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## PREDATION BY OWLS IN THE SIERRAN FOOTHILLS OF CALIFORNIA

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In the course of ecological studies of rodents in the woodlands of the foothill ranges east of Madera, Madera County, California, owls attracted attention as predators which might affect the populations of these prey animals. In 1939, 1940 and 1941 at the San Joaquin Experimental Range, the rodent species present and the population densities of several kinds were investigated by intensive live-trapping and marking. In this same period and in 1946, the following pellets were collected and analyzed: 654 of the Horned Owl (*Bubo virginianus*), having 1471 prey items, and 240 of the Barn Owl (*Tyto alba*), having 517 prey items. These two food samples afford a basis for comparing the feeding of these two raptors with each other and with hawk, mammal and snake predators where all had the same choice of prey.

Owl pellets were collected at irregular intervals as time permitted. Those of Horned Owls were found at dozens of different places, over the entire 4600 acres of the Experimental Range, and probably represented a large number of individual owls. Many of them were found singly while others were found in small accumulations beneath favored perches or day roosts. The 240 Barn Owl pellets were found in much larger accumulations, in only four different places, one of them a perennial nesting site.

Pellets were collected by the writer, and several helpers, Freeman Swenson, Jack Ramley, Bernard Mitchell, Raymond Sharp, Oscar Hornback, Richard Loughery, Frank Ahern, and Alvin Dodge. Swenson also contributed records of prey items from nests and field observations on owls. Pellet material collected in 1939 and 1940 was analyzed by Howard Twining, Daniel F. Tillotson and John E. Chattin; that collected in 1946 was analyzed by the writer.

### HABITAT AND ASSOCIATED VERTEBRATE ANIMALS

The San Joaquin Experimental Range, where observations on owls were made, is in rolling foothills broken by numerous ravines. It is in the blue oak-Digger pine belt of the Upper Sonoran Life-zone, here characteristically a grassland interspersed with trees, clumps of chaparral and piles of large granite boulders. Elevation of the study area varies from 700 to 1500 feet.

Fifteen species of rodents and rabbits present on the Experimental Range provide food for several kinds of predators. The pocket gopher (*Thomomys bottae*) is the most abundant mammal, usually occurring in populations of several or many per acre, and increasing in spring in favorable locations to thirty per acre, or perhaps considerably more. It may breed several times annually. The kangaroo rat (*Dipodomys heermanni*) fluctuates in numbers over periods of years. Road counts and poisoning off of small areas in 1935 indicated a population as high as thirty per acre. Monthly census by ratio of marked kangaroo rats recaptured to original number marked on an 80-acre area in 1939, 1940 and 1941 indicated population changes within the limits of four to

seven per acre, but in early 1946 on this same area the average was only one per acre. The California ground squirrel (*Citellus beecheyi*), censused on this same area in five different years by exhaustive live-trapping, had a breeding population of between three and four per acre, but on most other parts of the Range its numbers were lower. The Audubon cottontail (*Sylvilagus auduboni*) in the summer of 1940, through road counts and live-trapping, was computed to have a population average of 0.6 per acre and in some other years it was more numerous, perhaps several times that figure. The woodrat (*Neotoma fuscipes*) occurs in populations of several per acre where brush, rock piles, or live-oaks provide adequate shelter, but it is scarcer on relatively open areas. The winter population on a five-acre plot trapped out in 1939 was found to be three per acre. This area was thought to be fairly typical of the range as a whole with respect to amount and distribution of cover. The pocket mouse (*Perognathus inornatus*) is a grassland species with a population of perhaps three per acre as estimated by live-trapping. Three cricetid "mouse" species, *Peromyscus boylii*, *P. truei* and *P. maniculatus*, each occur in populations of several per acre, in some situations at least. The first two are generally in rocky and brushy places, the last in grassland. Much scarcer and more localized rodent species on this area are the California pocket mouse (*Perognathus californicus*), meadow mouse (*Microtus californicus*), chipmunk (*Eutamias merriami*) and harvest mouse (*Reithrodontomys megalotis*). The jackrabbit (*Lepus californicus*) is also scarce in this part of the foothills. The house mouse (*Mus musculus*) has not been found away from buildings in this locality and was not represented among more than 7500 food items of various predators.

The California Quail (*Lophortyx californica*), an important game bird locally, was censused at the beginning of the nesting season in different years as follows: 1938, .43 per acre; 1939, .38 per acre; 1940, .26 per acre (Glading, 1941:35).

#### HORNED OWL

*Numbers.*—The Horned Owl (*Bubo virginianus pacificus*) is an abundant resident, usually occurring in pairs. These keep to their jointly occupied territories maintained against intrusion by other Horned Owls. Several times counts were made of those hooting on an area of between 1900 and 2000 acres, approximately 1½ miles wide by 2 miles long, to determine the numbers present. The first attempt at census was made on October 7, 1938, 6:30 to 9:30 p.m. Four different observers, evenly spaced on one edge of the area, walked slowly across it along parallel courses and plotted the location of each owl heard hooting. Twenty were recorded, of which fourteen were definitely or tentatively classed as members of pairs, while the remaining six were all so isolated from each other that they could not have been pairs. Two of those heard, instead of hooting, made the squalling sounds which are supposedly begging calls of young or females. It is probable that some of the adult owls had mates which remained silent. Several later counts were made on the same area, as shown in table 1.

Table 1  
Number of Horned Owls Heard on 2000-acre Area

Time of count	Number of paired adults	Number of birds heard singly	Total
October 7, 1938, 6:30-9:30 p.m.	14	6	20
April 4, 1939, 8:30-9:40 p.m.	12	13	25
November 27, 1939, 8:30-10:00 p.m.	8	17	25
February 20, 1940, 8:30-10:00 p.m.	10	7	17
November 8, 1940, 9:30-11:30 p.m.	6	8	14
February 19, 1941, 1:30-3:00 a.m.	8	7	15
January 13, 1947, 7:00-10:30 p.m.	8	8	16

Six observers participated in each of the counts in 1939 and 1940, five in the count in 1941. The count in 1947 was made by a different method, with only two persons traveling over the area by automobile and listening from several well distributed points. In the course of the counts, several Horned Owls were seen flying which did not hoot. Also, many hooting singly were probably paired, and in each count we failed to record any from extensive areas where they were known to occur. Therefore, it is believed that the counts are, in every instance, below the actual number present. They serve merely to indicate the minimum numbers present. They show that there was at least one owl to a hundred acres.

Horned Owls of a pair tend to stay near together and sometimes even perch in the same tree. They may hoot alternatively at intervals of a few seconds. Shortly after sunset they have been seen and heard hooting from high, conspicuous perches such as dead snags. Horizontal limbs of larger Digger pines provide perch sites during the night hours of activity, and accumulations of excreta and pellets often can be found beneath them. Such high perches may serve mainly for territorial hooting. In many instances at least, the perches used in actual hunting are lower, so that prey may be more readily detected and pursued at close range. Pellets and excreta have been found on large granite boulders at piles and outcrops. Such perches atop rock piles must be especially strategic locations for hunting since prey of several kinds, including cottontails, woodrats, brush mice and rock mice, center their activities about such shelter, hiding beneath the rocks and between their crevices. Other hunting perches are provided by fence posts, stumps, and logs.

The area covered in the course of a night's hunting was not definitely determined. Several times a pair was seen at dusk making a flight of a quarter of a mile or more across open fields to hunt on a wooded ridge opposite the one where they had roosted for the day. In other instances pairs heard hooting night after night apparently limited much of their activity to a few acres of certain favorite hillsides or ravines. In the spring and summer of 1946, a pair with grown young, heard regularly at the headquarters of the Experimental Range, shifted from time to time over different parts of their supposed territory. For a period of weeks in July and August they came almost nightly to the vicinity of the headquarters building and could be heard hooting from the roof, or from one of several near-by trees. An unusual concentration of cottontail rabbits attracted each night to lawns about the building by the green grass, which was unavailable elsewhere, probably induced the owls to shift their hunting to this place.

*Feeding.*—Day roosts of the owls were the site of the most successful pellet collecting. These were in well sheltered places such as wooded ravines, where perches were most often within the crowns of thick live oaks (*Quercus wislizenii*), but sometimes were in small, dense Digger pines (*Pinus sabiniana*). Occasionally as many as 20 or 30 pellets were found beneath such a roost. Often several small accumulations, probably of a single owl, or a pair, were found within a small area of one or a few acres. It is likely that change from one roost to another takes place frequently over periods of weeks or months. Molestation by jays and other birds may lead to such shifts. In some instances collections were made beneath the same roost on successive occasions, but more often no new accumulations were found after an original lot had been gathered. This tendency of the owls to shift frequently and to leave only small accumulations of pellets in well sheltered places made difficult the amassing of a large collection.

The 1471 prey items of the Horned Owl identified from 654 pellets are classified according to several major taxonomic groupings and listed in table 2 in order of frequency. In many instances the smaller invertebrates may not have been actual prey

of the owls but may have been in the stomachs of bird, lizard or amphibian prey. Small or medium-sized insects were found with most occurrences of the spadefoot toad; invertebrates found with them and probably eaten by them included: 13 *Amara*, 3 *Coni-ontis*, 4 *Pterostichus*, and one each of *Chlaenius*, a small carabid, *Amphicyrta*, *Bolbo-ceras*, *Pleocoma*, and a snail. An ant and *Romalium* were found in the same pellets with flicker remains. A small scarabeid was found in the same pellet with a whiptail lizard, which probably had eaten it. The larger kinds of insects and other arthropods are taken regularly by the owls, although by bulk they do not comprise any significant part of the diet. The Jerusalem cricket, however, is the most frequent of all items, and in each of the eleven months that pellets were collected, it occurred with about the same relative frequency. Errington, Hamerstrom and Hamerstrom (1940:808) suggest that predation on arthropods is most characteristic of the young owls which are inexperienced hunters; however, Jerusalem crickets were favorite morsels throughout the year for both adults and young in the area of this study.

Table 2

## Foods Taken by Horned Owls

Group	Common name	Scientific name	Number of occurrences	
MAMMALS	Woodrat	<i>Neotoma fuscipes</i>	240	
	Cottontail	<i>Sylvilagus auduboni</i>	205	
	Kangaroo rat	<i>Dipodomys heermanni</i>	201	
	Pocket gopher	<i>Thomomys bottae</i>	115	
	White-footed mice	<i>Peromyscus boylii, truei,</i> and <i>maniculatus</i>	34	
	Ground squirrel	<i>Citellus beecheyi</i>	13	
	Meadow mouse	<i>Microtus californicus</i>	10	
	Pocket mice	<i>Perognathus inornatus</i> and <i>californicus</i>	21	
	Rodents, unidentified		8	
	Harvest mouse	<i>Reithrodontomys megalotis</i>	3	
	Opossum	<i>Didelphis virginiana</i>	1	
	Spotted skunk	<i>Spilogale gracilis</i>	1	
	Gray squirrel	<i>Sciurus griseus</i>	1	
	Red bat	<i>Nycteris borealis</i>	1	
	Pallid bat	<i>Antrozous pallidus</i>	1	
	BIRDS	California quail	<i>Lophortyx californica</i>	10
		Birds, unidentified		6
		House finch	<i>Carpodacus mexicanus</i>	5
		Scrub jays	<i>Aphelocoma coerulescens</i>	4
		Fringillids, unidentified		3
Red-shafted flicker		<i>Colaptes cafer</i>	3	
Screech owl		<i>Otus asio</i>	2	
Sparrow hawk		<i>Falco sparverius</i>	2	
Coot		<i>Fulica americana</i>	2	
Spotted towhee		<i>Pipilo maculatus</i>	2	
Mexican bluebird		<i>Sialia mexicana</i>	2	
Acorn woodpecker		<i>Balanosphyra formicivora</i>	1	
Oregon junco		<i>Junco oreganus</i>	1	
Bullock oriole		<i>Icterus bullockii</i>	1	
Water bird, unidentified, possibly a grebe			1	
REPTILES	Gopher snake	<i>Pituophis catenifer</i>	20	
	California racer	<i>Coluber lateralis</i>	7	
	Rattlesnake	<i>Crotalus viridis</i>	4	
	Snakes, unidentified, one possibly a night snake, <i>Hypsiglena</i>		4	
	King snake	<i>Lampropeltis getulus</i>	2	
	Yosemite skink	<i>Eumeces gilberti</i>	2	

Group	Common name	Scientific name	Number of occurrences	
REPTILES	Fence lizard	<i>Sceloporus occidentalis</i>	1	
	Whiptail lizard	<i>Cnemidophorus tesselatus</i>	1	
	Alligator lizard	<i>Gerrhonotus multicarinatus</i>	1	
	Lizard, unidentified		1	
	Reptile, unidentified		1	
AMPHIBIANS	Spadefoot toad	<i>Scaphiopus hammondi</i>	24	
CARRION			2	
INVERTEBRATES	Jerusalem cricket	<i>Stenopelmatus</i>	325	
	Beetles	Scarabeids		3
		<i>Phobetus</i>		2
		<i>Bolboceras</i>		1
		<i>Pleocoma</i>		11
		<i>Polyphylla</i>		2
		Tenbrionids		3
		<i>Coniontis</i>		4
		<i>Eleodes</i>		2
		Carabids		3
		<i>Harpalus</i>		2
		<i>Pterostichus</i>		20
		<i>Chlaenius</i>		1
		Cerambycid		1
		<i>Ergates</i>		7
		<i>Prionus</i>		8
		<i>Amphicyrta</i>		10
		<i>Odontaeus</i>		2
		<i>Amara</i>		15
		<i>Romalium</i>		10
		<i>Dytiscus</i>		1
	Weevil		1	
	Beetles, unidentified		10	
	Ants		2	
	Grasshopper		1	
	Warble	<i>Cuterebra</i>	1	
	"Arachnids," probably <i>Eurypelma</i>		37	
Scorpions		15		
Centipede		1		
Snail		1		

The occurrence of two coots and another water bird in the pellets is puzzling, as coots have not been seen on the area, which is waterless for much of the year. Two small reservoirs in the vicinity of the Experimental Range headquarters were occasionally visited by migrating waterfowl and may have attracted the coots, which would have been highly vulnerable to owl predation in such a situation.

The relative importance of different prey species in the diet is not well brought out by a mere listing of number of occurrences for each, as some kinds are so much smaller than others that their proportion is relatively insignificant. Emlen and Evans (1947) have emphasized the importance of relative bulk of different prey species that occur in pellets. Within each prey species, size varies in adults and even more if young are considered. Nevertheless, this size variation is slight in most instances as compared with the size differences between prey species. The true composition of the diet can best be shown on the basis of the average weight for each prey species and the total number of its occurrences in pellets. Assuming such average weights for all items, the total weight of identified prey would have been 265.6 kg. distributed among the principal prey species in the percentages shown in table 3.

Table 3  
Calculated Composition by Weight of Horned Owl Food

Species	Prey		
	Average weight in grams	Occurrence in Horned Owl food 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
Gopher snake	500	20	3.7
Ground squirrel	500	13	2.4
Others	variable	677	6.1
Totals		1471	100.0

Of the "other" prey, none alone made up as much as one per cent in this computation. Quail, "bird," rattlesnake, "snake," coot, "rodent," mouse (*Peromyscus*), racer, king snake, gray squirrel, opossum, spotted skunk, flicker, jay, meadow mouse, screech owl and pocket mouse, in that order of importance, all comprised fractional percentages each more than 0.1 per cent. The remaining kinds of prey, harvest mouse, bat, woodpecker, towhee, bluebird, finch, sparrow hawk, skink, whiptail lizard, alligator lizard, fence lizard, spadefoot toad, and about 29 kinds of arthropods each comprised less than 0.1 per cent, or mere traces.

For most of the vertebrate prey species, identifications were ordinarily made from skulls (or mandibles), and the number of recorded occurrences represents the actual number of individuals with fair accuracy. The cottontail is a notable exception as skulls of this species ordinarily are too large to be swallowed whole by the owls, and identifications were usually made from vertebrae or limb bones. Obviously a cottontail is large enough to provide several owl meals. If return to such carcasses for successive meals is habitual, or if members of a pair share their meals, the same rabbit might be counted two or more times in different pellets. This may have resulted in erroneously high numbers of cottontails, and percentages by weight, in the food. Errington, Hamerstrom and Hamerstrom (1940:769) estimated that the skeletal remains of cottontails in the horned owl pellets analyzed by them averaged 13 per cent of the complete skeleton for adults and 70 per cent for young. The implication is that an adult cottontail might be used for 7 or 8 successive meals and represented in as many pellets. For such kinds of prey, too large to be eaten at a single meal, the number of occurrences may be considerably greater than the number of individuals represented. The cottontail is, however, the only important prey species which much exceeded the owls' food capacity for a meal. If its relative numbers in the pellets have been overestimated by the assumption of one individual for each occurrence, the other prey species have been correspondingly underestimated. The woodrat may conceivably comprise a greater part of the food weight. However, the calculated weight percentage of the cottontail was almost exactly the same in the 94 prey items recorded from nests as their weight percentage computed for the pellet items. It is doubtful whether a carcass, even of large prey, generally provides a series of successive meals. In the dry season at least, temperatures are usually so high that carcasses would deteriorate or decay from one night to the next, and the numerous scavenging mammals, birds and insects would soon consume them.

The estimated percentage of gopher snakes in the prey weight is doubtless somewhat high, as many of those eaten were young and the differential between young and adult weights is much greater than in mammalian prey species. None of the percentages

can be considered exact, but they bring out the fact that the cottontail and woodrat make up the bulk of the diet, with kangaroo rat, gopher, gopher snake, and ground squirrel of secondary importance, and a long list of mammal, bird, reptile, amphibian and arthropod species separately comprising hardly more than traces and combined making up only a small percentage.

Except in a few instances, seasonal changes in relative availability of different prey species on this area are not evident. The principal prey species are abundant the year around. The collection of pellets is not well adapted to show seasonal changes in feeding since for most of the pellets exact date, or even month, of deposition is not known with certainty. Especially during the dry season, pellets do not disintegrate rapidly, and those collected in fall might have been deposited at any time during late spring or summer.

Nearly all pellets were collected in the months of November (1939 and 1946), January (1940), February (1940), March (1940), and May (1940). In table 4, the numbers of various kinds of prey in these collections, classified as to months, are shown. The collection of 1946 is omitted from this month-to-month comparison since prey populations were known to have changed somewhat in the intervening years. Varying age of the pellets collected in any month, and differences in locations and individual owls represented in the monthly collections may tend to obscure seasonal trends.

Table 4

Seasonal Trends in Composition of Horned Owl Food

	Numbers in November	Numbers in January	Numbers in February	Numbers in March	Numbers in May
Rabbit	25 ( 9.8%)	25 ( 7.5%)	22 ( 7.4%)	22 (13.8%)	37 (19.8%)
Woodrat	21 ( 8.3%)	43 (12.8%)	46 (15.4%)	29 (18.1%)	17 ( 9.1%)
Kangaroo rat	41 (16.1%)	36 (10.7%)	31 (10.4%)	17 (10.6%)	27 (14.5%)
Pocket gopher	18 ( 7.1%)	10 ( 3.0%)	15 ( 5.0%)	9 ( 5.6%)	13 ( 6.9%)
Miscellaneous mammals	10 ( 3.9%)	34 (10.0%)	20 ( 6.7%)	6 ( 3.8%)	7 ( 3.7%)
Birds	6 ( 2.4%)	8 ( 2.4%)	7 ( 2.4%)	4 ( 2.5%)	7 ( 3.7%)
Reptiles	5 ( 2.0%)	6 ( 1.8%)	1 ( 0.3%)	1 ( 0.6%)	0
Toad	0	3 ( 0.9%)	1 ( 0.3%)	8 ( 5.0%)	12 ( 6.4%)
Jerusalem cricket	110 (43.3%)	98 (29.3%)	128 (43.3%)	56 (35.0%)	49 (26.2%)
Miscellaneous arthropods	18 ( 7.1%)	72 (21.5%)	27 ( 9.1%)	18 (11.2%)	18 ( 9.6%)

No marked seasonal changes in food sources are brought out in table 4. In most instances, predation may have occurred in a month previous to the one in which the resulting pellet was collected, since pellets must have averaged at least a month old when found. Thus, reptile remains found mainly in pellets collected in November and January, at a time when reptiles were largely in hibernation, in most instances probably were eaten in early fall. Many represent newly hatched snakes, especially gopher snakes. Heaviest predation on rabbits was in May, at the season when the proportion of young rabbits to adults is highest. In the January, February and March collections, woodrats outnumbered every other kind of vertebrate prey, while kangaroo rats were most numerous in the November sample. Kangaroo rats ordinarily reach their annual peak in numbers in late summer since reproduction occurs throughout spring and summer but almost ceases in late fall and early winter.

All the pellets of the collection of 1946 were gathered in the month of November. Those collected in November, 1939, had different proportions of prey species (see table 5), notably kangaroo rats, and are significant in showing changed availability after this seven-year interval.

Table 5  
Comparison of Horned Owl Food Composition after a Seven-year Interval

Kind of prey	Numbers in November, 1939	Numbers in November, 1946
Rabbit	25 ( 9.8%)	54 (13.3%)
Woodrat	21 ( 8.3%)	58 (14.3%)
Kangaroo rat	41 (16.1%)	12 ( 2.9%)
Pocket gopher	18 ( 7.1%)	43 (10.6%)
Other mammals	10 ( 3.9%)	16 ( 3.9%)
Birds	6 ( 2.4%)	6 ( 1.5%)
Reptiles	5 ( 2.0%)	23 ( 5.6%)
Jerusalem cricket	110 (43.3%)	181 (44.5%)
Other arthropods	18 ( 7.1%)	13 ( 3.2%)
Totals	254	406

The kangaroo rat's decrease from 16.1 per cent of the total number in the sample of 1939 to 2.9 per cent in the sample of 1946 paralleled its population decrease in the same period from seven per acre in July, 1939, to just one per acre in February, 1946, on the 80-acre census area. It might be expected that at the peak of its population cycle the species would become a major food source to the owls because of ready availability.

In 1939, prey items from five different owl nests totaling 67 woodrats, kangaroo rats, cottontails, ground squirrels, and pocket gophers, were recorded (Fitch, 1940:74). In 1941, 27 prey animals of the same five species were recorded from three different nests. Altogether in these two years there were found 28 cottontails, 30 woodrats, 18 kangaroo rats, 13 ground squirrels and 5 pocket gophers.

*Behavior.*—Most Horned Owls seen during this study were those flushed in the daytime from roosting places, usually in thick live oaks. In daylight they were shy and alert, seldom allowing a person to approach within 100 feet. Warning alarm chirps of ground squirrels often drew attention to owls which had flushed which otherwise would have escaped unnoticed in low, rapid and silent flight. They were encountered frequently; often several were seen in the course of a day's field work.

Although mainly nocturnal, they are often heard hooting in late afternoon or evening, and on many occasions have been seen shortly before dusk perched on prominent look-outs. That they often do hunt by daylight is shown by the frequent occurrence of ground squirrels among the prey items. Several instances of daytime hunting were observed. On February 24, at 3:15 p.m., an owl was discovered in a narrow ravine, eating a cottontail. It flushed carrying the prey. Confined on three sides by the steep walls of the ravine, and a thick tree, it flew toward the observer and passed so close to him that he touched the rabbit with his finger tips in attempting to catch it.

One summer afternoon several ground squirrels were heard giving the characteristic scolding chirps which observers had learned to recognize as indicating the presence of a snake. Investigation revealed that the cause of the disturbance in this exceptional instance was a Horned Owl on the ground beneath a live oak, with a freshly killed gopher.

At 5:30 a.m. on a summer morning, an owl, flushed from beneath a live oak, carried a three-foot gopher snake to a thick tree. When flushed again, it was so weighed down by the dangling snake that it failed to clear a barbed wire fence, and the snake was impaled and torn from the owl's grasp. Thrown off balance in flight, the owl swerved sharply and lit on the ground near the fence, but it flew away when approached. Two hours later it had returned, perhaps to retrieve the snake, and was sitting beneath a tree near the scene of its mishap.

On a moonlit night, an adult striped skunk (*Mephitis mephitis*) disturbed by a person's approach lumbered away and a Horned Owl evidently attracted by the com-



motion, hovered low over the chaparral where the skunk had sought refuge. When the observer made a squeaking sound, the owl flew toward him and circled within 20 feet. In several instances owls have been "called up" at night by imitating the distressed squealing of a rabbit. Under such circumstances they were sufficiently bold and indifferent to humans to perch in a near-by tree watching for the expected prey.

Varying degrees of aggressiveness were displayed by parent owls when their nests were examined. The usual reaction consisted of flying from tree to tree with bill-snapping and occasional hooting. However, on April 23, 1941, Swenson recorded in his field notes the following: "As I moved young owls . . . the adult female suddenly swooped—squirrel chirps warned me and I ducked, but she knocked my sun helmet off and it dangled from one claw for ten feet." Three days later at the same nest, Swenson recorded: "Adult female owl came in a long glide; when I ducked, she dipped and struck at me. She lacerated my left forearm, which saved my face, and nicked my left shoulder."

*Nests.*—Nests were found in a variety of situations, and several of those observed were unsuccessful. Those recorded in 1938 and 1939 were described in an earlier paper (Fitch, 1940:73). Other nests were discovered in 1940 and 1941, as follows:

1. March 13, 1940: 25 feet above ground, in depression on top of Digger pine stub; 3 eggs.
2. April, 1940: 15 feet above ground, on bole of cottonwood growing in stream bed; 3 eggs.
3. March 11, 1941: 45 feet above ground and about 25 feet out on horizontal limb; an old gray squirrel nest taken over.
4. April 15, 1941: 50 feet above ground in Digger pine, in a shallow depression of trunk where a large limb had broken off; 3 half-grown nestlings.
5. April 17, 1941: 65 feet above ground in crotch of main trunk of Digger pine; small (16×8 inches in widest dimensions), of large twigs and completely filled up by one young owl.
6. May 20, 1941: On ground, sheltered by edge of a large boulder; two nestlings.

A few days after its discovery, nest 2 was found to have been robbed of its eggs. Fresh raccoon tracks crossed a sand bar to the base of the tree, and it seemed likely that this mammal had robbed the nest.

The half-grown young in nest 4 were attacked by small blood-sucking flies (*Eusimulium clarum*) which were found to cause heavy mortality among nestling red-tailed hawks (Fitch, Swenson and Tillotson, 1946: 216). The owls' dense feathers seemed to provide effective protection, but their eyelids were scabbed from bites. The same week, the single young owl examined in nest 5 also had its facial region scarred by the bites of these flies. Four days after its discovery, nest 5 had collapsed, about half of it had fallen, and the nestling had disappeared. An old nest of a Horned Owl, found in summer after the nesting season, contained a single egg which had its shell punctured, possibly by a jay.

#### BARN OWL

This species is much less common than the Horned Owl on the Experimental Range. No definite count of its population was obtained. In course of the seven counts of Horned Owls, in which 132 were recorded, only two Barn Owls were heard. This probably does not provide a fair clue to the abundance of Barn Owls, as Horned Owls are more vocal. Barn Owls also tend to be more secretive in their daytime retreats. Their molted feathers were seldom seen and their pellets were found in only four places. It is certain that their numbers amounted to only a fraction of the population of Horned Owls, but probably there were several pairs on the area. Especially in the vicinity of the headquarters of the Experimental Range, they were often heard at night and occasionally were seen flying slowly over a large swale, hunting. In July, 1940, a Barn Owl was found roosting in a large eucalyptus tree in the headquarters area and 44 pellets beneath its perch had accumulated during the dry season. The prey items in these pellets were:

60 pocket mice, 41 gophers, 5 mice (*Peromyscus*), 3 each of young cottontail, kangaroo rat, and meadow mouse, and one skink.

In the spring of 1939, a Barn Owl was flushed repeatedly from a hollow in the top of an oak stub about 3 feet thick and 15 feet high. Apparently it was nesting in this cavity. In the spring of 1940, it was observed that the stub was again occupied by a Barn Owl. No further observations were made until the spring of 1946 when a Barn Owl was again flushed there several times. In the fall of 1946, the cavity was finally investigated. It was found to be divided into numerous chambers and niches by incomplete partitions of decaying wood, and the cavities had apparently served as nests over many years. Small accumulations of pellets, mostly from young owls, had formed in

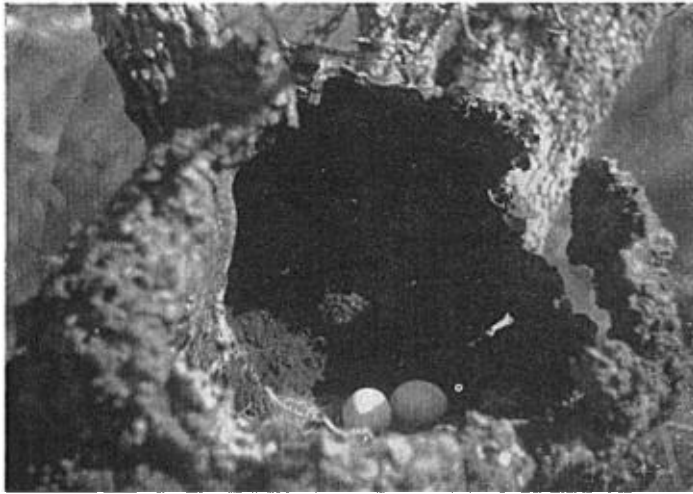


Fig. 24. Horned Owl nest in trunk of blue oak at San Joaquin Experimental Range.

several niches where they had escaped trampling. Most of the pellets probably had rolled into the interior of the stub where they were inaccessible. Those gathered obviously were of different ages. Some were of fresh appearance with a superficial glaze of dried mucous and evidently were those of the current season, whereas others were stained and weathered and may have been several or many years old. The prey items identified, representing mostly or entirely the spring and the nesting season, were: 58 pocket gophers, 35 pocket mice, 29 kangaroo rats, 6 mice (*Peromyscus*), 4 meadow mice, 3 spadefoot toads, and one each of cottontail (young), woodrat, and ground squirrel.

At another place more than a mile from this one, a roost was situated in October, 1946, in a large live oak in a canyon bottom near a hay field at the edge of the Experimental Range. Twenty-one pellets from this roost contained: 26 pocket mice (24 *P. inornatus*, 2 *P. californicus*), 10 pocket gophers, 8 mice (*Peromyscus*), 2 woodrats, 2 kangaroo rats, 1 meadow mouse.

The fourth location where Barn Owl pellets were found was more than a mile from any of the other three. Two thick live oaks about 100 feet apart were found to be alternative perches, in May, 1946, when all pellets beneath them were collected. At these same spots later accumulations from the same owl were gathered in early September, in October, and in November, providing a basis for showing seasonal changes in food

composition. For each lot, the percentages of total number of prey animals made up by the several species are shown in table 6.

Table 6  
Seasonal Change in Relative Numbers of Different Prey Animals in a Barn Owl's Pellets

	Numbers in May	Numbers in September	Numbers in October	Numbers in November
Pocket gopher	46 (56.9%)	31 (40.7%)	11 (26.2%)	15 (48.4%)
Pocket mouse	29 (35.8%)	39 (51.4%)	24 (57.1%)	10 (32.3%)
<i>Peromyscus</i>	3 ( 3.7%)	4 ( 5.3%)	6 (14.3%)	4 (12.9%)
Others	3 ( 3.6%)	2 ( 2.6%)	1 ( 2.4%)	2 ( 6.4%)

These figures show mainly that the numbers of pocket mice taken increase, in relation to gophers, in the dry season samples and are smaller in fall and spring, winter not being represented. This trend is to be expected, since pocket mice hibernate during several months of cool weather, and gophers are least active above ground during the dry season. Even during the season when they are least available, gophers made up most of the food of this owl.

For the total list of prey items taken by the Barn Owl, as for those of the Horned Owl, computation of weight percentages of each species, based on average adult weights, was made. The calculated percentages of the Barn Owl's food are shown in table 7.

Table 7  
Calculated Composition by Weight of Food of the Barn Owl

Species	Average weight in grams	Occurrence in Barn Owl food Number of occurrences	Computed percentage by weight of total recorded prey
Pocket gopher	100	192	71.4
Pocket mouse	10	223	8.5
Kangaroo rat	60	35	7.8
Woodrat	200	5	3.7
Cottontail (young)	200	4	3.0
Mouse ( <i>Peromyscus</i> )	20	36	2.7
Meadow mouse	30	9	1.0
Ground squirrel (young)	200	1	.8
Gopher snake	200(?)	1	.8
Skink	20	3	.2
Spadefoot toad	20	3	.2
Fence lizard	15	1	.1

In the foregoing listing, the 223 records of pocket mouse include five of the relatively large *Perognathus californicus*; the remainder are of *P. inornatus*.

Hawbecker (1945) made collections of pellets of the Barn Owl at ten different localities on the west side of the San Joaquin Valley and near Monterey Bay, at points 65 to 130 miles west of the present locality. His records, particularly those from the arid west side of the valley, have the same trend as those of the present study in indicating the gopher and San Joaquin pocket mouse as the most frequent prey. The pocket mouse was absent from the localities on Monterey Bay where the harvest mouse, brush rabbit, meadow mouse, woodrat, and various birds were important prey species. His more numerous records from varied habitats naturally revealed a much wider range of prey than that found in the present study.

At the Experimental Range, the Barn Owl is the only predator known to subsist principally on gophers, and the owls' numbers are few, in view of the great abundance of this prey species. Evidently factors other than food supply limit the population of this owl.

Factors which limit the population probably include distribution of favorable nesting sites in relation to tracts of open grassland, and predators. In October, 1946, remains of a recently killed Barn Owl were found under circumstances suggestive of predation by a Horned Owl. The remains were near a known Horned Owl roost. A trail of Barn Owl feathers for 100 yards along the bottom of a ravine disclosed the course of the predator as it ate the Barn Owl, parts of which, including a wing and a leg, had been dropped beneath three large trees. One of these trees was a Horned Owl perch beneath which pellets were gathered.

#### DISCUSSION

Comparison of the weight percentages made up by different prey species in the diets of the Barn Owl and the Horned Owl shows that there is little competition between them through overlapping food habits. Cottontails and woodrats comprised nearly four-fifths of the diet of Horned Owls (table 3), but only 6.5 per cent of the food of Barn Owls (table 7). Pocket gophers, making up more than 70 per cent of the Barn Owl diet, comprised less than six per cent of the Horned Owls' food, and pocket mice made up more than eight per cent for the Barn Owl as against a mere trace for the Horned Owl. Kangaroo rats were preyed upon to about the same minor extent by both species, 6.1 per cent for the Horned Owl and 7.8 per cent for the Barn Owl.

The Barn Owl is the more specialized in its feeding; it took only twelve prey species, with medium to small rodents making up nearly all its food. There were rare occurrences of snake, lizard and toad, and none of arthropods or birds. In contrast, the Horned Owl fed mainly on rat-sized rodents and rabbits but varied this diet with several mammalian species from skunk and opossum to bats and small mice. It also took a dozen kinds of birds, including other raptors, most of the more common snakes and lizards, including the venomous rattlesnake, and a great variety of arthropods. The trends of feeding records for the two owl species bring out a difference in their place and manner of hunting: the Barn Owl's prey animals were those which might have been hunted and caught by beating over the swales and grassy slopes, namely, gophers, pocket mice, kangaroo rats, and meadow mice. The Horned Owl's prey, mainly cottontails and woodrats, would have been caught mostly about piles and outcrops of granite, and about the live oaks, which were always in such rocky situations.

The effect of owl predation on the rabbit and rodent populations is not readily apparent or demonstrable without knowledge of the exact number of owls and of the kinds and numbers of prey animals eliminated by each of them in a given area. However, the incomplete information at hand concerning the numbers of owls and the quantity of prey taken by them from roughly measured populations provides a clue as to their possible effect. The food weight necessary to maintain an owl, and the relationship of this weight to the prey actually killed (presumably some parts are discarded at times) are of significance in this connection. A fledgling Horned Owl kept in captivity for 17 days consumed 4 ground squirrels, 1½ cottontails, 2 kangaroo rats, 2 gophers, most of a gopher snake, a rattlesnake, a jay and a chipmunk, and disgorged 20 pellets. The food was not weighed but probably totalled about 2000 grams. It is probable that for an individual Horned Owl the daily food requirement approximates 120 grams. At least this seems a likely amount for a bird of this size and is roughly applicable for a similar sized raptor, the Red-tailed Hawk. Errington, Hamerstrom and Hamerstrom (1940:770) concluded, on the basis of skeletal remains in pellets, that a typical meal would be the equivalent of about 6 large mice, about ½ Norway rat, about 3⅓ passerine birds, ⅔ of a screech owl, pigeon or bob-white, or ⅓ of a pheasant. With an individual daily food requirement of 120 grams and a minimum population of

one to 100 acres, the average food consumption would amount to 1.2 grams per acre per day, or 440 grams per acre per year. According to the food percentages in the samples analyzed, this 440 gram weight would be distributed among the principal prey species as shown in table 8.

Table 8  
Quantity of Horned Owl Food in Relation to Existing Prey Populations

Kind of prey	Estimated weight in grams per acre taken annually by Horned Owls	Estimated percentage by weight of actual breeding population taken annually by Horned Owls
Cottontail	269	56.0
Woodrat	102	17.0
Kangaroo rat	19.8	5.5
Pocket gopher	18.9	1.9
Gopher snake	16.3	13.6
Ground squirrel	10.6	.7

It is evident that predation by Horned Owls on cottontails and woodrats is sufficiently severe so that their populations might be affected. For the cottontail especially, predation by Horned Owls must be a major ecological factor, since the weight eliminated annually is computed as more than half that of the actual breeding population. To the extent that young are taken, relatively larger numbers would be required; however, even during the owls' nesting season, when young cottontails were abundant, adults were numerous among those brought to the nest. The Audubon cottontail has a high reproductive potential. Orr (1940:143) states that its average litter size is 3.6 and that it produces 2 or 3 litters annually, so that each female might be expected to produce nine young during the breeding season. An even higher potential is indicated by the possibility of more than one generation annually, as Ingles (1941:243-246) cites an instance of a female, marked soon after birth, which had matured and produced a litter of its own at the age of six months. The woodrat has a comparable rate of reproduction. For the kangaroo rat, pocket gopher, and ground squirrel, and various mouse species, the numbers taken would amount to such a small portion of the annual increase that their populations could be but little affected.

In view of its sparser population and smaller size, the Barn Owl probably takes no more gophers locally than does the Horned Owl, although it subsists mainly on them. The high gopher population would hardly be affected by these two species of owls taking, as they do, only a small fraction of the potential annual increase. Indeed, from what is known of the numbers and feeding of the owls, hawks, coyotes, foxes, and snakes of the Experimental Range, it appears that all of them combined would scarcely exert appreciable predation pressure on gopher populations.

If the owls cannot be definitely credited with limiting the populations of their rodent prey, neither can they be blamed for any harmful predation on this particular area. The prey sample for the Barn Owl consisted almost entirely of animals generally considered harmful to agriculture—rabbits and rodents—with traces of reptile and amphibian prey. The prey sample for the Horned Owl also consisted mainly of "harmful" rabbits and rodents with only a small percentage of birds. Quail comprised only six-tenths of a per cent by weight, and the number taken could not amount to more than a small percentage of their annual increase. Certainly it would not appreciably affect the populations of this game bird.

The differing feeding trends of the two owls are of significance as a basis of comparison with those of the Red-tailed Hawk. The feeding of this latter raptor was investigated on the area during the same period (Fitch, Swenson and Tillotson, 1946). Percentages by weight calculated for each of the principal prey species are shown in the following table.

Table 9  
Comparison of Food Composition of Three Raptor Species on San Joaquin Experimental Range

Prey species	Weight percentages of food of Horned Owl	Weight percentages of food of Barn Owl	Weight percentages of food of Red-tailed Hawk
Cottontail	61.1	3.0	24.2
Woodrat	17.9	3.7	1.1
Kangaroo rat	4.5	7.8	.2
Pocket gopher	4.3	71.4	7.4
Gopher snake	3.7	.8	9.0
Ground squirrel	2.4	.8	49.5
Pocket mouse	.1	8.1	trace
Meadow mouse	.1	1.0	trace
Rattlesnake	.5	.....	2.1
Snake (unidentified)	.5	.....	1.6
Mouse ( <i>Peromyscus</i> )	.3	2.7	trace
Other species	(54+) 4.6	(2) .9	(57+) 4.9

Two other major predators on the area are the coyote and the rattlesnake. The coyotes' food composition by weight, as calculated from 1173 scats, consisted of cottontail 45.4 per cent, ground squirrel 31.2 per cent, gopher snake 6.0 per cent, woodrat 4.9 per cent, pocket gopher 3.5 per cent, kangaroo rat 3.3 per cent, others 5.7 per cent. The rattlesnakes' food composition by weight as determined from 271 items, consisted of ground squirrel 70.5 per cent, cottontail 15.2 per cent, kangaroo rat 5.9 per cent, pocket gopher 2.5 per cent, woodrat 1.7 per cent, others 4.2 per cent. Thus, the food composition for Horned Owls and for coyotes are similar, while that of rattlesnakes corresponds even more closely with that for Red-tailed Hawks.

#### SUMMARY

At the San Joaquin Experimental Range in the Upper Sonoran Life-zone of the Sierra Nevada foothills, Madera County, California, a study of predation by Horned Owls and Barn Owls was made. It was based on analysis of pellets: 654 of Horned Owl, containing 1471 prey items, and 240 of Barn Owl containing 517 prey items.

Prey populations were measured by live trapping and marking on selected areas. Of these prey animals the pocket gopher was the most abundant, attaining a maximum known population of more than 30 per acre; the kangaroo rat, woodrat, cottontail, ground squirrel, pocket mouse and white-footed mouse each at times attained populations of several per acre.

Seven counts of Horned Owls hooting on a 2000-acre area in five different years varied from 15 to 25 and probably some of those heard had mates which were silent during the times of the counts. A population of 1 to perhaps 1.5 per 100 acres is indicated.

Pellets of Horned Owls representing many individuals were gathered in small lots beneath day roosts, usually in thick live oaks, and beneath favorite night perches.

Among the prey items were definitely identified 17 kinds of mammals, 12 of birds, 8 of reptiles, one of toad, and 27 of invertebrates. There were 325 Jerusalem crickets, 240 woodrats, 205 cottontails, 201 kangaroo rats, 118 beetles (of several kinds), 115 pocket gophers, 52 arachnids including scorpions, 34 mice, 24 spadefoot toads, 21 pocket mice, 20 gopher snakes, 13 ground squirrels, 10 each of meadow mouse and quail, and small numbers of many other prey species.

Extensive samples collected in November, January, February, March and May showed only slight seasonal change in trends but the month of deposition was uncertain in most instances. The same group of prey species is available throughout the year. In a lot of pellets collected in November, 1946, kangaroo rats were less than one-fifth as frequent as in a collection made in November, 1939; the kangaroo rat population was known to have decreased correspondingly.

No definite figures as to the population of Barn Owls were obtained, but there was evidence of several pairs on the 2000-acre area.

The prey items identified were 218 San Joaquin pocket mice, 192 gophers, 36 white-footed mice, 35 kangaroo rats, 9 meadow mice, 4 cottontails, 5 each of woodrat and California pocket mouse, 3 each of skink and spadefoot toad, and one each of ground squirrel, fence lizard, and gopher snake.

Successive lots gathered in May, September, October, and November from beneath the same roost had a higher ratio of pocket mouse to gopher during the dry season months.

The Barn Owl is so scarce in relation to its principal prey species, the gopher, that it is unlikely that the gopher is appreciably affected. Even the combined effect of all predators seems insufficient to eliminate a substantial part of the gopher's annual increase in view of its numbers and reproductive potential.

Predation by Horned Owls would eliminate annually, for each acre of land, a rodent of woodrat to rabbit size, or its equivalent; more than half the prey (by bulk) is comprised by the cottontail, somewhat less than one-fifth by the woodrat. Nearly all the prey animals taken are of kinds either principally harmful or largely neutral in their economic bearings. For the Horned Owl an exception is the California Quail, which, however, made up less than one per cent of the food sample, and its populations probably would not be appreciably affected.

A comparison of composition by weight of the food of Horned Owl, Barn Owl and Red-tailed Hawk on the area showed that the three differ greatly in choice of prey, with greatest overlapping between the Horned Owl and Red-tailed Hawk in their predation on the cottontail, which was more than half of the owl's food and one-fourth of the hawk's food.

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