Table 8.

TABLE 8.—Cottontail Weights Consumed by Predators

Kind of predator	Population per acre		Food requirement per day in grams		Food weight per acre per day				Food per acre per year		Percentage of prey weight of cottontail		Weight of cottontail per acre eliminated annually by predators
Coyote	.0033	x	600	=	1.98	x	365	=	722	x	45.4	=	328.0
Rattlesnake	2.5	x	2	=	5.00	x	365	=	1825	x	15.2	=	277.4
Horned owl	.010	x	120	=	1.20	x	365	=	437	x	61.1	=	267.0
Gopher snake	.6	x	2	=	1.2	x	365	=	438	x	37.1	=	162.5
Fox	.0033	x	300	=	.99	x	365	=	361	x	35.6	=	129.0
Red-tailed hawk	.0062	x	120	=	.74	x	365	=	270	x	24.2	=	65.0
Total													1228.9 grams

This summation does not include the rabbits eliminated by bobcats and badgers, but both are among the more important cottontail predators.

Thus it appears that predation annually might eliminate a rabbit-weight of about double the nonbreeding population of adults and well grown young present in summer. Admittedly, at each stage of the computation a substantial margin of error is probable so that the figures obtained cannot be considered more than a rough indication of the magnitude of losses to each kind of predator. If, in the food composition of a predator, the proportion of young were higher among cottontail than among other kinds of prey, the percentage of cottontail computed would be too high. However, it is probably that the proportion of young among

the ground squirrel, woodrat, and gopher snake, in prey samples was fully as large as among cottontail. Each of these species has, like the cottontail, a high reproductive potential and a rapid population turnover with even greater differentials between young and adult weights and they were the only ones other than cottontail comprising substantial percentages of the diet in any of the predators. The populations of predator species are variable according to time and place, and all of them are computed on a somewhat doubtful basis for application to the experimental range as a whole; for the red-tailed hawk and horned owl, however, the figures used represent the absolute minimum. For rattlesnakes, gopher snakes, coyotes, and especially foxes, the population figures are less definite. The average daily individual food consumption under natural conditions is somewhat speculative. This is especially so in the case of the snakes, and the figure used is based on the average individual weight, assuming that each snake consumes twice its body weight during the growing season as suggested by data obtained from several kept in confinement. For the rattlesnake most feeding records were obtained in April and May when small cottontail are available—but from June through October rabbits are not breeding and their young have grown too large to be swallowed. Few feeding records were obtained for snakes during this latter two-thirds of their active season, as they are then secretive or nocturnal. But it may be surmised that kangaroo rats and gophers are then substituted for the young rabbits and squirrels taken in spring.

For the horned owl there is a probability that the numbers of cottontail assumed to have been eaten was too high, for, unlike the other prey species, the cottontail is large enough to furnish several owl meals. Thus one might be counted several times from its limb bones and vertebrae appearing in several pellets, whereas the other prey species were generally identified from skulls revealing accurately the actual numbers eaten.

The predation calculated is not necessarily too high; it seems entirely possible that the rabbits are adopted to withstand such pressure by virtue of high reproductive potential. Ingles (1941 :243-6) records an instance of a female marked soon after birth, which had matured an produced a litter of its own at the age of six months. Many of the young born early in the breeding season in fall, may mature in time to produce litters before the breeding season is ended by the drought conditions of the summer. Females that are mature in the fall at the beginning of the breeding season might be expected to produce nine young apiece during the seven or eight months of green growth if the average of 3.6 young per litter and two or three litters annually mentioned by Orr (loc. cit.) is representative. Females which lose their litters early might produce an even greater number. The young at birth probably weigh around 30 grams, and upon leaving the nest from 11 to 14 days later, they have increased to several times this weight. Growth during subsequent weeks is extremely rapid (Fig. 52).

In recent years ecologists have tended to minimize the importance of predation factors in controlling vertebrate populations. Errington (1946) has summed up the literature of predation, and presents a fairly convincing case to show that "intraspecific self-limiting mechanisms basically determine the population levels maintained by the prey. ***the patterns revealed may look remarkably little influenced by variations in kinds and numbers of predators."

Concerning rabbits, Errington (op. cit. 154-155) states that though more tolerant of crowding without intraspecific strife, "they are by no means free from automatic mechanisms [determining their upper and lower population limits in a given habitat.] ***again and again lagomorphs recovering from depressed levels show rapid population gains from one year to the next, the attentions of wild flesheaters notwithstanding."

The matter is not merely one of lagomorphs being prolific or of making their gains when enemies are either numerically or proportionally scarce, as there are too many instances of lagomorphs populations apparently conforming to patterns, even despite pronounced differences in numbers of such able hunters as horned owls and foxes."

On the San Joaquin Range there is no direct evidence that predation actually holds the cottontail population to any given level. The situation is complex, however, because several common predators take large numbers of cottontail without being entirely dependent on them; all could probably adjust themselves to absence of cottontail by taking larger numbers of the abundant ground squirrels, woodrats, and other rodents. The predators also prey to some extent upon each other, at least hawks, owls, coyotes and foxes all prey upon both rattlesnake and gopher snake. Individual predators are long-lived as compared with their rabbit or rodent prey, and survive fluctuations in the populations of the latter. Even on areas of a few acres, the cottontail, or rodents, are not uniformly abundant but are concentrated where conditions of food and cover favor them; they are sensitive to changing weather conditions which result in expansion or contraction of their preferred ecologic niches, and their numbers change in response. Each species is, however, favored by a different set of conditions, so that increase in one kind is apt to be accompanied by a more or less compensatory decrease in another. The kangaroo rat, for instance, is favored by arid conditions with sparse vegetation and its peak in numbers on the Experimental Range followed a series of dry years. The ground squirrel is also favored by a sparse forage crop, whereas the cottontail prefers a habitat with thickets providing surface cover. Response to such conditions can be seen in the varying abundance of rabbits and rodents on different parts of the Range; on the ungrazed headquarters area, having chaparral thickets and rank growth of swale vegetation, cottontails are more numerous than elsewhere, squirrels and kangaroo rats less so.

While changes in abundance of both cottontails and predators are known to have occurred since 1935, records are too fragmentary to show either clear cut correlation or lack of it. Coyotes were first controlled in the winter of 1935-36, and 35 were trapped during a few weeks period. Nearly as many were caught in each of several succeeding years, but by 1939 the population was much reduced. In August, 1936, at the time they were still numerous, Kenneth A. Wagnon recorded in his field notes that cottontail were extremely abundant around the Experimental Range headquarters, where as many as 50 congregated on the lawns in the evening, and he speculated that this high rabbit population might be the attraction for the coyotes. The reduction of coyotes to a fraction of their former numbers did not result in any noticeable increase in rabbits. The hawk and owl populations have been stable, but rattlesnakes over the Experimental Range as a whole, have doubtless been somewhat reduced by the continual drain on their population imposed by human activity.

Intraspecific, self-limiting mechanisms in the cottontail population of the Experimental Range were not evident, either. It is doubtful whether any mortality results from intraspecific strife—no fighting or other evidence of intolerance was observed even when many rabbits were concentrated on a small area. Their food supply is subject to even heavier use by other herbivores, particularly domestic stock, so that the amount remaining at the end of the dry season is not determined primarily by the number of cottontail. Conditions of critical severity with respect to availability of moisture may occur late in the dry season, for at this time cottontail congregate at water, and avidly seek any remaining succulent vegetation. Rabbits in situations where no water is available may compete severely with each other for preferred foods such as rushes, already so closely

cropped as to be unavailable to grazing stock. For young in the nest, weather conditions may be critical and heavy rains may result in their death by chilling or even drowning.

So far as observed, however, actual mortality in nearly all instances involved predation, upon individuals which were not obviously handicapped or diseased and which were well provided with food and shelter. That is, they were not part of a surplus population crowded out into a precarious marginal existence in critical periods, as in cases cited by Errington (op. cit.).

"Vulnerability" of the cottontail population may depend not so much on the conditions of food and shelter available to the rabbits as on the numbers of predators present and the relative availability to them of ground squirrels, woodrats, pocket gophers and kangaroo rats. At least it seems fairly certain that the medium to high populations of these several rodents make possible the existence of the predators which account for most of the rabbit mortality.

Disease.—Evidence of disease was rarely noticed among the rabbits trapped, through nearly all of them were heavily infested with large fleas. On one occasion a cottontail died suddenly for no apparent reason when it was being removed from a trap, suggesting the possible existence of shock disease in the population but no autopsies or laboratory tests were carried out to verify this hypothesis.

On February l7, 1941, a cottontail evidencing sluggish behavior was noticed, and it allowed an observer to approach within eight feet, then crawled into a rock crevice. It made no effort to escape when picked up and died two hours later. There was a swelling about the size of a walnut on the lower jaw, containing a yellowish white mass of cheesy consistency, and a slightly smaller inguinal swelling. The liver was somewhat darkened with well-separated yellowish spots on its surface. This rabbit had an unusually heavy infestation of fleas; it was estimated that there were at least 100 on its head alone. Other rabbits seen at this location on the same day and during subsequent weeks appeared to be normally healthy.

Herman and Jankiewicz (1943) examined 43 cottontails from the experimental range, and found coccidian infections prevalent; six different types were described. The infections did not appear to be acute and their effect on the rabbits is not known. Cottontail experimentally infected with *Eimeria stiedae*, a coccidial liver pathogen of domestic rabbits did not develop severe infections, as do domestic rabbits, suggesting partial immunity. The only ectoparasite recorded by these authors was a flea (*Ctenocephaloides felis*). The animals were shipped to these authors in Los Angeles and the ectoparasites were probably lost during handling prior to shipment. Internal parasites found by them included two intestinal protozoans (*Trichomonas*, *Chilomastix*), two nemoatodes (*Obeliscoides cuniculi* and *Nematodirus leporis*), and several cestodes (*Taenia pisiformis*, *Cittotaenia variabilis* and other species of the same genus and *Raillietaenia retractilis*).

Summary

The cottontail is abundant in open woodlands of the Sierra Nevada foothill belt in central California At the San Joaquin Experimental Range it competes heavily with livestock in use of the vegetation. During the summer dry season, the rabbits took grain baits freely, but during the growing season they preferred succulent natural foods.

Knowledge of the changing seasonal bait acceptance is of practical value in connection with management operations. At times, locally, it may be desirable to remove, by poisoning, cottontail populations which are known to be diseased, or which are causing obvious damage to cultivated crops or range forage. More often it may be de-

sirable to retain the cottontail population while removing certain harmful rodent species. Ground squirrels, for instance, are controlled by annual poisoning on many of the foothill ranges. Squirrel poisoning operations during the winter or spring months would result in relatively light losses to the cottontail population since grain bait is not especially attractive to the rabbits at that season; but summer or early fall squirrel poisoning might at the same time reduce the rabbit population even more drastically.

Live trapping and marking of rabbits through a three-year period resulted in 1,159 captures of 228 individuals, and indicated that these animals are attached to definite small areas. Diameters of "foraging areas" within which individual rabbits usually stayed were roughly perhaps 700 feet, but were variable and occasionally long foraging trips were made. Immature animals appear to range less widely than adults. Of 23 rabbits released at a distance from the point of capture, three made homing movements of 4,400, 3,550 and 3,150 feet respectively; 10 were recaptured near the place of release, and the others were not again recorded.

One rabbit was recorded to have shifted its range a distance of 3,300 feet. Such movements may be fairly common and important in the population turnover of small areas. Water and succulence in the dry season attract unusual concentrations of cottontails.

In censusing the population by the ratio of marked ones to others during the dry season of each year on the 80-acre study area, the following numbers were recorded: 1939, 153; 1940, 53; 1941, 95. Allowing for movements outside the 80 acres, the population density was calculated as one per 1.2 acres in 1939 and one per 2.6 acres in 1940. In its cottontail population, the 80-acres study area was below the average of the experimental range as a whole. Road counts over 1,754 acres of the experimental range compared with similar counts on the trapping area, indicated a population density for these pastures 1.7 times that of the study area.

Observations on the feeding habits indicated that in spring the common forage plants most used by cattle, soft chess, foxtail fescue, broadleaf filaree, popcorn flower, and gold fields, make up the bulk of the cottontail diet. Through the summer heavy use of soft chess continues, but as the forage crop in general dies out, there is a distinct tendency to concentrate on swale vegetation where succulence remains. Clovers, rush, and dock are swale plants especially sought at this time. Leaves, seeds, and stems of tarweed, and leaves and stems of turkey mullein are often taken in summer. These along with dock, constitute plants rather unpalatable to livestock, so that competition is somewhat reduced during the dry season. Cast seeds of foxtail fescue constitute an important food source during the dry season.

Numerous wildlife species predatory on cottontails occur in the region of the experimental range. In order of their importance, predators included the coyote, rattlesnake, horned owl, gopher snake, gray fox, and red-tailed hawk. From the proportion of rabbit found for each species in the course of numerous scat, pellet, and stomach examinations, the population density of these predators, and the individual food requirement of each kind, it was estimated that predation factors annually might consume a cottontail weight of 1,229 grams per acre. This greatly exceeds the weight of the cottontail population actually present in late summer, before the breeding season begins. Nevertheless, the cottontail may be able to withstand this severe predation pressure by virtue of this long breeding season with possibly several litters of young annually for each adult female.

One diseased and dying rabbit was found, but no evidence was obtained that disease causes extensive mortality or affects population trends in this locality.

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