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BEHAVIOR AND FOOD HABITS OF THE RED-TAILED HAWK

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Intensive study of certain phases of the habits of the Red-tailed Hawk (*Buteo jamaicensis*) was made by the writers at the San Joaquin Experimental Range in the foothills of Madera County, California, during 1939, 1940, and the early part of 1941. This wide-ranging, common, and important raptor is well known through such detailed studies as those of McAtee (1935), Bent (1937), and Sumner (1929). The present study was intended to reveal economic importance of the Red-tailed Hawk as reflected by its feeding habits in one particular region. The rather stereotyped behavior observed by us in such habits as choice of nest sites, choice of prey, territorial perches, and size of territory, should afford significant contrast with observations on this species under other environmental conditions elsewhere. Individual adaptability enables these hawks to take advantage of varying environmental conditions. Because of their ability to cover great distances, there must be continual interchange of individuals between populations of the narrow foothill belt where our study was made and nearby regions such as the San Joaquin Valley, the Coast Ranges, the timber belt of the Sierra Nevada and the arid Great Basin. Banding records show that individuals may travel hundreds of miles (Bond, 1939:56; Lincoln, 1939:360). Observations on general behavior were made incidentally as opportunities arose, but it was the primary purpose of our study to determine the effect of predation of the Red-tailed Hawk on rodent populations by gathering feeding records and data regarding the population density of the hawks.

This study was made under the direction of Mr. Everett E. Horn of the United States Fish and Wildlife Service as a phase of rodent ecology in foothill range lands. Field work was shared by Fitch and Swenson. Swenson collected most of the prey records from nests and made hundreds of precarious climbs, often at the risk of attack. The identifications of prey in pellet material were made by Daniel F. Tillotson and Howard Twining.

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TERRITORIALITY

The hawks are mostly permanently paired and resident in definite hunting and nesting territories, although a small part of the winter population may consist of transient individuals. Through intensive study of several pairs we learned to recognize each bird individually by peculiarities of behavior, markings, and, sometimes, loss of certain flight

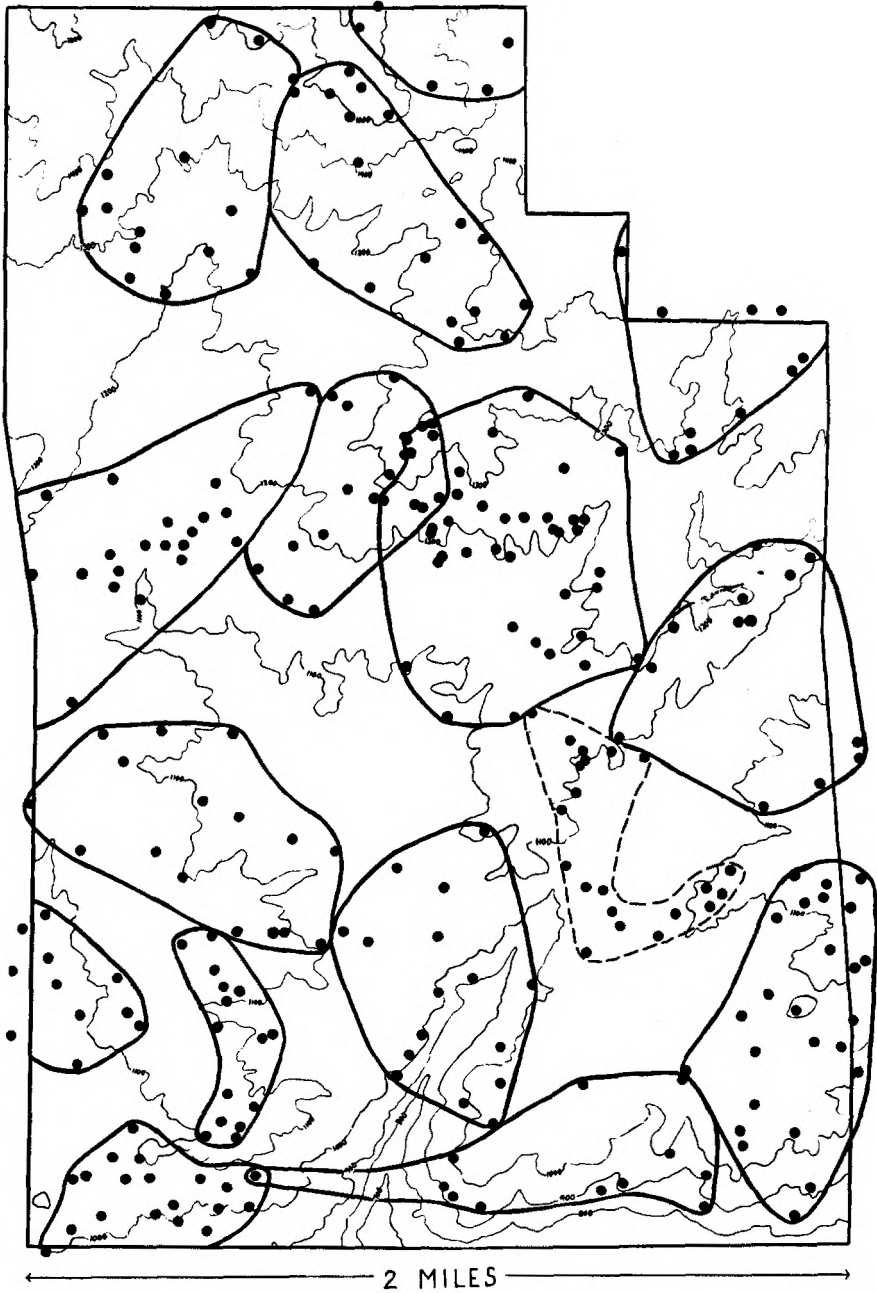


Fig. 43. Contour map of the San Joaquin Experimental Range, showing locations of some of the principal territorial perches of 16 pairs of Red-tailed Hawks in 1939; lines enclose perching area of each pair but do not represent territorial boundaries; broken line in right center indicates territory of pair which disappeared early in season.

feathers. The sexes are not always readily distinguishable, but the larger size of the female is often noticeable when the members of a pair are near together. The male hawk has a slightly more rapid cadence of wing beats, and in soaring moves in smaller circles than those of the female.

Territories tend to be circular or oval, but may vary greatly in size and shape according to the number and distribution of perch trees, food supply, territorial pressure, and physiographical features of the terrain. Frequently a ridge limits the territory of a pair on one or more sides, and the included small valley or swale comprises the hunting range. Such a ridge provides perches with views commanding extensive terrain and also provides rising air currents upon which the hawks may easily ascend from their perches.

Territories mapped from the distribution of perches covered 80 to 200 acres exclusive of the indefinite peripheral area also comprising a part of each. The perches and territories of the sixteen different pairs living partly or wholly on the San Joaquin Experimental Range were mapped in detail (see fig. 43). The entire area of the Experimental Range was used by the hawk population occurring on it and the behavior of the birds in continually contesting territorial boundaries suggested that the population was near the saturation point, with keen competition in an area otherwise favorable. The population density amounted to approximately one pair to half a square mile (320 acres); thus, on the average, as much as half of each territory was beyond the area enclosed by the perch trees. Territorial perches were recorded by observing the movements of the birds in the course of their daily activities. On foggy winter days when the hawks were unable to soar, they would fly directly from one perch to another, when flushed, and by following one for a short time, the observer could determine the general scope of its territory and the location of its favorite perches.

Adequate perches seem to be the most essential feature of a territory. The largest trees available are most apt to be used. Although scarcer than either blue oaks or live oaks, Digger pines furnish nearly all the territorial perches, being favored because of their greater heights and more open crowns. Live oaks generally do not afford suitable perches because of the dense outer foliage and too flexible and elastic outer branchlets. Of 272 trees recorded as used for perches 250 were Digger pines, 17 were blue oaks, and 5 were interior live oaks (all dead snags). The actual perches used are high horizontal limbs or sometimes the topmost branchlets. The fixed habit of the hawks in returning to the same trees does not extend to its constant use of the same branch and exact spot, for it may stop at any convenient location in the tree. Members of a pair often perch a few feet apart on the same limb or on adjacent limbs of the same tree. In the course of a day many different perch trees are used, but not in any definite sequence. One or a few perches are so much favored that a major portion of the bird's time is spent on them. During hot summer weather the hawks are apt to perch lower in the trees, in situations where main trunks or limbs provide some shade. As a result they are much less conspicuous at this season than in early spring when they perch more often in the tops of trees. On the Experimental Range trees suitable as perches are abundant but in other localities where they are scarce, Red-tailed Hawks may use large boulders or rock outcrops, or may even stop on the ground.

The boundaries of a territory are usually ill-defined and the area defended depends on the circumstances. The hawk protects from trespass certain trees and, with less interest, the area around them and the air above them. The degree of provocation required to incite a territorial attack varies according to the season, the weather conditions, the condition of the bird—whether alert and hungry or sluggish after a meal—and behavior of the mate. In flight the hawks often pass beyond the area where their perches are

located and spend much time soaring over areas where they seldom or never perch. One keeping at high altitude may pass unchallenged over the territory of another, whereas the same bird flying low among the tree tops would almost certainly be attacked. Fights may occur at high altitudes but such encounters are apt to be less violent than those which take place near the ground, consisting mainly of maneuvering and screaming. Territorial flights and combats are most frequent in early spring before the nesting period and seldom occur while the parent birds are occupied with the care of the young. Apparently much of the hunting at this time is done in a limited part of the territory, convenient to the nest, and the remainder of the territory is used less than at other seasons. During the summer months when many adults are still feeding young, and later when they are molting, little territorial activity is to be seen, but in the fall encounters are more conspicuous and frequent. During cold foggy weather or rain, in winter, relatively little time is spent by the birds in flight, and territorial combats are correspondingly infrequent.

Use by an intruding hawk of another's favorite territorial perch usually provokes an immediate attack. The resident birds close in with rapid and direct flight and, screaming, in turn swoop and strike at the trespasser. They may knock it from the perch if it does not take flight at once, but usually it attempts to escape, flying low and rapidly, and dodging in and out among trees. The pursuing hawks wheel and flap heavily after each swoop, to get high enough for another attempt. They usually pursue the intruder far beyond the limits of their own territory, then turn about abruptly and fly back to perch or maneuver.

The most frequent encounters are boundary disputes between pairs occupying adjacent territories. All four birds of the two rival pairs may be involved, or if the flight is of short duration, only two or three may participate. Sometimes they only circle close together and scream at each other with little actual fighting, or one may attack while the other merely moves to avoid its swoops without retreating, or the attacked bird may retaliate, each in turn swooping and then striving to get above the other again. Rarely, the commotion of a fight between two pairs may attract hawks of a third pair, so that five or more birds join in a territorial *melée*.

The objects of territorial attacks frequently are hawks which do not dominate areas of their own, chiefly juveniles, which either wander or stay permanently in chosen areas without defending them. Such individuals avoid conspicuous territorial perches and exist by eluding the aggressive mated birds residing in the area, which harry and pursue them on sight. Use of relatively low, inconspicuous perches, and usual abstinence from high, soaring flight characterizes the behavior of self-sustaining juveniles in areas dominated by paired adults.

The hawks are particularly hostile to eagles. Golden Eagles (*Aquila chrysaetos*) occurred frequently on the area and usually were seen when the attention of the observer was attracted by the commotion of one or more hawks harassing them. The eagles always retreated in observed instances, flying swiftly and dodging to avoid the hawks when they lunged too close. Being larger, heavier, and slower, the eagles were out-manuevered, but the hawks, despite their display of aggressiveness, showed respect for the eagle's greater size and strength, and avoided coming close except when swooping from above and behind. Eagles passing over were apt to be attacked successively by one pair of hawks after another, and when in sight were usually making strenuous attempts to escape. This constant harassment must here impose severe handicaps on their hunting and other activities. On the only occasion that a Bald Eagle (*Haliaeetus leucocephalus*) was seen on the Experimental Range, attention of the observer was

attracted to it by the screeching of a pair of hawks as they drove it away from their territory. Other large birds were treated with indifference by the hawks. On rare occasions, when excited, they have been observed to swoop at Turkey Vultures (*Cathartes aura*), but ordinarily the vultures, which are extremely common during the summer months, are allowed to patrol the hawks' territory unmolested.

VOICE

The most common vocal sound produced by this species is a high scream, *tsēē' ēēēē ārrr'*, of two or three seconds' duration. This call has many variations and is given on different occasions. Basically, however, it seems to be a territorial call which expresses defiance and hostility toward the object of the bird's attention. It may be hoarse and rasping or may have the mellow quality of a whistled note. Nestlings, even when they are less than half-grown, may occasionally give this call when disturbed by a person. When given by the young birds, the call lacks the piercing quality of the adults' scream and is a soft whistle.

Often the mere presence of a person is enough to cause a hawk to scream in defiance at intervals of a few seconds as it watches from some high perch, and usually one screams as it is flushed by a person approaching too closely. The scream is most often given while in flight. Usually it is uttered while soaring but at times of unusual stress, as in a territorial affray, it may be given in flapping flight, and the several wing beats given during the expiration impart a peculiarly quavering quality to the cry. The loudest and most persistent screaming is done during the course of territorial disputes. Occasionally a hawk may scream while hunting, and perhaps may even startle quarry into exposing itself by this means.

A modification of the usual scream appearing to express excitement and territorial assertion associated with courtship activity is most often heard on bright sunny days when the birds of a pair are soaring and maneuvering together, especially following an encounter with another pair or individual. Its quality is more that of a loud piercing chirp than of a scream, and it may be written as *chwirk*. Several such chirps are given in series and at intervals of about a second.

The hunger call of juveniles is frequently heard in late summer from the time the young birds leave the nest until they become independent. This is a two-syllabled scream, uttered in a series, *klēē'-ūck, klēē'-ūck, klēē'-uck*. Apparently it is not given by the young until after they have left the nest, but after the initial flight they become persistently noisy when hungry. One may utter its hunger calls for hours with only brief pauses. At sight of a parent bird approaching, the young calls louder and faster and crouches with its wings dangling loosely at its sides, flapping rhythmically.

In addition to the various cries described above, the adult hawks on certain occasions utter a low grunting or quacking, entirely different in nature, best represented by *gānk*, several times repeated. The sound produced is unhawk-like and has the nasal quality of a duck's voice. This is evidently a conversational sound between members of a pair when they are flying or perching near together under no particular excitement. It has been heard on only a few occasions, but it may be the hawks' most common utterance, as it lacks the carrying quality of the other calls and is noticed only at close range where the observer ordinarily would disturb the birds and prevent normal social behavior.

Low peeping notes of a soft, sleepy quality, somewhat like those of baby chicks, are given by small nestlings, usually when they are moving about in the nest or are aroused by arrival of one of the parents.

NESTING CYCLE

Courtship activity and the associated soaring maneuvers over the territory occur throughout the year on days when atmospheric conditions are favorable for protracted flight. Possession of a territory is necessary before pairing and nesting can occur. In most instances probably the territory and mate are acquired simultaneously as the bird inherits them in replacing another individual which has been eliminated. Usually it was not possible to recognize individuals with certainty over long periods, but it is believed that there were few instances of replacement over a two-year period in the pairs observed. Except where subject to human intervention, a pair of hawks may perhaps remain together and maintain the same territory over a period of years.

In courtship flights the hawks move in wide circles, sometimes drifting a distance in the course of each cycle. They may soar close together, almost touching, one immediately above and behind the other; often one extends its legs, allowing them to dangle loosely, and this is especially characteristic of the male when he is soaring above and behind the female. On at least one occasion, a female was seen reversing the usual procedure by dangling her legs while soaring over and behind the male, and members of a pair sometimes dangle their legs simultaneously. While engaged in this type of activity, the birds utter piercing screams at intervals of a few seconds. They may make short swoops at each other and briefly engage in combat-like maneuvers.

Courtship flights usually last from five to ten minutes. Often they are terminated by one of the birds making a series of long dives. It folds its wings, and heading downward, drops for perhaps as much as several hundred feet, gaining momentum all the while, then checks its fall by partly opening its wings causing it to swerve off its vertical course until its speed is lost and it goes into a stall. Then folding its wings it plunges downward again, and after a series of such dives it drops almost vertically into the top of some high territorial perch or it may soar upward again to continue its maneuvering.

In early spring, soaring flight correlated with territory or courtship is much more frequent than at other times of year. Actual mating is often preceded by a series of aerial maneuvers. On March 1, 1940, the female of a pair twice swooped and struck at the male, with her legs outstretched. Once he was hit sufficiently hard to be tipped sideways off his course, and he screamed in seeming protest. Later in the day when the pair was perched, the female twice postured, tilting forward until her body was nearly horizontal, and slightly opening her wings, she allowed them to hang loosely and flapped several times. The male made no response. Later the female flew to a perch beside the male and for about twelve minutes the birds nibbled at each other's head and neck feathers. In this the female was the more active, and the male abruptly terminated the proceedings by flying from his perch with a scream. On the following morning, after a typical courtship flight, the female alighted on a perch and postured as before; immediately the male spiralled down to her, and copulation occurred.

In all, eight records of actual copulation, involving several different pairs, were noted, one in 1939 and seven in 1940, and all within the period February 16 to March 2. In one instance the pair was perched near together just before mating; in all others the male was in flight and alighted on the back of the female. Copulation usually took from 5 to 12 seconds (20 in one instance). It was not always preceded by posturing of the female, and in one instance it was not preceded by soaring maneuvers. In some instances the male flapped slowly to maintain his balance during the process, in others he merely spread his wings to gain support of nearby twigs and branches. Mating often was followed by a period of soaring and aerial acrobatics, but in some instances the birds perched quietly. During late winter, hunger calls like those given by fledglings were

sometimes heard. On February 17 the female of one pair was seen and heard giving typical hunger calls, and on the following day this same pair was observed in the act of mating.

Hardly anything was discovered regarding nest building. On April 12 a female was flushed from a nest which was not yet completed. Careful search over the same area a week earlier had failed to reveal this nest, which on the latter date was conspicuous. Evidently it had been built during the time intervening. In other instances also, bulky new nests appeared with apparent suddenness where none had been known before. It seems evident that once a nest is begun, it is built rapidly, and that during the period of nest building the birds are extremely watchful and secretive to avoid discovery. Nests which were investigated by us during the period of building or laying were nearly all deserted by the birds.

Frequently old nests are used over, especially if they happen to be in favorable sites and are in a good state of repair at the beginning of the nesting season. Sticks and large twigs of blue oak, Digger pine, and buckeye are used and apparently are broken from the trees in most cases, rather than picked up off the ground, for in new nests the freshly broken ends are noticeable. The scanty lining is composed of softer material, shredded bark, and pine needles. Throughout the nesting season grass, such as soft chess, red brome, oats, and fescue, and various herbaceous plants are commonly brought to the nest, but probably these are snatched up and carried incidentally in the capturing of prey. Pellets disgorged by the hawks and trampled by them also form part of the nest lining. Through the entire nesting season, from early spring until the young are fledged, the adults frequently deposit green twigs in the nests. Twigs of buckeye, live oak, and blue oak were those most frequently observed. The significance of this habit is not clear but it may be associated with courtship behavior. Early in the season before a nesting site has been chosen, twigs may be deposited in several old nests within a short time by one pair of hawks.

Nests vary in size according to the type of support and tend to be larger when well supported, as by the main forks of a tree trunk, or smaller when built far out on lateral branches. In such locations they are difficult to find and the better concealment perhaps compensates for the poorer support. One pair early in the season was noticed evincing interest in a previously used bulky nest high in a large pine, and they deposited some green twigs there. After the investigator had climbed to this nest, however, the hawks lost interest in the site, and later built a new nest more than a quarter of a mile away, well concealed, in a thick clump of branches far out on the lateral limb of a pine. This nest was deserted after being robbed by a California Jay, and in the following nesting season the hawks returned to their original site. Certain individual birds tend to build larger nests than do others.

With one exception all nests seen were snugly built in a fork, either a crotch in one of the main tree trunks or a horizontal branching of a large limb. The one nest which was an exception rested on an old decaying gray squirrel nest, which collapsed beneath its weight and was destroyed during a heavy wind storm. Sites and dimensions of nests are illustrated in table 1, which consists of a sample of ten nests thought to be fairly typical.

The first nest recorded in table 1 was situated in a blue oak; all others were in Digger pines. Eight of the ten nests recorded above had pine needles as lining material and four of these had fine strips of bark (live oak or pine). Of the remaining two nests one had bark only as lining, the other had bark and leaves of blue oak.

In eighteen nests found before hatching, the average clutch was two and this num-

ber occurred in each of eight nests; five others each had a single egg, and five had three eggs each.

Table 1

Sites and Dimensions of Nests of the Red-tailed Hawk

Height	Position	Greatest diameter	Smallest diameter	Thickness	Depth of bowl	Diameter of bowl
30 feet	13 ft. out, 6 inches out on limb	30 in.	24 in.	10 in.	3 in.	14×10 in.
56 feet	Crotch of main trunk	29	27	15	2	11×11
40 feet	27 ft. out on limb	22	17	9	4	11×7
59 feet	Crotch of main trunk	29	25	18	3	14×12
50 feet	Crotch of main trunk	26	24	14	4	11×10
53 feet	14 ft. out on limb	27	24	15	4	13×10
68 feet	Crotch of main trunk	36	24	20	5	11×9
48 feet	Crotch in one of main trunks	38	20	17	5	14×8
50 feet	12 ft. out on limb	36	30	18	6	16×14
57 feet	Crotch of main trunk	35	28	16	6	15×11

In several observed instances the young required from 24 to 48 hours from the time they had pipped the eggshell to hatch. For a few hours after hatching the young hawk lies limp and exhausted, too weak even to raise its head. The downy plumage of the nestlings is white. On the second day the young are active; almost continuously while they are awake they give peeping calls, bounce up and down, and wave their stubby wings. This activity continues for several days. For the first few days the young pay no attention to the investigator while he is at the nest. Later they recognize his strangeness and quiet down at his appearance. The bouncing occurs only for the first few days, and after this period chirping is less continuous. At the age of six or seven days, young first begin to



Fig. 44. Brood of young Red-tailed Hawks, 1, 2, and 4 days old, left to right, removed from nest.

peck at prey in the nest, attempting to feed themselves. One six-day old hawk was found trying to swallow a headless fourteen-inch rattlesnake, recently brought by the parent hawk and still writhing feebly.

At the age of ten days or more the young give a high whistling note when the adult, soaring overhead, screams. At this age the young may show signs of resenting the presence of a person at the nest, and may even make a feeble peck at him. At sixteen days the

nestlings are beginning to acquire feathers, and some individuals are aggressive toward intruders. When three weeks old, some of the nestlings stand erect facing the intruder, with wings half spread, feathers ruffled out, and bills open, silent but ready, and strike with claws, bill, and wings when molested. Other nestlings of milder disposition allowed



Fig. 45. Twenty day old nestling, squirrel tail protruding from mouth.

themselves to be handled without any show of resentment or crouched passively in the nest. When a month or more of age the young begin to flap and stretch their wings, and thenceforth they exercise frequently. After this stage is reached, even the more mild individuals face an intruder in threatening, defensive pose, and the fledglings are now



Fig. 46. Nestlings one month old; note remains of ground squirrel at left.

sufficiently confident to walk about on the nest rim and on nearby limbs. The birds whose approximate hatching dates were known to us (four different nests) flew from the nest at the age of 45 or 46 days.

From the time of hatching until they become independent, the young are fed upon the same kinds of prey which the adults eat, but at all times ground squirrels appear to be the favorite food. Time after time, and at many different nests, it was noted that when an abundant and varied food supply had been brought by the parents, the ground squirrels were most apt to be eaten, while other prey often was left unused and eventually discarded.

Removal of unused prey within a day after capture is a habit of the parent hawks, and evidently the remnants are carried distances from the nest tree before they are dropped, for they were seldom found beneath the nest.



Fig. 47. Thirty-eight day old nestling.

Nestlings which died always disappeared from the nests soon afterward, and in several instances those which appeared in sickly or dying condition had disappeared on the following day, presumably having died and been carried away by the parents.

For a period of four or five weeks the parent birds feed the young, tearing the prey into pieces that can be swallowed. Later the adults merely deposit the prey in the nest for the young to feed on themselves. The fledglings lack sufficient strength and coordination to disarticulate the larger items, and sometimes merely eat some of the flesh and viscera, leaving the skeletons nearly intact. This results in a sharp decrease in the proportion of bone material consumed as they approach adult size. Tearing of the prey in feeding themselves doubtless contributes importantly to the development of the young. The adults less consistently remove unused food and the nest becomes littered with portions of old carcasses. The annoyance from insects attracted by this animal refuse may hasten departure of the young.

The 38 eggs recorded during the three seasons produced only sixteen fledglings—twelve eggs were eliminated before they had hatched and ten nestlings succumbed, mostly during the early stages of nest life. One pair whose nest was destroyed during incubation nested successfully later in the season, but six pairs whose nests failed before hatching and five pairs whose young all succumbed after hatching did not make second attempts.

Trends of nest fates differed significantly in the 1939 and 1940 seasons; in 1939 only 11 of 20 known eggs produced young, but in 1940 15 of the 16 known eggs hatched. One evidently was infertile. In 1939 all of the 11 young hatched survived, whereas in

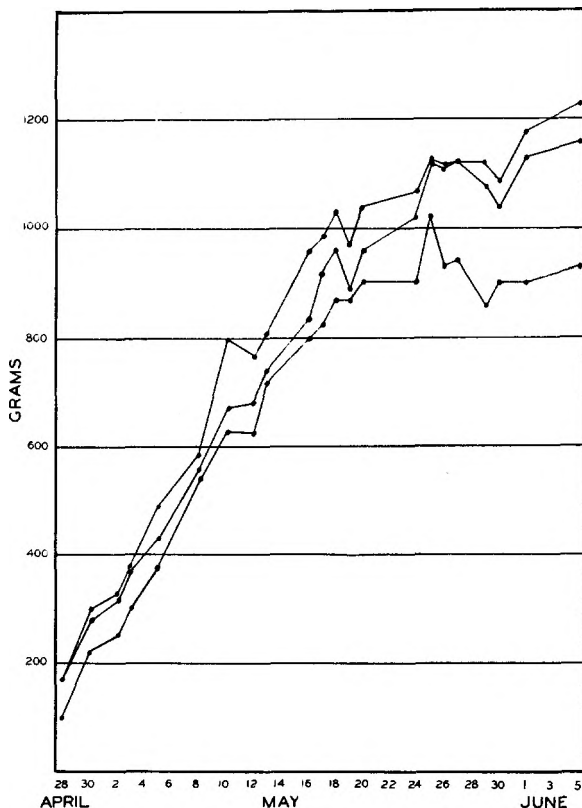


Fig. 48. Graph showing growth of three nestling Red-tailed Hawks during period of their stay in the nest.

1940 only 4 of the 15 young survived. These data illustrate that nesting success in any season may vary greatly due to weather and other circumstances. None of the nestling deaths was due to lack of sufficient food. Ordinarily the young were kept supplied far in excess of their needs, so that many of the items brought lay untouched until they began to spoil and were removed by the parents. At times the fortunes of hunting were such that the young went unfed for an entire day, but no visible ill effects resulted from these fasting periods. Among the causes of nest failures, desertion was important, but this probably was due to the disturbance to which the hawks were subjected by the investigators. Of other factors, the California Jay and a blood-sucking fly were found to be most important.

In one instance the actual robbing of a nest by a California Jay was witnessed by

an observer watching from a blind. The female hawk was sprawled low on the nest brooding her two eggs when the jay appeared and hopped up to the nest rim; then it sprang away suddenly, releasing a cloud of yellow pollen as it struck an overhanging pine twig. Almost immediately it returned to the nest rim, pulled out a twig, and flicked it away, all the while standing alongside the hawk's wing. The hawk made a thrust with its bill but the jay easily avoided the stroke and darted away, dislodging another cloud of pollen as it left. The hawk, aroused, stood up in the nest, then flew to the top of a tree and looked about. After a few seconds it flew again, and circled overhead. Immediately the jay returned to the nest but was driven away as the hawk made a sudden swoop at it. The hawk returned to the nest tree and perched, then screamed and flew to a tree 500 feet away where it perched six minutes and finally flew out of sight. Thirty minutes from the time the jay had been driven off, it (or possibly another one) returned to the rim of the nest, plunged its bill downward, and repeatedly performed drinking movements, reaching forward into the nest, then elevating its bill to swallow, as if it had punctured the egg and was consuming the contents. Several times the jay suddenly flew away from the nest interrupting its feeding in response to distant hawk screams, but each time it returned quickly. The hawk was not seen to return to the nest that day although watch was maintained for most of the afternoon. Several days later when the investigator climbed to the nest, by then definitely deserted, one intact egg still remained; the other was gone.

At another nest, the failure of which was tentatively attributed to jays, one of the two eggs was found punctured. Although a second egg remained intact, this nest likewise had been deserted.

Of eleven nestling hawks which were eliminated, one was found trampled and crushed, evidently killed accidentally by the parents. Another died suddenly from unknown causes when it was about half-grown. It was the only one of the brood and had appeared to be in good condition and developing normally. The day of its death was unusually hot and the nestling may have been killed by exposure to direct sunlight.

Seven young succumbed to the attacks of a blood-sucking fly, *Eusimulium clarum*. The destructiveness of *Eusimulium* during the 1940 season when we recorded six casualties may have been correlated with the heavy rainfall, since larvae of this insect are aquatic and it is dependent on standing water for breeding places. The 1939 season was unusually dry and no hawk mortality from *Eusimulium* was observed; in fact this parasite did not come to our attention at all until in 1940, when swarms were noticed about the nests between April 30 and May 8. At each nest they disappeared after a few days. The seven hawks which died from the effects of their attacks were from four to eight days old and still in downy plumage. The flies were not seen on more than three successive days at any one nest, and usually there was a swarm if any at all were present. They would alight on the downy plumage of a nestling and vigorously work their way through to the skin; in feeding they became so engorged with blood that their distended bodies were ruptured by a slight touch, rendering difficult the collection of an uninjured example. After its feeding the fly immediately forced its way out through the hawk's plumage and flew away.

The attacked nestlings showed evidence of acute suffering. They kept up a constant plaintive "cheeping," striking out frantically with their bills, flapping their short wings, and working their legs up and down continuously in an attempt to protect themselves. They became blinded as their eyelids were swollen shut, and all naked skin areas on exposed parts of their bodies became covered with scabs and flakes of dried blood. One larger nestling, 36 days old and already partly feathered out when the flies made their

appearance, survived as it was relatively well protected, with only small bare skin areas on its legs remaining exposed.

In the 1941 season, few observations on nests were possible, but one young hawk was known to have succumbed to attacks of *Eusimulium*. The spring of 1941, like that of 1940, was rainy and may have been similarly favorable to the development of these flies.

If our data for 1940 on nest mortality are at all representative, the limitations imposed by *Eusimulium* on the hawks' reproduction must be important. The number of flies doubtless fluctuates greatly from year to year according to weather conditions, and they are not oppressive every year. The situations of individual nests—whether or not readily available to the flies from their breeding places—determines the severity of their attacks. Mr. Thomas H. G. Aitken, to whom we are indebted for identifying this parasite, informs us that in 1937, at Patterson, Stanislaus County, California, an outbreak of these flies proved pestiferous to farm animals, particularly to chickens.

To summarize data on the fates of eggs, nests, and nestlings, seven of the 26 nests investigated failed to hatch young. Four of these were deserted, possibly because of the investigators' activities, and these four had three, two, one and no eggs, respectively. Desertion of two other nests, each with two eggs, was attributed to jays. Another nest with two incubated eggs was blown down in a wind storm. The remaining 19 nests all hatched young. Of these nests six were so inaccessible that they could not be closely observed and the number of young birds was not definitely known in any of them, but apparently all were successfully fledged. Young were fledged in eight other nests; in three with three young each, and in two with two young each, all were brought to maturity. In another nest having three young, two succeeded but the third succumbed early in its development. In another nest which had two young, one succeeded; but the other was sickly, stunted, and possibly diseased, and it died after a wetting from a heavy storm. In another nest having three young, two were fledged, the other was killed by blood-sucking flies (*Eusimulium*). In three other nests having 3, 2, and 1 young, respectively, all succumbed to attacks by these flies. The two remaining nests each had a single young bird, and both died suddenly from unknown causes.

In investigating hawk nests we found the parent birds aggressive and they nearly always swooped at anyone climbing to the nests, although ordinarily they swerved aside while still several yards distant. At one nest a hawk swooped between two climbers as one held the other in position to take a photograph. Another pair dived constantly while the climber was in their nest tree. The male of this pair never approached nearer than 25 feet but the female several times flicked the climber's back with her wing tips as she hurtled past, twice knocked his hat sidewise, and once dislodged his spectacles.

The female of another pair consistently made dangerously close swoops and became increasingly aggressive. Finally, as the observer was moving a nestling to examine prey beneath it, he was struck from behind with such force as to be momentarily stunned; clutching at the tree he was forced to dodge again as the hawk wheeled around and made another swoop. His back was lacerated from shoulder to hip where the hawk's talons had raked him, and there was a severe bruise between the lacerations where the hawk's breast bone had struck. Prior to this attack the hawk had threatened on many occasions, but afterward it became even more aggressive and would rise a hundred yards or more directly overhead, then would fold its wings and drop at the intruder. On these occasions it never missed by more than a narrow margin, and several times it might have found its mark but for the agility of the climber in dodging around the tree trunk to avoid it. After missing it would swerve upward and around the tree, then would wheel back abruptly and make another plunge.

Many times hawks swooping down at a climber crashed into branches which were sometimes knocked off; some were as much as two inches in diameter. Twice hawks partly stunned themselves in this way, narrowly avoided striking the ground, and rose with unsteady flight, but quickly recovered sufficiently to resume their attacks.

The female was the more aggressive of each pair encountered. Often an investigator approaching a nest found only one parent bird in the vicinity, but its angry cries would soon attract its mate, often from a distance of a quarter mile or more. On a few occasions neither adult hawk was near as a climb to an occupied nest was begun, but both always arrived in time to harass the climber.

On several occasions in late summer and fall, when we returned to examine nests that had been occupied earlier in the season, the resident pair of hawks circled low overhead and screamed in defiance with behavior similar to that displayed toward us when their young were still in the nest. Obviously these parent birds, after periods of weeks or even months, still retained memories of encounters with human intruders while attempting to defend their nests and young. Other pairs not disturbed during their nesting season showed no particular resentment at the presence of persons near their old nests at other times of year.

HABITS OF FLEDGED YOUNG

After leaving the nest, the young gradually become independent. The initial flight of the fledgling climaxes a period during which it becomes progressively bolder and more explorative and moves about on branches near the nest. The investigator climbing to the nest supplied the stimulus for the actual take-off in several instances, and the young hawks flew strongly to trees 100 yards or more away. The fledglings showed no tendency to leave the nest at any alarm until capable of sustained flight; serious injuries to the heavy-bodied young would occur if they faltered and crashed to the ground from the height of their nests.

On one occasion when a young hawk was making its first flight from the nest tree, the mother swooped down, struck it, and knocked it toward the ground. By hard flapping it reached a nearby tree short of its original goal. The adult's response at sight of this other hawk flying through her territory at a time when she was already angered and excited by the presence of persons at the nest was somewhat akin to that of members of a pair seen to make short swoops at each other while maneuvering and screaming overhead as a person climbs to the nest.

After leaving the nest the young hawk may stay in one tree for periods of days, not making extensive flights in the first week or two. A week after one fledgling had flown, eight fresh pellets were found under the tree where it had been located, 100 yards from the nest, suggesting that it may have been there continually. Six pellets of another young hawk were found under a tree 400 feet from the nest a week after the fledgling had left. Two weeks later the bird was relocated in a tree 670 yards from the nest, and at still another tree intermediate in location fourteen recent juvenal pellets, almost certainly those of the same bird, were collected. This indicates, perhaps, that the bird had spent the two-week period principally in the one tree and had disgorged a pellet daily. At still another perch 760 yards from the nest tree the bird remained almost a week more, but thereafter it became much less sedentary.

One young hawk left nest A on May 17; and intensive observations of its feeding and general behavior were made on May 20 and 21. All day May 20 it remained in the same tree, about 800 feet from the nest. At 9:00 a.m. the parents were perched together in a tree about 200 feet away. They spent much of the morning soaring together with no evident attempt to secure prey. At 2:23 p.m., the female began quartering about in low flight; two minutes later she made a successful plunge at a young ground squirrel, carried it to a tree, and ate the brain. Then she flew to the tree where the

young was waiting and began feeding it from the squirrel, at the same time eating some herself. At 3:42 p.m., the male appeared, carrying no food but with his crop distended, obviously having fed recently.

On the following day the young hawk had moved to another tree 100 yards away. As before, the adults spent much time soaring. At 10:41 a.m., the male brought a small ground squirrel and ate from it himself while feeding the young, which gave hunger calls all the while. During the middle of the day watching was discontinued. When the observer returned at 2:00 p.m., the young hawk was tearing at the hindquarters of a young cottontail, evidently brought by the female, as her crop was distended.

Two young left nest B on July 21 and July 28, respectively. On August 5 the family was kept under observation from dawn until dark. At 5:30 a.m., the smaller young which had left the nest on July 28 was located back in the home tree about five feet below the nest. The other young was perched low in a tree about 100 feet away. At 6:05 the smaller young gave hunger calls; shortly after the larger young began calling also, and both continued at intervals throughout the day. Several times during the day, the parent birds flew near the young but brought no food. The young usually were more vociferous when the parent birds were in sight. Several times the young moved from tree to tree, usually following one of the parents, but they made no attempt to hunt, and seemed fatigued even by these short flights.

On August 6 at 9:00 a.m., the adult male returning with a young ground squirrel came flying over a ridge and crossed the canyon in a long glide, perched on a large limb, and ate the brain. He then flew with the prey to the limb where the smaller young hawk was perched. The latter snatched it, and the adult promptly left. The larger young in a tree 100 yards away gave loud hunger calls while the adult was in sight, but made no attempt to leave its perch and share the food with the one which had received it.

The adults maneuvered together, and at 10:05 a.m. the female flew out of sight over a ridge. At 10:28 she returned, carrying a young ground squirrel to the larger young which saw her at a distance and hopped up and down excitedly, flapping its wings and giving hunger calls. The female came to rest beside it and both began tearing at the squirrel and feeding from it. At 10:32 the male swooped sharply to the ground and after a few minutes flew up, carrying still another young ground squirrel. He flew to a tree and ate it, not sharing it with either young.

On August 7 the family was again observed throughout most of the day. At 8:18 a.m. the adult female was located eating a small cottontail on the ground. At 9:09 the male brought in a ground squirrel from which he had already eaten the head. As he approached, the larger young hawk flew toward the nest, apparently in anticipation of being fed. While both were in flight the adult dropped the squirrel near the young which tried unsuccessfully to catch it, then flew down and retrieved it from the ground, carried it to a tree, and devoured it. At 1:00 p.m. the smaller young was seen giving hunger calls and pursuing the mother from tree to tree as she carried a ground squirrel and ate the entrails. After twenty minutes she allowed the young to take the remains, and flew away.

A third hawk of this same brood had been removed from the nest at an early age and hand fed until after it attained adult size. It was unconfined and gradually became independent, but for several weeks after it was able to fly it returned to be fed. On August 17 it was seen soaring for the first time. A few days later it was seen carrying a wood rat which it apparently had killed. Throughout the period of its association with humans, this hawk was tame and sociable, but as it learned to hunt, it became more aggressive and independent; when offered food it would fly down and snatch the morsel, but would then attempt to carry it away. It resented the proximity of persons while it was feeding. If unable to drag the prey away, it would crouch over it menacingly with plumage ruffled and would strike at anyone who came near, sometimes hopping forward to deliver blows with its feet. Rabbits and squirrels were shot to feed it, and when a person set out with a gun to secure one, the hawk would sometimes accompany him, flying ahead, or perching nearby to give hunger calls.

On August 27 when the territory containing nest B was again visited, numerous fresh pellets from the young hawks were found beneath the nest. Also there were remains of recently killed prey in the nest, indicating that after the young had learned to fly they had returned there to use it as a feeding station. One of the young seen on this date flew strongly. On September 3 the hand-reared young reappeared after an absence of ten days. For two hours after daylight it perched on a building near its usual feeding place and gave hunger calls persistently, then ceased calling abruptly, and was found on the ground feeding upon a cottontail which it had caught and killed.

On the same day one of the young from nest B was calling at intervals and was seen flying up and down the canyon, working in and out of ravines as if in search of prey. The parent birds were sometimes in sight but were not followed by the young, whose actions suggested that it had begun hunting for itself but still remained in the parental territory and perhaps depended on the adults for some of

its food. The other young could not be found. On September 10 the remaining juvenile and the adults were seen soaring together. The tame fledgling of this family made its final returns for food during the latter part of September. When a covey of quail was flushed by a person, this hawk watched attentively for an instant, then flew in pursuit and struck at one on the ground in dry grass and sparse brush, but it missed and flew out to a fence post, screeching. When a live cottontail was released, the hawk swooped down and knocked it from its feet, but after a few seconds of frantic kicking, the rabbit broke away. As it ran, the hawk flew in pursuit and struck, but the rabbit dodged each time and escaped. When a wood rat was released from a trap, the hawk flew down and snatched it without stopping, carried it to a high perch, and ate it. In October and early November, a hawk, almost certainly this one, was reported seen at a place about a mile farther east; it flew down to low perches and gave hunger calls as a person passed. After late November it was gone from this location.

The habits of older juveniles were studied from several other individuals. During the winter of 1938-39, one seen almost daily usually stayed within an area about 200 yards in diameter, although it sometimes made more extensive movements and occasionally wandered more than a quarter mile from its central perches. The relations of this hawk with others in adjoining areas were of significance. The favorite perch of a pair of adults was about a quarter of a mile southwest but a ridge intervened which seemed to be recognized by the adults as the boundary of their territory, for they seldom crossed it. The young hawk did not encroach on the territory of this pair, and was seldom molested by them, being out of sight from their perches. Immediately to the north, however, the range of this bird overlapped the large territory of another pair of adults, and the juvenile was constantly harried by these. Two large pines which were favorite perches of the young bird, seemed to be just south of the territory defended by the pair, and it was not apt to be molested while using these trees. But its use of any one of several large pines farther north was apt to provoke an attack by the adults. Apparently as a result of such encounters, the young bird was bedraggled in appearance with many flight feathers missing. Its existence was made precarious by the presence of adults dominating the area where it hunted. It was never seen soaring; either the poor condition of its plumage or fear of advertising its presence to the adults prevented this type of flight. Often when it flew, attention of one of the adults was attracted to it and a pursuit followed. The adult, attacking from above, would attempt to overtake it with a series of rapid and powerful wing beats, then would launch at it in a short glide to strike with its feet. The juvenile never resisted, but dodged in and out among trees in low erratic flight until the pursuit ended, usually only after it had been driven beyond the territory of the adults. In contrast to the perches used by paired adults, usually high up in the largest trees available, the perches chosen by this young bird were usually on branches within the tree crown partly concealing it on one or more sides, and sometimes in thick foliage. Its home range was partly on a hillside sparsely wooded with small trees, but with no large pines such as are preferred as perches by adults. Perhaps because it lacked such perch trees and lay between the territories of two pairs, this area was seldom used by any adult hawks and hence was a sanctuary where the juvenile was relatively safe from attack.

In the early winter of 1939-40, two juvenal hawks were found to be occupying jointly a territory previously held by a pair of adults. The adults had disappeared, probably having been shot. The juveniles were mutually tolerant and showed some tendency to keep together, but they did not display the close-knit partnership characteristic of paired adults. Their separate discovery and occupancy of the undefended territory and their association within it seemed to illustrate the early stages in formation of a pair and a nesting territory, but both had disappeared before the next nesting season.

In the fall of 1940 and the following winter, intensive observations were made on another juvenile. Four pines, all within a diameter of 200 yards, provided perches upon

which this bird spent most of its time; its foraging range was thus only a small fraction of the area included in the average adult territory. The territories of three different pairs of adults adjoined the range of this young bird. However, each of these territories was large so that territorial pressure was not severe in this buffer area between them. The juvenile asserted its territorial claim by often perching atop one of the largest trees in a commanding position like that of an adult in its own home territory. Nevertheless it was frequently subjected to attack by each of the adjoining pairs. Often it was seen to be intently watching adults soaring in the distance, and as such soaring adults moved nearer, it showed signs of uneasiness and occasionally moved to a lower and less conspicuous perch within the crown of the tree. Adults passing over sometimes swooped down at it and chased it beyond the limits of its usual range. After escaping, it would usually perch inconspicuously in a low tree, or even on a bush or rock. It was seen soaring only on rare occasions. A smaller juvenile, evidently a male, occupied a similar small area nearby. Twice the two young hawks were seen soaring together in maneuvers resembling the courtship flights of a pair of adults, except that there was no dangling of the legs and no swooping descents by the male. Perhaps this was an incipient stage of courtship.

On one occasion, when the larger juvenile mentioned above was under observation, it was seen craning its neck and watching intently. Suddenly another hawk came in in a low glide and lit beside it, making a low, nasal sound (as described in the foregoing section on "voice"). This visiting hawk was obviously a male, noticeably smaller than the young bird, and in the adult red-tailed plumage. For three minutes the birds perched close together watching each other warily and making hardly any movement. The adult's behavior did not seem hostile, but suggested courtship, as he stood erect with head thrown back, facing the juvenile. The latter stood sidewise to the male, crouching, with head lowered, and finally made a thrust at the male with its bill, but he avoided the stroke and flew away. This male probably was a mated bird from one of the adjoining territories. Late in March when most of the adults on the Experimental Range were nesting, this juvenal female was still unmated and was still occupying the same small area. During the summer and early fall of 1941 this bird could not be found in its former haunts, but in November and December it was there again and was still in juvenile plumage. While there was not absolute certainty that this individual was the same one observed there the year before, peculiarities of behavior and use of exactly the same perches and general area furnished strong support for this assumption.

FEEDING

As a basis for studying the feeding habits, two separate sets of records were used: food items brought to young in nests by the adults and the items identified in pellets. These two sets of records are more or less supplementary, as each type has certain inherent limitations. The nest records are of especial value in providing detailed information on the prey animals, with full identifications, time, and approximate place of capture, and even certain indications of the methods of killing and eating. The nest records are strictly seasonal, being confined to a period of weeks in late spring and early summer. Limitations of the pellet data lie in the fact that the actual number of pellet items cannot be determined with exactness and that dates are likewise indefinite.

Nest prey items.—During the nesting season, food records were obtained by daily visits to the nests containing young hawks. Prey found in the nests provides an index to the feeding during that season although certain very large items and very small ones may not be brought to the nest even when they are secured. Most adult ground squirrels,

for instance, are extremely fat in late spring, so that one may even weigh as much as an adult hawk and could not be lifted from the ground by the bird, much less carried to the nest. Adult cottontails are even heavier and are not represented among the nest items, but such large prey may be secured and fed upon by the adult hawks during the nesting season, as at other times of year. Insects and other very small prey found in the pellets have not been found in the nests, but since they are bolted entire, no trace would remain.

Many of the animals brought to the nests are not eaten, as at times parent hawks are excessively wasteful in bringing much more prey than can be eaten by themselves and their young. The prevailing high temperature during the nesting season results in rapid decomposition so that in general an animal is unfit for consumption on the day following its capture. Often the remains of an animal are removed from the nest by a parent on the same day it is secured, but sometimes dried carcasses may remain in a nest for several days. In our nest study we made it a practice to mark, by tail clipping or otherwise, all prey animals recorded, to avoid duplication in the records when the same animal still remained at the time of a later visit. Even when a nest was visited daily, it was not possible to record all prey items brought because some might be entirely eaten during the 24-hour interval between visits, and the discarded remains of others might be removed by the parent birds. Probably the number of food items missed through these causes was only a fraction of that which was recorded. Several full days were spent watching nests from blinds, and the prey which the parents were seen to bring during the course of the day did not much exceed in numbers those usually found when nests were visited.

The degree of distension of the nestlings' crops served as an indication of the amount of food taken. On several occasions, when no food remained in the nest, although the young were obviously gorged, records of the prey were obtained by looking into the gullets of the young birds. Ordinarily our visits to nests were made late in the afternoon, but with no fixed schedule, and occasionally when no prey was found at the nest at the time of the regular visits, a later visit disclosed some. Apparently the hawks had no fixed feeding times and might bring in prey at any time during the daylight hours but were least apt to make captures during the hot mid-day hours, perhaps because squirrels and other prey species were also relatively inactive at that time.

Prey brought to the nest consisted entirely of mammals, birds, and reptiles. Rodents and rabbits comprised all the mammals. The birds were of various sorts, having little in common except that nearly all were larger than sparrows but smaller than the hawks. The reptiles included snake and lizard species in equal numbers, although the lizards were slightly more numerous in individuals. The 625 prey items comprising the three years' records and pertaining to fourteen different nests were of 23 species, in the following numbers: 380 ground squirrels (*Citellus beecheyi*), 79 pocket gophers (*Thomomys bottae*), 62 cottontails (*Sylvilagus auduboni*), 13 wood rats (*Neotoma fuscipes*), 10 kangaroo rats (*Dipodomys heermanni*), 8 chipmunks (*Eutamias merriami*), 3 rock mice (*Peromyscus truei*), 2 gray squirrels (*Sciurus griseus*), 1 brush mouse (*Peromyscus boylii*), and 1 meadow mouse (*Microtus californicus*); 11 quail (*Lophortyx californicus*), 4 jays (*Aphelocoma coerulescens*), 3 towhees (*Pipilo fuscus*), 1 road-runner (*Geococcyx californianus*), 1 screech owl (*Otus asio*), 1 kingbird (*Tyrannus verticalis*), 1 lark sparrow (*Chondestes grammacus*), 1 unidentified bird; 17 whiptail lizards (*Cnemidophorus tesselatus*), 14 gopher snakes (*Pituophis catenifer*), 8 skinks (*Eumeces gilberti*), 2 rattlesnakes (*Crotalus viridis*), 1 fence lizard (*Sceloporus occidentalis*), 1 sharp-nosed snake (*Rhinocheilus lecontei*).

Some observed differences in representation of certain prey species in 1939 and 1940 may be due largely to individual preferences of the different hawks involved rather than to availability of prey populations. The records for 1939 were from five nests with 334 items in all and with 50 to 85 items per nest. The 254 items comprising the record for 1940 were from nine different nests, only three of which were the same pairs studied in 1939. All three of these pairs failed to rear their young to maturity in 1940 and hence they were poorly represented that season with only 21, 9, and 12 nest items—about one-sixth of the total. Pairs whose feeding was recorded in 1939 and again in 1940 did show the same trends in both years. The principal prey species were the same ones for each pair, but individual preferences were shown for the more unusual kinds. Thus, one pair of hawks took seven of the 10 kangaroo rats recorded, and in each of these years took more kangaroo rats than all the other pairs combined. In 1940 one pair, not observed in 1939, took 16 of the total of 22 lizards recorded. In the same season another pair took 8 of the 9 snakes, 7 of the 8 chipmunks, and 6 of the 7 quail recorded, although its total number of items was only one-fourth the total recorded for the season. In 1939 one pair took 5 of the 7 wood rats recorded, and another took all three of the jays. In 1940 another pair took 3 of the 5 wood rats recorded that year. The highest percentage of squirrels among the items for any nest, excluding those for which only a few records were obtained, was 92 per cent, and the same pair took this high percentage of squirrels in 1939 and again in 1940. One pair nesting in a location where squirrels were more abundant than anywhere else on the Range, preyed upon them least, both in 1939 (58 per cent, as against 71 per cent for all the pairs combined) and again in 1940 (38 per cent, as against 49 per cent for all the pairs combined). Their territory was also in good gopher habitat, and reduced predation on squirrels was mainly compensated by increased predation on gophers, which in 1939 made up 29 per cent of their nest items, as against 15 per cent gophers in all nests combined and comprised 29 per cent again in 1940 as against 11 per cent for all nests.

The relative numbers of different prey species among the nest items is clearly influenced by seasonal changes in availability. Nesting is timed so that newly emerged young squirrels are abundantly available as food for the young hawks, and in every nest the ground squirrel was the most frequent item. Appearance of the young squirrels was relatively late in the 1940 season, and for one early nest no young squirrels were available for two weeks after hatching. During this period 27 prey items were recorded: 7 chipmunks, 5 cottontails, 4 gopher snakes, 3 quail, 2 gophers, and 1 each of wood rat, rattlesnake, whiptail lizard, skink, fence lizard, and ground squirrel (the latter an adult female). During the subsequent period of observation on this same nest, from April 17 to May 21, 37 items were recorded: 25 ground squirrels (24 young and one adult), 4 cottontails, 3 quail, 2 gopher snakes, 2 rock mice, and 1 sharp-nosed snake. Thus, for this nest, ground squirrels far outranked all other items combined after the emergence of their young. They became eighteen times as important as they had been previously in the food of these particular hawks, increasing from 3.7 per cent to 67 per cent of the items taken. At all other nests, feeding of the young had not begun until young ground squirrels were available, and hence among those nests they comprise a consistently high percentage.

Pellet prey items.—Pellets of Red-tailed Hawks consist of the undigested residue of food from the stomach. Bone is readily dissolved by the digestive juices, and the pellets consist largely of hair, feathers, or scales. Varying amounts of bone remain, but the fragments have their exposed ends and edges corroded and are buried within the mass of fur and other matrix. The hawk pellets differ thus from owl pellets, in which small

and fragile bones frequently occur in almost perfect condition on the surface of the pellet mass. The degree to which bone is digested in hawk pellets probably depends upon the length of time it is retained in the stomach and the amount of material in which it is embedded, protecting it from digestive action. Commonly pellets consist entirely of scales or hair. Those composed of reptile scales are exceedingly fragile when dry. Ordinarily the skin, muscle, and connective tissue of the prey are digested, but occasionally an intact foot of a lizard, mouse, or squirrel, or even a section of a snake's body are found in a pellet, perhaps after the hawk has fed on a dried carcass especially resistant to digestion. A typical pellet is ovate, about two inches in length by one and one-half inches in width, but many are smaller, and sometimes the shape is attenuate. Frequently the pellet is nearly flat but with one side rounded, evidently in conformation with the outline of the bird's stomach; this shape may occur when the residue is of insufficient size to fill the stomach.

One tree known to be the night roost of a pair of hawks was one of the best sites in their territory for the collection of pellets, suggesting that some of these may be dropped at night, or in the morning before the birds begin their daily wanderings. On one occasion, a hawk, flushed as it was beginning to feed upon a freshly killed cottontail, was found to have dropped a pellet beside it, and in a few other instances pellets have been found away from perches at places where kills may have been made. Pellets, already formed when prey is secured, are likely to be disgorged before the hawk begins to eat; but in most instances a period probably intervenes between the time when one pellet is disgorged and the time the next prey is secured.

Pellets for our study were gathered from beneath the large trees which were the favorite territorial perches of the hawks. From month to month the birds often changed their habits so that a tree productive of many pellets on one occasion would yield few or none on the next collecting trip. Because of the large number of trees offering potential perching places in each territory, and the impracticability of observing closely the movements of each of the many hawks involved, accumulations of pellets often were not discovered for periods of months after they were begun. Even after thorough search beneath a perch tree, pellets were apt to be overlooked because they were scattered and hidden beneath growing vegetation, and they were especially hard to find during the spring. Best success in collecting was experienced during late summer and fall, when most of the vegetation had been grazed off so that the pellets could be readily seen. Many collected at that season were old ones remaining from spring, as indicated by greenish algal growth on their surfaces which must have formed before the cessation of the rainy season in April. Thus, most of the pellets collected could not be accurately dated.

The summary of pellet analyses presented below is based on all pellets of Red-tailed Hawks collected in 1939 and 1940. Most of these were collected on the Experimental Range, but some were collected on neighboring ranches, all within a radius of a few miles. Some were collected south of the Range in a more open and sparsely wooded type of environment, where prey populations and availability differed somewhat. One notable series was collected in an area where ground squirrels were controlled by poisoning.

In a total of 2094 pellets, the following mammalian occurrences were recorded: 1049 ground squirrels, 794 gophers, 322 rabbits, 147 unspecified "rodents," 59 wood rats, 34 kangaroo rats, 17 meadow mice, 12 pocket mice (*Perognathus* sp.), 8 mice (6 *Peromyscus* sp., 2 unspecified), 5 bats (4 *Lasiurus borealis*, 1 unspecified), 4 chipmunks, 2 gray squirrels, 1 mole (*Scapanus latimanus*), 1 harvest mouse (*Reithrodontomys megalotis*). Bird occurrences recorded were as follows: 117 unspecified "birds," 14 jays, 13 woodpeckers (8 *Balanosphyra formicivora*, 3 *Colaptes cafer*, 1 *Asyndesmus*

lewis, 1 unspecified), 7 towhees (*Pipilo fuscus* and *P. maculatus*), 6 quail, 5 meadowlarks (*Sturnella neglecta*), 2 sparrows (1 *Zonotrichia coronata*, 1 unspecified), 2 hawks (pellets composed mainly of *Buteo* feathers; of problematical significance), 1 warbler, 1 bluebird (*Sialia mexicana*), 1 linnet (*Carpodacus mexicanus*), 5 egg shells. The reptile occurrences recorded were: 237 whiptail lizards, 190 gopher snakes, 106 skinks, 70 rattlesnakes, 54 fence lizards, 51 unspecified lizards, 50 California racers (*Coluber lateralis*), 43 unspecified snakes, 32 unspecified "reptiles," 10 king snakes (*Lampropeltis getulus*), 5 alligator lizards (*Gerrhonotus multicarinatus*), 4 garter snakes (*Thamnophis* sp.), 1 brown-shouldered lizard (*Uta stansburiana*). The arthropod occurrences, mostly taken accidentally and not as actual prey, were as follows: 160 grasshoppers, 161 beetles (58 unspecified, 22 *Amara*, 18 tenebrionids, 13 *Coniontis*, 11 scarabeids, 9 *Pterostichus*, 7 carabids, 7 *Eleodes*, 4 *Phobetus comatus*, 2 buprestids, 2 *Acmaeodera*, 2 *Amphicyrta*, and one each of *Serica*, *Silpha*, *Polycesta*, *Nyctoporis*, *Hydrous*, and an elaterid), 99 Jerusalem crickets (*Stenopelmatus*), 8 flies and their larvae (5 *Lucilia*, 1 *Cuterebra*, and 2 unspecified), 22 hemipterans (1 corixid, 1 belostomatid, others unspecified), 18 ants, 9 unspecified "insects," 2 hornets (*Vespula*), 4 lepidopteran larvae, 1 Odonata; 1 scorpion, 20 unspecified arachnids, 2 centipedes. Also, 47 occurrences of carrion were recorded: 24 of cow, 6 of sheep, 6 of bobcat, 4 of coyote, 3 of horse, 3 of skunk, and 1 unspecified.

In the foregoing list items classed as rabbit consisted mostly or entirely of cottontail (*Sylvilagus auduboni*) but may have included a few jack rabbits (*Lepus californicus*). Items classed as "rodent" were small, fine-haired forms such as *Peromyscus*, *Microtus*, *Thomomys*, or *Dipodomys*, which could not be definitely identified because of minute quantities of remains present or their poor state of preservation. Remains of the three species of *Peromyscus* could not be distinguished from each other, and could have represented either *P. boylii*, *P. truei*, or *P. maniculatus*, but only the former two species were represented among the nest items. *Perognathus* remains could not be identified as to species, but probably were those of *P. inornatus* in most or all instances, as this species greatly outnumbers *P. californicus*, the only other kind occurring in this area. Material identified only as "mouse" could have pertained to any of the species of *Peromyscus*, *Perognathus*, *Microtus*, or *Reithrodontomys*. In the majority of bird occurrences in pellets, the feather material was in such poor condition that definite identifications could not be made, and the item was classed merely as "bird." Those kinds classed as "sparrow" and "warbler" or "woodpecker" were sufficiently diagnostic to reveal the general type of bird on the basis of size, shape, or color of the feather material, or bone fragments. Likewise, remains classed as "reptile," "snake," or "lizard" consisted of meager scale material insufficient for full identifications. Remains of insects and other arthropods were usually so minute and fragmentary that complete identifications could not be made; some were identified to family and others to genus.

In order to study differences in feeding habits under slightly differing ecologic conditions, two collections of pellets were made in the late summer and fall of 1940 off the Experimental Range and somewhat lower in the foothills, near the lower edge of the blue oak belt. One lot of pellets comprising 202 prey items was found under three adjacent trees and represented the accumulation of the entire dry season from a single family of hawks, many of them from the young birds still at the nest. On this area squirrels were abundant. The second collection comprised 581 prey items, and the pellets were from three different families of hawks. Accumulations from two different nest trees under which juveniles' pellets were found made up a large part of this collection. On this second area squirrels were controlled by annual poisoning and their numbers were

low. The relative abundance of different prey groups in the two collections are shown in table 2. These data illustrate the facts that squirrels are the principal food where they are present in abundance and that where the squirrel population is reduced, increased utilization of the other available food sources results. With an inadequate supply of squirrels in area 2, the pocket gopher became the most important prey species, while reptiles, birds, insects, and miscellaneous small mammals all were more important in the diet than they were on the area where squirrels were abundant.

Table 2
Relative Abundance of Prey Groups in Two Lots of Pellets

	Area 1 (squirrels not controlled)	Area 2 (squirrels controlled)
Squirrels	35 per cent	10 per cent
Pocket gophers	22	34
Reptiles	21	25
Birds	2	6
Other items	20	25

In a few instances concentrations of pellets were found on successive occasions under certain favored perches permitting comparison of food composition over different periods for the same pair. Data from one such series for spring, summer, and fall is shown in table 3; arthropod items were disregarded.

Table 3
Seasonal Change in Prey of an Individual Hawk

	February-March-April	May-June-July	August-September	October-November
Squirrel	37.5 per cent	24.6 per cent	26.1 per cent	19.6 per cent
Gopher	12.6	9.4	31.9	50.0
Rabbit	6.2	9.4	2.9	1.8
Other items	43.7	56.6	39.1	28.6

A series of pellets collected two miles south of the Experimental Range in less wooded and less brushy terrain where ground squirrels were subject to control showed the percentages of items, exclusive of arthropods, for different seasonal collections as summarized in table 4. Heavy predation on gophers and reptiles reflects the local scarcity of ground squirrels and rabbits where this sample was taken.

Table 4
Composition of Prey in Area of Controlled Squirrel Population

	June	July-August	September-November
Squirrel	0 per cent	12.1 per cent	7.8 per cent
Gopher	71.4	29.3	58.5
Rabbit	0	0	1.0
Bird	4.8	10.4	3.8
Reptile	19.2	46.0	20.9
Other items	4.6	2.2	8.0
Total items	21	58	106

Larger kinds of prey such as ground squirrels and rabbits often comprise the entire contents of a pellet, whereas the smaller kinds such as insects are almost invariably associated with other kinds of prey. In the 2094 pellets analyzed, prey was distributed as follows: 1 item in 923 (44.1 per cent), 2 items in 682 (32.7 per cent), 3 items in 297 (14.2 per cent), 4 items in 128 (6.1 per cent), 5 items in 45 (2.2 per cent), 6 items in 9 (0.5 per cent), 7 items in 7 (0.33 per cent), 8 items in 1 (0.05 per cent), 10 items in 1 (0.05 per cent). The associations of different kinds of items often are of significance;

for example, insects were most frequently found associated with lizard remains, suggesting that they had been eaten by the lizards and were not true prey items of the hawks. Of the pellets having single items, none contained lizard remains, and of those with two kinds of items only a little more than one-tenth had lizard remains. But of those pellets having four or more items, nearly three-fourths contained lizards. The reason for this is the usual occurrence of one or several kinds of insects in the stomach of each lizard eaten by the hawks and their subsequent association with lizard remains in the pellets produced.

The "occurrences" of various kinds of prey in our pellet records do not necessarily represent exactly the same numbers of individual prey animals killed by the hawks. Identifications of rodents, for instance, were made from hair and there was no certainty whether one or several individuals of a species were represented by an occurrence in a pellet. Also there was the possibility that one individual animal might appear in more than one pellet.

To obtain information concerning the relationship of pellets to the actual food, we kept an adult Red-tailed Hawk in a small cage for two months. During this period, the time of each feeding and the amount and kind of food were recorded, and the resulting pellets were analyzed. The kind of food was varied from day to day, and the same kinds of animals eaten by wild hawks were offered. It was found that a pellet may represent the accumulation of several meals over a period of several days, but occasionally pellets were dropped on successive days. In 61 days a total of 23 pellets was produced. Remains of a prey animal were best represented in the first pellet dropped after a meal, but often small quantities appeared in later pellets, even after periods of more than a week following the meal. On the average the captive hawk consumed 140 grams of food daily—about one-sixth of its own weight—but sometimes it voluntarily fasted for a day. The animals provided mostly were offered alive, and the hawk gorged itself after killing its prey. This adult ate even more than a large nestling, which during the latter half of its growing period consumed an average of 134 grams of food daily over a fifteen-day period (see fig. 49), and both ate much more than a hawk observed over a period of days in the wild.

Glading, Tillotson, and Sellick (1943) have discussed critically the use of pellets as an index to food habits of raptors and especially of hawks. They indicate various sources of error inherent in this approach and especially under the conditions of their own experiments. Among the points mentioned by them, the impracticability of determining actual numbers of individual prey animals from the fur, feathers, and scales in pellets and the likelihood of misidentifying or even missing entirely the remains of some small prey species are perhaps equally applicable to our own study. However, the results from their young hawks fed daily, with two or more kinds of animals at a meal, would not be representative of adult birds in the wild which feed less than once a day, and then usually make an entire meal of one kind of prey animal. The actual data of Glading *et al.* on food presented to the captive hawks and later identified in the pellets seems to bear out the idea that, very roughly, each pellet occurrence corresponds to one individual prey item. With the large numbers of pellets in our series, occasional oversight of a minute item or differences between numbers of occurrences and numbers of individual prey animals represented would tend to average out so that at least they would not be major sources of error. A considerable margin of error does exist, yet thousands of pellet records certainly afford a qualitative indication of the kinds of prey taken and also, in a general way at least, the relative importance of the several prey species which make up most of the food.

Predation on rodents.—Every genus of rodents on the Experimental Range (except that of the house mouse, here closely confined to buildings) was recorded as prey from nests or pellets or both. There was only one occurrence of the harvest mouse, which because of its small size, active and nocturnal habits, and scarcity on the area, would not be apt to fall prey to the hawks. All other kinds were represented by several or many occurrences.

The gray squirrel with two occurrences as pellet items and two as nest items was one of the most poorly represented. Both gray squirrels found in nests were young. The species is moderately common on the Range, and it keeps almost entirely to the scattered Digger pines which are also favorite perch trees of the hawks. Apparently these squirrels are too elusive to be caught by the hawks, so that only the inexperienced young

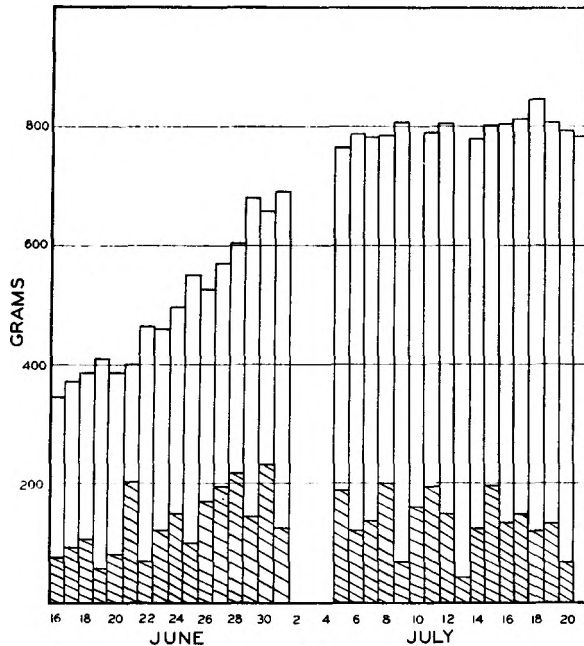


Fig. 49. Histogram showing daily weight (open columns) of a hand-reared nestling of the Red-tailed Hawk and the weight of food (lined columns) consumed by it.

or otherwise handicapped individuals are preyed upon. Their usual immunity from capture was illustrated on several occasions when individuals were seen climbing in trees which contained nests with young hawks.

Occurrences of the mainly nocturnal wood rat, kangaroo rat, and pocket mouse among the prey items was surprisingly frequent in view of their limited availability to these strictly diurnal raptors. They must be easy for the hawks to catch when they happen to be out in the daytime. By far the greater part of the hawks' food consisted of the ground squirrel, gopher, and cottontail, all terrestrial and relatively large species, partly, at least, diurnal in their habits.

Predation on birds.—No species of bird was commonly preyed upon. Most of those identified were California woodpeckers, California jays, meadowlarks, quail, and towhees—all types small enough to be easily overpowered but large enough to furnish a

meal. It is perhaps significant that all these are breeding species on the Experimental Range, for most of the birds taken may be young. At least many of those found as nest items were fledglings. Of the quail, however, nearly all those found as nest items were adult birds. The percentage of quail found as nest items was much higher (more than ten-fold) than the year-round percentage derived from the pellet items. The adult birds must be more vulnerable to such predators as the Red-tailed Hawk at the season when pairs have scattered from their coveys in order to nest. They are then deprived of the collective safety afforded by the continual watchfulness of all members of the flock and take further risks in guarding their nests and young.

The small birds identified were represented by one occurrence each for "sparrow," Golden-crowned Sparrow, bluebird, Linnet, and warbler; rarity of these occurrences seems to show that they are incidental. Fearlessness toward the hawks was demonstrated by Linnets on many occasions. Almost all the occupied hawk nests had occupied nests of Linnets (or less commonly those of other small passerines) built in their basal portions. The Linnets were constantly singing and hopping about on sticks of the hawk nest and on nearby branches even when a parent hawk was at the nest. So far as observed, the Linnets and their nests were not molested by the hawks.

Small birds of sparrow size ordinarily seem to be passed unnoticed by the hawks, but one seen fluttering on the ground in helpless condition might be pounced upon. This was observed when a White-crowned Sparrow was caught by the wing in a mouse trap and a Red-tailed Hawk attracted from a distant perch flew down to secure it. Ordinarily, hundreds of these sparrows foraged on the ground beneath the perch trees of the hawk daily without attracting its attention.

No poultry was found among the pellet and nest items. For most of the individual hawks whose feeding was studied there was no opportunity to secure poultry in or near their territories, but one pair well represented both in nest items and pellet collections had a territory adjoining a farm where chickens, turkeys, and guinea fowl were kept. An open field a quarter of a mile or more across separated the rugged wooded land where the hawks perched from the farm buildings where the poultry stayed, and although the hawks often soared over the field, they seemed to avoid coming near the buildings. Poultry raising is not important in the foothill belt, but most of the farms have a few chickens. The absence of poultry among the 4661 recorded items may not be a fair indication of complete abstinence from this type of predation; occasional individuals situated near farmyards might be potentially destructive.

Predation on reptiles and amphibians.—Of the 15 reptile species known to occur on the Experimental Range, there were only three not recorded among the food items—the small, secretive, and mainly nocturnal snakes, *Diadophis* and *Hypsiglena*, which would seldom be exposed to capture by the hawks, and the horned toad (*Phrynosoma*). The absence of the last fairly common and easily captured species from our extensive sample of food items would seem to have some special significance. The spiny head would constitute a formidable object for ingestion by a hawk, but the remainder could be eaten without difficulty.

The brown-shouldered lizard, which is by far the most common lizard species on the Range, occurred but once among the food items. Its minute size and speed must render it difficult to capture. The skink, although active above ground for only a few weeks in spring, occurred nearly twice as often as the fence lizard, common almost the year around. Apparently the skink's habit of frequenting open grassy places makes it much more susceptible to hawk predation than the fence lizard, which is shy and mostly confined to rock piles here.

Although the rattlesnake is frequently preyed upon, the relatively few occurrences of this common and sluggish, but dangerous species, as compared with the occurrences of the gopher snake, suggest selection on the part of the hawks. In human experience, the rattlesnake is encountered on the Range about five times as often as the gopher snake, yet in the combined records of nest and pellet items, the numbers of gopher snakes and rattlesnakes are 225 and 83, respectively. As a hawk would hardly have the opportunity to acquire respect for the venomous qualities of the rattlesnake through individual experience, it is possible that there may be a specific instinctive caution toward rattlesnakes.

Since many of the pellet items were identified merely as "reptile," "snake," or "lizard," the relative numbers of the various reptile species actually identified may not represent with accuracy the frequency with which they are taken. Some species may be more difficult than others to identify as pellet items and hence may have been recorded merely as "reptile" in many of their occurrences.

Although amphibians are well represented in the feeding records of Red-tailed Hawks elsewhere (McAtee, 1939), none of the seven species known to occur on the Range was found as food by us. As a group, their largely nocturnal and subterranean habits would protect them from hawk predation, yet such common species as the Pacific tree-toad and the California toad must be seen frequently by the hawks. If they are eaten, perhaps they are completely digested, leaving no hard parts in the pellets to be identified, but none was found among the nest items either.

Predation on arthropods.—In actual bulk of food consumed, insects made up only an insignificant portion of the total and were estimated to comprise less than two-hundredths of one per cent of the weight of all recorded items; but in number of occurrences they were slightly more than one-eighth of the total in pellets. Of the 534 arthropods identified in pellets, all were insects except two centipedes, one scorpion, and 22 "arachnids." Arthropods made up more than one-fourth of the total number of species among the pellet items, but were far less important in the diet of the Red-tailed Hawk than this fact might suggest and were almost invariably associated with vertebrate remains. Only two pellets were composed entirely of arthropods (grasshopper and Jerusalem cricket). The arthropod species occurring in pellets may be grouped in four general categories, although many occurrences are problematical. First are those pursued and captured by the hawks as actual prey, definitely including the Jerusalem cricket (*Stenopelmatus*), grasshopper (in some of its occurrences), giant water bug (*Belostoma*), giant water beetle (*Hydrous*), and perhaps others. A second group includes those species taken casually or accidentally by the hawks because they are attracted to the flesh or carrion on which it is feeding; included are the greenbottle fly (*Lucilia*), yellow jacket (*Ves-pula*), carrion beetle (*Silpha*), certain scarabeid beetles, ants, and probably others. A third group includes those eaten by small vertebrates, which themselves later become victims of a hawk. The chitinous remains of the insects disgorged in the pellets are apt to be associated with remains of the animals that ate them. In this class come the majority, both in number of individuals and number of species, of the arthropod items. They include buprestid, carabid, and tenebrionid beetles, *Amara*, *Amphicyrta*, *Coni-ontis*, *Eleodes*, *Nyctoporis*, *Pterostichus*, *Phobetus*, lepidopterous larvae, and certain arachnids—mostly small forms, some of vegetarian habits. More than half the grasshoppers recorded were with remains of either whiptail lizard or skink, and the majority of hemipterans, coleopterans, and arachnids were with one of these two kinds of lizards. Ants were with remains of fence lizards in six of the 18 occurrences; in all but one occurrence they were with either bird or lizard remains. A fourth category of arthropod

items includes those attached as parasites to the prey animals and taken accidentally by the feeding hawk. Only one such item was found in our records, a larval *Cuterebra*.

Frequency of feeding.—In the late fall and winter of 1940-41, an unmated juvenal hawk was made the subject of intensive observations to obtain an idea of the amount of food normally killed and eaten and thus to evaluate the effect of predation on prey populations. The hawk selected for these observations was an unusually tame one, and its movements were largely restricted to an area within the 200 yards' distance separating its favorite perch trees. Observations were made with binoculars at distances of 200 to 300 yards. It could be readily discerned whether the bird had fed recently by the prominently distended crop after a meal. On a few occasions when momentarily out of sight, the hawk may have eaten some small food item such as a beetle or Jerusalem cricket, but this is improbable, and such small unrecorded items could not have comprised more than an insignificant percentage of the food. Each full meal was evident.

For a total of 21 full days, the actions of this hawk were followed in detail and every meal taken by it was recorded. The periods of consecutive watching were as follows: 6 days, 3 days, 3 days, 2 days, 2 days, 2 days, 2 days, 1 day. During this period a total of only five kills were made, from which meals were eaten on eight different days. On the remaining thirteen days, no food, with the possible exception of minute items, was taken. The longest period of fasting extended over five consecutive days. During the latter part of this long period of fasting the bird became restive, moved more frequently, and covered an area several times the size of its usual range. The kills recorded in the 21 days were 1 five-foot gopher snake, 1 adult cottontail, and 1 adult ground squirrel (each fed upon for two successive days), 1 mouse (*Peromyscus boylii* or *P. truei*), and one unknown item, suspected to have been a gopher from the site of its capture and the subsequent degree of distension of the hawk's crop. The combined weights of these prey animals was computed to be somewhat over two kilograms. Thus, during the period it was observed, the hawk averaged about 100 grams of prey per day. Since some portions of the snake, the cottontail, and the ground squirrel were discarded, the food actually eaten by this hawk amounted to somewhat less than 100 grams per day, perhaps scarcely more than half the amount consumed by a caged adult. This may be near the minimum food requirement, and as observations extended over one long fasting period, it seems probable that on the average hawks in the wild use considerably more, eating at least 100 grams a day in addition to perhaps an equal amount which is discarded.

The habit of returning on successive days to feed from a kill too large to be consumed at a single meal may be characteristic during cool weather, but during the hot dry weather, prevailing for at least seven months of the year, prey ordinarily would not be available for more than a single meal. Decomposition begins within a few hours after death and carcasses are soon found by vultures, which patrol the Experimental Range in large numbers. Therefore, it may be assumed that in summer a separate kill is generally made for each meal taken. Evidence that both members of a mated pair may feed from the same animal when one has killed large prey was obtained on several occasions when pairs of hawks were flushed from the ground under circumstances that suggested they may have been sharing a meal. If such sharing occurs commonly, it must reduce appreciably the amount of prey necessary to maintain a pair.

Comparison of feeding data from pellets and nests.—In an attempt to determine the importance of various prey species in the food of the hawks, computations of the relative weight or bulk of each prey species in relation to the diet as a whole were made (table 5). These computations were made separately for the two sets of prey records, from nests and from pellets. An average individual weight for each prey species was

multiplied by its number of occurrences, and by adding these totals, the actual weight of food taken by the hawks to produce the pellets collected, or the remains found at nests, was estimated. The percentages of this total comprised by each species are significant, although these weights are of course merely approximations. Choosing a representative average weight for each species was difficult, even though for many species a large number of weight records were on hand showing seasonal, sexual, and age variation. In the case of the ground squirrel, for instance, individuals preyed upon by the hawks may weigh from 100 to 1200 grams. During the season when small young squirrels are abundant, they are taken in disproportionately large numbers as compared with adults. For this reason, a weight of 200 grams was used as representative of squirrels brought as nest prey while a weight of 500 grams was used for the year around sample in the pellets including adults and grown young as well as small ones.

Variation in weight among individuals of a species, and selection by the hawks, and, in the case of the pellets, inexact correspondence in number of occurrences and number of individuals would introduce errors. Nevertheless, prey species differ so much from each other in size that the general proportions comprised in the hawk diet can be readily shown.

Important differences exist between the set of feeding records based on pellet examinations and that based on nest items. In some instances the reasons for these differences are apparent from the nature of the material, but in other instances they are obscure. In reflecting the feeding habits of the Red-tailed Hawk in this locality, the two sets of records agree essentially in showing that three mammalian species, the ground squirrel, cottontail, and pocket gopher, and one reptile, the gopher snake, comprise the staple year-round diet with the first named species by far the most important, and that these are supplemented by a long list of rodents, snakes, lizards, and birds.

Table 5
Comparison of Prey Determined from Nest and Pellet Items

Kind of prey	Average weight in grams	Per cent weight of total pellet items	Per cent weight of total nest items
Ground squirrel	500 (in pellets) 200 (in nests)	49.50	60.80
Rabbit	800	24.20	26.50
Gopher snake	500	8.95	3.80
Pocket gopher	100	7.40	4.30
Rattlesnake	300	2.10	trace ¹
Snake (unidentified)	400	1.61
Rodent (unidentified)	100	1.39
Wood rat	200	1.10	1.40
Quail	160	trace	1.00
Bird (unidentified)	78	0.86	trace
Whiptail lizard	25	0.56	0.30
Racer	150	0.75
Reptile (unidentified)	200	0.65
Gray squirrel	500	trace	0.40
Chipmunk	70	trace	0.40
Kangaroo rat	60	0.19	0.40
Road-runner	430	0.30
Skink	20	0.20	trace
King snake	280	0.26
All arthropods	up to 1 (variable)	trace

¹ Traces are less than one-tenth of one per cent.

Additional traces (less than one-tenth of one per cent) for the pellet items included mice of the genera *Peromyscus*, *Reithrodontomys*, *Microtus*, and *Perognathus*, bat, towhee, meadowlark, woodpeckers (*Balanosphyra*, *Asyndesmus*), Linnet, sparrow, warbler, bluebird, garter snake, fence lizard, alligator lizard, brown-shouldered lizard, and unidentified lizard; and for the nest items included mice of the genera *Peromyscus* and *Microtus*, towhee, Screech Owl, Lark Sparrow, and sharp-nosed snake.

The absence of insects from the nest items and their frequent occurrences in pellets constitutes one of the most striking differences between the two sets of records; probably any insects brought to the nests are bolted entire, and hence are not found.

Rodents and rabbits combined comprise almost ten per cent less by weight in the pellet records than in the nest records. Their scarcity was compensated for mainly by greater abundance of reptiles in the pellets, although reptile activity is at its annual peak during the nesting season of the hawks and it would seem that reptiles are then much more available than at other times of year. Possibly the smaller reptiles are usually eaten where they are captured by the parents and hence are not represented in their true proportions for that season.

Methods of hunting.—The two principal methods of hunting are, first, waiting on a high perch until some prey exposes itself, then dropping upon it with a sudden direct swoop, and, second, quartering back and forth in low flight to pounce upon some animal in the open and to take it by surprise before it can reach shelter.

It is probable that most of the hawks' food is secured through the first method. The keenness of the hawks' eyesight enables them to discover and identify any small animals moving about within a radius of perhaps more than a hundred yards. The victim is usually unaware of the hawk and may be watched until it has moved into a position where it can be caught; then the bird glides toward it on set wings and strikes. From the point where the prey is situated, movement is almost imperceptible, as the hawk launches into flight, approaching in a straight line, with wings and body rigid. The hawk gains speed in its downward course, and the last few yards are covered in a fraction of a second so that even after it became aware of its danger, the victim, especially some near-sighted animal such as a snake or gopher, would scarcely have time to move before being struck.

On December 3, 1940, a hawk was observed for the entire morning and during this period it changed perches five times, making only short flights from one tree to another. At about noon it suddenly left its perch in a long glide to the ground 225 feet away, and swerving beneath low-hanging branches of a live oak, it crashed through dense but brittle dead brush for a distance of three feet as it struck at its quarry at the edge of a rock outcrop. The prey, partly protected by dead brush, was apparently not well secured at first. The hawk was obliged to lunge a second time to catch it, and then forced its way five feet farther through the brush, emerged, climbed on a boulder, and ate the animal, a large mouse (*Peromyscus truei* or *P. boylii*). Later it was flushed twice by the investigator, but otherwise it made only one short flight during the afternoon before its final flight at dusk to its night roost.

On the following morning at 8:12 a.m., this same hawk was seen to make another capture. It was perched on the same limb from which it had swooped at the mouse and dropped off with wings half folded in a straight 250-foot glide to the ground. The prey was in the open on a flat rock but was knocked for a distance of several feet as the hawk struck it. Although partly hidden from view, the hawk could be seen flapping violently as it struggled with the prey on the ground. Investigation revealed that it had caught a five-foot gopher snake. The snake evidently had been seized first at the middle of the body, then caught by the neck and bitten in the neck and head until dead. In eating the snake the hawk began at the head. About two minutes after the attack the bird was flushed from the ground by the observer and temporarily abandoned its prey, which was still writhing feebly although its head was partly eaten. The ease and rapidity with which this large reptile was dispatched may have been due in part to the cool weather, preventing it from becoming fully active.

On January 30, at 1:16 p.m., having made ten flights earlier in the day, this hawk suddenly dropped at a 45-degree angle from its 15-foot perch on a dead oak snag to catch an adult cottontail.

The rabbit must have emerged from brush at the foot of the tree to cross an open space, completely unaware of the danger, and as the hawk seized it, a struggle began, but the details could not be seen. It was almost two minutes before the struggles of the rabbit had subsided. Then the hawk, hopping laboriously, dragged it back under the edge of the brush and began to eat it there.

On one occasion a Red-tailed Hawk made a long glide down from its perch on an oak and took by surprise a ground squirrel which was chasing another at a distance from their burrows. Another time a hawk was seen to drop at a steep angle, with claws outstretched, from its perch on top of a high pine; three minutes later it flew up with a young ground squirrel.

An instance of success in more active hunting was observed on May 20; a hawk was seen quartering back and forth over rolling hills, staying at about the height of the tree tops; suddenly it veered sidewise and plunged at a small ground squirrel. The squirrel dived into a hole and escaped by a split second as the hawk struck, raising dust from the burrow mound. As the bird plunged, sharp alarm chirps were given by the intended victim and other squirrels in the vicinity. The hawk swerved upward about 25 feet and gave a loud scream. At this instant another small squirrel which had been in concealing vegetation made a dash for its burrow, almost directly beneath the hawk, which dropped and picked it up without stopping.

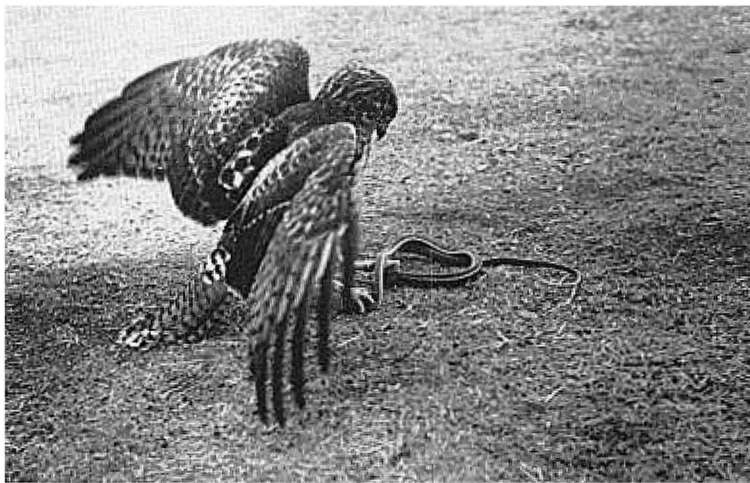


Fig. 50. Red-tailed Hawk killing California Racer.

On several occasions hawks hunting by flying low and erratically among trees, rock outcrops, hillsides, and ravines, in a manner likely to bring them suddenly within close range of a victim, have been seen to miss, and an effective defense is provided by the sharp warning chirp of the ground squirrels, given by each one in turn as it sights the bird. Where the squirrels are common, each one is thus warned and put on the alert well in advance of the hawk's approach.

Often the prey is torn to pieces and bolted on the ground at the spot where it is captured, within a few minutes. If the place of capture is near a convenient tree, and the prey is not too heavy, it may be carried to a perch and eaten. Prey too large to be carried may be dragged to a sheltered spot if one is accessible and eaten on the ground until it is partly consumed; then the remains may be carried to a perch. Remains of carcasses often are seen hanging over limbs of favorite perch trees or lying on the ground beneath them.

SUMMARY AND DISCUSSION

The Red-tailed Hawk is a resident species of the Digger-pine belt of the western Sierra Nevada foothills. Adults are permanently paired, and members of a pair jointly

occupy a territory which they defend against others of their own species and against eagles. Size of territories appears considerably larger than necessary for food supply, and intolerance of the hawks for individuals other than their mates prevents further crowding. Territories average about half a square mile in extent and, in undisturbed areas favorable to the hawks, are occupied in their entirety, although some parts are used more than others. High perches are an essential part of the territory, and the larger Digger pines are favored for this purpose. Dozens of perch trees within a territory may be used, but a few are used more than others. Juvenal hawks remain unpaired, probably for at least two years, and although they may settle within limited areas, they do not defend these against other hawks and are constantly pursued and harassed by paired adults.

Courtship activity, in the form of aërial maneuvers by members of a pair, continues throughout the year and is closely correlated with occupancy and defense of the territory. Nesting begins in March or even in late February. Nesting sites are high (30 to 70 feet) in large pines or, rarely, in blue oaks. Nests are often used in successive years. There are one, two, or three eggs to a clutch. Young are active and vociferous during the first week. When ten days old they may behave aggressively toward intruders, and they become increasingly aggressive as they grow older. At the age of a week they first begin to peck at prey in an attempt to feed themselves, and during the latter part of their stay in the nest, the parents leave prey almost intact for them to tear themselves. After a period of hopping and flapping about on limbs near the nest, they leave at the age of about 45 or 46 days and can fly strongly at the first attempt.

A high proportion of the eggs and nestlings perish. For 38 eggs in 19 nests, fates were as follows: 6 deserted before hatching (probably an unnaturally high loss introduced as a result of disturbance by the investigators), 4 destroyed by jays, 2 blown down, 7 hatched but young destroyed by blood-sucking flies, 2 hatched but young died from unknown accident or disease, 1 hatched but young crushed by parent, 1 hatched but destroyed by storm (apparently diseased also), 16 fledged. Six other nests inaccessible to us for detailed study also were apparently successful to the extent of fledging at least one young each.

After leaving the nest the young remain in the parent territory for several weeks and are fed by the adults as they gradually acquire skill in flying and hunting until they become self-sustaining. After becoming independent they wander away from the parent territory and possibly wander for long distances. They may take up residence in marginal areas between the territories of paired adults, where they lead a precarious existence, constantly chased and molested by any of the adults which happen to see them.

Feeding of the hawks during the nesting season was studied from records of 625 prey items brought to nests by parent hawks. Ground squirrels were by far the most important food, and the 380 recorded exceeded in numbers all other kinds of prey combined. The pocket gopher and cottontail were next most important with 79 and 62 records, respectively. Other items consisted of five species of reptiles, seven of birds, and six of mammals. Individual preferences were marked, and proportions of the different prey species varied greatly for different nests. Observations of certain nesting pairs in successive years showed that individual trends in proportions of various prey species were consistent even though prey populations varied somewhat.

Feeding throughout the entire year was studied from an analysis of 2094 pellets with 4036 individual occurrences of prey items. Trends of the pellet items differed from the nest items most significantly in having a lower proportion of ground squirrels (1049 occurrences), and apparently most severe predation pressure on this species is exerted

during the nesting season when young squirrels are abundantly available. Another important difference was the frequent occurrence of arthropods as pellet items whereas none occurred among the nest items. The combined data from the nest and pellet studies indicate that the ground squirrel is the principal prey species the year around, and that the gopher, cottontail, and gopher snake also are important. Other species which are taken regularly, although comprising only a small percentage of the diet, include whip-tail lizard, skink, wood rat, quail, California jay, and rattlesnake. Nearly every species of the small mammals and reptiles and many of the bird species occurring locally are occasionally eaten. However, many small vertebrates including most of the small common birds of the San Joaquin Experimental Range are not preyed upon by these hawks except under exceptional circumstances.

Often a pellet represents several meals and several days' feeding, but this depends upon the kind of food taken. Larger kinds of prey are not completely eaten, but flesh is torn away from the bones and skin with the result that relatively small amounts of indigestible material contributing to the contents of the pellet is taken. The smaller kinds of vertebrate prey and insects are eaten entire, and the pellets produced may be larger and more frequent.

Observations on hawks in the field and in captivity indicate that on the average a prey weight of from less than 100 grams to 140 grams is eaten daily, and an equal amount may be discarded. About half this weight is made up of ground squirrels. Thus, it is estimated that on the average a squirrel is killed every four or five days by each hawk. Predation on squirrels is much increased during the nesting season when one hawk may kill several in the course of a day in order to keep its young supplied with food. On the average, perhaps 72 squirrels would be eliminated by a hawk during the course of a year from its territory, and the two birds of a pair thus would eliminate 144 squirrels from a 320-acre area, or one to every 2.2 acres. This predation pressure would appear to be only a minor factor among those which hold a squirrel population in check, since it amounts to only a small fraction of the annual increase. The cumulative effect of several kinds of predators, including, besides these hawks, the coyote, gray fox, and rattlesnake, each feeding principally on squirrels, might have an important stabilizing influence.

The ground squirrel as the principal prey species is probably more affected than any of the other kinds of animals eaten. Although almost four gophers are taken for every five squirrels, the gopher is much less affected because it occurs in much denser populations; and having a more rapid rate of increase, it is adjusted to withstand more severe predation pressure. The cottontail, although taken less than a third as often as the ground squirrel, may be affected as much because it occurs in only a fraction of the population density of the squirrels and has a comparable rate of reproduction. Other species preyed upon commonly are taken in relatively small numbers in proportion to the populations in which they occur, and it must be concluded that the direct effect of predation by the Red-tailed Hawk is only a minor factor in their local ecology.

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