RED-TAILED HAWK AND HORNED OWL POPULATIONS IN WISCONSIN

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In the winter of 1953 we began a three-year investigation of interactions between populations of the Red-tailed Hawk (*Buteo jamaicensis*) and the Horned Owl (*Bubo virginianus*) on 95 square miles of open farm land in southern Green County, Wisconsin. The study area included all of Sylvester and Jefferson townships and parts of Clarno and Monroe townships. Additional observations were made on land within one-quarter mile of the area since birds nesting there fed partly in the study area. In the three-year period 90 nests of Red-tails and 48 nests of Horned Owls were examined.

The original vegetation of the area, as determined from surveyors' records by Dr. J. T. Curtis, Department of Botany, University of Wisconsin, consisted of a tongue of maple (*Acer saccharum*)–basswood (*Tilia americana*) forest bordered on the east and northwest by a belt of oak-basswood (*Quercus-Tilia*) forest which continued across the north-central portion of the area. The southeast part and most of the northern edge of the area were covered primarily by tall grass prairie with small islands and extensions of the forest. Extensive agriculture has greatly altered this original vegetation so that only small woodlots remain (fig. 1). Maple-basswood has replaced the oak-basswood chiefly on the north slopes, but oak dominates the drier slopes. The prairie areas are still essentially treeless with only a few scattered fence-row willows (*Salix*), American elms (*Ulmus americana*), and black cherries (*Prunus serotina*) (fig. 2). The principal farm crops are corn, hay, and oats. Much of the land is in pasture.

The other avian raptors breeding on the area were Screech Owls (*Otus asio*), a few Sparrow Hawks (*Falco sparverius*), and Cooper Hawks (*Accipiter cooperi*). Broad-winged Hawks (*Buteo platypterus*), Sharp-shinned Hawks (*Accipiter striatus*), and Marsh Hawks (*Circus cyaneus*) visited the area during migration, and Short-eared Owls (*Asio flammeus*) were uncommon in winter. Rough-legged Hawks (*Buteo lagopus*), sometimes as common as Red-tails between mid-November and mid-April, were the only other large raptors on the area in any numbers.

The word "competition" has been used to refer to a confusing variety of relationships between individuals, but recently Andrewartha and Birch (1954) have given good reasons for restricting the use of that term. Therefore, in this paper we have adopted the following terminology: *Interaction,* any relationship among individuals of the same or differing species; *competition,* the demand of individuals upon any common resource which is in short supply; and *interference,* any detrimental interaction not falling into the class of competition as just defined.

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THE RED-TAILED HAWK POPULATION

Winter population.—Throughout the winter the Red-tails moved about considerably, often sitting and hunting in small groups. We encountered birds throughout the area but most frequently in the wooded portions. Rough-legged Hawks, on the other hand, were most common on the prairie areas.

Of considerable interest was the scarcity of immature Red-tails in the winter. From November 30, 1953, to February 15, 1954, we observed 39 adults and 10 immature

Fig. 1. Typical scene on study area showing small woodlots, scattered trees along a stream, and cropland.

birds. In a comparable period the following winter, we saw 36 adults and two immatures. Many immature birds may migrate to the Gulf coast, as we have three winter recoveries from this region of nestlings banded in Green County (table 1).

In early autumn we often saw paired birds over their nesting woods, but this was not observed in the winter. Yet Fitch, Swenson, and Tillotson (1946) found that California birds were paired and permanently resident in definite hunting and nesting territories. On our study area all resident birds were paired on their territories by the end of February and only migrants travelled singly or in groups.

Breeding population.—The huge, relatively flat nests of the Red-tail, built on large horizontal branches, often at considerable distance from the trunk, were easily located in winter and readily identified. We noted the location of all old nests in the winter since many of them would be repaired or new ones built upon their foundations.

New nests apparently were built in a few days. We observed birds building only twice. On January 30, 1952, we saw two birds carrying sticks to a nearly completed nest and watched building at another nest on March 6, 1954. Twigs used in new nests were obviously broken from larger branches, as the fresh ends were conspicuous. Corn husks were used as lining material in all nests we studied.

Although nests were sometimes built as early as late January, incubation did not start at such an early date. We flushed our earliest incubating bird from a nest on March 1, 1953. We found the first incubating birds in 1954 and 1955 on March 13 and 11, respectively. By aging the young at the time of banding and using an incubation

period of about 35 days (Hardy, 1939), we estimated that the first eggs were laid in the first week of March but that most of them were laid in the second and third weeks. Both sexes participated in incubation. Twice we observed the replacement of one bird by the other.

None of the nests under observation was used three years in succession by Red-tails, but ten nests were used two years in succession. Eight new nests were built in the same woods as the old one, and sometimes the Red-tails re-used a nest after it had remained

Table 1

Recoveries of Nestling Red-tailed Hawks Banded on the Study Area

Date banded	Date recovered	Place recovered	Age at recovery	Distance and direction from banding location
May 26, 1951	July 25, 1951	Monroe, Wis.	3 months	.....
May 10, 1952	Dec. 23, 1952	San Augustin Co., Texas	8 months	800 miles SSW
May 12, 1952	March 9, 1953	Brownview, Point Coupe Parish, La.	10½ months	850 miles SSW
May 2, 1953	Dec. 1, 1953	Jersey, Buchanan Co., Iowa	7 months	120 miles W
May 2, 1953	Nov. 3, 1953	Elgin, Kane Co., Illinois	6 months	80 miles SE
May 8, 1953	Aug. 10, 1953	Dakota, Waushara Co., Wis.	3½ months	110 miles N
May 9, 1953	Sept. 4, 1953	Basco, Dane Co., Wis.	4½ months	25 miles N
May 9, 1953	Dec. 27, 1953	Lake City, Columbia Co., Fla.	8 months	950 miles SE
May 23, 1953	Jan. 30, 1954	Evansville, Rock Co., Wis.	9 months	23 miles NE
May 6, 1954	July 27, 1954	Juda, Green Co., Wis.	2½ months	2 miles NE
May 20, 1954	July 13, 1954	Stevenson, Ill.	2 months	½ mile S
May 20, 1954	Dec. 7, 1954	Fairbury, Livingston Co., Ill.	7 months	120 miles SE
May 22, 1954	Sept. 3, 1954	Monroe, Wis.	3½ months	2 miles W

unused for one season. Often Horned Owls used the old Red-tail nests, and sometimes the two species used the same nest in alternate years.

Although elms were outnumbered by both sugar maples and white oaks (*Quercus alba*), 52 of the 90 nests we found were in elms, perhaps because these trees are common along streams and fence-rows, and because their large, spreading branches provide many suitable nest sites. We found 15 nests in sugar maples, 9 in white oaks, 6 in basswoods, 5 in willows, 2 in red oaks (*Quercus borealis*), and one each in burr oak (*Quercus macrocarpa*), black walnut (*Juglans nigra*), and cottonwood (*Populus deltoides*).

The height of 49 nests ranged from 30 to 90 feet and averaged 57 (±13.1) feet. Nine nests were enclosed by dense woods so that the adults had to fly through trees to reach them. Twenty-three were on the edges of dense woods with access from the open air to the nest (fig. 4*a*). Fifty-seven nests were situated in isolated trees or in open stands of four to several dozen trees with unobstructed access to the nest from several sides (fig. 4*b*). Because Red-tails will nest in such open situations, the prairie regions of our study area were inhabited by them (fig. 3).

In 1954 there were 33 nesting pairs and six non-nesting pairs (0.41 pairs per square mile), while in 1955 there were 27 nesting pairs and one non-nesting pair (0.29 pairs per square mile). Only after a careful search of the area and a study of the birds' behavior did we call pairs non-nesters. In the only other study of Red-tail populations known to us, Fitch, Swenson, and Tillotson (1946) report that in Madera County, California, the density was one pair per 320 acres, a population about five times as dense.

In warm weather food not eaten was removed quickly from the nest, but small bits

sometimes were trampled into the bottom of the nest and caused a considerable stench. Green branches were brought to the nest throughout the fledgling period. They may serve as a clean resting place for the nestlings.

The young, which leave the nest in early June, are dependent on the adults for an unknown period (fig. 5). Recoveries of banded birds shot by local farmers in late July may indicate that independent hunting has started by then (table 1).

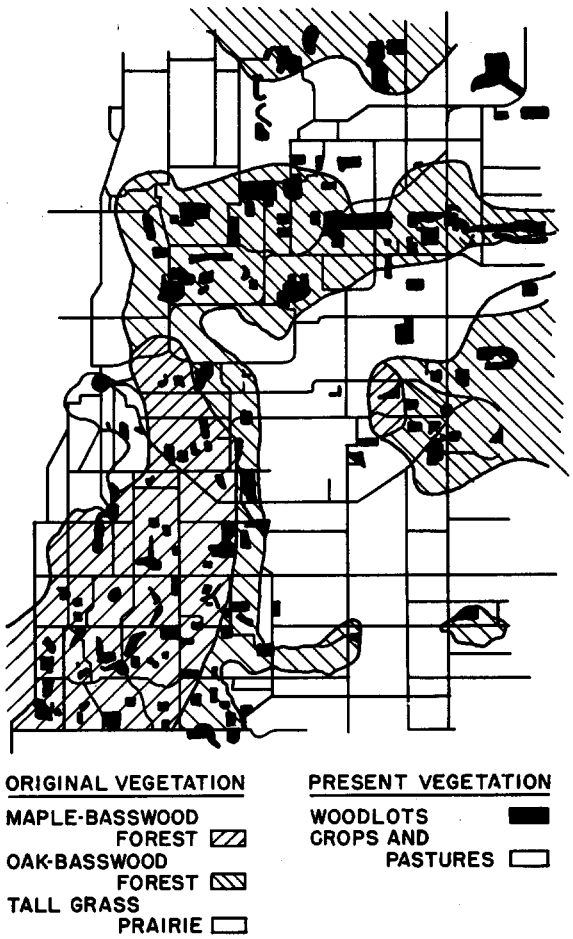

Fig. 2. Original and present vegetation on study area. Scale: 5 mm. = 1 mile.

Nesting success.—We consider a nest successful if one young bird is raised to an age when it can be expected to leave the nest. In 1953, 48 young were reared in 27 nests (1.8 young per nest): one bird in each of six nests, two in 12, and three in six; three nests failed. In contrast, only 36 young were raised in 33 nests in 1954 (1.1 young per nest): one young in each of seven nests, two in 13, and three in one; 12 nests failed. Of the 27 nests in 1955 (1.4 young per nest), four had one young, nine had two young, six had three, and eight failed, making a total of 40 nestlings reared (table 2).

Causes of nesting failure were difficult, and in most cases impossible, to determine. In the critical period when the nestlings were under two weeks of age, there was no

unusually cold weather in any of the three years, but weather may play an undiscovered role in causing nesting failure, as the Red-tail is not tenacious in its brooding. Our presence at one nest just before a sudden thunderstorm caused one failure.

As the only two young we found dead in the nests had been dead too long for us to ascertain the cause, we have no direct evidence of nestling deaths from either starvation or disease. Populations of pheasants and cottontails, the two principal prey species,

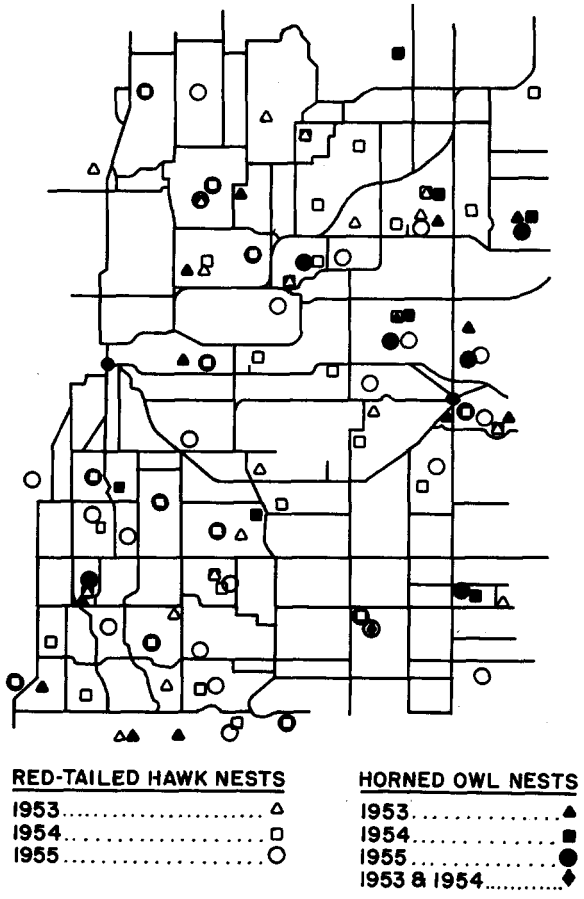

Fig. 3. Locations of nests of Red-tailed Hawks and Horned Owls.

showed no great fluctuations in Green County in the course of our study, according to Wisconsin Conservation Department hunting kill records (table 3). Of the three years, 1954 should have been the year of greatest prey-availability and yet this was the year of poorest Red-tail productivity.

While we have observed no evidence of direct Horned Owl predation on nestling Red-tails, we feel it is a possibility that should not be overlooked, as Hamerstrom and Hamerstrom (1951) report that a tethered fledgling Red-tail was killed by Horned Owls.

One nest failure of 1955 can be correlated with the death of one of the adults which we found shot beneath the nest.

Fitch, Swenson, and Tillotson (1946) attributed the nest failures in their study to

four known causes: desertion probably caused by the intrusion of the investigators; jays, which were observed robbing one nest and held responsible in another case; blood-sucking flies; and trampling by a parent which killed one nestling.

Table 2

Nesting Success of Red-tailed Hawks and Horned Owls

Species	Year	Number of pairs	Pop.* density	Number of nests	Fail-ures	Young/nest 1	2	3	Average number young/nest	Aver. no. young/suc-cessful nest
Red-tailed Hawk	1953	....	.....	27	3	6	12	6	1.8	2.0
	1954	38	0.41	33	12	7	13	1	1.1	1.7
	1955	28	0.29	27	8	4	9	6	1.4	2.1
Horned Owl	1953	20	0.22	13	4	4	5	0	1.1	1.6
	1954	19	0.20	17	1	2	12	2	1.9	2.0
	1955	12	0.12	11	3	3	4	1	1.3	1.8

* Population density expressed as pairs per square mile.

Food.—Our food data for the Red-tail is based entirely on nest remains because pellets do not accurately represent the Red-tail food. In the nests we found: 46 adult Ring-necked Pheasants (*Phasianus colchicus*), 26 cottontails (*Sylvilagus floridanus*), 20 chickens, 9 American Crows (*Corvus brachyrhynchos*), 8 mice (*Microtus*), 6 thirteen-lined ground squirrels (*Citellus tridecemlineatus*), 5 Redwings (*Agelaius phoeniceus*), 2 meadow jumping mice (*Zapus hudsonius*), 2 Yellow-shafted Flickers (*Colaptes auratus*), 2 domestic pigs, 2 domestic turkeys, 2 short-tailed shrews (*Blarina brevicauda*), 3 meadowlarks (*Sturnella* sp.), 1 Cowbird (*Molothrus ater*), 1 Starling (*Sturnus vulgaris*), 1 Rock Dove (*Columba livia*), 1 gray squirrel (*Sciurus carolinensis*), 1 fox squirrel (*Sciurus niger*), and 1 frog (*Rana* sp.).

We found manure on the feathers of many of the chickens in the nests and believe, as do a number of local farmers, that Red-tails pick up dead chickens which are spread on the fields with the manure.

The variability of Red-tail food in southern Wisconsin is seen when our data are compared with those of Errington (1933:27). He found the following prey items in nests in southern and central Wisconsin: 49 thirteen-lined ground squirrels, 42 *Microtus*, 18 chickens, 18 cottontails, 11 arboreal squirrels, 5 *Blarina*, 4 *Peromyscus*, 4 snakes, and 3 eastern chipmunks (*Tamias striatus*). The most striking differences are the complete absence of pheasants, the most numerous item in our study, and the large number of thirteen-lined ground squirrels which Errington found. Green County is one of the best pheasant areas in Wisconsin and the Red-tails on our study area are fully utilizing this abundant food supply.

Red-tails in California eat more rodents and reptiles, and birds are apparently a minor item (Fitch, Swenson, and Tillotson, 1946). The following data from their paper are taken from a list of 625 prey items from 14 nests over a three-year period: 380 Cali-

Table 3

Estimates of Pheasant and Rabbit Kills in Green County*

Year	Pheasant kill	Rabbit kill
1952 (fall)	19,647	27,115
1953 "	20,424	34,625
1954 "	15,380	31,230

* From Wisconsin Conservation Department records.

fornia ground squirrels (*Citellus beecheyi*), 79 pocket gophers (*Thomomys bottae*), 62 cottontails (*Sylvilagus auduboni*), 13 wood rats (*Neotoma fuscipes*), 10 kangaroo rats (*Dipodomys heermanni*), 8 Merriam chipmunks (*Eutamias merriami*), 7 additional rodents, 23 birds, and 23 reptiles.

Plumage variations.—The Red-tailed Hawk is noted for its wide variety of plumages, particularly in the western portion of its range. On our study area no extremely

Fig. 4*a*. Red-tailed Hawk nest in a red oak (*Quercus borealis*) on the edge of dense woods.

Fig. 4*b*. Red-tailed Hawk nest in a basswood (*Tilia americana*) on the edge of an open, heavily grazed woodlot.

white individuals have been observed, but we saw black individuals on ten occasions in the autumn, winter, and early spring. The only immature black bird observed closely was recorded in the company of a "normal" adult on March 28, 1953.

We saw black adults four times at rather widely scattered localities on the southern portion of the area in November, 1952, and we believe at least three individuals were present. On March 22, 1953, we saw one which seemed to be paired to a "normal" bird, but we could not relocate it and we think it left the area. In March, 1954, three different black adults were observed, two of which were migrating north at medium elevation. The third again appeared to be one of a pair and acted as though it were nesting, but it could not be found again later. In 1955 one black adult was observed on March 16.

Black Red-tails were never seen on the area in December or January, but they were observed at that time off the study area in southern Green County. Birds in this plumage were never observed in the summer in southern Wisconsin, and there is no evidence that they ever breed there.

THE HORNED OWL POPULATION

Winter population.—In the late fall and winter, owls roosted in the larger and denser stands of timber, but they used small ones if no large woodlots were available. By visiting each woodlot on the area several times throughout the winter we are certain that we located every bird on the area.

Birds were reluctant to leave the cover of their roosting woods and after being flushed several times they doubled back, often quite close to us. Birds of a pair generally roosted in the same woodlot and by early January the shift to the nesting area, if any, had been made. Similarly, Errington (1932*b*) found that all but one of 29 pairs moved into their nesting areas in late fall and Baumgartner (1938) stated that the nesting site is selected several months before the eggs are laid.

Fig. 5. Young Red-tailed Hawks nearly ready to leave the nest. At this age they begin to jump from the nest at the approach of the climber.

Population density.—There were 20 pairs of Horned Owls and one unpaired bird on the study area in 1953 (0.22 pairs per square mile), 19 pairs in 1954 (0.20 pairs per square mile), and 11 pairs and 4 single birds in 1955 (0.12 pairs per square mile). Near Prairie du Sac, Wisconsin, Errington, Hamerstrom, and Hamerstrom (1940) found 0.5 pairs per square mile, but we know of no other accurate census of Horned Owl populations over significant areas. Baumgartner (1939) heard three or four hooting males per square mile near Lawrence, Kansas, and estimated the population at two pairs per square mile. In California, Fitch (1940, 1947), also counting hooting birds, estimated three to four pairs per square mile. In neither of these instances, however, was the hooting count followed by an intensive search for nests so that it is impossible to judge the accuracy of this method of sampling Horned Owl populations.

Breeding.—Since we searched all woodlots and scattered trees on the area carefully, we believe that for the three years of the study we found all the breeding and non-breeding birds on the area. We began intensive searching for nests in mid-February

when nearly all birds had begun incubating. However, we made no attempt to investigate nests before there were young for fear the eggs would be chilled in the cold winter weather. We calculated the date of egg laying by estimating the age of young at the time of banding, using an accurately dated nest for reference, and adding to that the 33- to 37-day incubation period (Hoffmeister and Setzer, 1947; Elder, 1935).

Most birds laid their eggs between February 5 and 15 but one pair in each of two years laid in the last five days of January. In 1954 one bird did not lay until February 25, the latest laying date for the 48 nests studied.

The birds on our study area used old tree nests of hawks, crows, herons, and squirrels. We found no evidence that owls ever built or remodelled any of these nests and Errington (1932*b*) reports the same for 29 additional Wisconsin nests. Watson (1933) found an old Red-tailed Hawk nest which had been enlarged and newly lined with owl feathers and thought that owls had done the building. Lang (*fide* Baumgartner, 1938), reported a nest at Indian Head, Saskatchewan, Canada, which was built closer to his house than crows had previously chosen, and he was positive that owls had built it entirely. However, in neither instance were owls seen to carry sticks. We have seen owls take over nests freshly repaired by Red-tails and doubt that the Horned Owl builds.

Of the 48 Horned Owl nests we found in the course of the study, 31 were in old Red-tailed Hawk nests, 4 in Cooper Hawk nests, 3 in crow nests, 2 in fox squirrel nests, 1 in a Great Blue Heron (*Ardea herodias*) nest, and 7 in nests of unknown origin. Even if a nest had not been used for several years, we could recognize old Red-tailed Hawk nests by their construction and location. Of 29 nests in southern and central Wisconsin found by Errington (1932*b*), 13 were in Red-tailed Hawk nests, 8 in crow nests, 3 in hollow trees, 2 in unidentified stick nests, 2 in holes in rock faces, and one in a fox squirrel nest. Most Horned Owls in the eastern part of the United States nest in trees (Baumgartner, 1938; Kirkwood, 1925), but in the west, cliff sites are frequently used (Dixon, 1914) and even ground nests are found (Fitch, 1947). In spite of the adaptability of the Horned Owl we feel that on our study area, where there are no cliffs and the trees are cut before they are old enough to have large cavities, the population of Red-tailed Hawks aids the owls greatly in the breeding season by providing many suitable nests.

Thirteen nests were enclosed on all sides by dense woods, 5 were on the edges of woods, 19 were on open, grazed woodlots, and 4 were in very open localities where the few trees were more than 50 feet apart. The locations of nests are shown in figure 3. The nests we measured ranged in height from 25 to 91 feet with an average of 59 (±16.99 feet). The owls sometimes moved as far as one-half mile from their roosting site to find a suitable nest but occasionally a pair left its roosting woods for no obvious reason. One pair left a woods containing eight Great Blue Heron nests and one Red-tailed Hawk nest and used a crow nest only 25 feet from the ground one-third mile away.

Since the nests used by the owls are already at least one year old, they are generally usable for only one year. We found only one nest used two years in succession and by the end of the second year most of it had fallen from the tree. Sometimes, however, nests were repaired and used by Red-tailed Hawks the following year and then were used again by the owls.

The unpaired birds on the area may serve the important function of replacing mated birds which die in the course of the breeding season. This was not observed on the study area, but 30 miles to the north on March 4, 1954, we found an adult male, which had been dead for only a few hours, about 200 feet from a nest. A careful search revealed no owls in the vicinity other than the incubating female. When we revisited the nest on March 9 there were two birds and they successfully raised two young. We do not

know how or where the female acquired her new mate. Such replacements may occur more frequently than our records indicate, as these situations are difficult to detect.

Non-breeding pairs formed a characteristic part of the owl population. Six pairs out of 20 in 1953, 6 pairs out of 19 in 1954, and 1 pair out of 11 in 1955 failed to breed. When a nest could not be located, we searched the area carefully several times to be certain that a hollow tree or ground site had not been overlooked. Failure to breed might be caused by human disturbance, but since several times we observed successful nesting in woodlots that were being selectively lumbered we feel that this is unlikely. Lack of a suitable nest could be advanced as a factor in some instances but on three occasions pairs used nests a second year which were present the year they failed to nest. We think that a likely cause of non-nesting could have been that one of the pair was a yearling incapable of breeding, but we did not collect any birds to test this.

Horned Owls in Wisconsin brood their young constantly for several weeks. In cold weather we could not flush incubating birds by pounding on the tree trunks and we observed an adult brooding one-month-old young on a day when the temperature was 70°F. This brooding tenacity is in marked contrast to the behavior of the Red-tailed Hawk and would seem to be necessary if the species is to nest as early as it does.

It was not possible for us to determine the length of time the young normally remain in the nests as our visits caused many of them to leave prematurely. We closely observed a number of fledglings that had left the nest earlier than normal, and all of them survived. One young bird moved into an old fox squirrel nest where the adults continued to feed it. Since newly fledged birds are so clumsy that they have great difficulty in landing on tree branches, it must be several months before they are able to catch their own prey. The young of the smaller Tawny Owl (*Strix aluco*) are totally dependent upon their parents for three months after leaving the nest (Southern, 1954).

We considered a nest successful if one young bird was raised to the age where it could be expected to leave the nest. Our observations show that most nestling mortality occurred in the first three weeks after hatching. The success of Horned Owl nests for the three years was 1.6, 2.0, and 1.8 young per nest (table 2).

With the exception of one nesting failure in 1954 correlated with logging in the vicinity of the nest, we do not know the causes of nesting failure and cannot explain the differences between the years. Clutch size may vary from year to year, but this is doubtful.

After nests failed we searched the vicinity for adults and always found both parents, so that failure could not have been due to the death of one of the birds. If cold weather were the cause, 1954 should have been the poorest nesting year and not the best, as March of that year was very cold, while the other winters were comparatively mild and snowless. As we were unable to census the populations of the chief prey species (other than by kill records—table 3) on the study area we do not know how likely it is that the young starved. We never found dead young in the nests to examine. Even if prey were plentiful, it might be that a few nights of bad hunting at hatching time would prove fatal to the tiny young. Horned Owls also hunt in the daytime with some success (Fitch, 1947; Vaughan, 1954; Packard, 1954), but prey taken in daylight may be insufficient to offset night failure.

Nestlings vanished from unsuccessful nests and they may have been taken by predators. We feel that the Red-tailed Hawk is the most likely predator species. Fitch (1940) thought that the Red-tail was the most likely predator of one California nest. Other California failures were due to weather, raccoons, and unsanitary conditions created by uneaten prey (Fitch, 1940, 1947).

In the course of the study we banded over 70 young owls, but we have only one recovery, a nestling banded on March 27, 1954, and recovered on October 9, 1954, one-half mile south of the banding location. Errington (1932*b*) obtained three recoveries

from 13 birds banded, all at points 13 to 20 miles from the banding location. We found one adult which had died of a virus infection (Animal Disease Diagnostic Laboratory, University of Wisconsin). The symptoms were similar to those of a dead bird found by Errington (1932*a*), but unfortunately specific determination of the virus was not possible. Golden Eagles sometimes kill owls in the western states (Dixon, 1937; Carnie, 1954) but we know of no important predator of adult owls in Wisconsin.

Fig. 6. Young Horned Owls in nest with remains of an adult cottontail, their principal food on the study area.

Food.—Our studies of the food of the Horned Owl have been limited to the late winter and spring. Pellets collected near the nests contained the following food items: 100 *Peromyscus,* 34 *Microtus,* 17 cottontails, 5 *Mus musculus,* 4 *Blarina brevicauda,* 4 *Rattus norvegicus,* 3 woodchucks (*Marmota monax*), 2 crayfish (*Cambarus*), 1 thirteen-lined ground squirrel, 1 Screech Owl, 1 meadowlark (*Sturnella* sp.), and 1 unidentified passerine.

In the nests we found the remains of 43 cottontails, 30 Ring-necked Pheasants, 7 Yellow-shafted Flickers, 5 American Crows, 3 Rock Doves, 4 meadowlarks, 4 Grackles (*Quiscalus quiscula*), 1 Robin (*Turdus migratorius*), 1 *Peromyscus* sp., 1 *Microtus* sp., 1 chicken, and one Starling.

Cottontails seem to be the chief food of the Horned Owl over much of its range (fig. 6). In California, cottontails formed 61 per cent by weight of the food of the owls (Fitch, 1947), and in parts of the north-central states the percentage is even higher (Errington, Hamerstrom, and Hamerstrom, 1940). The owls on our study area ate far more pheasants than in any other region where they have been studied.

DISCUSSION

Populations.—In this three-year study, the population density of Red-tails varied from 0.41 to 0.29 pairs per square mile. That of the Horned Owls ranged from 0.21 to

0.14 pairs per square mile. However, if the prairie areas, where the owls do not nest, are subtracted from the total area, we have an owl population density of 0.38 to 0.22 pairs per square mile for the three years. There is no evidence which would indicate that human interference other than habitat alteration kept the numbers down.

Thirty-one of the 48 owl nests were built by Red-tails, and as the hawks often re-use their nests, these two species sometimes compete for nests. We saw hawks working at a nest in early February, 1952, but owls were using it in March. On April 11, 1955, we found a Red-tail incubating on a nest which the owls had been using in February. In the course of the study, both species simultaneously nested in the same woods 14 times. Flushed owls were never attacked by adult hawks but we did see immature hawks diving at owls flying in the open on several occasions. On February 21, 1954, we saw an adult Red-tail dive several times at an incubating owl.

In 1954 owl nesting success was best (1.9 young per nesting pair), but in this year the Red-tail success (1.1 young per nesting pair) was the poorest of the three years (table 2). A combination of competition for food and direct interference may be responsible, but more evidence is needed. For unknown reasons the numbers of both species decreased between breeding seasons of 1954 and 1955.

Food relationships.—When considering the food of the Red-tailed Hawk and the Horned Owl the following limitations of our data must be kept in mind: (a) Pellets cannot be used to give a fair quantitative appraisal of the food of the Red-tail. (b) Data were obtained only in the breeding season. (c) The data for the Red-tail were obtained a month later than those for the Horned Owl. (d) Only a few of the most abundant prey species can be discussed profitably because of the small number of data.

It is interesting that pheasants and cottontails were the principal food of both the Horned Owl and Red-tailed Hawk in Green County throughout these breeding seasons. We do not know how similar the food is in the remainder of the year, but our data from the breeding season suggest that these two species have converged in their food selection until they are more similar than various groups of closely related species of birds which have been studied (Lack, 1944, 1945, 1946). This suggests that it would be worthwhile to study the interactions between diurnal and nocturnal predators hunting the same prey species in the same area.

Timing of the breeding season.—With the exception of an occasional crossbill, Horned Owls are the first birds to breed in central and northeastern North America, egg-laying beginning at the coldest time of year. This may be because their food is most readily obtainable early in the spring or because the long post-fledgling period must be completed before cold weather returns.

The critical period for food would seem to be the first few weeks after hatching when one adult must hunt for its brooding mate and young in addition to itself. If breeding began later, it would be possible for both adults to hunt without danger of the young being chilled. It is therefore surprising to find that the numbers of both pheasants and cottontails are lowest at this time when we would expect the greatest strain upon the hunting adult. Before the middle of April, young cottontails are hidden in their nests where apparently they are not vulnerable to predation by owls. The breeding season of pheasants does not begin until May and June, long after the young owls have left the nest.

In spite of their small numbers, however, the prey species may be more vulnerable in early spring when the snow disappears and the flattened vegetation offers the least protection to ground-dwelling animals of any time of the year. Southern (1954) states that woodland owls must breed early in the year, in spite of the cold weather, to enable them to feed their young before the growth of vegetation on the forest floor effectively

conceals their favorite prey, whereas field owls are able to hunt with greater ease throughout the summer so that breeding can be much later and more prolonged. It is difficult to classify the Horned Owl into either of these two categories. In most of eastern North America the species is predominately a forest inhabitant but in the mid-west and far west, it may hunt almost exclusively in open country. In southern Wisconsin it must hunt regularly in both places.

On the other hand, the breeding season may be early because postfledgling survival is better in early broods which learn to hunt and disperse in the early autumn when hunting is easy. Until we have more information on the activities of the young in that crucial period when they are becoming independent of their parents, it is impossible to say which of the two reasons is the important one, or if the breeding season is a compromise between the two.

Table 4

The Food of Four Important Rodent Predators in California*

Prey species	Horned Owl	Coyote	Red-tailed Hawk	Rattlesnake
Cottontail	61.1	45.4	24.2	15.2
Woodrat	17.9	4.9	1.1	1.7
Kangaroo Rat	4.5	3.3	0.2	5.9
Pocket Gopher	4.3	3.5	7.4	2.4
Gopher Snake	3.7	6.0	9.0	.....
Ground Squirrel	2.4	31.2	49.5	70.5
Others	6.1	5.7	8.6	4.2

* Data from Fitch (1947); per cent composition by weight.

The study of animal populations.—Our studies of the Red-tailed Hawk and Horned Owl show that these two species occupy and forage over the same areas, and that pheasants and cottontails are the most important foods for both of them in the breeding season in southern Wisconsin. The studies of Fitch (1947) in California give further evidence of the similarity of the food selected by unrelated species of predators inhabiting the same area (table 4). Pitelka, Tomich, and Treichel (1955) stated that in northern Alaska lemmings formed the chief food for a variety of unrelated predators, namely, Pomarine Jaeger (*Stercorarius pomarinus*), Snowy Owl (*Nyctea scandiaca*), Short-eared Owl (*Asio flammeus*), arctic fox (*Alopex lagopus*), and least weasel (*Mustela rixosa*). Many other examples of this could be cited.

Lack (1944, 1945, 1946) studied many closely related species of birds and found that they all differed strikingly in food and habitat requirements. The same has been found for snakes (Carpenter, 1952) and insects (Diver, 1940). Elton (1946) and Moreau (1948), examined the species composition of a number of arbitrarily defined animal communities and found fewer closely related species occurring together than would be expected if species were randomly distributed. That closely related species, in these cases, differ in habitat and food requirements is interpreted by these authors as indicating that no competition occurs between them today. They have therefore assumed that it must have occurred in the past when the two species came together after their differentiation in geographical isolation from one another. Where their ranges overlapped they "competed" and drove each other into different niches. It is also assumed that the species evolved differences in behavior and structure in response to that niche in which they were successful. But as Andrewartha and Birch (1954:463) have stated, if we assume that "related species have differentiated in geographic isolation, the chances are that they would also have developed different habits and preferences, so

that when they were later brought into the same territory, they would select different sorts of places in which to live. It is not obligatory to suppose that these preferences were developed as a result of 'competition'."

We feel that the study of closely related species that has dominated the attention of students of population ecology in the past two decades may not lead to so complete an understanding of certain dynamics in natural communities as has been expected. Since closely related species seldom occupy the same habitat, the worker is forced to postulate what he thinks must have happened in the past, and to pose hypotheses which can be neither proved nor disproved. We believe that it is equally desirable to study *unrelated* species which are coming into frequent contact with one another. Then it is not necessary to postulate what we think must have happened in the past but we can directly study the present-day levels of interaction among the species of a community. As Elton (1946) pointed out, little is known about the relationships among species drawing on a common resource, the most frequent of all species interactions. That this type of study has been neglected testifies to the unfortunate grip of the "competition in the past" theory on ecological thought and stresses the need for a widening of approach.

SUMMARY

The populations of the Red-tailed Hawk and Horned Owl on 95 square miles of farm land in Green County, Wisconsin, were studied for three years. In this time we believe all resident birds of both species were located and all nests were found.

Red-tailed Hawks hunted singly or in groups throughout the winter but were paired on territories by the end of February. There were 27 nests in 1953, 33 in 1954, and 27 in 1955. Nests were built as early as the end of January but eggs were never laid before March. Nesting success was 1.8 young per nest in 1953, 1.1 young per nest in 1954, and 1.4 young per nest in 1955. The causes of nest failure could not be determined.

Horned Owls did not build their own nests but used old nests of hawks (35), crows (3), herons (1), and squirrels (2). There were 13 nests in 1953, 17 in 1954, and 11 in 1955. All pairs on our area moved into their nesting area by early January and the first eggs were laid by the end of the month. Nesting success was 1.1 young per nest in 1953, 1.9 young per nest in 1954, and 1.3 young per nest in 1955. Thirty-one of the 48 Horned Owl nests we found were in old Red-tailed Hawk nests, and we feel that Red-tails greatly aid the owls by providing a large number of excellent nests.

Pheasants and cottontails were the principal foods of both the Red-tailed Hawks and Horned Owls in the breeding season, and the two predator species may compete for food. They sometimes competed for nests. They may occasionally prey directly upon each other's young.

The authors believe that unrelated species offer the best opportunity to study the interactions of animal populations as they occur together in most habitats. The study of closely related species inevitably leads to postulations of what the observer feels must have happened in the past to produce present-day differences.

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