September 1940

The great horned owl and its prey in north-central United States

Paul L. Errington
Iowa State College

Frances Hamerstrom
Iowa State College

F. N. Hamerstrom Jr.
Iowa State College

Follow this and additional works at: http://lib.dr.iastate.edu/researchbulletin

Part of the Agriculture Commons, and the Zoology Commons

Recommended Citation
Available at: http://lib.dr.iastate.edu/researchbulletin/vol24/iss277/1

This Article is brought to you for free and open access by the Iowa Agricultural and Home Economics Experiment Station Publications at Iowa State University Digital Repository. It has been accepted for inclusion in Research Bulletin (Iowa Agriculture and Home Economics Experiment Station) by an authorized editor of Iowa State University Digital Repository. For more information, please contact digirep@iastate.edu.
The Great Horned Owl and Its Prey in North-Central United States

By Paul L. Errington, Frances Hamerstrom and F. N. Hamerstrom, Jr.

Agricultural Experiment Station
Iowa State College of Agriculture and Mechanic Arts

Entomology and Economic Zoology Section

United States Biological Survey
American Wildlife Institute
Iowa Conservation Commission

Cooperating

Ames, Iowa
## CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foreword</td>
<td>759</td>
</tr>
<tr>
<td>Summary</td>
<td>760</td>
</tr>
<tr>
<td>Introduction</td>
<td>763</td>
</tr>
<tr>
<td>Feeding trends of the great horned owl in the north-central region</td>
<td>768</td>
</tr>
<tr>
<td>General comparison of data for cold and warm weather seasons</td>
<td>776</td>
</tr>
<tr>
<td>Winter to summer transitions in diet as illustrated by data from</td>
<td>771</td>
</tr>
<tr>
<td>family groups of owls</td>
<td></td>
</tr>
<tr>
<td>Summer to winter transitions in diet as illustrated by data from</td>
<td>782</td>
</tr>
<tr>
<td>miscellaneous sources</td>
<td></td>
</tr>
<tr>
<td>Analysis of horned owl predation upon different groups of prey</td>
<td>784</td>
</tr>
<tr>
<td>Rabbits and hares</td>
<td>785</td>
</tr>
<tr>
<td>Norway rat</td>
<td>787</td>
</tr>
<tr>
<td>Mice</td>
<td>788</td>
</tr>
<tr>
<td>Sciurids and miscellaneous rodents</td>
<td>791</td>
</tr>
<tr>
<td>Carnivores and insectivores</td>
<td>793</td>
</tr>
<tr>
<td>Passerine and related small and medium-sized birds</td>
<td>794</td>
</tr>
<tr>
<td>Shorebirds, rails and allies, and miscellaneous water birds</td>
<td>796</td>
</tr>
<tr>
<td>Domestic chicken</td>
<td>798</td>
</tr>
<tr>
<td>Wild gallinaceous birds</td>
<td>799</td>
</tr>
<tr>
<td>Wild ducks</td>
<td>805</td>
</tr>
<tr>
<td>Lower vertebrates</td>
<td>806</td>
</tr>
<tr>
<td>Invertebrates</td>
<td>807</td>
</tr>
<tr>
<td>Discussion</td>
<td>808</td>
</tr>
<tr>
<td>The horned owl and the complex of vertebrate predation</td>
<td>810</td>
</tr>
<tr>
<td>Influence of horned owl predation upon population levels of</td>
<td>817</td>
</tr>
<tr>
<td>prey animals</td>
<td></td>
</tr>
<tr>
<td>The question of economic status of the horned owl in north-central</td>
<td>824</td>
</tr>
<tr>
<td>United States</td>
<td></td>
</tr>
<tr>
<td>Literature cited</td>
<td>827</td>
</tr>
<tr>
<td>Appendix</td>
<td>832</td>
</tr>
<tr>
<td>(A) Family studies</td>
<td>832</td>
</tr>
<tr>
<td>(B) Special phase studies</td>
<td>847</td>
</tr>
</tbody>
</table>
FOREWORD

The original data on predator food habits and prey populations forming the basis for this bulletin were obtained mainly from two cooperative studies. The first was the Wisconsin Quail Investigation, 1929-32, established at the University of Wisconsin by the Sporting Arms and Ammunition Manufacturers' Institute and the United States Biological Survey; the second, the Iowa wildlife research program, 1932-35, Iowa State College and Iowa Fish and Game Commission, aided by financial contributions from J. N. (''Ding'') Darling. Particular acknowledgement is made of help with specimen material by the Division of Food Habits Research of the Biological Survey and of the willingness of a third and current Cooperative Unit to have the senior author conclude partially on its time the necessary manuscript work. The junior authors had official responsibilities in connection with the horned owl research from 1932 to 1935.

In a study covering many years and such wide areas and bound up with other researches to the extent that this one has been, it would be manifestly impossible to list individually all persons who have in some way cooperated; hence our policy will be to give credit in the bibliography and in appropriate places in the text for the more important contributions.

1 Iowa State College in cooperation with the United States Biological Survey, the American Wildlife Institute and the Iowa Conservation Commission, 1935-40.
SUMMARY

Along with other predatory species, the great horned owl has been studied in north-central United States, particularly in Iowa and southern Wisconsin localities in which ecological research upon certain prey types has been carried on contemporaneously. After investigation by field and laboratory methods involving experimentation with captive horned owls and observation in nature, it became obvious that the mass data on feeding trends required by the program could be best obtained through pellet studies supplemented by whatever additional techniques would yield information.

The horned owl food habits data upon which this bulletin is partly based were gathered largely between 1930 and 1935 and were the product of experience with 84 horned owl nests, examination of 4,815 pellets and 23 food-containing stomachs and records of direct predation. The prey types studied were chiefly upland game birds, waterfowl and fur-bearers, though many other forms were observed incidentally. The general procedure was to continue, so far as feasible, work on predation and population year after year on specific areas and to correlate the data from both; in this way, not only have some of the reasons for pronounced changes in food habits of predators become evident, but a superior background for evaluating effects of predation upon population levels of prey species has also resulted.

Data on horned owl feeding trends are less complete for the warmer half of the year, during which but 20 percent of the examined pellets were gathered, and are only fragmentary for late summer and early fall. The field data on prey populations are similarly weak for these months, so our knowledge of predation and population phenomena at the season of maximum abundance of active predators and prey, alike, is distinctly limited. For the remainder of the year, the data appear reasonably adequate.

On the whole, it seems doubtful if north-central horned owls and associated predators exert a dominant influence upon populations of prey animals taken. The predators, even in numbers as great as many may themselves tolerate or can maintain locally, seldom appear to utilize more than a small proportion of the staple foods, i. e., rabbits and mice, conveniently available to them and, as a rule, turn to other mammals or to birds when these temporarily become more available than the prey staples. Overpopulation of habitats by nonstaple prey species has been ac-
panied by some of the most pronounced rises in representa-
tion of these types in diets of such flesh-eaters as the horned owl; 
crises precipitated by weather, destruction of environment, hu-
man activities, etc., were often reflected, as well, by response of 
predators to increased vulnerability of given prey animals.

Predator-prey relationships studied in the north-central region 
were flexible, and predators did not always respond to apparent 
changes in availability of prey. Nevertheless, unrelieved basic 
insecurities of prey populations were often attended by response 
of some predators sufficient to compensate, at least in part, for 
lack of utilization by others; and compensatory tendencies in loss 
rates of prey animals were noted under a wide range of conditions 
having little evident connection with kinds and densities of pre-
dators.
Fig. 1. Adult great horned owl with young in nest. Photo by Stanley F. Stein.
The Great Horned Owl and Its Prey
In North-Central United States

By
PAUL L. ERRINGTON, FRANCES HAMERSTROM AND F. N. HAMERSTROM, JR.

The opportunism that governs much of the preying of the great horned owl (*Bubo virginianus*) (fig. 1) has been brought out by correlation of its food habits, among those of other predators, with data on contemporaneous and local status of certain prey populations (46). Such a background for the appraisal of predation phenomena makes study of this owl's feeding trends of exceptional biological interest. We may see, for instance, that unusual representations of non-staple prey in its diet reflect to a considerable extent insecurity of animal populations due to over-crowding, intraspecific friction, evictions from habitats and miscellaneous natural emergencies (44, 46). Even what may look like routine utilization of staples, such as rabbits and mice, can be conditioned by factors appearing far from simple in analysis.

Food habits data—including some published in an earlier paper (31) but corrected and recast for present use—resulted mainly from research carried on between 1930 and 1935 in Iowa and southern Wisconsin, supplemented by information gained prior to, and after, these years. They are the product of field observations, experience with 84 horned owl nests and examination of 4,815 pellets and 23 food-containing stomachs.

Of the methods used, the study of pellets proved the most satisfactory approach to the technical problems of the investigation. Full consideration has been given the objections of Brooks (18) to the use of pellets in raptorial food studies, and the possible application of these objections to the research program as conceived in Wisconsin in 1929 was explored through experimentation and field investigation (30). Feeding and pellet formation of the horned owl and the salient advantages and disadvantages of pellet studies of this species have been recently discussed (46); let it therefore suffice for the requirements of this bulletin to give the gist of the evidence we have and that to be found in the pertinent literature.

2 Project 330 of the Iowa Agricultural Experiment Station.
3 The reader interested in subspecies of the horned owl occurring in the north-central region is referred to the recent study by Swenk (116).
Horned owl pellets, which are regurgitated castings, usually show the remains of prey animals in fairly identifiable condition. Fur or feathers may or may not be appreciably reduced during digestion; but bones, as a rule, come through without much change, except those of very small size or of cartilaginous consistency (46, 105). It is probable that occasionally a horned owl may eat some animal such as a tadpole or an earthworm, evident debris of which might not appear in pellets; but we have found remains of soft-bodied caterpillars, small amphibians and very immature, small mammals and birds.

The horned owls studied in captivity and in the wild gave the carcasses of food animals a rough dressing, if any at all, and typically swallowed chunks of flesh with accompanying fur, feathers and pieces of bone. The pellet of fig 2 consisted in large part of feathers too bulky to be taken into the owl’s stomach. We have occasionally found rabbit feet, wings of medium-sized birds, or similar material attached to pellets. Flesh may be picked away from bones or tough skin of exceptionally large food animals, but, in the instances coming to our attention, quantities of fur or feathers were also ingested. The only record we have of an important item in the diet of free-living horned owls not being represented in pellet contents relates to spring scavenging upon a freshly skinned cow carcass (32).

If the horned owl pellets are gathered with proper precau-
tions, the risk of contamination with pellets from barred owls (*Strix varia*) and other owls may be reduced to negligible proportions in non-coniferous country of the north-central states (30, 46). Lots totaling hundreds of pellets were discarded as of questionable origin, having been deposited mostly in fall and early winter before breeding season intolerances restricted the use of certain feeding and roosting sites to individual owls or pairs. For the balance of 4,815 pellets judged eligible for study, the incidence of contamination is believed to be considerably lower than 3 percent.

Pellets may be collected in large lots in localities where it would be difficult to secure more than a limited number of stomachs or observational data of quantitative significance and may thus supply the mass data on feeding trends needed for correlation with population studies of given prey species. Under favorable circumstances, time of deposition of the Wisconsin and Iowa pellets could be ascertained with some exactness from mucus content and appearance; even when months old, it was frequently possible to date them within a few weeks by the aid of meteorological records. Contained prey items, especially remains of migratory birds, also yielded useful phenological information.

The familiarity with the habits and idiosyncrasies of individual horned owls, or of family groups, that is often essential in judging the reliability of pellet collections may be gained only occasionally and usually with difficulty except when the owls are scarce or during the months of social and breeding intolerance. Accordingly, we have made special efforts to obtain pellets deposited after the beginning of the period of evident territorial activity as manifested by vigorous hooting, which Baumgartner (10) found occurred between late November and about the first of January at Lawrence, Kan., and about a month later at Ithaca, N. Y. In southern Wisconsin it was observed that many, but not all, horned owls wintered in the vicinity of future nesting sites. Variable quantities of freshly ejected pellets could be gathered about used nests from February to late April or early May. Although dependent upon their parents for food until midsummer or later, the young, if permitted to remain free, would gener-

4 The barred owl, although nearly the same size in outline as the horned owl, is distinctly the more slenderly built and weaker. At times when small mammals, small birds, snakes, amphibians and large invertebrates may be abundant or from some cause highly vulnerable to predation, the prey taken by the two owls may differ only slightly (56), but, in localities where we have worked, the barred owl seldom seems to attack adult rabbits and hares (*Leporidae*), which often constitute staple food for the horned owl.

5 Experimentation has been done to investigate changes in different types of pellets through the action of weathering or of plants and animals. Where usually found, pellets maintained their form rather well during the months when precipitation fell as snow but tended to disintegrate quickly in the spring rains. During the warm, humid weather of late spring and midsummer, they would, in a few weeks, either become covered with saprophytic growths or remain visible only as scattered and bleached bone fragments; after that, it would not be long before they were buried in the humus or soil.
Fig. 3. Young horned owl tethered for purposes of study. Note the slope of the ground which allows the pellets to roll out of the space trampled by the owl.

ally terminate opportunities for pellet collecting by leaving the vicinity of the nest; hence, it proved advantageous to fasten them with chains, swivels and leather anklets (30) on sloping ground down which pellets from food currently supplied by adults could roll out of reach of trampling feet (fig. 3). By means of this technique, data on feeding trends of given family groups have been procured in good sequence to July or August.

Of 4,838 pellets and stomach contents, 3,852 or 80 percent were from late fall to early spring; 986 or 20 percent, from the warmer half of the year. Three hundred and six of the 3,852 from late fall to early spring were known to have been ejected by nestling owls, and at least 709 of the 986 late spring to early fall pellets were from young owls almost wholly dependent upon their parents.

The seasonal food habits picture is the most out of balance for late summer and early fall, when pellets of unquestionable identity were found in very limited numbers. Not only does there seem to be erratic movement on the part of young owls subsequent to "weaning," which apparently occurs at about this time of year (14, 32), but the adults also use specific roosting stations in deciduous woods with much less regularity. Furthermore, the ground vegetation may be so dense as to interfere with searches for pellets, and clues as to the origin of pellets discovered at random have diminished value because of the common feeding of many large and medium-sized raptorial birds upon the arthropods and young vertebrates so liberally available by autumn in this region.

The specimen material was handled as two main groups. Most of the Wisconsin series of 2,266 pellets and stomachs were gathered by Errington, given a preliminary examination by him, then

---

6 As a rule, the vertebrate food of the adults corresponds to that fed the young—free or tethered—but the occurrence of invertebrate items in pellets of different sources may frequently be difficult to interpret (see later discussions in this writing).
submitted to the United States Biological Survey for the final analyses, which were made principally by Arnold L. Nelson, Robert H. Gensch and Clarence F. Smith.

In other states, Malcolm McDonald, Parsons College, Fairfield, Iowa, contributed 196 pellets from that neighborhood; Ralph T. King, then of the University of Minnesota, 60 pellets from the Forestry Station at Cloquet, Minn.; W. J. Breckenridge, University of Minnesota, 308 pellets from the vicinity of Fridley and Anoka, Minn.; and the remaining 2,008 pellets and stomachs were collected largely by the authors and Mrs. Ruth Dudgeon Adams. Preliminary examinations were usually made by the junior authors and Mrs. Adams, with the aid of a fairly complete reference series of skins and skeletons of midwest mammals and birds and the entomological collection of Iowa State College. Errington subsequently reworked all of the Iowa, Minnesota, and South Dakota pellets, sending the more difficultly identifiable items to the Biological Survey.

The summarized results of analyses of pellet lots having special bearing upon the subject matter of this bulletin are given in the appendix. Food items are listed by names expressing the most precise identifications made, with exceptions to be explained. Two species of meadow mouse (Microtus pennsylvanicus and M. ochrogaster, of which the latter was less common) were often recognized, but these are not differentiated in this paper. "Deer mouse" includes Peromyscus leucopus, P. maniculatus bairdi, and remains of many individuals of Peromyscus not further identified. Insects are designated by genera for convenience and space-saving, even when specifically determined.

Insofar as rabbits and hares comprised the greater part of the horned owl's staple prey, it was thought that arrangement of food types in descending phylogenetic order would facilitate comparisons of feeding trends. This arrangement was followed not only in the appendix but also as conscientiously in the tabular presentations as the necessity for lumping data allowed. Obviously such categories as resident and migratory birds included many species only remotely related; and, even in less comprehensive groupings, bitterns and herons (Ardeidae) and grebes (Colymbidae) were placed with certain other water-frequenting birds as shore birds (Charadriioidea) and rails and allies (Rallidae).

\*\*Nomenclature used for birds was that of the 1981 checklist of the American Ornithologists' Union (5); for mammals, Anthony's Field Book (7), except for weasels (71); for lower vertebrates and invertebrates, authorities used by the Biological Survey and Iowa State College for general purposes.
FEEDING TRENDS OF THE GREAT HORNFED OWL 
IN THE NORTH-CENTRAL REGION

In the following presentations of data, subregion I refers to southern Wisconsin (work was done chiefly in Dane, Sauk and Columbia Counties); II, southern and central Iowa (Story, Polk, Jefferson and Wapello Counties); III, northwestern Iowa (Palo Alto and Emmet Counties); and IV, central Minnesota (Anoka and Carlton Counties) and western South Dakota (Haakon County).

The data summarized are from pellets and stomachs only, as those from other sources—whatever their occasional qualitative importance—were of practically no value in quantitative studies because of the disproportionate conspicuousness of feathers and remains of large prey (30, 46). For information on uneaten or fragmentary prey items found about nests and feeding places, the reader may consult the Wisconsin family studies in the appendix (A), 1929-32; in later years, the practice of recording such non-pellet remnants was largely discontinued unless the killing or eating of certain animals by the owls was in itself of interest. Food remains encountered at random in the field were chiefly of rabbits, small owls, gallinaceous and passerine birds; infrequently, of smaller mammals, such as mice.

The food habits data we have can usually be expressed in number of times remains of prey animals or groups are represented in collections of pellets or as percentages of pellets containing representations. Each representation of medium-sized prey—or even small prey—should not necessarily be thought of as remains of a separate individual, for it has been plain from field and experimental studies, alike, that a given victim may serve as food for more than one owl or as more than one meal for a single owl.

Individuals of small animals distinguished in the pellet analyses are given as total numbers or as average numbers per containing pellet when for any reason that seemed desirable. For small mammals and small birds, the individual counts probably included some duplication but hardly enough to have a significant effect on the totals arrived at.

Bones sorted out of hundreds of pellets taken at random from our collections give ratios of minimum numbers of prey individuals to times represented for the following medium-sized species (table 1): cottontail rabbit (*Sylvilagus floridanus*), snowshoe or varying hare (*Lepus americanus*), Norway or barn rat (*Rattus norvegicus*), muskrat (*Ondatra zibethica*), pocket gopher (*Geomys bursarius*), screech owl (*Otus asio*), domestic pigeon (*Columba livia*), coot (*Fulica americana*), ring-necked pheasant (*Phasianus colchicus torquatus*), bob-white quail (*Colinus vir-
ginianus) and Hungarian or European partridge (*Perdix perdix*).

Attempts to ascertain the volume of the horned owl’s food made up of different prey groups as originally eaten were of course handicapped because of the natural short-comings of the pellet specimen material. The skeletal debris of 1,135 of the Iowa

### TABLE 1—DATA ON PROPORTION OF MEDIUM-SIZED PREY INDIVIDUALS PER PELLET REPRESENTATION IN RANDOM SERIES.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Number of pellets containing prey remains</th>
<th>Minimum number of prey individuals distinguished by bone counts</th>
<th>Average fraction of a complete prey skeleton per representation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cottontail* adult</td>
<td>1391</td>
<td>175</td>
<td>0.13</td>
</tr>
<tr>
<td>Cottontail* young</td>
<td>152</td>
<td>107</td>
<td>0.70</td>
</tr>
<tr>
<td>Snowshoe hare</td>
<td>59</td>
<td>11</td>
<td>0.19</td>
</tr>
<tr>
<td>Norway rat</td>
<td>103</td>
<td>47</td>
<td>0.46</td>
</tr>
<tr>
<td>Muskrat, chiefly young</td>
<td>29</td>
<td>17</td>
<td>0.59</td>
</tr>
<tr>
<td>Pocket gopher</td>
<td>36</td>
<td>14</td>
<td>0.39</td>
</tr>
<tr>
<td>Sooty owl</td>
<td>51</td>
<td>16</td>
<td>0.31</td>
</tr>
<tr>
<td>Domestic pigeon</td>
<td>18</td>
<td>7</td>
<td>0.39</td>
</tr>
<tr>
<td>Coot</td>
<td>34</td>
<td>9</td>
<td>0.26</td>
</tr>
<tr>
<td>Phesant</td>
<td>168</td>
<td>33</td>
<td>0.20</td>
</tr>
<tr>
<td>Bob-white</td>
<td>88</td>
<td>29</td>
<td>0.33</td>
</tr>
<tr>
<td>Hungarian partridge</td>
<td>40</td>
<td>12</td>
<td>0.30</td>
</tr>
</tbody>
</table>

*Considerable numbers of the pellets containing cottontail remains were so broken or scattered when found as to make complete reassembling virtually impossible; for adult cottontails, at least, the figures are thought to be out of line, especially in view of the ratio shown by the somewhat larger snowshoe hare.

It was considered a matter of some interest that, while parts of as many as 3 skeletons of adult bob-whites have been found in a single horned owl pellet, individuals are seldom eaten entire at one feeding. Twenty quail-containing pellets were selected for completeness and looked through for bones of diagnostic importance; the tally was 6 skulls, 7 sterns, 5 right humeri, 7 left humeri, 6 synsacra, 5 right femora, 6 left femora, 2 right tarsometatarsi, and 5 left tarsometatarsi. Each quail representation, then, was the equivalent of remains of about one-third of a bird or in agreement with the ratio for the larger but unselected series of table 1.
and Minnesota pellets was, however, studied in sufficient detail to permit (after consideration of the anatomy of the prey animals and the probable feeding procedure of the owls) a fairly clear reconstruction of volumetric proportions of items in terms of stomach contents before reduction to pellets; and the resulting percentages of food types by bulk are incorporated in table 5.

In table 3 the volumetric proportions of foods in subregional diets of the owls were based upon less detailed data and are probably liable to more error due to personal judgment. These figures were derived from a study of tabulated food representations, ratios of prey individuals or representations, and data showing numbers or fractions of prey individuals the remains of which comprise typical full pellets of essentially unmixed composition. It was computed that a full, unmixed meal would be the equivalent of about 6 large mice, about \( \frac{1}{2} \) of a Norway rat, about 3 \( \frac{3}{5} \) passerine birds of the kinds ordinarily taken by the owls, about \( \frac{2}{3} \) of a screech owl, domestic pigeon, or bob-white, about \( \frac{1}{2} \) of a coot, \( \frac{1}{3} \) of a pheasant and so on. Incompleteness of many of the pellets containing cottontail remains interfered with translation of representations of medium-sized mammals into volumetric equivalents, but this was the only major group for which satisfactory values could not be obtained from the available totals of representations and individuals of prey. We may therefore fill in this hiatus by subtracting from 100 percent the sum of the percentages from the other more easily manipulated groups.

Representation percentages do not greatly exceed volumetric for medium-sized mammals, and remains of small prey in pellets made up principally of cottontail, etc., are often roughly equal to the traces and minor fragments of the latter victims that may be found in debris predominantly of lesser forms. When pellets may consist wholly of remains of many small animals of the same species or genus, volume and representation may thus be synonymous; but, on the whole, representations of the smaller sizes of prey tend to have numerical values out of proportion to volume of remains, either as freshly eaten food or as pellet material.

**GENERAL COMPARISON OF DATA FOR COLD AND WARM WEATHER SEASONS**

Tables 2 and 3 summarize fall to spring and spring to fall feeding trends by subregions. Table 2 deals with prey groups that will be discussed later in the section on analysis of horned owl predation. Representation percentages only are given, as it was felt that the data from all of the pellets and stomachs did not justify volumetric calculations in the detail required by certain of the groups. Lesser inaccuracies, nevertheless, should be
offset by the breadth of the categories used in table 3, in which both representation and volumetric percentages are compared.

Subregions I and II showed little difference in cold and warm weather feeding on medium-sized mammals, although in II it took increased utilization of rats and miscellaneous rodents in the warmer months partially to make up for lessened importance of rabbits. Rabbits were likewise of decreased importance in the summer diet for IV, but the utilization of miscellaneous rodents was insufficient to change the trend for medium-sized mammals, collectively. This holds true for III to an even greater degree. Consumption of mice by the owls was less in warm weather than in cold in all subregions except IV, and the seasonal difference was decidedly more pronounced in I.

Resident as well as migratory birds were more prominent in the warm weather diets of the owls. Wild gallinaceous birds of I were preyed upon less heavily in late spring and summer, but, in this subregion, there was a notable increase of local pressure upon domestic chickens as young poultry became available. Warm weather increases in utilization of lower vertebrates were most evident in I and II; of invertebrates, I and IV.

WINTER TO SUMMER TRANSITIONS IN DIET AS ILLUSTRATED BY DATA FROM FAMILY GROUPS OF OWLS

Availability of prey naturally varies to some extent with the seasons, and the food habits of certain family groups of owls can be followed practically from day to day for weeks or months during the winter-spring-early summer transition period. Diets may best be described, however, by the use of longer than daily or weekly intervals.

Horned owl studies have shown few, if any, food preferences (32, 46); still, the question frequently arises whether apparent changes in feeding trends may not more correctly reflect individual differences in hunting routines rather than changes in general or local availability of prey. To reduce unknowns as much as possible, we have attempted to restrict the winter to summer transition data to those from individual or closely associated owls of fairly well-ascertained identity—mated pairs and their current offspring. This has meant excluding pellets deposited in fall and early winter, unless we had reason to believe that none but the owls nesting had been present so early in the territories or that the pellets from transients were so few that their inclu-
<table>
<thead>
<tr>
<th>Subregion</th>
<th>Prey groups</th>
<th>Fall to Spring</th>
<th>Spring to Fall</th>
<th>Fall to Spring</th>
<th>Spring to Fall</th>
<th>Fall to Spring</th>
<th>Spring to Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Rabbit and hares*</td>
<td>66.8% 63.2% 75.0%</td>
<td>4.9% 13.4% 66.0%</td>
<td>4.8% 37.7%</td>
<td>43.8% 87.8%</td>
<td>75.2% 3.8%</td>
<td>17.9% 0.8%</td>
</tr>
<tr>
<td></td>
<td>Norway rat</td>
<td>6.3% 12.5% 19.2%</td>
<td>15.6% 29.3% 42.4%</td>
<td>16.8% 32.1%</td>
<td>40.5% 52.8%</td>
<td>75.9% 3.8%</td>
<td>17.9% 0.8%</td>
</tr>
<tr>
<td></td>
<td>Mice</td>
<td>49.8% 34.5% 34.4%</td>
<td>34.5% 34.5% 34.5%</td>
<td>32.9% 34.5%</td>
<td>37.8% 37.9%</td>
<td>29.9% 28.6%</td>
<td>17.9% 0.8%</td>
</tr>
<tr>
<td></td>
<td>3.3 av. per containing pellet</td>
<td>2.4 av. per containing pellet</td>
<td>2.3 av. per containing pellet</td>
<td>2.3 av. per containing pellet</td>
<td>2.3 av. per containing pellet</td>
<td>2.3 av. per containing pellet</td>
<td>2.3 av. per containing pellet</td>
</tr>
<tr>
<td></td>
<td>Scirpids and mice</td>
<td>1.8% 3.8% 1.6%</td>
<td>6.3% 6.3% 6.3%</td>
<td>3.4% 6.4%</td>
<td>7.9% 14.3%</td>
<td>14.3% 7.6%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Carnivores and insectivores</td>
<td>4.1% 5.2% 4.7%</td>
<td>2.9% 2.9% 2.9%</td>
<td>2.1% 1.0%</td>
<td>4.3% 7.6%</td>
<td>7.6% 14.3%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Passerine and related small and medium-sized birds</td>
<td>8.9% 22.6% 14.2%</td>
<td>26.1% 26.1% 26.1%</td>
<td>11.4% 25.8%</td>
<td>10.5% 23.8%</td>
<td>23.8% 3.8%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Shorebirds, rails and allies and water birds</td>
<td>0.8% 7.6% 0.8%</td>
<td>4.2% 4.2% 4.2%</td>
<td>3.2% 20.5%</td>
<td>1.3% 3.8%</td>
<td>3.8% 14.3%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Domestic chicken</td>
<td>0.4% 8.4% 1.1%</td>
<td>3.4% 3.4% 3.4%</td>
<td>0.7% 2.3%</td>
<td>0.3% 4.8%</td>
<td>4.8% 14.3%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Wild gallinaceous birds†</td>
<td>5.3% 2.0% 7.8%</td>
<td>9.2% 9.2% 9.2%</td>
<td>20.5% 29.2%</td>
<td>7.6% 10.5%</td>
<td>10.5% 23.8%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Wild ducks,</td>
<td>0.5% 1.4% 0.8%</td>
<td>1.3% 1.3% 1.3%</td>
<td>3.9% 6.4%</td>
<td>0.3%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lower vertebrates§</td>
<td>1.9% 7.8% 1.3%</td>
<td>0.4% 0.4% 0.4%</td>
<td>0.9% 8.1%</td>
<td>1.3% 2.8%</td>
<td>2.8% 14.3%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Invertebrates</td>
<td>1.6% 41.7% 3.4%</td>
<td>20.6% 20.6% 20.6%</td>
<td>4.3% 20.0%</td>
<td>2.0% 23.8%</td>
<td>23.8% 3.8%</td>
<td>23.8% 3.8%</td>
</tr>
<tr>
<td></td>
<td>Representations...</td>
<td>1.0 av. per containing pellet</td>
<td>1.1 av. per containing pellet</td>
<td>2.0 av. per containing pellet</td>
<td>1.7 av. per containing pellet</td>
<td>1.7 av. per containing pellet</td>
<td>1.0 per containing pellet</td>
</tr>
<tr>
<td></td>
<td>Individuals...</td>
<td>0.0 av. per containing pellet</td>
<td>0.0 av. per containing pellet</td>
<td>0.0 av. per containing pellet</td>
<td>0.0 av. per containing pellet</td>
<td>0.0 av. per containing pellet</td>
<td>0.0 av. per containing pellet</td>
</tr>
</tbody>
</table>

* Largely cottontail except for jack rabbit (*Lepus townsendii campanius*) and snowshoe hare representations in some pellet lots from subregion IV.
† Predominantly bob-white, fall to spring, for subregions I and II; pheasant and bob-white, spring to fall, subregion II; pheasant with considerable Hungarian partridge, subregion III.
‡ Salamander (*Ambystoma* sp.), especially, fall to spring, subregion I; snakes, spring to fall, subregion I; salamander and fishes, fall to spring, subregion II; snakes and frogs (*Rana* sp.) spring to fall, subregion III.
§ Insects for the most part except for crayfish (*Cambarus* sp.) fall to spring, subregion II, and wolf spider (*Lycosa* sp.) spring to fall, subregion IV.

Sion with pellets from residents could not appreciably distort the evidence. Throughout the nesting season and until the tethered young were abandoned by their parents or lost, pellets were gathered with assurance that they came from circumscribed groups, if not known individuals.

Fourteen local areas were the scene of family studies for 2
TABLE 3. REPRESENTATIONS AND APPROXIMATE VOLUMETRIC PROPORTIONS OF MAJOR PREY TYPES IN PELLETS (INCLUDING STOMACHS) FROM COLD AND WARM WEATHER SEASONS,

<table>
<thead>
<tr>
<th>Subregion I</th>
<th>Subregion II</th>
<th>Subregion III</th>
<th>Subregion IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cottontail and other medium-sized mammals</td>
<td>72%</td>
<td>65%</td>
<td>75%</td>
</tr>
<tr>
<td>Mice and other small mammals</td>
<td>52%</td>
<td>28%</td>
<td>40%</td>
</tr>
<tr>
<td>Small and medium-sized resident birds, lower vertebrates</td>
<td>7%</td>
<td>3%</td>
<td>11%</td>
</tr>
<tr>
<td>Small and medium-sized migratory birds</td>
<td>8%</td>
<td>3%</td>
<td>25%</td>
</tr>
<tr>
<td>Lower vertebrates</td>
<td>2%</td>
<td>tr.</td>
<td>8%</td>
</tr>
<tr>
<td>Insects and other invertebrates</td>
<td>2%</td>
<td>tr.</td>
<td>42%</td>
</tr>
</tbody>
</table>

or 3 (usually consecutive) years. At least one member of a horned owl pair, as indicated by distinctive behavior, occupied each year the territories of family studies number 1 and 2, 16 and 17, 18 and 19, 20 and 21, 24 and 25, 30 to 32, and 35 and 36. Data from 4 and 5 and 26 and 28 do not reveal whether any of the occupants of the territories were the same in different seasons. Adults of 8 to 10 and of 11 and 12 were probably different owls each season, and those of 6 and 7, 22 and 23, and 39 and 40 were almost unquestionably so. Influx of new birds into previously vacant nesting territories was observed to take place from fall to February.

The approximate duration of each of 41 family studies is given in table 4. Average and median periods of productive study were about 5½ months, with extremes varying from 26 days (number 32) to perhaps 8 to 8½ months (numbers 15, 35 and 40). In 24 of the 26 instances in which family groups yielded data later than the first of May, one or more young owls were kept tethered

---

or 3 (usually consecutive) years. At least one member of a horned owl pair, as indicated by distinctive behavior, occupied each year the territories of family studies number 1 and 2, 16 and 17, 18 and 19, 20 and 21, 24 and 25, 30 to 32, and 35 and 36. Data from 4 and 5 and 26 and 28 do not reveal whether any of the occupants of the territories were the same in different seasons. Adults of 8 to 10 and of 11 and 12 were probably different owls each season, and those of 6 and 7, 22 and 23, and 39 and 40 were almost unquestionably so. Influx of new birds into previously vacant nesting territories was observed to take place from fall to February.

The approximate duration of each of 41 family studies is given in table 4. Average and median periods of productive study were about 5½ months, with extremes varying from 26 days (number 32) to perhaps 8 to 8½ months (numbers 15, 35 and 40). In 24 of the 26 instances in which family groups yielded data later than the first of May, one or more young owls were kept tethered

---

---

---

---
TABLE 4. APPROXIMATE LENGTHS OF TIME FAMILY STUDIES WERE PRODUCTIVE OF FOOD HABITS DATA.

<table>
<thead>
<tr>
<th>Period of productivity</th>
<th>Number of family studies</th>
<th>Serial numbers of family studies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Less than 1 month</td>
<td>1</td>
<td>32</td>
</tr>
<tr>
<td>Between 1 and 2 months</td>
<td>0</td>
<td>28, 19, 30, 36</td>
</tr>
<tr>
<td>Between 2 and 3 months</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>Between 3 and 4 months</td>
<td>1</td>
<td>5, 7, 8, 11, 16, 26, 28</td>
</tr>
<tr>
<td>Between 4 and 5 months</td>
<td>7</td>
<td>1, 5, 10, 13, 17, 20, 22, 23, 29, 31, 33</td>
</tr>
<tr>
<td>Between 5 and 6 months</td>
<td>11*</td>
<td>2, 4, 12, 14, 21, 24, 25, 27, 37, 38</td>
</tr>
<tr>
<td>Between 6 and 7 months</td>
<td>10</td>
<td>6, 34, 39, 41</td>
</tr>
<tr>
<td>Between 7 and 8 months</td>
<td>4</td>
<td>15, 35, 40</td>
</tr>
<tr>
<td>Between 8 and 9 months</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Over 9 months</td>
<td>0†</td>
<td></td>
</tr>
</tbody>
</table>

* Average and median periods of about 5½ months.
† Exceptionally favorable conditions for study in an island habitat permitted gathering of data representing nearly 13 months, but these data doubtless included some from owls not belonging to the original family group.

on the ground; the other instances related to one family on an island and to one probably re-nesting after loss of an earlier clutch of eggs.

Table 5 was prepared from the more specific data from family studies given in the appendix (A). Since pellets from only 13 family studies (numbers 24 to 26, 29 to 31 and 35 to 41) were studied with detailed volumetric calculations in mind, the majority of the feeding trends must be followed through the columns listing percentages of representations.

Family studies 1 to 21 were carried on in subregion I, southern Wisconsin. Data of numbers 1 and 2 are from partly wooded, level, agricultural land; 3 to 10, partly wooded, hilly land devoted to dairying and general farming; 11 to 14, heavily wooded, hilly land, with occasional tracts under cultivation; 15 to 21, partly wooded, chiefly agricultural land in the vicinity of lakes and marshes.

In subregion II, family studies 22 to 34 reflect winter to summer diet in central Iowa areas of rolling agricultural land with wooded stream borders.

The data from subregion III, northwest Iowa, were obtained from two very different types of environment: Numbers 35 to 38, more or less heavily wooded bottomlands in agricultural country; numbers 39 and 40, a wooded island in a marsh surrounded by pastured and cultivated ground.

Pellet material summarized as family study 41, subregion IV, was gathered largely by W. J. Breckenridge from a drained sand plain in central Minnesota. Scattered fields were in cultivation, but the principal growths were of wild brushy and herbaceous vegetation.

It is hard to make generalizations as to increasing or decreasing prominence of the most important prey types with the advent of warm weather. This is exemplified by the frequent lack of
### Table 5. Winter to Summer Changes in Percentages of Major Prey Types Shown Broadly by Representations in Pellets and, Where Data Permit, by Volumetric Calculations.

<table>
<thead>
<tr>
<th>Location</th>
<th>Study</th>
<th>Period Yielding Data</th>
<th>Mammals</th>
<th>Birds</th>
<th>Insects and Other Invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cottontail and Others of Medium Sizes</td>
<td>Mice and Others of Small Sizes</td>
<td>Resident (Incl. Probable)</td>
</tr>
<tr>
<td>Verona, Wis.</td>
<td>Study 1</td>
<td>Winter, 1929-30, through March</td>
<td>39</td>
<td>49%</td>
<td>92%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 5 to 27, 1930</td>
<td>27</td>
<td>81%</td>
<td>48%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 28 to May 15, 1930</td>
<td>22</td>
<td>59%</td>
<td>77%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Late winter, 1930-31, through March</td>
<td>21</td>
<td>86%</td>
<td>57%</td>
</tr>
<tr>
<td>N. E. Pine Bluff, Wis.</td>
<td>Study 3</td>
<td>Winter, 1930-31, through Feb.</td>
<td>33</td>
<td>76%</td>
<td>48%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Early March to March 22, 1931</td>
<td>9</td>
<td>78%</td>
<td>56%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March 23 to April 8, 1931</td>
<td>6</td>
<td>100%</td>
<td>83%</td>
</tr>
<tr>
<td>W. Pine Bluff, Wis.</td>
<td>Study 4</td>
<td>Late winter, 1930-31, to March 22</td>
<td>28</td>
<td>57%</td>
<td>61%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March 23 to April 25, 1931</td>
<td>12</td>
<td>67%</td>
<td>42%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 26 to May 30, 1931</td>
<td>21</td>
<td>81%</td>
<td>52%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 31 to June 25, 1931</td>
<td>10</td>
<td>100%</td>
<td>31%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 26 to July 15, 1931</td>
<td>10</td>
<td>90%</td>
<td>50%</td>
</tr>
<tr>
<td>Locality</td>
<td>Appendix (A) reference</td>
<td>Period yielding data</td>
<td>No. pellets</td>
<td>Mammals</td>
<td>Birds</td>
</tr>
<tr>
<td>---------------------------</td>
<td>------------------------</td>
<td>----------------------</td>
<td>-------------</td>
<td>---------</td>
<td>------</td>
</tr>
<tr>
<td>N. E. Prairie du Sac, Wis.</td>
<td>Family study 5</td>
<td>July 17 to Aug. 8, 1931</td>
<td>15</td>
<td>100%</td>
<td>20%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fall, 1931, to Feb. 23, 1932</td>
<td>23</td>
<td>57%</td>
<td>79%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feb. 24 to April 1, 1952</td>
<td>39</td>
<td>41%</td>
<td>85%</td>
</tr>
<tr>
<td>E. Prairie du Sac, Wis.</td>
<td>Family study 6</td>
<td>Fall, 1930, through March, 1951</td>
<td>30</td>
<td>80%</td>
<td>47%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April, 1951</td>
<td>25</td>
<td>84%</td>
<td>64%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 1 to 24, 1931</td>
<td>26</td>
<td>69%</td>
<td>65%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 25 to June 10, 1951</td>
<td>13</td>
<td>85%</td>
<td>31%</td>
</tr>
<tr>
<td></td>
<td>Family study 7</td>
<td>About Feb. 1 to 21, 1932</td>
<td>9</td>
<td>67%</td>
<td>67%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feb. 22 through March, 1932</td>
<td>50</td>
<td>66%</td>
<td>44%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Early April to May 6, 1932</td>
<td>42</td>
<td>81%</td>
<td>57%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 7 to 30, 1932</td>
<td>20</td>
<td>45%</td>
<td>70%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter, 1930-31, through March</td>
<td>35</td>
<td>77%</td>
<td>43%</td>
</tr>
<tr>
<td></td>
<td>Family study 8</td>
<td>About April 1 to 9, 1931</td>
<td>13</td>
<td>85%</td>
<td>15%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fall to Dec. 21, 1931</td>
<td>5</td>
<td>80%</td>
<td>20%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dec. 22 to Feb. 21, 1932</td>
<td>30</td>
<td>47%</td>
<td>47%</td>
</tr>
<tr>
<td></td>
<td>Family study 9</td>
<td>Dec., 1932, to Jan. 9, 1933</td>
<td>11</td>
<td>91%</td>
<td>36%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jan. 10 to March 8, 1933</td>
<td>17</td>
<td>53%</td>
<td>59%</td>
</tr>
<tr>
<td>Locality</td>
<td>Appendix (A) reference</td>
<td>Period yielding data</td>
<td>No. pellets</td>
<td>Mammals</td>
<td>Birds</td>
</tr>
<tr>
<td>----------------------------</td>
<td>------------------------</td>
<td>----------------------</td>
<td>-------------</td>
<td>---------</td>
<td>-------</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Cottontail and others of medium sizes</td>
<td>Mice and others of small sizes</td>
</tr>
<tr>
<td>S. E. Prairie du Sac, Wis.</td>
<td>Family study 11</td>
<td>March 9 to April 27, 1933</td>
<td>8</td>
<td>50%</td>
<td>50%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter, 1929-30, to about March 25</td>
<td>35</td>
<td>50%</td>
<td>69%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>About March 26 to April 13, 1930</td>
<td>36</td>
<td>97%</td>
<td>11%</td>
</tr>
<tr>
<td></td>
<td>Family study 12</td>
<td>Fall, 1931, through March, 1932</td>
<td>32</td>
<td>56%</td>
<td>56%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>About April 1 to 20, 1932</td>
<td>20</td>
<td>95%</td>
<td>25%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 21 to May 18, 1932</td>
<td>14</td>
<td>71%</td>
<td>21%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter, 1929-30, to about April 7</td>
<td>10</td>
<td>60%</td>
<td>70%</td>
</tr>
<tr>
<td></td>
<td>Family study 13</td>
<td>April 8 to May 7, 1930</td>
<td>6</td>
<td>100%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter, 1931-32, through March</td>
<td>39</td>
<td>62%</td>
<td>74%</td>
</tr>
<tr>
<td></td>
<td>Family study 14</td>
<td>About April 1 to May 3, 1932</td>
<td>34</td>
<td>100%</td>
<td>29%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 4 to 30, 1932</td>
<td>20</td>
<td>90%</td>
<td>15%</td>
</tr>
<tr>
<td></td>
<td>Family study 15</td>
<td>Fall to mid-winter, 1930-31</td>
<td>48</td>
<td>88%</td>
<td>58%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Late winter to early April, 1931</td>
<td>11</td>
<td>100%</td>
<td>45%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Early April to April 24, 1931</td>
<td>21</td>
<td>81%</td>
<td>29%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 25 to May 21, 1931</td>
<td>34</td>
<td>62%</td>
<td>32%</td>
</tr>
<tr>
<td>Local-</td>
<td>Appendix</td>
<td>Period yielding data</td>
<td>No. pel-</td>
<td>Mammals</td>
<td>Birds</td>
</tr>
<tr>
<td>--------</td>
<td>-----------</td>
<td>---------------------------------------------</td>
<td>-----------</td>
<td>---------</td>
<td>------</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>others of</td>
<td>others</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>medium sizes</td>
<td>small sizes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. Mad-</td>
<td>Family</td>
<td>May 22 to July 10, 1931</td>
<td>20</td>
<td>65%</td>
<td>50%</td>
</tr>
<tr>
<td>son,</td>
<td>study 16</td>
<td>Winter, 1930-31, through Feb.</td>
<td>22</td>
<td>86%</td>
<td>45%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March 5 to April 10, 1981</td>
<td>14</td>
<td>86%</td>
<td>21%</td>
</tr>
<tr>
<td>Family</td>
<td>Family</td>
<td>Winter, 1932-33, to Mar. 5</td>
<td>33</td>
<td>79%</td>
<td>30%</td>
</tr>
<tr>
<td>study</td>
<td>study 17</td>
<td>March 6 to April 29, 1933</td>
<td>24</td>
<td>71%</td>
<td>42%</td>
</tr>
<tr>
<td>Middle-</td>
<td>Family</td>
<td>Late winter, 1930-31, to March 10</td>
<td>28</td>
<td>78%</td>
<td>57%</td>
</tr>
<tr>
<td>ton,</td>
<td>study 18</td>
<td>March 11 to April 6, 1931</td>
<td>15</td>
<td>100%</td>
<td>27%</td>
</tr>
<tr>
<td>Family</td>
<td>Family</td>
<td>Middle of March to April 1, 1932</td>
<td>18</td>
<td>94%</td>
<td>39%</td>
</tr>
<tr>
<td>study</td>
<td>study 19</td>
<td>April 2 to 14, 1932</td>
<td>17</td>
<td>106%</td>
<td>35%</td>
</tr>
<tr>
<td>Family</td>
<td>Family</td>
<td>April 15 to June 3, 1932</td>
<td>35</td>
<td>83%</td>
<td>51%</td>
</tr>
<tr>
<td>study</td>
<td>study 20</td>
<td>Fall, 1930, through March, 1931</td>
<td>17</td>
<td>82%</td>
<td>35%</td>
</tr>
<tr>
<td>Family</td>
<td>Family</td>
<td>About April 1 to 11, 1931</td>
<td>8</td>
<td>63%</td>
<td>63%</td>
</tr>
<tr>
<td>study</td>
<td>study 21</td>
<td>Winter, 1931-32, to April 26</td>
<td>66</td>
<td>83%</td>
<td>39%</td>
</tr>
<tr>
<td>Family</td>
<td>Family</td>
<td>April 27 to May 24, 1932</td>
<td>8</td>
<td>75%</td>
<td>50%</td>
</tr>
<tr>
<td>study</td>
<td>study 22</td>
<td>May 25 to June 25, 1932</td>
<td>22</td>
<td>100%</td>
<td>23%</td>
</tr>
<tr>
<td>S. Des-</td>
<td>Family</td>
<td>Winter, 1932-33, to March 11</td>
<td>25</td>
<td>92%</td>
<td>24%</td>
</tr>
<tr>
<td>Moines,</td>
<td>Family</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iowa</td>
<td>study 22</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 5—Continued

<table>
<thead>
<tr>
<th>Localit</th>
<th>Appendix (A) reference</th>
<th>Period yielding data</th>
<th>No. pel-</th>
<th>Mammals</th>
<th>Birds</th>
<th>Lower vertebrates</th>
<th>Insects and other invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Localit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Localit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W. Fam,</td>
<td>Family study 23</td>
<td>March 12 to April</td>
<td>68</td>
<td>78%</td>
<td>35%</td>
<td>7%</td>
<td>16%</td>
</tr>
<tr>
<td>Ames,</td>
<td></td>
<td>28, 1933</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iowa</td>
<td></td>
<td></td>
<td>Fall and early, 1934-35</td>
<td>24</td>
<td>79%</td>
<td>13%</td>
<td>21%</td>
</tr>
<tr>
<td>N. W.</td>
<td>Family study 24</td>
<td>Late winter to April 14, 1935</td>
<td>25</td>
<td>92%</td>
<td>16%</td>
<td>8%</td>
<td>4%</td>
</tr>
<tr>
<td>Ames,</td>
<td></td>
<td>Winter, 1932-33, through March</td>
<td>13</td>
<td>66%</td>
<td>23%</td>
<td>15%</td>
<td>15%</td>
</tr>
<tr>
<td>Iowa</td>
<td></td>
<td>About April 1 to 30, 1933</td>
<td>70</td>
<td>81%</td>
<td>33%</td>
<td>6%</td>
<td>23%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 1 to 28, 1933</td>
<td>21</td>
<td>57%</td>
<td>52%</td>
<td>19%</td>
<td>43%</td>
</tr>
<tr>
<td>N. E.</td>
<td>Family study 25</td>
<td>Fall, 1934, to March 22, 1935</td>
<td>22</td>
<td>64%</td>
<td>21%</td>
<td>36%</td>
<td>4%</td>
</tr>
<tr>
<td>Ames,</td>
<td></td>
<td>March 23 to May 16, 1935</td>
<td>33</td>
<td>79%</td>
<td>9%</td>
<td>21%</td>
<td>39%</td>
</tr>
<tr>
<td>Iowa</td>
<td></td>
<td>Late winter, 1932-33, to April 22</td>
<td>23</td>
<td>100%</td>
<td>39%</td>
<td>13%</td>
<td>4%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 23 to May 21, 1933</td>
<td>21</td>
<td>76%</td>
<td>52%</td>
<td>5%</td>
<td>19%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 22 to June 23, 1933</td>
<td>31</td>
<td>87%</td>
<td>55%</td>
<td>6%</td>
<td>10%</td>
</tr>
<tr>
<td>N. E.</td>
<td>Family study 27</td>
<td>Fall, 1933, to April 8, 1934</td>
<td>54</td>
<td>69%</td>
<td>44%</td>
<td>13%</td>
<td>9%</td>
</tr>
<tr>
<td>Ames,</td>
<td></td>
<td>April 9 to 28, 1934</td>
<td>15</td>
<td>100%</td>
<td>20%</td>
<td>47%</td>
<td>7%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter, 1934-35, to March 15</td>
<td>20</td>
<td>85%</td>
<td>45%</td>
<td>15%</td>
<td></td>
</tr>
<tr>
<td>Iowa</td>
<td>Family study 28</td>
<td>March 16 to April 26, 1935</td>
<td>7</td>
<td>86%</td>
<td>14%</td>
<td>20%</td>
<td></td>
</tr>
<tr>
<td>E. Fam,</td>
<td>Family study 29</td>
<td>Late winter, 1932-33, to April 23</td>
<td>17</td>
<td>100%</td>
<td>82%</td>
<td>12%</td>
<td>18%</td>
</tr>
<tr>
<td>Location</td>
<td>Appendix (A) reference</td>
<td>Period yielding data</td>
<td>No. pellets</td>
<td>Mammals</td>
<td>Birds</td>
<td>Lower vertebrates</td>
<td>Insects and other invertebrates</td>
</tr>
<tr>
<td>----------</td>
<td>------------------------</td>
<td>----------------------</td>
<td>------------</td>
<td>---------</td>
<td>-------</td>
<td>------------------</td>
<td>-----------------------------</td>
</tr>
<tr>
<td>S. E. Ames, Iowa</td>
<td>Family study 30</td>
<td>April 24 to May 28, 1933</td>
<td>27</td>
<td>74% 60%</td>
<td>19% 4%</td>
<td>33% 20%</td>
<td>14% 19% 2%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 29 to June 23, 1933</td>
<td>26</td>
<td>92% 74%</td>
<td>19% 8%</td>
<td>27% 15%</td>
<td>15% 42% 3%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 24 to July 21, 1933</td>
<td>13</td>
<td>69% 52%</td>
<td>23% 8%</td>
<td>62% 11%</td>
<td>30% 30%</td>
</tr>
<tr>
<td></td>
<td>Late April 21, 1933</td>
<td>23</td>
<td>52% 51%</td>
<td>30% 8%</td>
<td>26% 11%</td>
<td>39%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>May 22 to June 11, 1933</td>
<td>11</td>
<td>64% 62%</td>
<td>18% 9%</td>
<td>27% 21%</td>
<td>6% 27% 2%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June 12 to July 6, 1933</td>
<td>20</td>
<td>95% 80%</td>
<td>15% 5%</td>
<td>15% 8%</td>
<td>4% 45% 3%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter, 1933-34</td>
<td>40</td>
<td>85% 69%</td>
<td>33% 23%</td>
<td>10% 5%</td>
<td>8%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>to April 8, 1934</td>
<td>31</td>
<td>69% 53%</td>
<td>30% 26%</td>
<td>18% 18%</td>
<td>3% 12%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>April 9 to May 13, 1934</td>
<td>24</td>
<td>94% 65%</td>
<td>56% 20%</td>
<td>15% 3%</td>
<td>12% 15%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>April 29 to May 15, 1935</td>
<td>16</td>
<td>50% 45%</td>
<td>75% 31%</td>
<td>13% 8%</td>
<td>16% 6% 6%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>About April 20 to May 15, 1935</td>
<td>11</td>
<td>100%</td>
<td>27%</td>
<td>18%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. Ames, Iowa</td>
<td>Family study 32</td>
<td>Winter, 1934-35</td>
<td>20</td>
<td>90%</td>
<td>35%</td>
<td>5%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>through March</td>
<td>About April 1 to March 29, 1935</td>
<td>22</td>
<td>86%</td>
<td>9%</td>
<td>23% 5%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fall, 1934, to late March, 1935</td>
<td>44</td>
<td>86%</td>
<td>20%</td>
<td>9% 25%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>About March 28 to April 25, 1935</td>
<td>33</td>
<td>97%</td>
<td>15%</td>
<td>6% 27% 9%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 26 to June 7, 1935</td>
<td>28</td>
<td>96%</td>
<td>29%</td>
<td>4% 32% 11%</td>
<td></td>
</tr>
<tr>
<td>S. Wallingford, Iowa</td>
<td>Family study 33</td>
<td>Fall, 1933, to April 29, 1934</td>
<td>91</td>
<td>57% 43%</td>
<td>38% 24%</td>
<td>33% 34% 7%</td>
<td>1% 1%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 29, 1934</td>
<td>90</td>
<td>57% 43%</td>
<td>38% 24%</td>
<td>33% 34% 7%</td>
<td>1% 1%</td>
</tr>
</tbody>
</table>

**TABLE 5—Continued**
## TABLE 5—Continued

<table>
<thead>
<tr>
<th>Location</th>
<th>Local- dixity</th>
<th>Period yielding data</th>
<th>No. of pellets</th>
<th>Mammals</th>
<th>Birds</th>
<th>Lower vertebrates</th>
<th>Insects and other invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Cottontail and others of medium sizes</td>
<td>Mice and others of small sizes</td>
<td>Resident (incl. probable)</td>
<td>Migratory (incl. probable)</td>
</tr>
<tr>
<td>S. W. Wallingford, Iowa</td>
<td>Family study 37</td>
<td>April 30 to May 29, 1934</td>
<td>10</td>
<td>40%</td>
<td>25%</td>
<td>30%</td>
<td>25%</td>
</tr>
<tr>
<td>W. Emmetsburg, Iowa</td>
<td>Family study 38</td>
<td>April 30 to May 21, 1935</td>
<td>10</td>
<td>25%</td>
<td>30%</td>
<td>50%</td>
<td>19%</td>
</tr>
<tr>
<td>N. Ruthven, Iowa</td>
<td>Family study 39</td>
<td>April 30 to May 21, 1935</td>
<td>26</td>
<td>35%</td>
<td>38%</td>
<td>82%</td>
<td>27%</td>
</tr>
<tr>
<td>Mud Lake, N. Ruthven, Iowa</td>
<td>Family study 40</td>
<td>April 30 to May 21, 1935</td>
<td>26</td>
<td>35%</td>
<td>38%</td>
<td>82%</td>
<td>27%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 29 to July 12, 1934</td>
<td>42</td>
<td>55%</td>
<td>34%</td>
<td>62%</td>
<td>40%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 29 to July 12, 1934</td>
<td>42</td>
<td>55%</td>
<td>34%</td>
<td>62%</td>
<td>40%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Early spring to April 29, 1935</td>
<td>9</td>
<td>57%</td>
<td>40%</td>
<td>44%</td>
<td>19%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fall, 1934, through March, 1935</td>
<td>33</td>
<td>70%</td>
<td>64%</td>
<td>45%</td>
<td>23%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter, 1933-34, to April 24, 1935</td>
<td>23</td>
<td>91%</td>
<td>77%</td>
<td>30%</td>
<td>14%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April 25 to May 29, 1935</td>
<td>47</td>
<td>72%</td>
<td>48%</td>
<td>51%</td>
<td>16%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 29 to June 10, 1935</td>
<td>19</td>
<td>42%</td>
<td>26%</td>
<td>42%</td>
<td>10%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Late spring to June 18, 1933</td>
<td>27</td>
<td>19%</td>
<td>11%</td>
<td>26%</td>
<td>9%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 19 to July 24, 1933</td>
<td>18</td>
<td>22%</td>
<td>16%</td>
<td>11%</td>
<td>6%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fall, 1934, to March 30, 1935</td>
<td>105</td>
<td>84%</td>
<td>71%</td>
<td>33%</td>
<td>13%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March 31 to May 16, 1935</td>
<td>43</td>
<td>60%</td>
<td>38%</td>
<td>35%</td>
<td>10%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 17 to June 1, 1935</td>
<td>16</td>
<td>38%</td>
<td>19%</td>
<td>31%</td>
<td>7%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 2 to July 15, 1935</td>
<td>12</td>
<td>75%</td>
<td>63%</td>
<td>8%</td>
<td>3%</td>
</tr>
</tbody>
</table>
Table 5—Continued

<table>
<thead>
<tr>
<th>Locality</th>
<th>Appendix (A) reference</th>
<th>Period yielding data</th>
<th>No. pellets</th>
<th>Mammals</th>
<th>Birds</th>
<th>Lower vertebrates</th>
<th>Insects and other invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anoka, Minn. Family study 41</td>
<td>Early winter, 1932-33, to Feb. 25</td>
<td>17 17</td>
<td>88% 70%</td>
<td>35% 18%</td>
<td>12% 6%</td>
<td>1%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Late winter and spring, 1932-33, to about April 20</td>
<td>166 166</td>
<td>87% 71%</td>
<td>42% 21%</td>
<td>8% 5%</td>
<td>3%</td>
<td>1% tr.</td>
</tr>
<tr>
<td></td>
<td>About April 21 to May 21, 1933</td>
<td>54 54</td>
<td>80% 63%</td>
<td>39% 19%</td>
<td>9% 6%</td>
<td>10%</td>
<td>4% 2% tr.</td>
</tr>
<tr>
<td></td>
<td>May 22 to June 18, 1933</td>
<td>32 32</td>
<td>78% 64%</td>
<td>25% 12%</td>
<td>28% 13%</td>
<td>10%</td>
<td>41%</td>
</tr>
</tbody>
</table>

Uniformity of feeding trends revealed by table 5 and the appendix (A). Nevertheless, the limited volumetric data in table 5 may be plotted—excluding family studies 39 and 40 because of their unique marsh setting and consequent overweighting of migratory birds—in a way adequate to give the reader an idea of the foods depended upon as staples in much of the region covered by the research (fig. 4). It may be seen that the trend of medium-sized mammals is irregular but low in late spring when migratory birds are at a temporary peak and also low when resident birds reach their high midsummer level; small mammals gradually decline and lower vertebrates rise rather sharply between early summer and midsummer; invertebrates remain a minor food from late spring to midsummer.

**Summer to Winter Transitions in Diet as Illustrated by Data from Miscellaneous Sources**

We have, as previously indicated, a paucity of data on food habits of horned owls in late summer and early fall and few from what we have reason to believe were the same individuals or groups. Only two local areas have yielded even fair data for this time of year, and they are not very typical of the region as a whole: the island in Mud Lake, north of Ruthven, northwest Iowa (special phase study 1, appendix (B)), and the vicinity of a dry creek north of Philip, western South Dakota (special phase study 2, appendix (B)). A truer picture of seasonal feeding trends is doubtlessly shown by the miscellaneous data.
of special phase studies 3 and 4 (appendix (B)), which were derived largely from stomachs and isolated pellets of clear origin in subregions I and II, respectively.

Table 6 gives the representation percentages of major prey types for special phase studies 1 to 4. Except for special phase study 2, the proportion of pellets and stomachs containing invertebrate remains is not high, but owls utilizing this prey type at all usually did so rather heavily—which suggests feeding by inexperienced or clumsy juveniles (49).
TABLE 6. SUMMER TO WINTER CHANGES IN FEEDING TRENDS SHOWN BY PERCENT OF PELLETS (INCLUDING STOMACHS) IN WHICH MAJOR PREY TYPES WERE REPRESENTED.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Appendix (B) reference</th>
<th>Period yielding data</th>
<th>No. pellets</th>
<th>Mammals</th>
<th>Birds</th>
<th>Lower vertebrates</th>
<th>Insects and other invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mud Lake, N. Ruthven, Iowa</td>
<td>Special phase study 1</td>
<td>July 25 to early fall, 1933</td>
<td>20</td>
<td>45%</td>
<td>15%</td>
<td>5%</td>
<td>70%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Late fall, 1933, to Feb. 10, 1934</td>
<td>24</td>
<td>63%</td>
<td>8%</td>
<td>17%</td>
<td>25%</td>
</tr>
<tr>
<td>N. Philip, S. Dak.</td>
<td>Special phase study 2</td>
<td>Early Aug. to Aug. 25, 1934</td>
<td>13</td>
<td>69%</td>
<td>23%</td>
<td>15%</td>
<td>15%</td>
</tr>
<tr>
<td>Southern Wis.</td>
<td>Special phase study 3</td>
<td>Late summer through early fall, 1930</td>
<td>10</td>
<td>60%</td>
<td>70%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Late fall through early winter, 1930-32</td>
<td>35</td>
<td>54%</td>
<td>46%</td>
<td>20%</td>
<td>6%</td>
</tr>
<tr>
<td>Southern central Iowa</td>
<td>Special phase study 4</td>
<td>Early fall through early winter, 1932-33</td>
<td>25</td>
<td>84%</td>
<td>40%</td>
<td>16%</td>
<td>4%</td>
</tr>
</tbody>
</table>

* Invertebrates eaten were chiefly wolf spiders (Lycosa sp.)

ANALYSIS OF HORNED OWL PREDATION UPON DIFFERENT GROUPS OF PREY

The preying of the great horned owl upon conveniently available forms of life may seem easy to understand, but the factors conditioning different degrees of availability may be many and involved. Predation, in our experience, has rarely seemed just a matter of a predator having a predilection for a given prey species and taking its victims when and where it presumably wished. Development by an individual predator of hunting routines in habitats characterized by certain prey types does not necessarily mean that the predator has a special "taste" for the prey found there, as is illustrated by the promptness with which many predators may take advantage of increased availability of other prey.

It is logical to expect mammals that hibernate or estivate, migratory birds, young of various species, etc., to be utilized at times when actively present in considerable numbers; but there appears to be little evident uniformity in the proportions in
which these or other animal groups may be represented in the diet of an efficient general feeder such as the horned owl. Many fluctuations in representation do not seem to differ essentially from the "waves" in capture of prey species observed in studying the marsh hawk \((Circus hudsonius)\), the diet of which showed transitory prominence of various items \((50)\).

"Wave" phenomena, when compared with contemporaneous population and ecological data, may reflect changes in vulnerability of prey populations that at times may be very significant. Some of the clearest examples will be given later in the discussion of predation upon the muskrat and the bob-white, both of which have been studied with particular thoroughness.

We know so little about the ecology of the majority of species preyed upon by the horned owl, however, that discussions of them must of necessity be in many ways incomplete or inconclusive. Variations in fundamental predator-prey interactions due to geographical peculiarities may also complicate efforts at analysis— as Errington and Stoddard \((57)\) have brought out in comparing the findings from their respective quail investigations in north-central and southeastern United States.

**RABBITS AND HAARES**

Members of the Leporidae, remains of which were represented in 3,315 or 68.5 percent of 4,838 pellets and stomachs, usually constitute the main staple fare of the horned owl over nearly all of that species' range on this continent. Special phase study 5 (appendix \((B)\)) illustrates the winter and spring dominance of snowshoe hare over cottontail prey in the northern part of the region with which this writing deals. Snowshoe hare remains were recognized in 85 percent and those of cottontail in 10 percent of 81 pellets collected from the Forestry Station near Cloquet, Minn., chiefly by R. T. King and students. Bird \((15)\) found snowshoe hare remains in 53 percent of 114 pellets gathered in southern Manitoba during the spring and early summer of 1928.

On the whole, the cottontail seems to comprise about the same proportion of the horned owl's diet in north-central states during years that the rabbit populations are low that it does in years marked by high densities. This is exemplified by table 7 for an area near Prairie du Sac, Wis., that has been under close observation for many years. The cottontail population was judged by a careful resident observer, A. J. Gastrow, to be only about one-third "normal" for the winter of 1936-37, yet remains occurred in 69 percent of 51 owl pellets or at a higher rate of representation than the average of 66 percent of 543 pellets for 8 winters. By the winter of 1937-38, the cottontail population had recovered noticeably, though no exact figures for this area are
TABLE 7. REPRESENTATIONS OF COTTONTAIL REMAINS IN WINTER HORNED OWL PELLETS COLLECTED ON THE SAME AREA* OVER A PERIOD OF YEARS.

<table>
<thead>
<tr>
<th>Winter</th>
<th>Number of pellets examined</th>
<th>Percentage of pellets containing cottontail remains</th>
<th>Approximate status of cottontail population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>31</td>
<td>74%</td>
<td>Density within limits of what seems &quot;normal&quot;, for area</td>
</tr>
<tr>
<td>1930-31</td>
<td>60</td>
<td>73%</td>
<td>&quot;</td>
</tr>
<tr>
<td>1931-32</td>
<td>161</td>
<td>66%</td>
<td>&quot;</td>
</tr>
<tr>
<td>1932-33</td>
<td>99</td>
<td>66%</td>
<td>&quot;</td>
</tr>
<tr>
<td>1933-34</td>
<td>21</td>
<td>76%</td>
<td>&quot;</td>
</tr>
<tr>
<td>1934-35</td>
<td>42</td>
<td>21%</td>
<td>Decidedly low density</td>
</tr>
<tr>
<td>1935-36</td>
<td>No data</td>
<td>No data</td>
<td>Higher density than 1937-37 but still rather low</td>
</tr>
<tr>
<td>1936-37</td>
<td>51</td>
<td>69%</td>
<td>&quot;</td>
</tr>
<tr>
<td>1937-38</td>
<td>78</td>
<td>76%</td>
<td>&quot;</td>
</tr>
<tr>
<td>Total</td>
<td>543</td>
<td>66%</td>
<td></td>
</tr>
</tbody>
</table>

* Five square miles near Prairie du Sac, Wis.

at hand. (The reader, if interested in differences in local feeding trends of these owls for the latter two winters, may turn to special phase studies 6 and 7 in the appendix (B)).

Leopold and Anderson (88) state, "It may . . . be concluded that a rabbit [cottontail] scarcity prevailed throughout southern Wisconsin in 1936 . . .", and it was plain that central Iowa cottontails were also scarce that year. Nevertheless, a large number of horned owl pellets examined superficially in the field during the spring of 1937 contained about the same proportion of cottontail remains as pellet lots from previous years.

The evidence of possible thresholds of comparative security from predation for rabbits and hares is scanty and difficult to appraise. Williams (118) records an instance of what looks like virtually annihilative pressure by foxes upon a local rabbit population in northeastern Ohio following drought and other ecological upsets. Criddle (21) describes very severe predator pressure upon low densities of the snowshoe hare in southern Manitoba after a cyclic decline of that species; Sheldon’s (109) observations in Alaska were similar. On the other hand, certain data from southern Wisconsin suggest that cottontails may be able to live in some security at rather low densities despite hunting by wild predatory enemies, much as did the mice Kalabuhov and Raewski studied in the North Caucasus (61). (See also discussion of predation upon mice in the present bulletin, page 789.)

Only 1 (3 percent) of 30 winter pellets from strong cottontail habitat on the outskirts of Madison, Wis., 1929-30, contained cottontail remains (special phase study 8, appendix (B)). At the time that the pellets were collected, there were still cottontails to be seen, but it was thought that fall and early winter
human hunting had reduced their numbers to the point of virtual security from wild enemies even as formidable as the horned owl. Cottontail remains were found in 9 (27 percent) of 33 pellets from an adjacent estate that was not so freely accessible to shooters (special phase study 9, appendix (B)). It cannot be said positively that these two lots of pellets were not contaminated with pellets of the barred owl, but field evidence indicated that such contamination, if it existed, was slight.

At this stage of our knowledge, we can hardly say whether rabbit or hare populations really do have thresholds of security from predation that become operative after their densities are reduced to low levels, or whether decreasing mathematical chances of predators finding prey at low densities may account for the apparent security of populations occasionally observed. The fact remains that, even after the drastic periodic declines of the northern wilderness hares followed by intense searching on the part of desperate predators having practically no other food, there are enough hares surviving to permit recovery to top-heavy peaks within a short space of years.

NORWAY RAT

Representations of Norway rat remains in 289 (6.0 percent) of the total pellets and stomachs show what is believed to be pressure disproportionate to the densities of this alien species occurring away from buildings. For the cold months, the representations were in 200 (5.2 percent) of 3,852 pellets; from late spring to fall, in 89 (9.0 percent) of 986 pellets. While the rats constituted a food item of greater dietary importance in the southern half of the north-central region in which studies were made, Bird (15), writing of the food habits of the horned owl in Manitoba in spring and early summer, 1928, lists 5 representations in 114 pellets for which contents were tabulated.

Very high representations of rat remains in owl pellets (up to 70 percent for some fair-sized lots) are to be noted in local collections rather than in those from extensive areas, and this may hold true for pellets from owls other than the horned owl (35). Family studies 1, 4, 27 and 29 of appendix (A) and special phase study 10 (appendix (B)) illustrate conspicuously heavy pressure. Special phase study 10 was based upon pellets from near a lake, where rats lived in abundance along the shores.

Vulnerability of Norway rats living, or trying to live, away from human habitations is apparently linked with localization of winter food sources and with habits that may predispose them to attack by our native owls (37). In southern Wisconsin, field-wintering rats seemed preyed upon at all observed densities and

11 Wild predators should be considered in a different category from selective and ingenious man, aided by guns, dogs and other equipment.
usually left the fields or suffered annihilation by spring. With
the return of warm weather, the fields were repopulated by
animals spreading out from farm buildings, dumps and other
favorable quarters capable of maintaining populations the year
around. We have known rats in southern Iowa to succeed in
wintering in field-shocked corn, in the vicinity of game bird
feeding stations, etc., especially during mild winters; but here,
too, they seemed exceedingly vulnerable to predation.

MICE

In the 4,838 pellets and stomachs, mouse remains were found
in 1,934 (40 percent). The total of 5,080 mouse individuals listed
in the analyses of these pellets includes jumping mice (Zapus
hudsonius), house mice (Mus musculus), red-backed mice (Clet-
trionomys gapperi), lemming mice (Synaptomys cooperi) and
harvest mice (Reithrodonatomy megalotis), as well as meadow
mice and deer mice, but the last two kinds far outnumber the
others.

For the cold months, 1,601 (41.6 percent) of 3,872 pellets con-
tained remains of mice—4,578 individuals or an average of 2.9
per containing pellet. Warm weather representations in 333
(33.8 percent) of 986 pellets showed remains of 503 individual
s or an average of 1.5.

Meadow mouse representations in 800 pellets and deer mous
in 1,400 give a 36.4 to 63.6 ratio to each other; and recognized
remains of individuals total 1,281 for meadow mouse and 3,414
for deer mouse, thus occurring in a ratio of 27.3 to 72.7 for all
seasons. Apportioned according to the colder and warmer halves
of the year, the data show representations of Microtus and Per-
omyssus of 37.3 to 62.7 from late fall through early spring and
of 29.8 to 70.2 from late spring through early fall. There is
slightly less difference in the ratios of individuals of these gen-
era taken by the owls over the year, the cold weather ratio
being 27.7 to 72.3 and the warm weather ratio, 23.3 to 76.7.

Hendrickson and Swan (77) observed during a central Iowa
winter study of the short-eared owl (Asio flammeus) that ‘‘... as
the temperature went down the percentage of Microtus [in
pellets] went down and the percentages of Peromyscus in-
creased.'’ Vulnerability of Microtus seemed to increase as their
tunnels were exposed by the melting of the ice and snow. In
southern Wisconsin, meadow mice, although exceptionally
abundant, received such protection from deep snow during mid-
winter, 1929-30, that foxes hardly preyed upon them at all
(39) and barn owls (Tyto alba pratincola) evidently dependent
upon them died of cold and hunger in at least one locality (29,
31).

The question of possible thresholds of security in mouse popu-
lations has not to our knowledge been adequately explored. Very suggestive are the findings of Kalabuchov and Raewski whose work on mice in the North Caucasus has been referred to by Gause (61). These investigators found that, after the mouse populations they were studying had been reduced to certain levels, the remnant only rarely lost from predation and hence remained constant in numbers; biological peculiarities of predatory enemies as well as densities of the mice and qualities of mouse habitats seemed to determine the levels of comparative security operative for these rodent populations.

Of mice of the genera Microtus and Peromyscus, the former are seemingly more subject to pronounced fluctuations. As Hamilton (75) states in reviewing the literature, the evidence points to a 4-year population cycle in Microtus. The same author found populations of M. pennsylvanicus reaching densities of 160 to 230 per acre in New York in the winter of 1935-36; and Elton, Davis and Findlay (26) report densities of M. agrestis of between 100 and 200 per acre on the Scottish Border in the spring of 1934. Occasionally peak populations greatly in excess of these occur, as in the "mouse plagues" described by Bailey (8), Piper (104) and others. Declines following such peaks may be sudden and drastic and have taken place in the spring in instances recorded by Middleton (96), Elton et al (26) and Hamilton (75).

Meadow mice had manifestly reached an abundance peak in south-central Wisconsin by the summer of 1929. It is not clear just when the most abrupt drop in numbers took place, but, by early summer, 1930, few animals or fresh "signs" could be found in fields criss-crossed by the trails and burrows of the preceding year. While at the height of their abundance, the mice were preyed upon by a great variety of creatures, including crows (Corvus brachyrhynchos), domestic chickens, and American bitterns (Botaurus lentiginosus), as well as serving as the chief item in the diet of field-hunting house cats (Felis domestica), red fox (Vulpes fulva), grey fox (Urocyon cinereoargenteus) (39), marsh hawk (33, 50), barn owl, long-eared owl (Asio wilsonianus) and screech owl (31). The short-eared owl fed more on deer mice 12 (31; see also 77). Seventy entire pellets and fragments of about 15 others from probably a single saw-whet owl (Cryptoglaux acadica) contained nearly four times as many Peromyscus skulls as Microtus.

That the horned owl did not turn to the extraordinarily numerous meadow mice as an exclusive diet is plain from table 8, which was prepared from data from localities known to have

12 Snyder and Hope (110) discovered much heavier feeding by short-eared owls upon meadow mice during a peak year in Ontario and even greater proportion of meadow mice to deer mice in the diets of the owls the following year, though at that time both owls and mice were less numerous.
TABLE 8. MEADOW MICE AND DEER MICE IN THE DIET OF THE GREAT HORNED OWL IN SOUTH-CENTRAL WISCONSIN LOCALITIES, 1929-31*

<table>
<thead>
<tr>
<th>Locality</th>
<th>Period with which data are concerned</th>
<th>Number of pellets</th>
<th>Meadow mouse</th>
<th>Deer mouse</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Percent of pellets containing mouse remains</td>
<td>Average of individual mouse remains in pellets</td>
<td>Percent of pellets containing mouse remains</td>
</tr>
<tr>
<td>Verona</td>
<td>Winter, 1929-30, through March</td>
<td>39</td>
<td>64%</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>April 5 to 27, 1930</td>
<td>27</td>
<td>26%</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>April 28 to May 15, 1930</td>
<td>22</td>
<td>9%</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>Winter, 1930-31, through March</td>
<td>21</td>
<td>33%</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>April 1 to 25, 1931</td>
<td>8</td>
<td>13%</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>April 26 to May 21, 1931</td>
<td>29</td>
<td>14%</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>May 22 to Aug. 5, 1931</td>
<td>39</td>
<td>8%</td>
<td>0.1</td>
</tr>
<tr>
<td>Pine Bluff</td>
<td>Winter, 1929-30, through March</td>
<td>10</td>
<td>70%</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>Late winter, 1930-31, to March 22</td>
<td>28</td>
<td>18%</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>March 23 to April 25, 1931</td>
<td>12</td>
<td>25%</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>April 26 to May 30, 1931</td>
<td>21</td>
<td>5%</td>
<td>tr.</td>
</tr>
<tr>
<td></td>
<td>May 31 to Aug. 8, 1931</td>
<td>44</td>
<td>5%</td>
<td>tr.</td>
</tr>
<tr>
<td>Roxbury</td>
<td>Winter, 1929-30</td>
<td>106</td>
<td>37%</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Winter, 1930-31</td>
<td>40</td>
<td>13%</td>
<td>0.2</td>
</tr>
<tr>
<td>Middleton</td>
<td>Winter, 1929-30</td>
<td>19</td>
<td>47%</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Winter, 1930-31</td>
<td>43</td>
<td>5%</td>
<td>tr.</td>
</tr>
<tr>
<td>Stoughton</td>
<td>Winter, 1929-30</td>
<td>21</td>
<td>62%</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Fall, 1930, to April 11, 1931</td>
<td>25</td>
<td>24%</td>
<td>0.6</td>
</tr>
<tr>
<td>Prairie du Sac</td>
<td>Winter, 1929-30, to March 25</td>
<td>36</td>
<td>22%</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>March 26 to April 12, 1930</td>
<td>36</td>
<td>8%</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>Fall, 1930, through March, 1931</td>
<td>65</td>
<td>14%</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>April, 1931</td>
<td>38</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>May 1 to June 10, 1931</td>
<td>39</td>
<td>8%</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>Winter, 1929-30</td>
<td>231</td>
<td>44%</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>Spring, 1930</td>
<td>85</td>
<td>14%</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>Winter, 1930-31</td>
<td>222</td>
<td>15%</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Spring, 1931</td>
<td>320</td>
<td>7%</td>
<td>0.1</td>
</tr>
</tbody>
</table>

* The summer of 1929 and the winter of 1929-30 were seasons of conspicuous abundance of meadow mice, which apparently fell off sharply in numbers in the spring of 1930; deer mouse populations were not known to have fluctuated unusually during the periods with which this table deals.
been heavily populated by *Microtus* in 1929 and up to the spring of 1930 and then underpopulated for many months. During the meadow mouse peak, deer mice were generally taken in greater numbers and their predominance became even more marked after the decline of the meadow mice.

SCIURIDS AND MISCELLANEOUS RODENTS

Although representations of fox squirrel remains in 20 (0.4 percent) of the pellets and stomachs and of ground squirrels (*Citellus* spp.) in 8 (0.2 percent) relate to the greater part of the region in which studies were made, other sciurid representations reflect horned owl pressure on a more restricted scale. The majority of the pellets containing flying squirrel (*Glaucomys* spp.) and chipmunk (*Tamias striatus*) remains [27 (0.6 percent) and 10 (0.2 percent) of the 4,838 total, respectively] were collected from Dane County, Wis.

Predation upon *Glaucomys volans* by barred owls (31) as well as by horned owls has seemed remarkably severe in proportion to detected evidence of these mammals in southern Wisconsin woodlots, but they may have been more abundant than was believed. The diurnal sciurids, conversely, appear to be preyed upon by large owls less in proportion to numbers than according to chance opportunities for predation. Allen (4) writes of activities of chipmunks at about daybreak and gives one instance of an animal gathering food in the dusk after sundown, and it is probably at these times that they are usually caught by owls. Unpublished notes describe crepuscular unrest on the part of fox squirrels, some of which was manifested by scolding and chasing in the dim light of evening in a manner one would think inviting attack by any horned owls that might be in the neighborhood.

The miscellaneous rodents referred to under this heading are chiefly muskrats and pocket gophers. Remains of the gophers were found in 47 (1.0 percent) of the total number of pellets and stomachs, with Iowa and Minnesota lots containing the most representations. Bird (15) lists remains of the Western pocket gopher (*Thomomys talpoides*) in 16 (14 percent) of 114 horned owl pellets from Manitoba and comments further that it is an important food item during the latter part of May, when it spends much time above ground in search of mates.

A distinct rise in representations of *Geomys bursarius* in the diet of Iowa red foxes during the drought spring and summer of 1934 over that of "normal" 1933 was attributed to increased foraging above ground (and hence increased vulnerability for these fossorial animals) necessitated by sparseness of vegetation during the drought (40).

---

13 Seton (108) gives testimony of many authors indicating gregarious habits and astonishing local abundance.
The only Iowa horned owl food data strictly contemporaneous with the fox data for 1933 and 1934 and pertaining to specific localities come from the vicinities of Ames and Ruthven. None of 45 Ruthven pellets for 1933 and 15 for 1934 contained pocket gopher remains. The Ames collections contained remains of this prey in 6 (2.3 percent) of 263 pellets for 1933 and in none of 65 pellets for 1934. Over the state as a whole, representations in 7 (1.6 percent) of 451 spring and summer pellets for 1933 and in 5 (1.8 percent) of 278 for 1934 show little difference that can be associated with drought-accentuated vulnerability of the gophers.

There appears to be a similar lack of association between the drought of 1934 and horned owl pressure upon muskrats, although drought conditions were accompanied by increased representation of muskrats in the diet of red foxes (40). During the drought of 1936, the increase of vulnerability of muskrats to mink also was striking (47). Nevertheless, horned owls may respond to increased vulnerability of muskrats resulting from overpopulation or inferiority of occupied habitats.

Of muskrat representations in 37 (0.8 percent) of the pellets and stomachs for the region, 29 were from lots totalling 134 pellets picked up during single seasons in three areas. Relative to the most illuminating instance of horned owl predation upon muskrats, we may quote directly (46):

"The muskrat populations in the areas under observation in northwest Iowa were in the early stages of recovery from a drought when the Iowa cooperative program was begun in 1932. Aided by a closed trapping season during the fall and winter of 1933-34 and favorable breeding conditions during the summers of 1933 and 1934, the animals reached exceptional abundance by the trapping season of 1934-35, when the Mud Lake Fur Farm alone reported a catch of 2,528 muskrats or about 8.5 per acre from about 300 acres of privately owned marsh near Ruthven, Iowa (letter, Joe Kautzky, Jr., March 23, 1938).

"Despite the patently high fall density for 1934 and a probable density close to five muskrats per acre in the fall of 1933 when no trapping was done, 209 horned owl pellets collected from a wooded island in Mud Lake from early spring, 1933, to early spring, 1935, contained no muskrat remains, which seems explainable in terms of the excellence of the habitat even for such large numbers of animals.

"In late spring and early summer, 1935, stands of Cyperaceae covering roughly one-third of Mud Lake died out from some undetermined cause, and this was followed by the horned owls responding in a spectacular manner to the consequent exposure of a large part of the muskrat population. Of 43 pellets from April and May, one of those from late May contained muskrat remains; then 5 of 16 pellets from June showed this item; and
also 8 of 12 July pellets. In the 8 Muskrat-containing pellets from July, remains of 1 adult and 11 young individuals were distinguished. The population was at perhaps half the density that the marsh had accommodated with evident security the year before, yet it apparently became more conspicuously vulnerable by reason of drastic changes in a very important constituent of its environment—the cover.”

[See family study 40 appendix (A) for closer dating of the above pellet lots and listings of other food items].

The pressure revealed by family study 26 (appendix (A)), May 22 to June 23, 1933, was centered upon young muskrats in small and shallow oxbow potholes that subsequent studies have shown to be of doubtful habitability.

Concerning the third instance of severe local horned owl predation upon muskrats (special phase study 11, appendix (B)), we are not sure that the muskrats were overpopulating their environment, but this is implied by the indirect evidence (46).

**CARNIVORES AND INSECTIVORES**

Remains of shrews, mostly short-tailed (*Blarina brevicauda*), were represented in 130 (2.7 percent) of the total pellets and stomachs; moles (*Scalopus aquaticus*), in 40 (0.8 percent); carnivores, in 27 (0.5 percent). The carnivore representations were 19 of various weasels (*Mustela* spp.), 2 of mink (*Mustela vison*), 1 of spotted skunk (*Spilogale interrupta*), 4 of striped skunk (*Mephitis* sp.), and 1 of young gray (?) fox. Other representations of mammals were 1 of bat (probably a vespertilionid) and 6 of opossum (*Didelphis virginiana*).

We feel that we know little of what governs availability of insectivores to the owls except possibly relative numbers (91) and the hunting routines of the owls themselves. Moles, their fossorial habits notwithstanding, are preyed upon also by barred owls (56) and to some extent by red-tailed hawks (*Buteo borealis*) (27, 51), foxes (40) and other north-central higher vertebrates.

Insectivores are obviously regarded with distaste by some predators, especially mammalian, including individual foxes (99), minks and house cats, which may leave carcasses uneaten after killing. Raptorial birds in central Iowa seemingly discard part-eaten remains of shrews more often than they do remains of other small mammals captured in similar proportions, but, relished or not, insectivores may in some localities enter importantly into the diets of owls. Guérin (70), in his study of the European *Strix aluco*, and Davis (22), from work on the barn owl in Texas, give interesting examples.

Among the mustelids, weasels seem more likely to be killed and left uneaten by mammals such as foxes than are skunks (39, 40).
All are freely eaten by horned owls, and Mustela spp. with such surprising frequency that one may wonder if weasel intrepidity may not lead its possessors into a disproportionate amount of danger that weasel prowess cannot get them out of.

PASSERINE AND RELATED SMALL AND MEDIUM-SIZED BIRDS

Grouped under the above heading are members of 5 of the last 10 orders of birds as arranged in the fourth edition of the A. O. U. checklist (5): Columbiformes, Strigiformes, Caprimulgiformes, Piciformes and Passeriformes. Also included, for lack of a better place to put them, are the hawks (Falconiformes). Together, remains of these birds were detected in 665 (13.7 percent) of the pellets and stomachs.

Caprimulgiformes were represented in only 2 pellets, 1 each of nighthawk (Chordeiles minor) and whip-poor-will (Antrostomus vociferus). Representations of Falconiformes were in 5 pellets—3 of sparrow hawk (Falco sparverius), 1 of sharp-shinned hawk (Accipiter velox) and 1 of the possible goshawk (Astur atricapillus) mentioned under special phase study 5, appendix (B). Field evidence of horned owl predation upon another sparrow hawk, a Cooper’s hawk (Accipiter cooperi) and a nestling red-tailed hawk likewise was noted.

Remains of Columbiformes were found in 47 (0.9 percent) of the pellets: 30 representations of domestic pigeon and 17 of mourning dove (Zenaidura macroura). Remains of Piciformes in 69 (1.4 percent) were predominantly of flicker (Colaptes auratus) and red-headed woodpecker (Melanerpes erythrocephalus).

Strigiformes representations in 90 (1.9 percent) comprise 65 of screech owl, 21 of Asio spp., 1 of burrowing owl (Speotyto cunicularia), 1 of saw-whet owl and 2 of young horned owl, the latter being remains of a tethered young killed by fire (family study 41, appendix (A)). In addition, we have field evidence of all other north-central owls eaten by the horned owl except adults of its own kind 

\[14\] Cannibalism occurs not uncommonly when two or more adult horned owls are held captive together in confined quarters. We do not regard as cannibalism the killing and eating of owls belonging to other species.
of 591 individuals, 476 were identified at least to the family and, except Fringillidae, mostly to the species.

Comparatively few of 149 fringillid remains were further identified, but those that were traced down represent a fair sample of native sparrow populations at all seasons, resident and migratory forms, alike: snow buntings (Plectrophenax nivalis), longspurs (Calcarius spp.), song sparrows (Melospiza melodia), white-throated sparrows (Zonotrichia albicollis), tree sparrows (Spizella arborea), juneos (Junco hyemalis), vesper sparrows (Poecetes gramineus), cardinals (Richmondena cardinalis), etc.

Among remains of 163 icterids were 27 of grackles (Quiscalus quiscula), 94 of marsh blackbirds (both red-winged, Agelaius phoeniceus, and yellow headed, Xanthocephalus xanthocephalus), 29 of meadowlarks (Sturnella spp.) and 13 determined only to family or to sparingly represented genera as Molothrus, Euphagus and Icterus. Thirty-nine of 58 Turdidae were robins (Turdus migratorius); the balance, bluebirds (Sialia sialis), hermit thrushes (Hylocichla guttata) and a few not further identified. Data on corvine remains in pellets are hard to interpret in terms of individual victims, principally because of the large size of the crows, but, of bones of 47 individuals reasonably well distinguished, 23 were of crows and 24 of bluejays (Cyanocitta cristata).

Fifty-nine passerine birds belonging to miscellaneous families were recognized from pelletal remains: 11 English sparrows (Passer domesticus), 4 warblers (Compsothlypidae), 4 vireos (Vireo sp.), 4 starlings (Sturnus vulgaris) 2 kinglets (Regulinae), 4 brown thrashers (Toxostoma rufum), 6 catbirds (Dumetella carolinensis), 3 wrens (Troglodytidae), 2 creepers (Certhia familiaris), 3 nuthatches (Sittidae), 1 titmouse (Baeolophus bicolor), 2 chickadees (Penthestes atricapillus), 9 swallows (Hirundinidae) and 4 horned larks (Otocoris alpestris).

There have been in recent years a considerable number of comprehensive studies of the life history and ecology of American passerine birds. Examples of resulting publications include those on the house wren (Troglodytes aedon) by Baldwin and Kendeigh (9, 82, 83); the song sparrow by Nice (101, 102); the bank swallow (Riparia riparia) by Stoner (114); the oven-bird (Seiurus aurocapillus) by Hann (76); and the wren-tit (Chamaea fasciata) by Erickson (28). As concerns vulnerability of passerine birds, Nice's (102) findings are of notable interest and significance—illustrating a connection between quality of Ohio song sparrow environment and severity of losses from predation—and it seems probable that they may have wider application to populations of small birds.

Some changes in horned owl pressure upon marsh blackbird
populations on Mud Lake, north of Ruthven, Iowa, are suggestive (family studies 39 and 40, appendix (A)). Ten (22 percent) of 45 pellets deposited from late spring to July 24, 1933, contained remains of 14 red-winged blackbirds and 5 (11 percent) remains of 5 yellow-heads. In 71 pellets deposited between March 31 and July 15, 1935, there were remains of 17 red-wings in 12 (17 percent), which does not indicate a significant difference in pressure; but remains of 27 yellow-heads were found in 20 (28 percent) of the pellets. The heavy rise in representation of yellow-heads seemed to coincide with the dying out of the Cyperaceae described under the discussion of predation upon muskrats. The yellow-heads, living deep in the marsh, were presumably rendered more vulnerable by the collapse of the central stands of vegetation than were the edge-dwelling red-wings. A possible flaw in this cause-and-effect reasoning may be indicated by the fact that four of five yellow-heads taken by the owls between June 2 and July 15, 1935, were young, banded birds living in habitat somewhat apart from the main area affected by the die-off of the Cyperaceae; one pellet was made up largely of remains of three banded in a nest a few days previously.

So far as we can see, passerine birds in migration are preyed upon roughly in proportion to their numbers. This is in keeping with McAtee’s (91) principle, which, however, refers more to combined than to specific predation. Marked congregation at other times, as on wintering grounds, seemingly may or may not be attended by proportional predation, depending upon relationships too complex and as yet too imperfectly understood to be discussed here.

It is logical that types of habitats and hunting routines of individual horned owls may influence the actual order in which prey species are taken, even when the apparent availability of the prey may be about the same over sizeable tracts of land. Without knowing much about many of the details of detection and capture of prey by the owls, one can readily conceive of an individual's utilization of migratory birds in part of its hunting territory being conditioned by whether or not it caught a cottontail enroute. Again and again, pellet contents and field data reflect opportunistic hunting in different habitats characterized seasonally by certain types of available prey animals.

SHOREBIRDS, RAILS AND ALLIES, AND MISCELLANEOUS WATER BIRDS

Grebes and herons (orders Colymbiformes and Ciconiiformes) are for convenience included here with the Rallidae of the Gruidae and the shorebirds and Laridae of the Charadriiformes.

\(^{15}\) G. A. Ammann carried on life history and ecological studies of local marsh blackbirds, especially yellow-headed, during the period covered by the horned owl work at Mud Lake (6).
Remains of these forms collectively were represented in 144 (3 percent) of the pellets and stomachs.

Twelve representations of shorebirds were mainly of different or of undetermined species that seem to have been preyed upon lightly and at random. Comment is hardly warranted upon single representations of the black tern (Chlidonias niger), Forster’s tern (Sterna forsteri), Bonaparte’s gull (Larus philadelphia) and green heron (Butorides virescens), nor upon four representations of the least bittern (Ixobrychus exilis).

Fifty-nine representations of coots and gallinules (Gallinula chloropus) (mostly the former), 55 of rails and 19 of grebes manifest predation upon both migrant and breeding populations. Relative to pressure upon breeding birds, the data from Mud Lake, in the vicinity of Ruthven, Iowa, are most pertinent.

A recent paper by Friley, Bennett and Hendrickson (58) sums up data on Mud Lake coot and grebe populations gathered by Iowa State College investigators between 1932 and 1935. Bennett, in the spring of 1933, estimated that 20,000 coots rested for a time on this marsh, then of about 350 acres in area. On June 25, 1932, 189 coot nests were counted on one-fourth of the marsh; for the summer of 1935, the resident coot population for the marsh is given at approximately 100 pairs. In the summer of 1935, over 60 pairs of pied-billed grebes (Podilymbus podiceps) and a colony of eared grebes (Colymbus nigricollis) nested on Mud Lake;" grebe data for previous seasons are incomplete, but the authors quoted state that there were no eared grebes nesting there in 1932 and that other species of birds, except the abundant coots, were less numerous that year—which apparently was also true of the pied-billed grebes. No numerical data on rail populations are given, but three nesting species are referred to as “numerous”, at least for 1935."

As may be seen from family study 39 (appendix (A)) and special phase study 1 (appendix (B)), 65 horned owl pellets were collected from the vicinity of Mud Lake during the 1933 breeding season of water birds. Representations of Rallidae and grebes: coot (including 2 pellets with remains of young), 10 (15 percent); sora (Porzana carolina), 2 (3 percent); Virginia rail (Rallus limicola), 1 (2 percent); king rail (Rallus elegans), 1 (2 percent); pied-billed grebe (including 1 pellet with remains of young), 5 (8 percent).

The last 71 pellets of family study 40 (appendix (A)), likewise collected at Mud Lake, though in 1935, are not wholly comparable with the 1933 pellets, but the two lots are similar enough.

For information on the shorebirds of northwest Iowa, where most instances of predation occurred, see papers by Bennett (12) and Spawn (112).

The eared grebe colony has been described by Friley and Hendrickson (59).

Bennett (11) has published a general account of marsh-nesting birds in northwest Iowa, especially those of Mud Lake.
in size and seasonal chronology to make the following representations of interest: coot (including 1 pellet with remains of young), 14 (20 percent); sora, 11 (15 percent); Virginia rail, 6 (8 percent); king rail, 1 (1 percent); pied-billed grebe, 4 (6 percent); probable eared grebe, 1 (1 percent).

Fryley, Bennett and Hendrickson (58) do not give figures on coot nesting populations for 1933, but Errington, who spent some time on and about Mud Lake in 1932 and much more in 1933, does not believe that there was any great difference for these two seasons in the vicinity of the island where the pellets were picked up. If this be true, the 1935 pellets show a higher rate of predation upon a considerably lower coot population. Whether the previously described failure of the marsh cover increased the vulnerability of the coots is not clear, but such an explanation would seem plausible.

Rails, coots and grebes in migration are preyed upon rather regularly by horned owls but seemingly not out of proportion to the numbers of migrants using the flyways.

DOMESTIC CHICKEN

Depredations by the horned owl upon domestic chickens were generally light but sometimes occurred on a heavy local scale. Seventy-five (1.6 percent) of the pellets and stomachs contained chicken remains, including some evidently eaten as carrion. As a rule, poultrymen’s losses were of young chickens, from mid-summer to fall.

Family study 2 (appendix (A)), between May 22 and Aug. 5, 1931, revealed the severest pressure of which we have record. Nineteen (49 percent) of 39 pellets contained remains of chickens, mostly of young and sometimes of more than 1 individual in a pellet. This pressure was becoming progressively heavier up to the time when the parent owls stopped feeding the tethered young, and it is suspected that chickens remained a staple in the diet of the parents for unknown days or weeks thereafter. Depredations by the owls of family study 29 were also increasing by the last of the period of productive investigation; 1 of 4 pellets, July 4 to 8, 1933, contained remains of adult chicken; 3 of 3 pellets, July 9 to 15, adult chicken; and 1 of 2 pellets, July 16 to 21, young chicken (2 individuals).

Further evidence of poultry loss to horned owls at seasons poorly covered by pellet data was obtained by Errington in August, 1934, while visiting a western South Dakota ranch of which the terrain, buildings and economy were familiar to him. Shortly after the middle of August, and largely after the deposition of the pellets collected for special phase study 2 (appendix (A)), one fresh pellet containing remains of two chicken heads was found on Feb, 17, 1934, at the edge of an Iowa farmyard about which other chicken heads were freshly scattered as cut off by the farmer while killing or dressing poultry.
dix (B)), poultry losses became very noticeable. The depredating owls seemed mainly self-hunting juveniles, judging from a specimen examined and from the calling heard at night from trees bordering a creek near by. The stomach contents of the specimen, shot in the evening of Aug. 25 as it came up to the yard, were remains of young rabbit or hare and domestic chicken (included in the summary for special phase study 2).

The other data in hand revealing heavy local pressure upon poultry—family studies 4 and 38 (appendix (A))—do not show ascending importance of this item in the diets of the owls in the terminating days of the studies. From June 26 to July 16, 1931, 5 of 10 pellets of number 4 contained remains of young domestic chickens; from July 17 to Aug. 8, 0 of 15. Representations of young chickens were in 5 of 19 pellets from number 38, May 29 to June 5, 1934; in 0 of 11, June 6 to 10.

This type of predation upon barnyard flocks appears comparable to that described for the red-tailed hawk (33, 51). One family of red-tails lived almost exclusively upon young domestic chickens from the last of April, 1931, to early in June; from June 8 to about June 20, on cottontails and ground squirrels, with some chicken; and from the last third of June to July 9, on little except cottontails, ground squirrels and mice. In another instance, data from May to July, 1931, showed heaviest pressure upon chickens between May 21 and June 5.

Little is known of the circumstances under which horned owl predation upon chickens was most severe except as concerns family study 2 (appendix (A)) and that following special phase study 2 (appendix (B)). The owls of the family study had access to inadequately housed chickens that roamed and roosted at the edge of a large tract of woods. Those at the South Dakota ranch not only picked up chickens about the buildings and environs but also took birds roosting in cattle sheds. Well-kept coops seemed to afford roosting chickens a substantial measure of security from horned owls, and some owls apparently avoid human habitations, as do wary red-tailed hawks (33), and seldom molest chickens that remain localized about the yards.

WILD GALLINACEOUS BIRDS

Horned owl predation upon northern bob-white populations has been summarized in one paper (44) and discussed to a varying extent elsewhere (34, 36, 46, 53). It may, therefore, be unprofitable to devote more space to this subject in the present writing than is necessary to review our findings and perhaps to amplify descriptions of certain relationships.

The greater part of the horned owl predation upon bob-white quail [181 (3.7 percent) of the pellets and stomachs contained remains of this species] was born by quail populations exceed-
ing the winter carrying capacities of their habitats in southern and central Iowa and southern Wisconsin, as determined by year-to-year studies on specific areas (53). Vulnerability of wintering overpopulations was manifested by predation either upon excess birds occupying good range or upon those wandering away from occupied coverts or stationing themselves in inferior or uninhabitable environment.

The clearest example of the latter type of vulnerability pertains to a lethal territory in which quail, attempting to winter, consistently suffered annihilative losses if they didn’t leave (34, 53). The owls of family study 7 (appendix (A)) hunted over this territory, and the occurrence of quail remains in 15 percent of 101 pellets deposited from February to May 6, 1932, coincides with the shrinkage of the doomed covey from 16 to 2 birds between Feb. 3 and March 23 (34).

The winter and early spring data of family studies 5, 15 and 17 (appendix (A)) illustrate horned owl pressure upon moderate bob-white surpluses on areas for which existing carrying capacities were reasonably well ascertained. Six representations of bob-white in 62 pellets, 6 in 59, and 6 in 57 give close to 10 percent of the pellets with quail remains. Relative to “normal” representations of bob-white in horned owl pellets, we may quote (44): “Experience . . . has shown that quail remains in less than 6 percent of winter pellets (in good-sized lots) ordinarily means a fairly light horned owl pressure upon quail populations running from 30 to 100 birds per square mile.” This represents losses of the sort that even well-situated populations may be expected to suffer and seems largely to take the place of the losses from age and accident which would obviously go on anyway in the total absence of predators.”

The food habits data summarized as special phase study 12 (appendix (B)) show quail representations in 5 (10 percent) of 50 pellets. Contemporaneous with the hunting of the owls, the two nearest quail coveys were reduced to the carrying capacities of their respective territories—one from 28 to 22 birds and the other from 22 to 17 (53 pp. 343 and 346, territories number 20 and 29, 1932-33).

More severe predation tends to take place when bob-whites concentrate during starvation crises in habitats where food is still to be had. Eight (19 percent) of the 42 pellets of special phase study 13 (appendix (B)) contained quail remains, which reflects pressure by horned owls at the time of the following situation (44):

“This tract of land had a carrying capacity of around 53 bob-whites, as calculated on the basis of the numbers that had successfully wintered there in previous non-emergency years.

25 The usual range of winter densities in Iowa and Wisconsin “quail country.”
As nearly as the 1934-35 story could be pieced together from almost continual field studies, 72 quail started the winter and 50 were surviving by spring; but in the meantime there had been much movement in, some movement out, and a mortality that could be fairly closely determined at 54 birds, or a loss exceeding the number that wintered.

"As long as the quail occupying this tract filled it up only to the limit of its known carrying capacity, the population suffered negligible losses from predation, from horned owls as well as from other resident predators. But whenever the environment became filled with quail past carrying capacity, the surplus birds soon departed (or their equivalent number did), or increased pressure from enemies cut the population down to the level of carrying capacity again."

During the winter of 1934-35, Malcolm McDonald gathered some remarkable lots of horned and barred owl pellets from the vicinity of Fairfield, Iowa. Not only were the quail representations in the barred owl pellets the highest that Errington and McDonald found in their study of food habits of that owl (56), but bob-white remains in 19 (22 percent) of 85 horned owl pellets also stands as our record for a large series. McDonald et al (95) explain this extreme pressure: "The bob-whites were taken during a blizzard week when there was a particularly heavy concentration of bob-whites in the park; 59 individuals were banded within a week in the few acres of woodland where they had taken refuge from the surrounding fields." Bands of five bob-whites were recovered from owl pellets. Another lot of 65 pellets from an area a few miles away where the bob-white population was presumably more "normal" had remains in four (6 percent). For purposes of contrast, the contents of these lots are given in the appendix (B) as special phase studies 14 and 15.

In spring and summer, predation rates were at times accelerated as an accompaniment of breeding excitement among the birds or perhaps for unknown reasons (44). Survival of the season's young in the face of predation from all usual sources has been, so far as worked out in the north-central region, in inverse ratios to the densities of the adult populations, regardless of observed kinds and numbers of predators (53, 54).

Ruffed grouse (Bonasa umbellus) populations in the north-central region seem to be in many ways vulnerable to, or relatively secure from, predation much as are bob-white populations (20, 42, 84).

The right hand column of table 9, prepared from data on

---

21 We have found bob-white remains in 10 or 33 percent of one lot of 30 pellets—see family study 9 (appendix (A)), Dec. 22, 1931, to Feb. 21, 1932.

22 In southeastern United States, the predator-quail equations may be considerably different (57, 85, 113).
TABLE 9. REPRESENTATIONS OF RUFFED GROUSE REMAINS IN PELLETS COMPARED WITH WINTER POPULATION STATUS OF THE GROUSE ON AN AREA OF 5 SQUARE MILES NEAR PRAIRIE DU SAC, WIS.*

<table>
<thead>
<tr>
<th>Winter</th>
<th>Number of pellets examined</th>
<th>Percentage of pellets containing ruffed grouse remains</th>
<th>Status of ruffed grouse population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Individuals, December</td>
</tr>
<tr>
<td>1929-30</td>
<td>53</td>
<td>4%</td>
<td>20 ?</td>
</tr>
<tr>
<td>1930-31</td>
<td>150</td>
<td>4%</td>
<td>20 ?</td>
</tr>
<tr>
<td>1931-32</td>
<td>232</td>
<td>1%</td>
<td>25</td>
</tr>
<tr>
<td>1932-33</td>
<td>99</td>
<td>5%†</td>
<td>33</td>
</tr>
<tr>
<td>1933-34</td>
<td>31</td>
<td></td>
<td>18</td>
</tr>
<tr>
<td>1934-35</td>
<td>42</td>
<td>††</td>
<td>19 ?</td>
</tr>
<tr>
<td>1935-36</td>
<td>No data</td>
<td>No data</td>
<td>15</td>
</tr>
<tr>
<td>1936-37</td>
<td>51</td>
<td></td>
<td>15</td>
</tr>
<tr>
<td>1937-38</td>
<td>78</td>
<td>8%</td>
<td>15</td>
</tr>
</tbody>
</table>

* Data for winters 1929-30 through 1935-36 were taken from Errington's (42) paper on winter carrying capacity of marginal ruffed grouse environment in north-central United States; those for the last two winters from notes of A. J. Gastro and special phase studies 6 and 7 (appendix B).
† Lenses from horned owls were heavier than as indicated by pellets gathered.
†† Non-pellet remains of two grouse killed by horned owls were found.

Marginal environment (42 and unpublished), shows what seems to be a threshold of security for wintering adults at about 18 birds for an area of 5 square miles east of Prairie du Sac, Wis. King (84) obtained the following figures on densities on 1,800 acres of good ruffed grouse range near Cloquet, Minn., during years of high populations: October, 1931, 525 birds; April, 1932, 443; October, 1932, 750; April, 1933, 455; October, 1933, 995; April, 1934, 452. During the winter of 1933-34, the reduction of the unusually high fall density to the approximate spring densities of 1932 and 1933 was accompanied by the most severe predation observed in 7 years of intensive study. Neither the pellets of table 9 nor those of special phase study 5 (appendix B) reveal striking representations of grouse remains for any season. But, at both Prairie du Sac and Cloquet, populations top-heavy for their respective wintering environments were evidently insecure from horned owls as well as from other predators. Of the 4,838 horned owl pellets and stomachs from the north-central region, mostly from environment occupied by few if any ruffed grouse, 22 (0.5 percent) contained remains of the species.

Edminster (25), analyzing results obtained by the New York ruffed grouse investigation between 1930 and 1937, found that, in every case where fall densities surpassed a bird per 4 acres on the best range, "immediate reaction set in in the form of dispersion and accelerated decimation." The New York data, however, show less connection between the severity of winter predation and recognizable carrying capacity than the north-central data seem to, if one may judge from Edminster's tabulations for the 2,304-acre Connecticut Hill area and the 816-acre Adirondack area. It is possible that biotic relationships in the north-central and northeastern regions may differ some-
what like those described for north-central and southeastern quail habitats (57).

Most of the data we have on horned owl predation upon populations of ring-necked pheasants and Hungarian partridges have been summarized (46), and these are used as a basis for Table 10. Representations of pheasant were recorded in 201 (4.2 percent) of the total pellets and stomachs; Hungarian partridge, in 46 (1.0 percent); and the great majority of these remains were in the pellets from northwest Iowa (subregion III).

In northwest Iowa for the winter of 1934-35 "... representation of pheasant remains in but 10 or 6.4 percent of 156 horned owl pellets suggests that these birds [pheasants] may have been wintering at densities near some sort of threshold of security. The spring and summer representation ... was higher ... but at this time of year predation upon gallinaceous birds studied seems to be more in proportion to their actual numbers than in winter" (46).

On areas under observation for the last 7 years in the vicinity of Ames, central Iowa, the pheasant wintering densities have been maintained at about the same level or have perhaps increased slightly. Random counts of birds under favorable census conditions and usually with the aid of good tracking snows have indicated densities averaging between 1 per 32 and 1 per 80 acres. Green (68) estimated in 1935 a late fall population (before the hunting season) of approximately 1,000 pheasants or an average of 1 per 4.9 acres on 8 sections of land under observation in north-central Iowa, of which about half of the birds entered the winter; these densities, we believe,

<table>
<thead>
<tr>
<th>Season</th>
<th>Number of pellets</th>
<th>Percent of pellets containing pheasant remains</th>
<th>Percent of pellets containing partridge remains</th>
<th>Remarks on comparative population status of pheasants and partridges</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter, 1933-34</td>
<td>224</td>
<td>21%</td>
<td>5%</td>
<td>Pheasants had declined from a high level of the previous year but were still numerous. Partridge densities seemed to have risen somewhat from moderately low levels of 1932-33.</td>
</tr>
<tr>
<td>Spring and Summer, 1934</td>
<td>147</td>
<td>37%</td>
<td>10%</td>
<td>This season was one of severe early drought that seemed to be attended by slightly greater consequences for the partridges.</td>
</tr>
<tr>
<td>Winter, 1934-35</td>
<td>156</td>
<td>6%</td>
<td>4%</td>
<td>Pheasants were present in considerable abundance but their numbers were evidently lower than for the preceding two winters. Partridge densities were not known to be much different than for the winter of 1933-34.</td>
</tr>
<tr>
<td>Spring and Summer, 1935</td>
<td>143</td>
<td>23%</td>
<td>8%</td>
<td>Spring and summer pheasant densities were lower than those of 1934. Partridge densities were thought to have been about the same both breeding seasons.</td>
</tr>
</tbody>
</table>
were probably rather close to those often existing in the northwestern part of the state from which owl pellets were collected.

Family studies 24, 25 and 29 to 34 (appendix (A)) were made on the Ames areas. Only 2 (1 percent) of 162 winter horned owl pellets contained pheasant remains, and field "sign" of pheasants having been killed by the owls was rarely encountered. The spring and summer pressure was obviously heavier, as pheasant representations were found in 17 (4.4 percent) of 388 pellets, and pheasant feathers were commonly seen about horned owl feeding places. In northwest Iowa, family studies 39 and 40, with pheasant remains in 4 percent of 221 pellets, were made in pheasant environment thought to be not only somewhat superior to, but also less populated23 than, the sites of family studies 35 to 38, the pellets from which had remains in 33 percent of 334.

Yeatter (119) reports an average early spring density for 1933 of 13.1 Hungarian partridges per 100 acres or about 1 bird per 8 acres on 3 sample plots in southern Michigan. Data for 1931 and 1932 show early spring densities of about 1 bird per 19 acres and 1 per 11 acres, respectively, on his principal study area near Blissfield. Leopold (86) gives densities averaging about 1 bird per 6.5 acres in generally superior partridge range of Wisconsin, Illinois and Indiana, 1925 to 1928. The winter and spring partridge populations reported by Green and Hendrickson (69) for a 4,900-acre observational area in north-central Iowa varied from 16 birds (1 per 306 acres) to 140 (1 per 35 acres) between 1935 and 1938; but Leopold (87, p. 85) lists maximum densities for northwest Iowa counties (including Palo Alto, in which much of our work on the horned owl was done) up to a bird per 2.5 acres.

The task of trying to arrive at conclusions regarding carrying capacities of Hungarian partridge habitats in northern Iowa is—even when population data of evident reliability are available—greatly complicated by the occurrence of varying but usually more or less high densities of pheasants on the same land 24. The intra- and interspecific relations appear similar to those observed between pheasants and bob-whites, in which case the quail were intolerant of overcrowding either by their own kind or by the pheasants (53). The rise of partridge densities recorded by Green and Hendrickson (69) occurred after the drastic decline of the pheasants in the winter of 1935-36 (68), which was in turn followed by poor breeding seasons of the latter birds. Prior to the winter of 1935-36, our impression from field work in northwest Iowa was that since 1932 there had been a grad-__

23 Lower pheasant densities in the vicinity of Mud Lake, north of Ruthven, were attributed in part to overshooting.
24 Readers particularly interested in this phase of the subject should consult Leopold's (87, p. 83-85) discussion of mixed populations of gallinaceous game birds.
nal increase of Hungarian partridges attending incomplete recovery of pheasant populations from overshooting, among other things. Green and Hendrickson (69) conclude their paper with the sentence: "Possibly when and if the pheasant population is built up to the same level it held before the disastrous winter of 1935-36, the European Partridge will lose the little advantage it has gained in the last year, and the old situation of low, fairly constant densities will result."

The 1934 drought was thought to have increased the vulnerability of partridges to red foxes (40) but not to marsh hawks (50) or horned owls (55).

The four representations of prairie chicken (*Tympanuchus cupido americanus*) in the 269 pellets of family study 41 (Anoka, Minn., appendix (A)) are all that our pellets and stomachs show of this species, although prairie chickens are found as sparse breeding populations or in wintering flocks or "packs" in south-central Wisconsin and northern Iowa. Breckenridge (16) has described the floral and faunal characteristics of the sand plain area from which the Anoka pellets were gathered. Ruffed grouse, prairie chickens, bob-whites and ring-necked pheasants were present at approximately the same spring and summer densities: 10 to 15 per square mile (1 to 43-64 acres), with bob-whites slightly more numerous and pheasants slightly less. Corresponding representations of wild gallinaceous bird remains in 223 spring and summer pellets: pheasant, 10; bob-white, 0; prairie chicken, 4; ruffed grouse, 2.

Since 1935, the junior authors have been working on horned owl-prairie chicken relationships in central Wisconsin, but this study is as yet incomplete. Remains of 11 sharp-tailed grouse (*Pediocetes phasianellus campestris*) and prairie chickens were found in 571 pellets from the winter of 1936-37 (Frances Hamerstrom and Oswald Mattson, MS), when the combined population of the two grouse was estimated at 1 bird per 85-100 acres (73). The field ratio was about 3 sharp-tails to every prairie chicken, but the ratio of these in pellets (including questionable identifications) was 4 to 7.

**WILD DUCKS**

Wild duck remains in 64 (1.3 percent) of the total pellets and stomachs reflect very seasonal and local pressure by the owls. Family study 15 (appendix (A)), late winter to May 21, 1931, shows duck representations (almost entirely of mallard, *Anas platyrhynchos*) in 11 (17 percent) of 66 pellets—by far the highest incidence observed in collections from the vicinity of lakes, marshes or streams in southern Wisconsin. Representations in 3 (4 percent) of 70 pellets of family study 24, about April 1 to 30, 1933, and in 4 (12 percent) of 34 of family study
29, late winter to May 28, 1933, illustrate the heaviest pressure upon migrating ducks noted along central Iowa streams.

The spring losses of ducks to horned owls were of course heavier in the well-populated waterfowl marshes of northwest Iowa. No duck remains were found in 27 pellets deposited from late spring to June 18, 1933, at Mud Lake, north of Ruthven (see family study 39, appendix (A)) nor in 15 spring pellets for 1934, but there were duck representations in 8 (8 percent) of 105 pellets from family study 40, fall, 1934, to March 30, 1935 (chiefly spring), and in 3 (7 percent) of 43 pellets, March 31 to May 16. Special phase study 16 (appendix (B)) relates to another marsh; of 14 pellets, spring to May 3, 1934, 5 (36 percent) contained duck remains.25

The pellets of special phase study 1 (appendix (B)) were collected from the vicinity of Mud Lake and constitute the best evidence we have of horned owl predation upon ducks concentrated during the fall migration. There were representations in 9 (45 percent) of 20 pellets deposited between July 25 and early fall, 1933, and in 3 (13 percent) of 24 pellets, late fall, 1933, to Feb. 10, 1934.

Bennett’s (13) 5-year study of the blue-winged teal (Querquedula discors) was carried on to a large extent in the area about Ruthven, including the area from which our horned owl pellet collections were made. Only slight indications of losses of nesting ducks to the owls were found except three representations of blue-winged teal (including 1 pellet with remains of both adult and young birds), 1 of mallard, and 1 of undetermined duck in 18 pellets of family study 39 (appendix (A)), June 19 to July 24, 1933. No duck remains were recorded from 28 pellets of family study 40, May 17 to July 15, 1935.

LOWER VERTEBRATES

One hundred sixteen (2.4 percent) of the pellets and stomachs contained remains of lower vertebrates, principally snakes, salamanders and frogs. Fish26 remains were numerous only in pellets from scattered areas (special phase studies 17 and 18, appendix (B)).

Snakes and frogs seem to be preyed upon irregularly. The heaviest pressure upon salamanders is during the period of spring mating, but some are taken in the fall when large numbers are often seen on highways in some localities. The 42 pellets

25 The apparently greater total of duck representations to be seen in appendix data is due to the occurrence of more than one species in individual pellets.
26 We know little of the horned owl’s technique in capturing fishes but have some reason to think that in winter it gets them mainly from concentrations about open springs or holes in the ice at the edge of lakes or water courses. Victims from such places are usually of small sizes, but fishes weighing a pound or more may sometimes be brought to nests. It may be that the owls scavenge upon fishes stranded, washed ashore or left by other animals.
of family study 35 (appendix (A)), May 29 to July 12, 1934, had about the highest incidence of lower vertebrates that we have noted: representations in 12 (29 percent).

INVERTEBRATES

Remains of invertebrate animals—insects, with some spiders and crayfishes—were represented in 392 (8.1 percent) of the pellets and stomachs. Of 933 individuals distinguished, the majority were of large-sized species available chiefly from May to July. Crayfishes were taken mainly in spring in southern and central Iowa; the big wolf spiders, in late summer, western South Dakota.

The question of whether insects occurring in horned owl diet are eaten directly by the owls or are simply stomach contents of other victims cannot always be answered. Insects that associated items or appearance show practically without doubt to be owl prey are usually rather conspicuous crawlers, carrion feeders, predators, etc., including scarabaeids, lucanids, silphids, carabids, Lepidoptera larva, belostomids and Orthoptera. Many of these are attracted to carcass fragments about feeding places, both of free and of tethered owls.

The amount of insect material found in pellets of tethered owls that may be prey they themselves manage to catch is also difficult to judge. Insect remains may be similarly represented in the pellets from adult owls and their tethered young (family study 15, appendix (A), April 25 to July 10, 1931); more in pellets of adults than of young (family study 4, April 26 to May 30, 1931); or more in pellets of young than of adults (family study 35, May 29 to July 12, 1934).

Nearly all pellets of some early and midsummer lots contained insects: family studies 15 and 21, May 22 to July 10, 1931, and May 21 to June 25, 1932. Special phase study 2 (appendix (B)), which brought out extensive utilization of South Dakota wolf spiders in late summer, probably reflects both high availability of the spiders at this season and the partial dependence of inexperienced young owls upon types of prey that are easy to catch, including invertebrates. Errington and Bennett (49), finding that the proportion of burrowing owl pellets containing remains of vertebrate prey was about the same as the proportion of adult to young owls to be seen in northwest Iowa in late August, 1933, write: "Hence, the temptation is to suspect that the adults were the owls taking the vertebrates, while

---

27 See family studies 1, 2, 4, 6, 7, 14, 15, 19, 21, 24, 29, 30, 35, 39, 40 and 41 of appendix (A) and special phase study 2, appendix (B).

28 Examples: insect debris mixed only with that of non-insectivorous forms or exoskeleton pieces too large to have been swallowed by insectivorous animals represented in containing pellets.

29 In other years, late summer feeding upon large spiders by avian and mammalian predators also has been noted in central and northwest Iowa.
the clumsy youngsters, not being adept enough at this stage to
catch their own mice and frogs and not being able to live off the
old ones any more, had to eat insects and similar slow small prey
or nothing at all. A darting mouse may be unavailable to a young
owl, but it doesn't require any great skill to pick up dung
beetles. This seems to be of general applicability to the feed­
ing of many immature predatory birds and mammals when they
are learning to hunt (43, 50, 51).

Diets of the more typically insectivorous predators as the
skunk (74) and sparrow hawk (17) follow closely the summer
and fall periods of conspicuous availability of Orthoptera and
certain other common large insects. Predators having a wider
range of hunting prowess, or at least somewhat different adapta­
tions for obtaining food, may or may not respond to apparent
changes in insect availability in this manner. During the
drought spring of 1934, insect debris in the fecal passages of Iowa
red foxes rose to about 10 percent by bulk from the 1.5 percent
of the spring before (40), but a comparison of the data given
under the horned owl family studies (appendix (A)) for those
seasons reveals no changes in insect representations that may
be considered significant.

DISCUSSION

Gause and co-workers (61, 62, 63, 64, 65) have studied com­
petition and predation in experimental cultures of microorgan­
isms to establish general principles of interactions. We cannot
say how much the findings from such investigations of biological
phenomena, reduced to relationships between few organisms in
microcosms, may apply to situations found in nature. However,
MacLulich (89) concluded that the relaxation oscillations applied
by Gause to animal populations also describe periodic fluctua­
tions of the snowshoe hare in Canada. In this instance, with
disease substituted for predation in the reaction, the resulting
concept is one of hares being reduced to low levels from previous
peaks, whereupon the depressive organisms tend to lose con­
tact with the victimized species enough to allow recovery of the
latter before significant pressure is resumed.29

In Gause's (61) experiments with protozoa, the predatory
Didinium nasutum devoured the unprotected prey, Paramecium
caudatum, and then themselves died; likewise the predatory mite,
Cheyletus eruditus, eliminated another mite, Aleuroglyphus
agilis, but with rapidity varying with the accessibility of the prey

29 Periodic die-off of snowshoe hares evidently need not be due to infectious micro­
organisms, according to the findings on "shock disease" of Green and Larson (67).
31 Muir (98) comments on the diminishing contact of insect parasites with hosts at
low host densities. Predation and parasitism, though often differing in a pronounced
manner, nevertheless may have much in common, especially as concerns response
to availability of prey or hosts.
in different environments (64). Feeding by Paramecium bus-
saria upon yeast (Saccharomyces exiguus) did not terminate in
complete destruction of either; a certain threshold concentration
of yeast cells sedimenting on the bottom of the container and
elsewhere was not destroyed by the predators; and the predators
did not seriously decrease in concentration until the destruction
of prey down to this threshold, which had in no way a fixed value
but depended upon the concentration of the yeast (64).

As Gause (63) points out, the complexity of populations of
microorganisms on glass plates submerged in natural waters is
intermediate between that of "highly complex field biocenoses
and extremely simple laboratory mixed populations" but affords
opportunity to study elements of complexity in relatively simple
form. The advantages of such procedure we recognize, despite
our approach to the study of predation and population from the
other direction. Many of the natural interactions that we have
tried to appraise not only yield pertinent data with extreme
slowness, but the data in hand also seem to be frequently beyond
our ability to interpret.

The data from our field research, admittedly beset by their full
share of unknowns and unknowables but dealing with natural
events, do not by their portrayal of intricatecies disprove the
existence of fundamental patterns. Rather, one may conceive
of an underlying framework of basic reactions, which, however,
may seldom progress to their "ideal" termination under field
conditions because of the multiplicity of interruptions, deflec­
tions and compensations so often attending biotic interrela­tion­
ships. In nature, reactions of given predator and prey species
may indeed barely get started in predictable patterns before
deviations occur—if contacts between these forms are made at
all—and other predators and other prey may release or involve
the original participants.

One thing that has impressed us in our field studies has been
the apparent lack of rigidity in predator-prey relationships
observed in north-central United States. The Darwinian (24)
concept of sensitivity of organisms to variations in pressure
by enemies seems to be borne out by our findings only to the
extent that such pressure may have truly limiting influence—
which it may not necessarily have even when conspicuously heavy.
Comparatively few of the innumerable changes associated with
the interrelationships and ecology of the species we have been
studying appear to be of decisive consequence; in other words,
the inherent limitations of animal populations and their resilien-
ces may serve to nullify alike many of the seeming advantages
and disadvantages to which fortune may subject them.
THE HORNED OWL AND THE COMPLEX OF VERTEBRATE PREDATION

The horned owl’s efficiency as a hunter and its general feeding have been discussed (46), also its tendency to be lethargic when satisfied (32, 46). It appears, moreover, to be about as “unimaginatively” opportunistic as any of the predators with which we have worked and evidently takes its prey much in order of the ease with which such may be secured. Size limits of prey species that may be readily caught or handled (large insects toward the bottom of the scale and adult striped skunks, opossums, geese, turkeys, etc. toward the top) should be borne in mind when considering availability of prey animals to horned owls; so, obviously, should specific habits of prey animals and factors regularly or irregularly affecting their relative vulnerability or security.

Horned owls may or may not respond as expected to evidently increased availability of prey animals. The extremely high incidence of young muskrats in horned owl diet for family study 40 (appendix (A)), June 2 to July 15, 1935, which was associated with an observed dying and collapse of marsh cover, illustrates prompt response. Conversely, nothing that can be called a departure in feeding habits is shown by the data from a Wisconsin area at a season when meadow mice were present in cyclic peak densities in the hunting range of the owls; representations of meadow mouse and cottontail in 40 pellets were 4 or in 10 percent and 37 or in 93 percent, respectively (special phase study 19, appendix (B)).

Lack of responsiveness of horned owls to increased availability of a given prey species, however, may often be accompanied by decidedly greater response on the part of other predators. In cases investigated, it appears to us that responsiveness of horned owls and other predators to exceptional availability of species that were staple prey for all had little mutual interdependence. Whether most or only a few predators responded, it did not inevitably follow that any particular species among the other predators either reacted likewise or differently.

Table 11 was prepared from more or less comparable data on the feeding upon cottontails and mice by foxes and horned owls, chiefly in central and northwest Iowa. It may be seen that the representations of mouse remains in the fox feces fell from 65 percent for the “normal” spring and summer of 1933 to 48 percent for the drought seasons of 1934, whereas the representations of cottontail did not differ materially. Cottontail representations differed even less in the horned owl pellets; but mouse representations rose from 29 percent to 48 percent for the drought spring and summer, and the average number of mouse individuals per horned owl pellet during the drought was 0.9, compared
TABLE 11. COMPARATIVE IMPORTANCE OF COTTONTAILS AND MICE IN THE DIETS OF RED FOXES AND HORNED OWLS DURING "NORMAL" SEASONS AND DROUGHT.

<table>
<thead>
<tr>
<th>Season</th>
<th>Predator</th>
<th>Number of feces or pellets</th>
<th>Percent of feces or pellets containing cottontail remains</th>
<th>Percent of feces or pellets containing mouse remains</th>
<th>Average of individual mouse remains in pellets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter, 1932-33 (&quot;normal&quot;)</td>
<td>fox</td>
<td>29</td>
<td>83%</td>
<td>45%</td>
<td>0.3</td>
</tr>
<tr>
<td>(&quot;normal&quot;)</td>
<td>owl</td>
<td>54</td>
<td>91%</td>
<td>21%</td>
<td></td>
</tr>
<tr>
<td>Spring and summer, 1933 (&quot;normal&quot;)</td>
<td>fox</td>
<td>1,175</td>
<td>43%</td>
<td>65%</td>
<td>0.4</td>
</tr>
<tr>
<td>(&quot;normal&quot;)</td>
<td>owl</td>
<td>328</td>
<td>59%</td>
<td>29%</td>
<td></td>
</tr>
<tr>
<td>Winter, 1933-34 (&quot;normal&quot;)</td>
<td>fox</td>
<td>50</td>
<td>52%</td>
<td>54%</td>
<td>0.7</td>
</tr>
<tr>
<td>(&quot;normal&quot;)</td>
<td>owl</td>
<td>431</td>
<td>62%</td>
<td>29%</td>
<td></td>
</tr>
<tr>
<td>Spring and summer, 1934 (drought)</td>
<td>fox</td>
<td>935</td>
<td>39%</td>
<td>48%</td>
<td>0.9</td>
</tr>
<tr>
<td>(drought)</td>
<td>owl</td>
<td>197</td>
<td>61%</td>
<td>48%</td>
<td></td>
</tr>
</tbody>
</table>

* Chiefly in central and northwest Iowa, from whence come our most comparable data.
† Stomach contents are included for convenience with fox fecal passages.
‡ Only cottontail representations determined with reasonable certainty are given; if all representations of Leporidae were included, the remains of unrecognized young jack rabbits would doubtless introduce considerable error into the fox figures, though not much into the figures for the horned owl.
§ Number of individuals of mouse prey could not be satisfactorily ascertained in the fox feces, so the right hand column pertains only to owl pellets.

with 0.4 for the corresponding seasons of the year before\(^{29}\). It may further be perceived from table 11 that the winter representations of mice and average number of individuals in the horned owl pellets for 1933-34 had also increased decidedly since 1932-33, which seems to make rather remote the possibility that drought had much influence on the owl’s utilization of this type of prey.

As concerns variations in utilization of non-staple prey species by predators, the bob-white furnishes the best material we have for analytical treatment. Predation upon this bird may not typify relationships between predators and even non-staple prey, but at least it has been studied for many years (44, 53, 57, 113).

The conditions favoring severe horned owl predation on bobwhites in north-central states were reviewed earlier in this writing and may be summed up largely in a few words: overpopulation by the quail of their wintering environment.

Recognized overpopulation has not always signified that large numbers of birds were occupying a given tract of land. It has simply meant that existing densities—whether few birds or many per unit of area—were in excess of the capacity for accommodation of the land, as demonstrated by the upper limit of spring survival of birds wintering over a period of years sufficiently long to reduce the chief variables due to underpopulation, climatic emergencies and human interference. The maximum num-

\(^{29}\) Marsh hawks near Ruthven, Iowa, also took a higher proportion of mice during the summer of 1934 [10 (6 percent) of 158 recorded prey items] than they had the previous summer [3 (1 percent) of 289 items] (50).
ber of quail that an area in established north-central range may accommodate may be either raised or lowered through ecological succession, land use or environmental manipulation but tends to be a rather constant property of given land units from year to year. Capacity for accommodation for bob-whites is not the same on all areas, nevertheless, and may be further influenced by pheasants or perhaps other cohabitants, including some that may not even be competitive except in the sense that their presence may cause the quail to avoid needed coverts (53).

As populations not beset by blizzard crises, starvation, etc., wintered within or below the carrying capacity of their habitats with comparative security from natural enemies of all kinds observed in the north-central region, so populations exceeding carrying capacity were in all known cases reduced approximately to that level by spring. Reduction of excess fall populations, when not accomplished by hunters (52), generally occurred through egress of the birds or through the medium of predation.

Analysis of this predation has brought out the existence of highly interesting compensatory trends. It was discovered that, although horned owls actually did most of the killing of excess birds, decreased horned owl pressure was followed or attended by increased pressure from other enemies often differing greatly in prowess and hunting tactics—the swift and formidable Cooper’s hawks, the clumsy buteos, the marsh hawks, foxes, house cats, small and medium-sized owls and lesser predators. Sometimes, insecure quail populations were relieved of horned owl attacks through death or departure of the owls; at other times, the owls preyed upon something else to the virtual exclusion of the quail; but in neither event did the birds escape for long the consequences of their basic insecurity nor did this bear appreciable relation to changes in kinds and numbers of predators (53).

A similar vulnerability is illustrated by the ruffed grouse data given in table 9. As low as the carrying capacity of the area at Prairie du Sac is for ruffed grouse, populations exceeding about 20 birds on 5 square miles have been distinctly insecure. The heavy predation losses in 1931-32 and 1932-33 varied with what was evidently the degree of overpopulation, whether the predators responding were horned owls, gray foxes or possibly enemies to which losses were not specifically traced (42).

In these instances relating to wintering bob-whites and ruffed grouse on agricultural lands in north-central United States, vulnerability to general predation seemed essentially restricted to population surpluses above thresholds of comparative security; but compensatory trends in predation rates by different kinds and densities of predators may often be apparent even when

---

Units of large size—several square miles in area—show definiteness of carrying capacity much better than do small acreages (53).
thresholds of security may not be recognized or, conceivably, may not be operative with any definiteness 34.

The possibility of something comparable to thresholds of security existing for wintering ring-necked pheasants has been touched upon in this paper, but the scanty evidence at hand suggests that such thresholds, if they do exist for this bird and its habitats, may be numerically less definite than those observed for northern bob-whites on given areas. The concept has been growing on us of a cross-play of predation, variable in source but compensatory in net effect, eliminating perhaps about the same proportion of the pheasants resident on an area, winter after winter. This is in many ways similar to McAtee's (91) thesis, and we furthermore suspect that its application may be extended to other birds wintering in the region, notably to species tolerant of concentrations in favored habitats.

Reproduction in the vertebrates we have studied is interlinked with behavior variables predisposing individuals to capture by enemies, and analysis of predation upon breeding adults is involved with corresponding uncertainties. It has been postulated (44) that, since one of the manifestations of overpopulation in wintering bob-whites has been increased friction among the birds themselves, the intolerance and excitement of mating may have the same effect as overpopulation in increasing vulnerability.

At any rate, the breeding season for the quail, and also for some other wild gallinaceous birds, may apparently be accompanied by predation more in proportion to actual population than during the cold weather months. Just what proportions of the prey population may be thus taken is not clear. In northwest Iowa, slight mortality of breeding pheasants was traced to predation (72), yet the food habits data from contemporaneous local studies of predatory species showed a pronounced increase in utilization of these birds in spring and early summer, especially by horned owls (see table 10) and red foxes. Ratios of pheasant carcasses of known sex found at fox dens were 98 cocks to 201 hens (1:2) for 1933 and 184 cocks to 307 hens (1:1.67) for 1934, or close to the sex ratios of the general pheasant population for the respective seasons (41).

Although the horned owl had little to do with the loss of eggs and immature young that we have recorded in our work on north-central pheasants and quail, the data on this type of predation by other animals are so revealing of compensatory trends that they merit space in this discussion.

For the northern bob-white, we have insufficient data on details of nesting losses and juvenile mortality to justify many con-

34 The authors do not at this time have further contributions to add to published discussions (53) of definiteness of carrying capacity for northern bob-white wintering environment.
TABLE 12. RATES OF RECOVERY OF RUFFED GROUSE POPULATIONS ON AN AREA OF 2,304 ACRES IN NEW YORK, ACCORDING TO EDMISTER (25).*

<table>
<thead>
<tr>
<th>Year</th>
<th>Spring (April) breeding population</th>
<th>September population</th>
<th>Rate of recovery from breeding level</th>
</tr>
</thead>
<tbody>
<tr>
<td>1930</td>
<td>63</td>
<td>140</td>
<td>122%</td>
</tr>
<tr>
<td>1931</td>
<td>130</td>
<td>272</td>
<td>120%</td>
</tr>
<tr>
<td>1932</td>
<td>199</td>
<td>437</td>
<td>100%</td>
</tr>
<tr>
<td>1933†</td>
<td>296</td>
<td>417</td>
<td>120%</td>
</tr>
<tr>
<td>1934</td>
<td>285</td>
<td>287</td>
<td>120%</td>
</tr>
<tr>
<td>1935</td>
<td>241</td>
<td>255</td>
<td>120%</td>
</tr>
<tr>
<td>1936</td>
<td>155</td>
<td>248</td>
<td>125%</td>
</tr>
<tr>
<td>1937</td>
<td>110</td>
<td>218</td>
<td>125%</td>
</tr>
</tbody>
</table>

* Tabular errors for 1936-37 in original publication were corrected upon advice of Edminster (letter to Errington, Jan. 18, 1939).
† "1933 figures calculated from sample data." (25, Table 1).

Conclusions, but the summer recovery rates of populations on southern Wisconsin study areas have proved very suggestive. It may be seen from published data (36, 53, 54) that the rates of recovery from breeding stock have been in inverse proportion to the densities of the adult birds. Survival of young following a curve having points as mathematically predictable as those shown by the Prairie du Sac records (53, 54), irrespective of decided changes in status of predator populations over the years, could hardly indicate any important predation upon immature bobwhites that wasn't compensatory as well as more or less predetermined by intraspecific and environmental mechanics.

The 2,304-acre Connecticut Hill area of the New York ruffed grouse investigations has yielded data having more complex recovery trends. Table 12 reproduces Edminster's (25) recent figures on rates of increase by fall from the spring breeding densities. If the recovery percentages be plotted on the ordinate and the breeding densities on the abscissa, what appear to be two curves may be seen, one for the years 1932 to 1935 and the other for 1930, 1931, 1936 and 1937. The falling of points for the middle years in a different curve from the points of the end years has occasioned the following comment from Edminster (letter to Errington, Jan. 18, 1939): "This relationship of productivity to the cyclic phase does appear to have some significance. Just how significant it is, I confess I am not certain." Aside from the possible bearing upon recovery rates of unknown cyclic factors, Edminster's data lead him to conclude his section on actual productivity with the words (25): "Thus, definite substance supports the contention that as populations approach the range

---

25 The reader should be cautious about drawing overbroad conclusions from these findings, which may or may not hold at other times, in other parts of the country or for other species. Cases in point are afforded by increased productivity of certain game bird populations following artificial reduction of the most serious enemies of their young (including eggs)—especially in the South and in the West (78, 81, 113).
carrying capacity, their productivity declines."

There is some evidence that survival of pheasant young in northwest Iowa may also be influenced by densities of adult birds already present (54). The seasonal shrinkage of broods from causes including predation progressed, however, at about the same average rate according to age classes, not only in northwest Iowa as a whole during the summers of 1933 and 1934, but also in localities in which the densities of known enemies of pheasant young varied from abundance to virtual absence. For example, marsh hawks on one area preyed rather severely upon young pheasants, but the average decline in size of the pheasant broods at that place was no more rapid than the decline of broods on an area a few miles distant where marsh hawks were seldom seen.

The Iowa researches on the blue-winged teal (13, 48) and the muskrat (47 and unpublished) have brought out some as yet imperfectly evaluated predator-prey interactions that seem at least partially of compensatory nature; the waterfowl studies of Kalmbach (80, 81) in North Dakota, Saskatchewan and Alberta and of Furniss (60) in Saskatchewan are likewise very suggestive. Incidental observations on general predation strengthen the concept of many prey species being, at given densities and in particular situations, vulnerable to a certain amount of predation, whether through the agency of one exceptionally efficient or abundant enemy or a combination of lesser ones.

The mind-picture that we have of vertebrate predation in the rich farming communities of Iowa and southern Wisconsin takes the following broad outlines: A supply of staple prey animals so bountiful that even after cyclic declines some species may be preyed upon by their usual enemies in much the same proportions as before; non-staple prey species that suffer severe predation chiefly as their vulnerability may be accentuated by overpopulation, environmental evictions, climatic emergencies or disadvantages of other sorts; a predator population that may often be about up to the limits of density that many of the component species will themselves tolerate in their respective habitats, but

McAtee’s (94) discussions of self-regulation of populations have pertinent bearing upon this phenomenon. Very low populations of organisms, however, are not optimum for reproduction, and, indeed, in some gregarious forms, breeding is facilitated by high numerical densities (1, 2, 23).

These are the only seasons for which we have comparable data on pheasant brood losses (54).

Migratory or immature predators may fluctuate considerably in numbers from year to year. Breeding densities of such species as the horned owl appear to remain rather constant for given areas over long periods of time—close to one pair per 2 square miles both in the vicinity of Prairie du Sac, Wis. (5 square miles, 1929-38), and Ames, Iowa (8 square miles, 1932-38). Breeding densities of redtailed hawks near Prairie du Sac have been about the same as those of the horned owl; and these two species seemed to occupy the greater part of the nesting territory available for large raptorial birds. Excessive campaigning by man may, of course, keep territories underpopulated or even devoid of certain predators.
still a population essentially far below the limit of its easily accessible food.29

The greatest difference in this picture and those that may be drawn from some other parts of the continent seems to lie in the continued availability of staple prey or "buffer" species. Stoddard (113) and Komarek (85) have described the building up of populations of certain southeastern predatory mammals during ascendencies of their prey, cotton rats (Sigmodon hispidus), and the resulting increase of pressure upon bob-whites after decline of the rodents. MacLulich (89) has recently reviewed the extensive literature on dependence of lynx (Lynx canadensis) and other predators upon the snowshoe hare in the northern wilderness and the starvation that follows periodic die-off of the hares. In the north-central states areas under observation, few of the predators we have studied ever appeared primarily dependent on any one staple prey species for food at any critical time; such declines of staple prey animals as were observed accordingly did little to upset general predator-prey equilibria except occasionally (not always) to cause predators to turn to other staple species that were themselves well able to bear greatly increased pressure.40

Except for Asio owls and like forms having more inflexible hunting tendencies or specialized adaptations, north-central winter-active predators seem to have little trouble in shifting from one major mouse species to another or from mice to cottontails or from usual main staple foods to the various non-staples that for one reason or another may rise in prominence. During warm-weather months, there is the same ready utilization of rabbits and mice and temporary shifting to an even greater variety of non-staple prey, including ground squirrels, crayfish, May beetles (Phyllophaga spp.), grasshoppers (Melanoplus spp.) and perhaps other animals that may, in addition, constitute staple seasonal food for some of the predator species resident.

29 McAtee (94), among others, points out that few animal populations are limited by their food supply in nature, and we cannot see—making due allowance for apparent exceptions—that this holds any less true for most populations of predators in the north-central region.

40 "While the observed severity of predator pressure upon southeastern bob-whites was at least in part due to high densities of specific predators, Stoddard feels that many of the principal quail enemies there may be—even in times of abundance—numerically fewer than they normally are in north-central areas as the one near Prairie du Sac, with which he has long been familiar. The resulting picture has its imperfections, but it appears to suggest that lower predator densities in the southeast may in effect exert more severe pressure upon resident bob-white populations than may equivalent or higher predator densities in the north. The most noteworthy case in point is provided by the gray fox, which even at patently destructive densities in the southeast seldom approaches in numbers the Prairie du Sac winter average [according to the best figures in hand when the manuscript was prepared, 4.6 per square mile from 1930-31 to 1936-37]." (57)

41 There is an apparent connection between densities of these owls and populations of the mice upon which they prey, but much of the evidence we have for this region is obscure if not conflicting. Chitty (19) cites an interesting example of short-eared owl decline on the Scottish Border following epidemic disease in voles (Microtus agrestis) in 1934.
Making allowance as well as we can for variables and narrowing down our attention to what seem to be the broader aspects of our regional picture, we see a pattern of continuity and compensation that looks in many ways peculiarly reminiscent of McAttee’s (91) much-attacked thesis that predation collectively tends to be in proportion to population, later restated (92) to the effect that the proportion, however, rises and falls progressively with increase or decrease in numbers of the available food organisms.

Losses from predators of some species living in strong environment may be negligible, though their own and predator densities may be high; or losses of the same or other species in weak environment, or when over-crowding strong environment, may represent a clean sweep of populations or parts of populations; or, at times, densities of prey, as rodents and insects, may reach such peaks that predators can consume or kill but a very minor proportion of them under conditions most favoring predation; still other species may be conspicuously vulnerable only to few, or to particular, enemies. Even so, between the extremes and the exceptions, it would be hazardous to say that the majority of prey species treated with in this paper do not at most times suffer collective predation much as their relative abundance might lead one to expect. At any rate, it is apparent that relief from specific predators is not necessarily synonymous with that much net relief from predation as long as basic population insecurities continue unchanged. Given a prey species vulnerable because of over-population or eviction or for similar reason, the accelerated response of some predators may often compensate for lack of predation by others.

The horned owl is a redoubtable, if not a dominant, predator within the confines of its habitat in Iowa and southern Wisconsin. There it seldom lacks alternatives as concerns staple food, of which there is commonly a far greater abundance than it or associated predators can utilize. Within limits imposed by its own adaptations and behavior, it takes non-staple prey largely as circumstances permit or as these may exceed in availability the staple prey animals. Exceptional availability of non-staple prey may be superimposed upon the “normal” availability of the staple, and, if the horned owl doesn’t happen to respond, the chances are strong that some other predator, or predators, will.

INFLUENCE OF HORNED OWL PREDATION UPON POPULATION LEVELS OF PREY ANIMALS

One of the causes of the disputes often elicited by the mere mention of predation is confusion of the fact that predators prey upon certain animals with effect that such predation may have on numbers of the prey. The fact of predation may usually
be ascertained with relative ease through field or laboratory studies; evaluation of effect of predation upon population is another matter and one just beginning to receive a small measure of the attention that is its due.

It may then be appropriate to inquire, as critically as our knowledge may justify, into the influence of predation by horned owls and other predators upon populations of the prey groups with which we have dealt in this bulletin.

The infrequency with which predators or parasites completely destroy their respective prey or host species should not need emphasizing, in view of the obviously continued existence of predators and parasites along with the exploited species over vast periods of time. In late years, there has seemed to be, moreover, a gradual turning away of biological thought from the idea that predation, or parasitism, has a primary regulating effect on general abundance of animals or, at any rate, an effect commensurate with that of climate, specific habitat requirements and automatic adjustments on the part of the prey, or the hosts, themselves. This is illustrated by McAtee's (90, 91) quotations from the literature pertaining to natural checks upon insects; by Leopold's (87) discussions of properties of game populations; and, exceptions and modifications notwithstanding, by the writings of an increasing number of other workers on related topics.

Muir (98), in writing of the critical point of parasitism in insects, states that this comes when the parasite can exist but can produce no further effect upon the host population and that, fundamentally, the critical point is due to the psychology, physiology and morphology of an insect but is modified by physical and biological environments; differences and interactions of these factors cause the differences between the critical points of parasitism of different insects. If we might apply the term "critical point" in somewhat the above sense to predation, it would seem that the densities of the majority of predator species we have studied seldom rose far above it in the north-central region even when their own increase was checked mainly by intraspecific mechanisms.

Rodent, rabbit and insect populations, at peak abundances over large areas, appear to be far beyond the control of any vertebrate enemies that may, within reason, prey upon them. During mouse plagues, grasshopper outbreaks, etc., virtually all con-

42 Some of the most drastic effects of predation or parasitism on record have resulted from introduction of alien forms or have been otherwise associated with human activities. One should be especially careful not to impute primarily to predation differences in the status of prey species following pronounced environmental changes. Sumner's (115) description of deterioration of California quail (Lophortyx californica) habitat is pertinent, and the history of the rise and decline of prairie chickens on the north-central prairies (87) furnishes a good example of human influence at first favorable to a wild species, then adverse.
ceivable enemies may take toll without visibly affecting population densities, except perhaps where predators may concentrate on a local scale (110); and periodic rises of "cyclic" animals that are in turn staple foods for many important predators are of widespread occurrence in northern lands. Parasitism, as it is more likely to bring about collapse of top-heavy host populations, is not so comparable with predation in this respect.

It seems true from the writings of Tinbergen (117), Criddle (21), and others that predation, to have anything approaching a governing effect on northern mouse or rabbit populations, must occur at times when the latter are at low to moderate densities. Whether or not this holds for the north-central states, we cannot judge from the inadequate and involved data at our disposal. The extreme consequences of predation on mammals reported by Williams (118) in northeastern Ohio were linked with a drought emergency and perhaps also reflect predator-prey relations basically different from those with which we have worked.

In Iowa and southern Wisconsin, for all of the tremendous numbers of small and medium-sized mammals eaten as staple food by predators, we are not convinced that such utilization actually serves to keep populations significantly lower than they otherwise would have been. Lest this remark appear over-skeptical, we may say that unpublished data on the muskrat—related to the meadow mouse although treated in this paper as a nonstaple prey species—indicate not only that losses from intraspecific strife under given conditions may largely compensate for decreased predator pressure but also that unusually severe losses of young animals, as through disease or attacks of minks, may be followed by prolongation of breeding by adults to an at least partially compensatory extent.

The one area on which we have conducted year-to-year horned owl studies and on which legal or illegal hunting by man has not introduced a variable into the cottontail equation is the Des Moines Waterworks supply grounds at Des Moines, Iowa—a police-patrolled wildlife sanctuary of over 1,500 acres where wildlife management consisted of protection from human poachers and preserving an adequate balance of food and cover. The cottontail population of a sample under regular observation in connection with winter quail studies, 1932–39, maintained moderate to high densities with remarkable uniformity; seldom would one spend 2 hours on foot on the place without seeing from 6 to 10 cottontails, which may be compared with flushing rates given by Leopold and Anderson (88) for Wisconsin. Native

43 Including parasitism by plants and organisms of uncertain systematic position.
44 It may, however, at certain times and in certain situations, be preyed upon by some predators as a staple (46, 47).
predatory mammals were not abundant, but rabbit-hunting dogs 
were; and hawks and owls were generally about as numerous as 
anywhere noted in central Iowa, though not necessarily more 
so. Cottontail representations were found in 20 (69 percent) 
of 29 horned owl pellets collected, fall to spring, 1932-35 (special 
phase study 20, appendix (B)).

We must admit that, likewise, we know very little about the 
effects of horned owl predation upon the majority of mammal 
especies taken as nonstaple prey. One would not expect the 
capture of diurnal sciurids to be of much consequence from the 
standpoint of populations, but the situation possibly may be the 
reverse as concerns flying squirrels. In two of the three in-
stances of severe horned owl pressure upon muskrats given in 
this paper, the animals were living in precarious circumstances 
and even in the absence of the owls would probably have suffer-
ed heavy losses from other causes.

Heavy though horned and other owl pressure upon field-
living Norway rats may be (35, 37), it often occurs most con-
spicuously in localities where one might logically question, any-
way, the ability of the rats to winter away from buildings, dumps 
and the like. That there would be more rats were it not for the 
owls is not necessarily assured.

Although predation upon Mustela spp. does seem so intense in 
proportion to numbers that we suspect it may have a consider-
able depressive effect, this, too, may be easy to overestimate. 
Soper's (111) trapping experiences in western Canada during 
the winters of 1912-14, when weasels (mostly short-tailed) were 
very common, indicate populations of about 10 per square mile; 
the reported yield of about 200 minks of a 12-square mile lake and 
marsh area in South Dakota during a winter of abundance, 
1921-22, (45) may suggest somewhat greater densities, as may 
also unpublished data from marshlands in the vicinity of Ruth-
ven, Iowa. Minks suffer losses from general predation, but we 
have found carcasses of many minks killed by others of their 
kind. The role of intraspecific strife must then be considered 
along with predation and human exploitation or persecution 
before we may feel entitled to say much of what determines mink 
population levels for given habitats; and, if intolerance proves 
to be the ultimate check on mink numbers above certain densi-
ties, it may conceivably so function for the terrestrial weasels.

Since the publication of Howard's (79) book on territorial 
reactions of nesting birds, a tremendous amount of work has 
been done on this subject that has contributed to a clearer under-
standing of avian populations (100). Whether territorialism 
may be restricted to the breeding season or continued through-
out the year as in the case of the wren-tit (28), it tends toward 
the stabilization of population densities especially of passerine
birds and those of comparable habits. There is, in short, room for only about so may breeding territories in the environmental niches available to different species of common "song bird" types; and these territories are often pretty well filled to capacity and so compressible only to a minor degree. Interspecific competition and intolerance may sometimes favor or handicap one species or another; but intraspecific manifestations seem more general and evident.

Nicholson (103) has compared the system of balance in territory-holding populations with that of water in an overflowing reservoir, surplus individuals being harried or forced into unsuitable environments to the extent that their chances of surviving or of reproducing are greatly reduced. As concerns most passerine and related birds, we feel that the statements made by Erickson (28) for the wren-tit hold true: "Whether or not possession of a territory is essential to the success of the individual life, it is unquestionably essential to reproduction. The ultimate competition is for space."

We are aware of no more detailed study of predation on passerine birds by owls than that made by Allen (3) in 1922 on a bird sanctuary at Ithaca, New York. He kept adult-attended young screech owls caged at the nest site, and the feeding of these was observed for 45 days, during which time 77 small birds of 18 species were brought to the young. Contemporaneous studies of the local bird population provided the basis for the following conclusions:

"When both of a pair of birds were killed in the same night... that pair ceased to be represented in the sanctuary, but if only one were taken, the survivor secured a new mate almost immediately so that the destructiveness of the owls was in this way covered up.

"Birds are able to secure new mates rapidly because of the unmated immature birds which are usually available on account of their later migration period and the later maturation of their reproductive organs."

The local nesting populations of birds over a period of 7 years were given: 1917, 34 pairs, 18 species; 1918, 34 pairs, 22 species; 1919, 27 pairs, 16 species; 1920, 38 pairs, 19 species; 1921, 45 pairs, 15 species; the year of the observed heavy owl pressure, 1922, 42 pairs, 17 species; the year following the owl losses, 1923, 44 pairs, 18 species. Allen remarks that the total bird population of the area under consideration was not materially affected by the inroads of the owls but goes on to state that he did not wish to minimize the destructiveness of the latter. "It may well be that had it not been for the owls there would have been a very substantial increase in the bird population." (3).
Variability of nesting success and survival both of adults and young is revealed by all comprehensive life history studies of passerine birds that have come to our attention. Differences in population densities that may result from this variation in productivity seem mainly evident in the post-breeding months of the year unless following wholesale mortality from some unusual cause or cataclysmic change in environment. With the return of the breeding season such temporary gains or losses, within limits, may be cancelled out before reproduction begins, and we are reminded of the words of Erickson (28): "Even when an exceptionally large number of individuals are produced or survive to their first breeding season, the number that find places to breed will not be greatly increased. The potential geometric rate of increase is damped before it has a chance to get under way."

The large size and the increase (106) in numbers of the crow in recent years may cause one to wonder how much it may constitute something of a special case among passerine birds, but the literature does not seem to be as enlightening as one might wish. Of interest are the findings of Roebuck (107) on rook (a related but colony-nesting species, Corvus frugilegus) densities in England. A survey of rookeries on 5,305 square miles in 1928-30 gave average breeding densities of 1 bird per 27.4 acres; a second survey, 4 years later, showed little substantial change either in numbers or in distribution.

Among the north-central birds exhibiting breeding territorialism after the manner of passerine forms, the small and mediumsized owls are very nearly the only ones suffering predation from horned owls severe enough to look significant. Granted that it is logical to expect the smaller night-hunting owls to be peculiarly exposed to horned owls, the possibility should not be lost sight of that they may, in actuality, be preyed upon no more heavily in proportion to their local densities than many diurnal birds. Most of the owls taken are screech owls, which seem to hold up well not only under the horned owl pressure but also in the face of conspicuous mortality from motor traffic. Then too, insofar as the screech owl losses traced to barred owls (31) and marsh hawks (50) occurred in areas not known to have been hunted over by horned owls at the time, much predation on the screech owl may be compensatory in trend.

Evaluation of the significance of predation losses suffered by migratory birds on their flyways or wintering grounds from existing data is practically hopeless. This is broadly true for the whole semianual migration, game or nongame, warblers to waterfowl. What we may eventually expect to learn about the subject may be limited; but when, or if, we ever have reasonably accurate population figures to compare with loss rates from
areas showing different intensities of predatory attack, we should be in a better position to make preliminary calculations. After that, if predation losses prove to do much more than take the place of "natural" losses of the sort to occur anyway, it will be in order to consider the problem of what actual effect the greater mortality may have on productivity or maintenance of populations.

The distinction between severe losses from predation and apparent net influence of such losses upon population levels maintained by the bob-white in Iowa and southern Wisconsin has already been discussed in this bulletin and elsewhere (44, 53). Under conditions studied, even the heavy winter depredations upon this species by the horned owl—centered as they were upon birds essentially doomed because of insecurity of position—simply didn't seem to count. That these relationships may differ in other parts of the country has previously received mention.

On the other hand, the severity of predator pressure upon the ring-necked pheasant may very possibly signify material lowering of populations below levels that otherwise would have been maintained. It has been thought that the pheasant, being alien to this continent, might not be as well adjusted as native species to our predators. Instances of heaviest pressure from both horned owls and red foxes, however, were recorded from localities in Kossuth and Palo Alto Counties, northwest Iowa, well known to sportsmen for excellence of pheasant hunting.

Predator pressure upon the Hungarian partridge may be locally heavy, but our data are too limited and involved to permit much of an analysis. Yeatter's (119) study in the Lake States does not reveal losses from predation more striking than those recorded from studies of native gallinaceous birds. Emphasis upon "vermin" control in partridge management in Great Britain is traditional, but pertinent data and statements clearly having scientific standing are not so easy to find in the literature. We feel that Middleton and Chitty (97) have made one of the most accurate appraisals:

"In naturally favorable environments 'vermin' destruction and protection have allowed the partridge population to reach very high densities at certain times, but there is a limit to the carrying capacity of any area beyond which the population cannot be forced without changing one or more of the first three factors mentioned above [(1) food, (2) nesting cover, (3) summer cover and shelter for the very young birds]. The density limit is undoubtedly controlled, not by one of these factors alone but by the correct balance between them."

Horned owl predation may perhaps have some effect on local snake densities, but it is unlikely that population levels of other
lower vertebrates and of invertebrates are appreciably influenced thereby.

Before concluding this section, let us take up briefly a conspicuous, special type of predation—that upon animals artificially concentrated, as about poultry-raising or game-breeding establishments. Such “unnatural” densities may be highly attractive to predators in the neighborhood, and losses may also occur through species ordinarily nonpredacious in habits. Tales of weasel depredations in hen houses may grow into legends over the years, but in the literature are records of 160 chickens killed in a farmyard by a raiding fox family in two mornings (39), 28 quail in a propagating pen by a house cat in one night (113), and many other accounts of mass killings under like circumstances. Horned owls gravitate along with other flesh-eaters to such rich hunting grounds and avail themselves naturally and capably of the opportunities presented.

The population aspects of this sort of predation are, as usual, beclouded by unknowns. Although astonishing numbers of drifting predators may be shot or trapped on the premises of game breeders, Grange and McAtee (66) observe that “The yearly toll taken by predators on many game farms is almost constant, indicating that no real progress has been made even where wholesale control is attempted.” The continued maintenance of exceedingly vulnerable populations on these places is, of course, evidence that some compensatory loss trends have been partially overcome by artificial means. A thorough and objective study of predation on game farms, with observational techniques supplemented by planned experimentation, would no doubt yield data on questions concerning which our knowledge is only fragmentary, at present.

THE QUESTION OF ECONOMIC STATUS OF THE HORNED OWL IN NORTH-CENTRAL UNITED STATES

Except for Norway rats, mice and insects, the greater part of the horned owl’s regular diet in north-central states consists of species legally designated as game or protected nongame. Of forms taken from time to time, pocket gophers, weasels, moles, gerales and blackbirds, jays and crows, owls, snakes, salamanders, and frogs are creatures man may or may not—usually not—care for. Rabbits, the main staple food for the horned owl, may be regarded by the public either as pests or prized game animals. The “song bird” group enjoys rather general popularity, unless special interests as fruit growing, etc., are affected; this also may be said of waterfowl and upland game birds. Some of the loss relates to personal property—poultry or privately owned game birds in pens.

We shall not attempt to discuss comprehensively the values—
positive or negative—man may place upon the various items eaten by horned owls nor the criteria upon which such values may be based. Not only do we feel that consideration of these involved subjects would take us too far from what has been our field of inquiry, but we are also convinced that accurate appraisals of predation from either biological or economic standpoints must await better insight into the functioning of natural mechanisms than we as yet have.

In view of the looseness of predator-prey relationships and the patently incidental or secondary nature of common types of predation observed in the north-central region, it should not be taken for granted that destruction of prey by predators necessarily has significant influence on population densities maintained by the prey, even when losses may be heavy in proportion to numbers. We may, indeed, ask what, if any, of the prey species would have been, on the whole, more abundant, had it not been for the animals killed by the horned owls—or by any specific wild predator?

It seems probable that certain farmers would have raised more poultry but not the full equivalent of the birds lost to the owls. Perhaps there would have been more rabbits for hunters to shoot, to die of tularemia or simply to live at higher densities; perhaps, somewhat greater populations of flying squirrels, weasels and screech owls; maybe, more coots and pheasants, to the approval of some people and the disapproval of others. Conceivably, there may have been other differences in the biotic picture of which the imperfections of our knowledge permit neither recognition nor analysis.

The rights of farmers, poultrymen and game breeders to protect their interests from horned owls are recognized, and there is no doubt that the owls may otherwise be subjected to intelligent control. With its extensive wilderness and backwoods range, the species is possibly as secure as any wild creature on the continent—although in the East it appears to be held at quite low levels, presumably because of human persecution, and, for all of its general abundance, organized campaigning may keep it practically cleaned out of some localities.

The animosity of the public—especially hunters—toward the horned owl, however, seems needlessly extreme. Sporting factions, too, have rights and grievances, but flat claims that they must choose between game and "vermin" (i.e. natural enemies or competitors of game, collectively) are hardly entitled to acceptance without question or reservation. Judged by the bare details of what it may eat, the horned owl may logically be

---

45 Improved housing facilities, covered pens, etc., for poultry or propagated game may often give more efficacious protection than direct action against predatory species. See McAtee (93) for practical suggestions.
classed with the "worst" of so-called vermin (or, for that matter, as a species expressly to be encouraged for the sake of agriculture); but understanding of the interactions of predators and prey is not so easily gained. Still less readily may the effects of predation upon prey populations be evaluated without knowledge of densities, social behavior and habitats of the prey and of degrees of compensation that may exist in loss and recovery trends.
LITERATURE CITED

(3) Allen, A. A. A contribution to the life history and economic status of the screech owl (Otus asio). Auk, 41:1-16. 1924.


(41) Errington, Paul L. Food habits of the red fox in Iowa. American Wildlife, 26:5-6, 13. 1937.


(56) Errington, Paul L. and McDonald, Malcolm. Conclusions as to the food habits of the barred owl in Iowa. Iowa Bird Life, 7:47-49. 1937.


(70) Guérin, G. La vie des chouettes. II La hulotte et son régime. Lussand Frères, Fontenay-le-Compte. 1932.


(91) McAtee, W. L. Effectiveness in nature of the so-called protective adaptations in the animal kingdom, chiefly as illustrated by the food habits of Nearctic birds. Smithsonian Misc. Coll., 85 (7) (Publ. 3125). 1932.


(98) Muir, F. The critical point of parasitism and the law of Malthus. 
Musc. Publ. 32. 1936.
(100) Nice, M. M. The theory of territorialism and its development. Fifty 
years progress of American ornithology; American Ornithologist’s 
Union Memorial Volume. Lancaster, Pa. 88:89-100. 1933.
(101) Nice, M. M. Zur Naturgeschichte des Singnammers. Jour. für 
Ornithologie, 81:552-595; 82:1-96. 1933-34.
(102) Nice, M. M. Studies in the life history of the song sparrow. I. 
(105) Reed, C. J. and Reed, B. P. The mechanism of pellet formation 
in the great horned owl (Bubo virginianus). Science, N. S., 
(106) Roberts, Thomas S. The birds of Minnesota. 2. Univ. Minnesota 
Press, Minneapolis. 1932.
(107) Roebuck, A. The rook in the rural economy of the midlands. 
(108) Seton, Ernest Thompson. Lives of game animals, 4 (1). Doubleday, 
1930.
(110) Snyder, L. L. and Hope, C. E. A predator-prey relationship between 
the short-eared owl and the meadow mouse. Wilson Bul., 50:110- 
112. 1938.
(111) Soper, J. Dewey. Notes on Canadian weasels. Canadian Field-Na­ 
turalist, 33:43-47. 1919.
(112) Spawn, G. B. The 1934 fall migration of shore birds through Clay 
and Palo Alto Counties, Iowa. Iowa State College Jour. Sci., 
(113) Stoddard, H. L. and others. The bob-white quail. Scribner’s, New 
York. 1931.
(114) Stoner, Dayton. Studies on the bank swallow, Riparia riparia 
1936.
(115) Sumner, E. Lowell, Jr. A life history study of the California quail, 
with recommendations for conservation and management. California 
Fish and Game, 21 (3-4):165-256; 277-342. 1935.
(116) Swenk, Myron H. A study of the distribution and migration of 
the great horned owls in the Missouri Valley Region. Nebraska 
(117) Tinbergen, N. Die ernährungsökologischen Beziehungen zwischen 
Asto otus otus L. and ihren Beutetieren, insbesondere den Microtus- 
(118) Williams, Arthur B. The composition and dynamics of a beech- 
(119) Ycatter, Ralph E. The Hungarian partridge in the Great Lakes 
5. 1934.
APPENDIX

(A) FAMILY STUDIES

FAMILY STUDY 1—Verona, Wis.

Winter, 1929-30, through March.

Representations in 39 pellets from ADULT OWLS: cottontail, 9; Norway rat, 10; house mouse, 1; meadow mouse, 25 (42 individuals); deer mouse, 27 (110 individuals); short-tailed shrew, 3; fringillidae, 1; probable crow, 1; large bird, 1.

April 5 to 27, 1930.

Nonpellet food items: cottontail, 5; Norway rat, 2; meadowlark, 1; crow, 2; long-eared owl, 1; domestic pigeon, 2; domestic chicken, 2.

Representations in 12 pellets from ADULT OWLS: cottontail (including 1 pellet with remains of young), 7; Norway rat, 3; meadow mouse, 4; deer mouse, 7 (18 individuals); mouse, 2 (3 individuals); rodent, 1; crow, 2; domestic pigeon, 1; large bird, possibly domestic chicken, 1; salamander, 1.

Representations in 15 pellets from YOUNG OWLS: cottontail, 11; Norway rat, 2; meadow mouse, 3; deer mouse, 2; crow, 2.

April 28 to May 15, 1930.

Nonpellet food items: cottontail, 2; Norway rat, 1; crow, 1; bluejay, 1.

Representations in 1 pellet from ADULT OWL: mouse and domestic chicken.

Representations in 21 pellets from YOUNG OWLS: cottontail, 11; house mouse, 1 (2 individuals); meadow mouse, 2; deer mouse, 9 (18 individuals); mouse, 4; small rodent, 1; insectivore, 1; mammal, 2; crow, 1; bluejay, 1; passerine bird, 1; king rail, 1; young domestic chicken, 1; bird, 6; snake, 4; vertebrate, 1; insect, 3 (12 individuals: 3 Onthophagus, 1 Aphodius, 1 Trox, 3 Calosoma, 1 carabid, 1 Gryllus (♀), 2 acridians).

FAMILY STUDY 2—Verona, Wis.

Late Winter, 1930-31, through March.

Representations in 21 pellets from ADULT OWLS: cottontail, 16; Norway rat, 3; meadow mouse, 7; deer mouse, 11 (32 individuals); domestic pigeon, 1.

April 1 to 25, 1931.

Nonpellet food items: cottontail, parts of many carcasses; grackle, 1; pied-billed grebe, 1.

Representations in 8 pellets from ADULT OWLS: cottontail, 3; Norway rat, 1; meadow mouse, 1 (2 individuals); deer mouse, 6 (31 individuals).

April 26 to May 21, 1931.

Nonpellet food items: cottontail (including 2 young), 4; Norway rat, 2; rail, 1.

Representations in 27 pellets from ADULT OWLS: cottontail (including 10 pellets with remains of young), 21; Norway rat, 4; meadow mouse, 4; deer mouse, 14 (49 individuals); short-tailed shrew, 1; yellow rail (Colurnicops noveboracensis), 1; small bird, 1; insect, 4 (at least 4 individuals, including 2 Phyllophaga).

Representations in 2 pellets from YOUNG OWLS: cottontail, 1; Norway rat, 2.

May 22 to June 25, 1931.

Representations in 15 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 7; Norway rat, 4; house mouse, 1; meadow mouse, 1; deer mouse, 1; cricketine rodent, 2; domestic chicken (including 3 pellets with remains of young), 4; small snake, probably Natrix sipedon, 1; salamander, 1; insect, 6 (16 individuals: 1 Camponotus, 2 Phyllophaga, 3 Geotrupes, 2 Aphodius, 3 Necrophorus, 3 Calosoma, 2 Lepidoptera larvae).
June 26 to August 5, 1931.

Representations in 24 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 9; Norway rat, 2; meadow mouse, 2; deer mouse, 1; mouse, 1; weasel (*Mustela frenata noveboracensis* or *M. cinerea*), 1; domestic chicken (including 13 pellets with remains of 15 young individuals), 15; frog, 1; insect, 10 (19 individuals: 1 curculionid, 1 *Phyllophaga*, 1 *Geotrupes*, 5 scarabaeids, 2 *Pseudolucanus*, 1 lucanid, 3 *Necrophorus*, 2 *Carabus*, 3 carabids).

**FAMILY STUDY 3—N. E. Pine Bluff, Wis.**

Winter, 1930-31, through February.

Representations in 33 pellets from ADULT OWLS: cottontail, 26; meadow mouse, 12 (30 individuals); deer mouse, 15 (45 individuals); cricetine rodent, 1; flying squirrel, 1; snake, 2; insect, 1 (individual: *Geotrupes*).

**Early March to March 22, 1931.**

Representations in 9 pellets from ADULT OWLS: cottontail, 7; meadow mouse, 2 (3 individuals); deer mouse, 4 (9 individuals); cricetine rodent, 1.

March 23 to April 8, 1931.

Nonpellet food items: cottontail, 3; coot, 1.

Representations in 6 pellets from ADULT OWLS: cottontail, 6; meadow mouse, 2; deer mouse, 4 (6 individuals); small passerine bird, 1; garter snake (*Thamnophis sirtalis*), 2.

**FAMILY STUDY 4—W. Pine Bluff, Wis.**

Late winter, 1930-31, to March 22.

Nonpellet food items: cottontail, 1; long-eared owl, 2.

Representations in 28 pellets from ADULT OWLS: cottontail, 15; Norway rat, 1; meadow mouse, 5; deer mouse, 14 (51 individuals); chipmunk, 1; mourning dove, 1; domestic pigeon, 1; ruffed grouse, 1.

March 23 to April 25, 1931.

Nonpellet food items: cottontail (including 4 very young individuals), 5; bluejay, 1; flicker, 1.

Representations in 10 pellets from ADULT OWLS: cottontail, 5; Norway rat, 1 (2 individuals); meadow mouse, 3; deer mouse, 4 (37 individuals).

Representations in 2 pellets from YOUNG OWL: cottontail (including 1 pellet with remains of young), 2.

April 26 to May 30, 1931.

Nonpellet food items: cottontail and Norway rat, parts of many carcasses; flicker, 2.

Representations in 8 pellets from ADULT OWLS: cottontail, 5; Norway rat, 2; house mouse, 1 (2 individuals); deer mouse, 3 (4 individuals); cowbird (*Molothrus ater*), 1; crow, 1; flicker, 1; whip-poor-will, 1; domestic pigeon, 1; insect, 5 (22 individuals: 13 *Phyllophaga*, 4 *Geotrupes*, 1 scarabaeid, 1 *Necrophorus*, 1 carabid, 2 Lepidoptera larvae.)

Representations in 13 pellets from YOUNG OWL: cottontail (including 5 pellets with remains of young), 10; Norway rat, 3; meadow mouse, 1; deer mouse, 4 (6 individuals); cricetine rodent, 2; fringillid, 2 (3 individuals, of which 1 was probably *Zonotrichia*); catbird, 1; small passerine bird, 1; flicker, 2; screech owl, 1; insect, 1 (2 individuals: scarabaeids).

May 31 to June 25, 1931.

Representations in 19 pellets from YOUNG OWL: cottontail (including 2 pellets with remains of young), 13; Norway rat, 5; deer mouse, 6; fox squirrel, 1; striped skunk, 1; bird, 1; insect, 3 (4 individuals: 1 *Vespa*, 1 *Geotrupes*, 1 elaterid, 1 *Necrophorus*).

*This hornet, *V. maculifrons*, was associated in the pellet only with remains of young cottontail, so was probably taken as owl prey instead of as stomach contents of the skunk. The skunk remains were in a pellet deposited later.
June 26 to July 16, 1931.
Representations in 10 pellets from YOUNG OWL: cottontail, 5; Norway rat, 4; young striped skunk, 1; mourning dove (1), 1; young domestic chicken, 5; insect, 1 (2 individuals: carabids).

July 17 to Aug. 8, 1931.
Representations in 15 pellets from YOUNG OWL: cottontail (including 3 pellets with remains of young), 9; Norway rat, 6; meadow mouse, 2; deer mouse, 1; chipmunk, 1; insect, 10 (24 individuals: 1 curculionid, 2 Meracantha, 1 chrysomelid, 2 scarabaeids, 3 Necrophorus, 2 Carabus, 10 carabids, 1 pentatomid, 2 other insects).

FAMILY STUDY 5—W. Pine Bluff, Wis.
Fall, 1931, to Feb. 23, 1932.
Representations in 23 pellets from ADULT OWLS: cottontail (including 2 fall pellets with remains of young), 11; Norway rat, 1 (2 individuals); meadow mouse, 8 (9 individuals); deer mouse, 17 (80 individuals); fox squirrel, 1; short-tailed shrew, 1; bob-white, 1.

February 24 to April 1, 1932.
Representations in 39 pellets from ADULT OWLS: cottontail, 15; meadow mouse, 11 (12 individuals); deer mouse, 30 (135 individuals); fox squirrel, 1; small passerine bird, 1; domestic pigeon, 1; bob-white, 5.

FAMILY STUDY 6—N. E. Prairie du Sac, Wis.
Fall, 1930, through March, 1931.
Representations in 30 pellets from ADULT OWLS: cottontail, 21; Norway rat, 3; house mouse, 3 (6 individuals); meadow mouse, 3; deer mouse, 13 (51 individuals); fringillid, 2 (4 individuals, including 1 Melospiza); passerine bird, 1; domestic chicken, 1; bob-white, 1; salamander, 2 (3 individuals); insect, 2 (2 individuals: 1 Sitona and 1 acridian).

April, 1931.
Non-pellet food items; cottontail, fragments of many; crow, 1; flicker, 2; screech owl, 1; domestic chicken, 1; ruffed grouse, 2.

Representations in 15 pellets from ADULT OWLS: cottontail, 13; jumping mouse, 1; deer mouse, 10, (39 individuals); mouse, 1; salamander, 1; small bird, 1.

Representations in 10 pellets from YOUNG OWLS: cottontail (including 3 pellets with remains of young), 8; Norway rat, 1; deer mouse, 6 (7 individuals); short-tailed shrew, 1; meadowlark, 1; birds, mostly small, 4 (5 individuals): insect, 1 (2 individuals: 1 Formica and 1 Phyllophaga).

May 1 to 24, 1931.
Representations in 26 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 17; Norway rat, 3; meadow mouse, 3; deer mouse 13 (23 individuals); cricetine rodent, 2; fringillid, 2; meadowlark, 2; brown thrasher, 1; crow, 1; passerine bird, 6; possible red-headed woodpecker, 1; screech owl, 1; Virginia rail, 1; rail, 1; fish, 1; insect, 7 (14 individuals: 10 Phyllophaga, 1 elaterid, 3 Necrophorus).

May 25 to June 10, 1931.
Representations in 13 pellets from YOUNG OWLS: cottontail (including 8 pellets with remains of 11 young individuals), 11; deer mouse, 4 (9 individuals); hermit thrush, 3 (7 individuals); small bird, 1; insect, 11 (38 individuals: 2 curculionids, 1 cerambycid, 1 Anomala, 18 Phyllophaga, 4 Geotrupes, 2 Copris, 1 Canthon, 1 Stilpa, 5 Necrophorus, 1 Calliphora, 1 Lepidoptera larva, 1 other insect).

FAMILY STUDY 7—N. E. Prairie du Sac, Wis.
About February 1 to 21, 1932.
Representations in 9 pellets from ADULT OWLS: cottontail, 5; Norway rat, 1; deer mouse, 5 (25 individuals); mouse, 1; bob-white, 2 (3 individuals).
Feb. 22 through March, 1932.
Representations in 50 pellets from ADULT OWLS: cottontail, 33; meadow mouse, 2; deer mouse, 23 (91 individuals); meadowlark, 3; bob-white, 8; small birds, 3 (4 individuals); salamander, 1.

Early April to May 6, 1932.
Nonpellet food items: cottontail, fragments of many carcasses; fringillid, 1; meadowlark, 1; robin, 1.

Representations in 2 pellets from ADULT OWLS: cottontail, 2; deer mouse, 2 (11 individuals).

Representations in 40 pellets from YOUNG OWLS: cottontail, 32; house mouse, 1; deer mouse, 22 (33 individuals); fox squirrel, 1; fringillid, 6 (9 individuals); cowbird, 1; meadowlark, 3; hermit thrush, 1; robin, 1; crow, 4; bluejay, 4; horned lark, 1; flicker, 1; Florida gallinule, 1; domestic chicken (?), 1; bob-white, 5; bird, 6 (7 individuals); salamander, 2.

May 7 to 30, 1932.
Representations in 20 pellets from YOUNG OWLS: cottontail, 9; house mouse, 4; meadow mouse, 1; deer mouse, 9 (15 individuals); mouse, 2; mole, 1; mammal, 2; fringillid, 2; brown thrasher, 1; passerine bird, 3; night hawk, 1; killdeer (Oxyechus vociferus), 1; bird, 1; insect, 14 (103 individuals: 1 ant, 1 Ithycerus, 4 curculionids, 93 Phylophaga, 1 Serica, 1 Aphodius, 1 elaterid, 1 Necrophorus).

FAMILY STUDY 8—E. Prairie du Sac, Wis.
Winter, 1930-31, through March.
Nonpellet food items: cottontail, 1; crow, 1; bob-white, 3.

Representations in 33 pellets from ADULT OWLS: cottontail, 23; Norway rat, 4; meadow mouse, 6 (7 individuals); deer mouse, 11 (38 individuals); cricetine rodent, 1; mouse, 1; bluejay, 1; passerine bird, 1; bob-white, 2.

Representations in 2 pellets from YOUNG OWL: deer mouse, 1 (2 individuals); crow, 1; bob-white, 1.

About April 1 to 9, 1931.
Nonpellet food items: cottontail, 2.

Representations in 13 pellets from ADULT OWLS: cottontail, 11; deer mouse, 2 (4 individuals); cricetine rodent, 1; crow, 2; probable hairy woodpecker (Dryobates villosus), 1; bob-white, 2.

FAMILY STUDY 9—E. Prairie du Sac, Wis.
Fall to Dec. 21, 1931.
Representations in 5 pellets from ADULT OWLS: cottontail, 3; Norway rat, 1; deer mouse, 1; domestic pigeon, 1.

Representations in 30 pellets from ADULT OWLS: cottontail, 10; Norway rat, 4; meadow mouse, 3; deer mouse, 13 (24 individuals); little shrew (Cryptotis parva), 1; mole, 1; English sparrow, 1; domestic pigeon, 1; bob-white, 10; ruffed grouse, 1; small bird, 1.

FAMILY STUDY 10—E. Prairie du Sac, Wis.
Dec., 1932, to Jan. 9, 1933.
Representations in 11 pellets from ADULT OWLS: cottontail, 10; flying squirrel, 2; shrew (Sorex sp.), 1; insect, 1 (1 individual: acridian).

Jan. 10 to March 8, 1933.
Representations in 17 pellets from ADULT OWLS: cottontail, 9; meadow mouse, 3; deer mouse, 8 (14 individuals); mole, 1; fringillid, 1; bluejay, 1; bob-white, 3.

March 9 to April 27, 1933.
Representations in 8 pellets from ADULT OWLS: cottontail, 4; deer mouse, 4 (6 individuals); bluebird, 1; ruffed grouse, 1; insect, 1 (individual: Geopinus).
FAMILY STUDY 11—S. E. Prairie du Sac, Wis.
Winter, 1929-30, to about March 25.
Nonpellet food items: cottontail, 1; robin, 1; bob-white, 1.
Representations in 36 pellets from ADULT OWLS: cottontail, 17; Norway rat, 2; meadow mouse, 8 (17 individuals); deer mouse, 24 (87 individuals); mouse, 1; fringillid, 1; passerine bird, 1; bluejay, 1; bob-white, 2; ruffed grouse, 1.

About March 26 to April 13, 1930.
Nonpellet food items: cottontail, 5; Norway rat, 1; longspur, 1; domestic pigeon, 1; bob-white, 1; ruffed grouse, 1.
Representations in 16 pellets from ADULT OWLS: cottontail, 14; Norway rat, 1; meadow mouse, 2; deer mouse, 1; short-tailed shrew, 1; bob-white, 2; ruffed grouse, 1.
Representations in 20 pellets from YOUNG OWLS: cottontail, 20; meadow mouse, 1.

FAMILY STUDY 12—S. E. Prairie du Sac, Wis.
Fall, 1931, through March, 1932.
Representations in 32 pellets from ADULT OWLS: cottontail, 18; house mouse, 1; meadow mouse, 2; deer mouse, 15 (68 individuals); flying squirrel, 2; short-tailed shrew, 1; small bird, 1 (3 individuals).

About April 1 to 20, 1932.
Nonpellet food item: robin, 1.
Representations in 5 pellets from ADULT OWLS: cottontail, 4; deer mouse, 1 (11 individuals); small bird, 1.
Representations in 15 pellets from YOUNG OWLS: cottontail, 15; deer mouse, 4 (5 individuals); fringillid, 1 (2 individuals); bluebird, 1; passerine bird, 2.

April 21 to May 16, 1932.
Representations in 14 pellets from YOUNG OWL: cottontail (including 2 pellets with remains of young), 10; meadow mouse, 1; deer mouse, 2; fringillid, 4 (7 individuals, including 4 white-throated sparrows); meadowlark, 1; horned lark, 1; small passerine bird, 1 (2 individuals); flicker, 1; woodpecker, 1; gallinule, 1; ruffed grouse, 1; small birds, 2 (3 individuals).

FAMILY STUDY 13—Roxbury, Wis.
Winter, 1929-30, to about April 7.
Representations in 10 pellets from ADULT OWLS: cottontail, 6; meadow mouse, 5 (9 individuals); deer mouse, 5 (10 individuals); ericetine rodent, 2; salamander, 3 (4 individuals).

April 8 to May 7, 1930.
Nonpellet food items: cottontail, 6; Norway rat, 1; flicker, 1; young great horned owla, 1; domestic chicken, 3; bob-white, 1; diving duck (Nyroca, probably affinis), 2; garter snake, 1.
Representations in 6 pellets from ADULT OWLS: cottontail, 5; fox squirrel, 1; robin, 1.

FAMILY STUDY 14—Denzer, Wis.
Winter, 1931-32, through March.
Representations in 39 pellets from ADULT OWLS: cottontail, 24; meadow mouse, 3; deer mouse, 28 (133 individuals); short-tailed shrew, 3; fringillid, 1; English sparrow, 2; ruffed grouse, 1; bird, 2.

* Of the two young owls in the small tree cavity in which the nest was situated, one was conspicuously smaller and weaker than the other. It evidently died from trampling and starvation, to be eaten by its thriving nest mate. Note also a similar occurrence recorded in family study 37.
About April 1 to May 3, 1932.
Nonpellet food items: cottontail, 8; mole, 1; domestic pigeon, 1; ruffed grouse, 1.
Representations in 5 pellets from ADULT OWLS: cottontail (including 1 pellet with remains of young, 5; deer mouse, 3 (6 individuals); fringillid, 1; domestic pigeon, 1.
Representations in 29 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 29; Norway rat, 1; deer mouse, 7; passerine bird, 1; ruffed grouse, 1; small bird, 1.

May 4 to 30, 1932.
Representations in 20 pellets from YOUNG OWLS: cottontail (including 6 pellets with remains of young), 18; deer mouse, 3 (4 individuals); bluejay, 1; passerine bird, 1; shorebird, 1; bob-white, 1; ruffed grouse, 1; garter snake, 1; insect, 6 (13 individuals: 1 ant, 7 Phyllophaga, 2 Aphodius, 1 scarabaeid, 2 Silpha).

FAMILY STUDY 15—S. W. Madison, Wis.

Fall to midwinter, 1930-31.
Representations in 48 pellets from ADULT OWLS: cottontail, 31; jumping mouse, 1; Norway rat, 17; meadow mouse, 12 (19 individuals); deer mouse, 24 (46 individuals); flying squirrel, 1; short-tailed shrew, 1; meadowlark, 1 (2 individuals); coot, 1; bob-white, 5; reptile, possibly garter snake, 1.

Late winter to early April, 1931.
Representations in 11 pellets from ADULT OWLS: cottontail, 11; deer mouse, 5 (7 individuals); bob-white, 1; mallard, 2.

Early April to April 24, 1931.
Nonpellet food items: cottontail, 1; deer mouse, 1; robin, 1; domestic chicken, 1; bob-white, 2; mallard, 3.
Representations in 21 pellets from ADULT OWLS: cottontail, 16; Norway rat, 3; meadow mouse, 2 (4 individuals); deer mouse, 5 (7 individuals); robin, 1; coot, 3; mallard, 4; snake, 1.

April 25 to May 21, 1931.
Nonpellet food items: sora, 1; mallard, 1.
Representations in 10 pellets from ADULT OWLS: cottontail, 7; Norway rat, 2; meadow mouse, 2; deer mouse, 2; lesser yellow-legs (Totanus flavipes), 1; coot, 1; sora, 1; bob-white, 1; mallard, 1; pied-billed grebe, 1; small bird, 2; snake, 1; insect, 1 (9 individuals: Phyllophaga).
Representations in 24 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 11; Norway rat, 3; meadow mouse, 5 (6 individuals); deer mouse, 4; cisticine rodent, 1; robin, 1; bluejay, 1; passerine bird, 1; shorebird, 1; coot, 1; sora, 3; Virginia rail, 3; mallard, 3; duck, 1; pied-billed grebe, 1; small bird, 1; garter snake, 2; vertebrate, 2; insect, 5 (7 individuals: 3 Phyllophaga, 4 Geotrupes).

May 22 to July 10, 1931.
Nonpellet food item: Norway rat, 1.
Representations in 3 pellets from ADULT OWLS: cottontail (including 2 pellets with remains of young), 3; meadow mouse, 1; rodent, 1; insect, 2 (unknown number of individuals: 1 curculionid, several Phyllophaga, 1 Geotrupes, 1 Canthon).
Representations in 17 pellets from YOUNG OWL: cottontail (including 3 pellets with remains of young), 5; Norway rat, 3; young muskrat, 2; deer mouse, 4; fox squirrel, 1; chipmunk, 5; passerine bird, 1; coot, 2; bob-white, 2; least bittern, 1; small snake, probably Natrica sipeodon, 1; insect, 17 (48 individuals: 1 curculionid, 16 Phyllophaga, 1 Trox, 12 Geotrupes, 1 Onthophagus, 1 scarabaeid, 8 Necrophorus, 3 Harpalus, 3 carabids, 1 beetle, 1 Lepidoptera); spider, 1.
FAMILY STUDY 16—S. Madison, Wis.

Winter, 1930-31, through February.
Nonpellet food items: cottontail, 1; crow, 1.
Representations in 22 pellets from ADULT OWLS: cottontail, 18; Norway rat, 1; meadow mouse, 1; deer mouse, 8 (12 individuals); flying squirrel, 2; weasel (Mustela frenata noveboracensis), 1; short-tailed shrew, 1; rusty blackbird (Euphagus carolinus), 1.

March 5 to April 10, 1931.
Representations in 14 pellets from ADULT OWLS: cottontail, 12; deer mouse, 2 (3 individuals); short-tailed shrew, 1 (3 individuals); bluejay, 1.

FAMILY STUDY 17—S. Madison, Wis.

Winter, 1932-33, to March 5.
Representations in 33 pellets from ADULT OWLS: cottontail, 26; meadow mouse, 10 (18 individuals); deer mouse, 2 (5 individuals); bobwhite, 3.

March 6 to April 29, 1933.
Representations in 24 pellets from ADULT OWLS: cottontail, 17; meadow mouse, 8 (15 individuals); deer mouse, 6 (8 individuals); short-tailed shrew, 2; grackle, 4; meadowlark, 1; robin, 6; passerine bird, 1; woodcock (Philohela minor), 1; pheasant, 4; bob-white, 3; small bird, 1.

FAMILY STUDY 18—Middleton, Wis.

Late winter, 1930-31, to March 10.
Nonpellet food items: lean meat from a skinned cow carcass; cottontail, 1; fox squirrel, 1; domestic pigeon, 1.
Representations in 28 pellets from ADULT OWLS: cottontail, 21; meadow mouse, 2; deer mouse, 16 (66 individuals); domestic chicken, 2.

March 11 to April 6, 1931.
Representations in 15 pellets from ADULT OWLS: cottontail, 15; Norway rat, 1; deer mouse, 4 (5 individuals).

FAMILY STUDY 19—Middleton, Wis.

Middle of March to April 1, 1932.
Representations in 18 pellets from YOUNG OWLS: cottontail, 17; house mouse, 1; deer mouse, 6 (9 individuals); coot or gallinule, 3; domestic chicken, 1; salamander, 1.

April 2 to 14, 1932.
Nonpellet food item: sparrow hawk, 1.
Representations in 6 pellets from ADULT OWLS: cottontail, 6; deer mouse, 2 (3 individuals); salamander, 1 (4 individuals).

April 15 to June 3, 1932.
Representations in 35 pellets from YOUNG OWLS: cottontail (including 8 pellets with remains of young), 27; Norway rat, 3; deer mouse, 9; young fox, probably gray, 1; short-tailed shrew, 2; fringillid, 1; red-winged blackbird, 1; robin, 1; catbird, 1 (3 individuals); crow, 1; flicker, 1; sora, 3 (4 individuals); rail, 1; domestic chicken, 1; blue-winged teal, 1; bird, 4; snake, 3; insect, 12 (40 individuals: 38 Phyllophaga, 1 Trox, 1 Necrophorus).
FAMILY STUDY 20—Stoughton, Wis.
Fall, 1930, through March, 1931.

Representations in 17 pellets from ADULT OWLS: cottontail, 13; Norway rat, 1; meadow mouse, 3 (8 individuals); deer mouse, 4 (12 individuals); short-tailed shrew, 2; probable short-eared owl, 1; screech owl, 1; bird, 1.

About April 1 to 11, 1931.

Nonpellet food items: cottontail, Norway rat, meadow mouse and deer mouse, remains of many carcasses; meadowlark, 1; crow, fragments of several carcasses; short-eared owl, 1; screech owl, 1; ruddy duck (Eriscula jamaicensis rubida), 1; pied-billed grebe, 1; exoskeleton fragments of many crayfish.

Representations in 8 pellets from ADULT OWLS: cottontail, 5; meadow mouse, 3 (7 individuals); deer mouse, 1; weasel (Mustela frenata nubeoracensis or M. cincognanti), 1; shrew (Sorex sp.), 1 (2 individuals); fringillid, 1; robin, 1; gallinule, 1; duck, 1; snake, 1; crayfish, 1.

FAMILY STUDY 21—Stoughton, Wis.
Winter, 1931-32, to April 26.

Representations in 66 pellets from ADULT OWLS: cottontail, 54; Norway rat, 2; meadow mouse, 5 (6 individuals); deer mouse, 18 (51 individuals); weasel (Mustela rixosa), 1; short-tailed shrew, 4; red-winged blackbird, 2 (3 individuals); starling, 2; owl (Asio, probably wilsonianus), 2; bird, 2; snake, 2.

April 27 to May 24, 1932.

Representations in 8 pellets from YOUNG OWL: cottontail (including 3 pellets with remains of young), 6; Norway rat, 1; house mouse, 1; meadow mouse, 1; deer mouse, 1; short-tailed shrew, 2; red-winged blackbird, 1; swallow, 1; bird, 1; snake, 3; insect, 4 (4 individuals: Phyllophaga).

May 25 to June 25, 1932.

Representations in 22 pellets from YOUNG OWL: cottontail (including 8 pellets with remains of young), 22; Norway rat, 1; house mouse, 2; deer mouse, 3; mouse, 1; screech owl, 1; medium-sized bird, 1; snake, 4; insect, 21 (82 individuals: 1 Formica, 4 Ithycerus, 9 Phyllophaga, 2 Trox, 26 Geotrupes, 14 Onthophagus, 2 elaterids, 3 Tachinus, 20 Necrophorus, 1 Calosoma).

FAMILY STUDY 22—S. Des Moines, Iowa.
Winter, 1932-33, to March 11.

Representations in 25 pellets from ADULT OWLS: cottontail, 23; meadow mouse, 3 (4 individuals); deer mouse, 4 (10 individuals); shrew (Sorex sp.), 1 (2 individuals); long-eared owl, 1.

March 12 to April 28, 1933.

Nonpellet food items: cottontail, 1; grackle, 1; flicker, 1; short-eared owl, 1; bob-white, 1.

Representations in 59 pellets from ADULT OWLS: cottontail (including 4 pellets with remains of young), 48; Norway rat, 1; meadow mouse, 8 (11 individuals); deer mouse, 14 (46 individuals); mouse, 1; fox squirrel, 1; shrew (Sorex sp.) 1; opossum, 2; fringillid, 1; red-winged blackbird, 1; yellow-headed blackbird, 1; hairy woodpecker, 1; flicker, 3; long-eared owl, 1; screech owl, 1; bob-white, 3; bird, 1; snake, 1; frog, 3; insect, 1 (1 individual: beetle); crayfish, 5.

Representations in 9 pellets from YOUNG OWLS: cottontail, 3; meadow mouse, 5 (9 individuals); deer mouse, 3; short-tailed shrew, 1; thrush, 1; flicker, 2; short-eared owl, 1; insect, 1 (1 individual: beetle).
FAMILY STUDY 23—S. Des Moines, Iowa.

Fall and early winter, 1934-35.

Representations in 24 pellets from ADULT OWLS: cottontail, 18; jumping mouse, 1; Norway rat, 1; meadow mouse, 1; lemming mouse, 1 (2 individuals); deer mouse, 3 (7 individuals); mole, 1; domestic pigeon, 1; domestic chicken, 2; bob-white, 2; frog, 1.

Late winter to April 14, 1935.

Representations in 25 pellets from ADULT OWLS: cottontail, 23; deer mouse, 2; mole, 2; bob-white, 2; blue or snow goose (Chen sp.), 1.

FAMILY STUDY 24—N. W. Ames, Iowa.

Winter, 1932-33, through March.

Representations in 13 pellets from ADULT OWLS: cottontail, 9; Norway rat, 1; lemming mouse, 1; deer mouse, 2 (4 individuals); flicker, 1; short-eared owl, 1; pheasant, 1; bob-white, 1.

About April 1 to 30, 1933.

Representations in 24 pellets from ADULT OWLS: cottontail (including 2 pellets with remains of young), 19; house mouse, 1; meadow mouse, 7 (8 individuals); deer mouse, 3 (7 individuals); harvest mouse, 1; short-tailed shrew, 1; grackle, 2; vireo, 1; robin, 1; bluejay, 1; flicker, 1; killdeer, 1; bob-white, 2; blue-winged teal, 1; crayfish, 2.

Representations in 46 pellets from YOUNG OWLS: cottontail (including 4 pellets with remains of young), 34; Norway rat, 2; house mouse, 2; meadow mouse, 12 (15 individuals); deer mouse, 2; pocket gopher, 3; fox squirrel, 1; song sparrow, 1; fringillid, 1; meadowlark, 1; robin, 2; flicker, 1; mourning dove, 1; bob-white, 1; shoveller (Spatula clypeata), 1; pintail (Dafila acuta tsitsihoa), 1; bird, 1.

May 1 to 28, 1933.

Representations in 21 pellets from YOUNG OWLS: cottontail (including 5 pellets with remains of young), 10; young jack rabbit, 2; jumping mouse, 1; Norway rat, 1; meadow mouse, 3 (4 individuals); deer mouse, 8 (13 individuals); mole, 1; fringillid, 1; grackle, 3; robin, 1; red-headed woodpecker, 1; screech owl, 1; mourning dove, 3; sora, 1; Virginia rail, 1; pheasant, 1; bob-white, 1; pied-billed grebe, 1; insect, 12 (29 individuals: 1 Phyllophaga, 13 Geotrupes, 2 Copris, 1 Canthon, 1 Silpha, 1 Necrophorus, 3 Harpalus, 1 Pasimachus, 4 carabids, 2 beetles).

FAMILY STUDY 25—N. W. Ames, Iowa.

Fall, 1934, to March 22, 1935.

Representations in 28 pellets from ADULT OWLS: cottontail, 16; jumping mouse, 2 (4 individuals); Norway rat, 1; meadow mouse, 2; deer mouse, 5 (13 individuals); mole, 1; young opossum, 1; flicker, 1; screech owl, 4; domestic pigeon, 2; bob-white, 5; insect, 1 (1 individual: carabid).

March 23 to May 16, 1935.

Representations in 26 pellets from ADULT OWLS: cottontail (including 5 pellets with remains of young), 22; Norway rat, 5; deer mouse, 2; pocket gopher, 2; young rodent, 1; junco, 1; grackle, 1; icterid, 1; robin, 1; white-breasted nuthatch (Sitta carolinensis), 1; horned lark, 1; passerine bird, 1; screech owl, 1; coot, 1; pheasant, 4; bob-white, 1; bird, 1.

Representations in 7 pellets from YOUNG OWLS: cottontail, 1; Norway rat, 2; spotted skunk, 1; fringillid, 1; grackle, 1; young icterid, 1; English sparrow, 1; robin, 1; passerine bird, 3; young long-eared owl, 1; mourning dove, 2; insect, 1 (trace, probably from stomach of avian prey).
FAMILY STUDY 26—N. E. Ames, Iowa.

Late winter, 1932-33, to April 22.
Representations in 23 pellets from ADULT OWLS: cottontail (including 3 pellets with remains of young), 22; Norway rat, 3; meadow mouse, 4 (5 individuals); deer mouse, 5; short-tailed shrew, 1; domestic chicken, 1; pheasant, 1; bob-white, 1; small bird, 1.

April 23 to May 21, 1933.
Representations in 21 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 16; house mouse, 2; meadow mouse, 1; deer mouse, 8 (14 individuals); harvest mouse, 1; pocket gopher, 1; dickcissel (Spiza americana), 1; brown thrasher, 1; red-headed woodpecker, 1; mourning dove, 1; bob-white, 1.

May 22 to June 23, 1933.
Representations in 31 pellets from YOUNG OWLS: cottontail (including 4 pellets with remains of young), 18; Norway rat, 3; house mouse, 2; muskrat (all but one representation of young animals), 9; meadow mouse, 9; deer mouse, 7 (10 individuals); striped ground squirrel (Citellus tridecemlineatus), 1; fringillid, possibly clay-colored sparrow (Spizella palillida), 1; robin, 1; sapsucker (Sphyrapicus varius), 1; young screech owl, 1; pheasant, 1; bob-white, 1; insect, 3 (4 individuals: 1 Phyllophaga, 1 Dorcus, 2 Necrophorus).

FAMILY STUDY 27—N. E. Ames, Iowa.

Fall, 1933, to April 8, 1934.
Representations in 54 pellets from ADULT OWLS: cottontail (including 3 pellets with remains of young), 32; Norway rat, 4; house mouse, 1; meadow mouse, 9 (15 individuals); deer mouse, 14 (19 individuals); harvest mouse, 2 (4 individuals); mouse, 1; short-tailed shrew, 4 (5 individuals); opossum, 1; tree sparrow, 2; junco, 1; icerid, 1; bluebird, 1; downy woodpecker (Dryobates pubescens), 1; red bellied woodpecker (Centurus carolinus), 1; screech owl, 1; domestic chicken, 4; young bob-white, 2; frog, 2; pike (Esox sp.), 1; crayfish, 3.

April 9 to 28, 1934.
Representations in 15 pellets from YOUNG OWLS: cottontail (including 4 pellets with remains of young), 13; Norway rat, 8; meadow mouse, 1; deer mouse, 2; song sparrow, 1; fringillid, 1; meadowlark, 1; robin, 1; chickadee, 1; mourning dove, 2; coot, 1; insect, 1 (1 individual).

FAMILY STUDY 28—N. E. Ames, Iowa.

Winter, 1934-35, to March 15.
Representations in 20 pellets from ADULT OWLS: cottontail, 17; meadow mouse, 5; deer mouse, 4; mole, 1; screech owl, 1; domestic chicken, 1; bob-white, 1.

March 16 to April 26, 1935.
Representations in 7 pellets from YOUNG OWL: cottontail, 6; blue-jay, 1; coot, 2.

FAMILY STUDY 29—E. Ames, Iowa.

Late winter, 1932-33, to April 23.
Nonpellet food items: bluebird, 1; barred owl, 1.
Representations in 17 pellets from ADULT OWLS: cottontail (including 1 pellet with remains of young), 17; pheasant, 1; bob-white, 1; baldpate (Marcrea americana), 2; bird, 1.
April 24 to May 28, 1933.

Representations in 27 pellets from YOUNG OWLS: cottontail (including 4 pellets with remains of young), 18; Norway rat, 2; muskrat, 1; meadow mouse, 1; deer mouse, 4; red-winged blackbird, 1; bluebird, 1; brown thrasher, 1; bluejay, 3; red-headed woodpecker, 1; screech owl, 3; mourning dove, 1; coot, 1; sora, 1; pheasant, 4; blue-winged teal, 2; pied-billed grebe, 1; insect, 5 (9 individuals: 4 Phyllophaga, 1 Pseudolucanus, 2 Harpalus, 2 beetles).

May 29 to June 23, 1933.

Representations in 26 pellets from YOUNG OWLS: cottontail (including 7 pellets with remains of young), 20; Norway rat, 10; meadow mouse, 3; deer mouse, 1 (2 individuals); mole, 1; fringillid, 1; hairy woodpecker, 1; screech owl, 3; bob-white, 4; least bittern, 1; small bird, 1; insect, 11 (15 individuals: 6 Phyllophaga, 7 Pseudolucanus, 1 dytiscid, 1 beetle).

June 24 to July 21, 1933.

Representations in 13 pellets from YOUNG OWLS: cottontail, 6; Norway rat, 9; meadow mouse, 3; mole, 1; screech owl, 2; domestic chicken, 5 (including 1 pellet with remains of 2 young); bob-white, 1; insect, 2 (2 individuals: Pseudolucanus).

FAMILY STUDY 30—S. E. Ames, Iowa.

Late April to May 21, 1933.

Representations in 2 pellets from ADULT OWLS: cottontail, 2; pheasant, 1.

Representations in 21 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 10; house mouse, 1; meadow mouse, 4; deer mouse, 2; dickeissel, 1; cardinal, 1; grackle, 1; red-headed woodpecker, 1; domestic pigeon, 2; mourning dove, 1; lesser yellow-legs, 1; coot, 2; pheasant, 1; bob-white, 2; blue-winged teal, 1; small bird, 1.

May 22 to June 11, 1933.

Representations in 2 pellets from ADULT OWLS: young cottontail, 1; meadow mouse, 1; short-tailed shrew, 1; insect, 2 (3 individuals: 1 Phyllophaga, 1 Harpalus, 1 Pasimacius).

Representations in 9 pellets from YOUNG OWLS: cottontail, 4; Norway rat, 1; meadow mouse, 1; pocket gopher, 1; grackle, 1; young flicker (?), 1; screech owl, 1; domestic pigeon, 1; bob-white, 1; insect, 1 (5 individuals: 1 Dorcus, 4 earabids).

June 12 to July 6, 1933.

Representations in 20 undifferentiated pellets from both ADULT and YOUNG OWLS: cottontail (including 4 pellets with remains of young), 16; Norway rat, 1; meadow mouse, 1; deer mouse, 1 (2 individuals); young pocket gopher, 1; short-tailed shrew, 1; opossum, 2; grackle, 1; robin, 1; domestic pigeon, 1; very young domestic chicken, 2; insect, 9 (12 individuals: 3 Phyllophaga, 1 Geotrupes, 5 Pseudolucanus, 2 Calosoma, 1 beetle).

FAMILY STUDY 31—S. E. Ames, Iowa.

Winter, 1933-34, to April 8.

Representations in 37 pellets from ADULT OWLS: cottontail, 29; Norway rat, 3; house mouse, 1; meadow mouse, 7 (16 individuals); deer mouse, 8 (20 individuals); pocket gopher, 1; fox squirrel, 1; weasel (Mustela frenata spadix), 1; cardinal, 1; short-tailed owl, 1; screech owl, 3; small bird, 1.

Representations in 3 pellets from YOUNG OWLS: cottontail, 1; Norway rat, 2; meadow mouse, 1.
April 9 to 28, 1934.
Representations in 34 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 31; meadow mouse, 8 (9 individuals); deer mouse, 14 (33 individuals); fox squirrel, 1; short-tailed shrew, 1; Harris sparrow (Zonotrichia querula), 1; Baltimore oriole (Icterus galbula), 1; flicker, 2; screech owl, 3; dove, 1; bob-white, 2; gallinaceous bird, 1; green heron, 1; pied-billed grebe, 2; insect 1 (1 individual).

April 29 to May 13, 1934.
Representations in 16 pellets from YOUNG OWLS: cottontail, 8; house mouse, 3; meadow mouse, 4 (5 individuals); deer mouse, 11 (20 individuals); vesper sparrow, 1; fringillid, 1; robin, 1; flicker, 2; bob-white, 2; snake, 1; insect, 1 (1 individual: Necrophorus).

FAMILY STUDY 32—S. E. Ames, Iowa.
About April 20 to May 15, 1935.
Representations in 11 pellets from YOUNG OWLS: cottontail (including 7 pellets with remains of young), 11; deer mouse, 3 (7 individuals); fringillid, 2.

FAMILY STUDY 33—S. Ames, Iowa.
Winter, 1934-35, through March.
Representations in 20 pellets from ADULT OWLS: cottontail, 17; jumping mouse, 1; Norway rat, 1; house mouse, 1; meadow mouse, 2; deer mouse, 5 (9 individuals); mole, 1; tree sparrow, 1.
About April 1 to 29, 1935.
Representations in 22 pellets from ADULT OWLS: cottontail (including 5 pellets with remains of young), 18; jumping mouse, 1; deer mouse, 1; pocket gopher, 2; grackle, 1; pheasant, 5.

FAMILY STUDY 34—N. Ames, Iowa.
Fall, 1934, to late March, 1935.
Representations in 44 pellets from ADULT OWLS: cottontail, 37; Norway rat, 2; meadow mouse, 3; deer mouse, 6 (12 individuals); harvest mouse, 1; fringillid, 2; grackle, 1; meadowlark, 4; icterid, 1; English sparrow, 1; robin, 3; crow, 2; bob-white, 3.

About March 28 to April 25, 1935.
Representations in 26 pellets from ADULT OWLS: cottontail, 26; meadow mouse, 1; deer mouse, 2; mouse, 1; bluebird, 1; crow, 3; flicker, 1; domestic pigeon, 1; insect, 1 (1 individual: beetle).
Representations in 7 pellets from YOUNG OWLS: cottontail (including 1 pellet with remains of young), 6; meadow mouse, 1; icterid, 1; robin, 1; crow, 1; woodpecker, 1; screech owl, 1; insect, 2 (2 individuals: Geotrupes).

April 26 to June 7, 1935.
Representations in 28 pellets from YOUNG OWLS: cottontail (including 8 pellets with remains of young), 25; Norway rat, 5; meadow mouse, 2; deer mouse, 6 (7 individuals); mouse, 1; Franklin’s ground squirrel (Citellus franklini), 1; fringillid, 2; grackle, 1; robin, 1; red-bellied woodpecker, 2; mourning dove, 2; pheasant, 1; small bird, 5 (7 individuals of which 3 were young); insect, 3 (unknown number of individuals, including 1 Phyllophaga and some debris probably from the stomachs of avian prey).

FAMILY STUDY 35—S. Wallingford, Iowa.
Fall, 1933, to April 29, 1934.
Representations in 91 pellets from ADULT OWLS: cottontail (including 3 pellets with remains of young), 47; young jack rabbit, 1; Norway rat, 3; young muskrat, 1; meadow mouse, 29 (64 individuals); deer mouse, 25 (37 individuals); mouse, 2; short-tailed shrew, 1; fringillid, 1; flicker, 1;
short-eared owl, 2; screech owl, 5; pheasant, 23; Hungarian partridge, 5; small bird, 2; fish, 1.

April 30 to May 28, 1934.
Representations in 5 pellets from ADULT OWLS: house mouse, 1; deer mouse, 4 (7 individuals); harvest mouse, 1; warbler, 1; red-headed woodpecker, 1; pheasant, 2; snake, 1.
Representations in 5 pellets from YOUNG OWLS: cottontail (including 2 pellets with remains of young), 3; young jack rabbit, 1; deer mouse, 1; mouse, 1; king rail, 1; pheasant, 1.

May 29 to July 12, 1934.
Representations in 10 pellets from ADULT OWLS: cottontail (including 2 pellets with remains of young), 3; meadow mouse, 1 (3 individuals); deer mouse, 3 (5 individuals); domestic pigeon, 1; pheasant, 4; Hungarian partridge, 3; snake, 2; frog, 1; insect, 3 (at least 4 individuals: 1 Chrysocinus, 1 Necrophorus, 1 Harpalus, and other beetles).
Representations in 32 pellets from YOUNG OWLS: cottontail (including 13 pellets with remains of young), 17; Norway rat, 5; young muskrat, 1; meadow mouse, 2; deer mouse, 3 (6 individuals); harvest mouse, 4 (7 individuals); mouse, 2; pocket gopher, 2; short-tailed shrew, 1; screech owl, 5; sora, 1; pheasant, 12; Hungarian partridge, 8; sparrow hawk, 1; snake, 6; frog, 3; fish, 1; insect, 15 (at least 26 individuals, including 6 Phyllophaga, 3 scarabaeids, 2 Necrophorus, 6 Harpalus, 9 beetles); crayfish, 1.

FAMILY STUDY 36—S. Wallingford, Iowa.
Early spring to April 29, 1935.
Representations in 9 pellets from ADULT OWLS: cottontail (including 4 pellets with remains of young), 6; meadow mouse, 1 (3 individuals); deer mouse, 3; coot, 1; sora, 1; pheasant, 3; frog, 1.

April 30 to May 21, 1935.
Representations in 10 pellets from ADULT OWLS: cottontail (including 1 pellet with remains of young), 3; young rabbit or hare, 2; jumping mouse, 4 (5 individuals); deer mouse, 7 (11 individuals); harvest mouse, 3; fringillid, 1; sora, 1; pheasant, 4; insect, 1 (1 individual).
Representations in 6 pellets from YOUNG OWL: cottontail (both pellets with remains of young), 2; deer mouse, 1; mouse, 1; meadowlark, 1; pheasant, 4.

FAMILY STUDY 37—S. W. Wallingford, Iowa.
Fall, 1934, through March, 1935.
Representations in 55 pellets from ADULT OWLS: cottontail (including 2 pellets with remains of young), 25; jack rabbit, 1; meadow mouse, 8; deer mouse, 9 (19 individuals); harvest mouse, 1; short-tailed shrew, 1; short-eared owl, 1; screech owl, 1; pheasant, 3; Hungarian partridge, 2; small bird, 1.

About April 1 to 20, 1935.
Nonpellet food item: young great horned owl. *
Representation in 1 pellet from ADULT OWL: pheasant.
Representations in 17 pellets from YOUNG OWLS: cottontail (including 4 pellets with remains of young), 13; young jack rabbit, 1; young rabbit or hare, 1; jumping mouse, 1; Norway rat, 2; meadow mouse, 1; deer mouse, 4; mouse, 1; fox squirrel, 1; weasel, 3 (including 1 Mustela frenata spadix and 1 M. ciongnani); spotted sandpiper (Actitis macularia), 1; pheasant, 9; Hungarian partridge, 4.

* This instance differs from the cannibalism recorded under family study 13 in that the victim was the smallest and weakest of a brood of 4 young—the largest brood we have found. To appearances, it—doubtless the last to hatch—simply failed to get enough to eat after its nest mates grew strong and active and was finally utilized the same as any other food in the nest.
April 21 to May 21, 1935.
Representations in 26 pellets from YOUNG OWLS: cottontail (including 10 pellets with remains of young), 13; young jack rabbit, 1; Norway rat, 3; house mouse, 1; meadow mouse, 3 (4 individuals); deer mouse, 5 (9 individuals); fox squirrel, 1; grackle, 2; meadowlark, 2; pheasant, 12; Hungarian partridge, 5; insect, 4 (9 individuals: 5 Geotrupes, 1 Hydrophilus, 1 Pasimachus, 1 beetle, 1 other insect).

FAMILY STUDY 38—W. Emmetsburg, Iowa.
Winter, 1933-34, to April 24.
 Representations in 23 pellets from ADULT OWLS: cottontail, 19; Norway rat, 4; meadow mouse, 2 (6 individuals); deer mouse, 5 (9 individuals); pocket gopher, 1; Franklin's ground squirrel, 1; young mammal, 1; fringillid, 1; screech owl, 1; young domestic chicken, 1; pheasant, 2; Hungarian partridge, 1; insect, 1 (4 individuals: 3 Phyllophaga, 1 beetle); crayfish, 1.

April 25 to May 28, 1934.
Representations in 10 pellets from ADULT OWLS: cottontail, 6; young jack rabbit, 1; house mouse, 1; deer mouse, 4 (7 individuals); harvest mouse, 2; mouse, 1; weasel (Mustela rizosa), 1; pheasant, 3; Hungarian partridge, 1; frog, 1.
Representations in 37 pellets from YOUNG OWLS: cottontail (including 17 pellets with remains of young), 25; young rabbit or hare, 1; Norway rat, 1; house mouse, 1; meadow mouse, 1; deer mouse, 13 (14 individuals); harvest mouse, 2; mouse, 3; fringillid, 2; titmouse, 1; red-headed woodpecker, 1; pheasant, 18; Hungarian partridge, 2; least bittern, 2; snake, 1; fish, 1; insect, 3 (3 individuals: 1 Phyllophaga, 2 beetles).

May 29 to June 10, 1934.
Representations in 1 pellet from ADULT OWLS: young cottontail; pheasant.
Representations in 18 pellets from YOUNG OWLS: young cottontail (1 pellet also contained remains of adult), 6; young jack rabbit, 1; Norway rat, 1; meadow mouse, 1; deer mouse, 6 (7 individuals); harvest mouse, 2; young domestic chicken, 5; pheasant (including 2 pellets with remains of young), 9; snake, 1; insect, 7 (7 individuals: 1 scarabaeid, 4 beetles, 2 other insects).

FAMILY STUDY 39—Mud Lake, N. Ruthven, Iowa.
Late spring to June 18, 1933.
Representations in 27 undifferentiated pellets from both ADULT and YOUNG OWLS: cottontail (including 1 pellet with remains of young), 5; meadow mouse, 4 (8 individuals); deer mouse, 3; mole, 1; fringillid, 1; red-winged blackbird, 8 (11 individuals); yellow-headed blackbird (including 1 pellet with remains of young), 4; long-billed marsh wren (Telmatoctyes palustris), 1; flicker, 1; black tern, 1; semipalmented sandpiper (Ereuntes pusillus), 1; coot, 4; sora, 2; Virginia rail, 1; king rail, 1; pheasant, 1; Hungarian partridge, 1; pied-billed grebe, 2; snake, 1; salamander, 1; insect, 5 (18 individuals: 1 Pseudolucanus, 3 Hydrophilus, 10 Lepidoptera larvae close to Tropisternus, 4 Lethoceras (?)).

June 19 to July 24, 1933.
Representations in 18 undifferentiated pellets from both ADULT and YOUNG OWLS: cottontail (including 3 pellets with remains of young), 4; meadow mouse, 1; deer mouse, 1; red-winged blackbird, 2 (3 individuals); yellow-headed blackbird, 1; flicker, 1; short-eared owl, 1; Forster's tern, 1; coot (including 2 pellets with remains of young), 5; young domestic chicken, 1; blue-winged teal (including 1 pellet with remains both of adult and young), 3; mallard, 1; duck, 1; pied-billed grebe (including 1 pellet with remains of young), 2; garter snake, 4; salamander, 1; insect, 5 (8 individuals; 5 Hydrophilus, 3 Dytiscus).
FAMILY STUDY 40—Mud Lake, N. Ruthven, Iowa.
Fall, 1934, to March 30, 1935.

Representations in 105 pellets from ADULT OWLS: cottontail (including 2 pellets with remains of young), 85; jack rabbit (including 1 pellet with remains of young), 2; jumping mouse, 1; Norway rat, 6; meadow mouse, 17 (24 individuals); deer mouse, 21 (35 individuals); mouse, 1; shrew (Sorex sp.), 1; fringillid, 1; red-winged blackbird, 1 (2 individuals); yellow-headed blackbird, 1; swallow, 1 (6 individuals, of which 5 seemed to be barn swallow, Hirundo erythrogaster); Bonaparte's gull, 1; coot, 1; sora, 2; domestic chicken (f), 1; pheasant, 6; Hungarian partridge, 3; diving duck (Nyroca affinis or collaris), 1; green-winged teal (Nettion carolinensis), 3; pintail, 2; baldpate, 1; mallard, 3; pied-billed grebe, 3; large bird, 1; insect, 2 (2 individuals: 1 Phyllophaga, 1 beetle).

March 31 to May 16, 1935.

Representations in 43 undifferentiated pellets from both ADULT and YOUNG OWLS: cottontail (including 10 pellets with remains of young), 19; young jack rabbit, 4; young rabbit or hare, 2; jumping mouse, 3; young muskrat, 1; meadow mouse, 1; deer mouse, 8 (13 individuals); harvest mouse, 2; mouse, 1; striped ground squirrel (including 1 pellet with remains of young), 2; swamp sparrow (Melospiza georgiana), 1; fringillid, 1; grackle, 1; red-winged blackbird, 3; yellow-headed blackbird, 6; catbird, 1; blue jay, 1; barn swallow, 1; probable bank swallow, 2; passerine bird, 2; red-headed woodpecker, 1; screech owl, 1; least sandpiper (Pisobia minimilla), 1; shorebird, 1; coot, 9; sora, 6 (10 individuals); Virginia rail, 6; king rail, 1; domestic chicken, 1; pheasant, 1; Hungarian partridge, 2; diving duck (Nyroca affinis or collaris), 1; blue-winged teal, 1; mallard, 1; pied-billed grebe, 2; probable eared grebe, 1; insect, 3 (at least 6 individuals, including 1 Hydrophilus, 3 dytiscids and 1 beetle).

May 17 to June 1, 1935.

Representations in 7 pellets from ADULT OWLS: young muskrat, 3; meadow mouse, 1; deer mouse, 1; swamp sparrow, 1; red-winged blackbird, 5 (9 individuals); yellow-headed blackbird, 5 (6 individuals); long-billed marsh wren, 1; coot, 1; sora, 1; Virginia rail, 1.

Representations in 9 pellets from YOUNG OWLS: cottontail, 1; jumping mouse, 1; muskrat (including 1 pellet with remains of young), 2; deer mouse, 1; mouse, 1; cowbird, 1; red-winged blackbird, 2; yellow-headed blackbird, 6 (10 individuals); icterid, 1; coot, 2; sora, 4; pied-billed grebe, 2; insect, 2 (2 individuals: beetles).

June 2 to July 15, 1935.

Representations in 1 pellet from ADULT OWL: young muskrat (2 individuals); deer mouse (2 individuals); red-winged blackbird (2 individuals); young yellow-headed blackbird; coot.

Representations in 11 pellets from YOUNG OWL: cottontail (including 1 pellet with remains of young), 2; muskrat (including 6 pellets with remains of 9 young individuals), 7; young red-winged blackbird, 1; young yellow-headed blackbird, 2 (4 individuals); young coot, 1; pheasant, 1; bird, 1; snake, 1; insect, 8 (at least 11 individuals: 1 Chrysochus, 5 adult and 1 larval Phyllophaga, at least 4 other beetles and insects); crayfish, 1.

FAMILY STUDY 41—Anoka, Minn.
Early winter, 1932-33, to February 25.

Representations in 17 pellets from ADULT OWLS: cottontail, 15; meadow mouse, 4 (5 individuals); red-backed mouse, 2; deer mouse, 2; short-tailed shrew, 1; shrew (Sorex sp.), 1; screech owl, 1; pheasant, 1.

Late winter and spring, 1932-33, to about April 20.

Representations in 106 undifferentiated pellets from both ADULT and
YOUNG OWLS: cottontail (including 4 pellets with remains of young), 140; jack rabbit, 1; jumping mouse (Zapus or *Napocozus* sp.), 1; muskrat, 1; meadow mouse, 30 (43 individuals); red-backed mouse, 2; deer mouse, 43 (74 individuals); mouse, 3; pocket gopher, 11; flying squirrel, 1; weasel (*Mustela cicognanii*), 3; short-tailed shrew, 4; shrews, 6 (7 individuals, including 1 *Microsorex* sp. and 4 *Sorex* sp.); mole, 1; longspur, 1; vesper sparrow, 1; fringillid, 3; bluebird, 1; robin, 1; red-headed woodpecker, 1; flicker, 3 (5 individuals); mourning dove, 1; pheasant, 11; bob-white, 1; prairie chicken, 1; gallinaceous bird, 1; small bird, 1; insect, 2 (2 individuals: *Phyllophaga*, 1 beetle).

About April 21 to May 21, 1933.

Representations in 45 undifferentiated pellets from both ADULT and YOUNG OWLS: cottontail (including 13 pellets with remains of young), 31; jack rabbit, 1; rabbit or hare, 1; Norway rat, 1; meadow mouse, 5 (7 individuals); deer mouse, 7 (9 individuals); mouse, 1; pocket gopher, 5; striped ground squirrel, 1; short-tailed shrew, 3; mole, 1; junco, 1; fringillid, 1; warbler, 1; bluebird, 2; robin, 2; catbird, 1; flicker, 1; young great horned owl*, 2; probable pheasant, 1; ruffed grouse, 1; gallinaceous bird, probably domestic, 1; frog, 2; salamander, 1; insect, 2 (2 individuals: *Phyllophaga*).

Representations in 3 pellets from ADULT OWLS: cottontail, 2; meadow mouse, 1 (2 individuals); deer mouse, 1.

Representations in 6 pellets from YOUNG OWL: cottontail (including 1 pellet with remains of young), 5; meadow mouse, 2; deer mouse, 2; pocket gopher, 2; Franklin's ground squirrel, 1; weasel (*Mustela cicognanii*), 1; flicker, 2; pheasant, 1; sparrow hawk, 1.

May 22 to June 18, 1933.

Representations in 6 pellets from ADULT OWLS: cottontail, 2; deer mouse, 2 (9 individuals); pocket gopher, 1; short-tailed shrew, 1 (2 individuals); fringillid, 1; insect, 1 (3 individuals: *Cotaipa*).

Representations in 26 pellets from YOUNG OWL: cottontail (including 6 pellets with remains of young), 22; Norway rat, 3; meadow mouse, 4 (5 individuals); pocket gopher, 3; short-tailed shrew, 2; brown creeper, 1; flicker, 1; screech owl, 6; prairie chicken, 3; ruffed grouse, 1; sparrow hawk, 1; bird, 1; insect, 12 (18 individuals: 1 cermubied, 10 *Geotrupes*, 1 elaterid, 2 *Necrophorus*, 1 silphid, 2 *Calosoma*, 1 beetle).

(B) SPECIAL PHASE STUDIES

SPECIAL PHASE STUDY 1—Mud Lake, N. Ruthven, Iowa.

July 25 to early fall, 1933.

Representations in 20 pellets: cottontail (including 1 pellet with remains of young), 8; Norway rat, 1; deer mouse, 2 (3 individuals); mouse, 1; shrew (*Sorex* sp.), 1; red-winged blackbird, 1; yellow-headed blackbird, 1; flicker, 1; coot, 1; pheasant, 1; diving duck (*Nyroca affinis* or *collaris*), 1; baldpate, 1; mallard, 8; pied-billed grebe, 1; insect, 1 (1 individual: *Dytiscus*).

Late fall, 1933, to Feb. 10, 1934.

Representations in 24 pellets: cottontail, 15; meadow mouse, 1 (2 individuals); deer mouse, 1; red-winged blackbird, 3 (6 individuals); yellow-headed blackbird, 1; screech owl, 1; coot, 1; pheasant, 3; diving duck (*Nyroca affinis* or *collaris*), 1; gadwall (*Chapteleasmus streperus*), 1.

* A tethered young owl of this family group was killed by a brush fire in late April, and the carcasses were evidently fed upon by one of the adults.
SPECIAL PHASE STUDY 2—N. Philip, S. D.

Early August to Aug. 25, 1934.
Representations in 13 pellets: young rabbit or hare (mainly jack rabbit with some cottontail remains), 9; meadow mouse, 1; heteromyid rodent, 2; meadowlark, 2; young domestic turkey (*Meleagris gallopavo*), 1; domestic chicken, 1; hog-nosed snake (*Heterodon* sp.), 1; insect, 11 (31 in total; individuals: 2 *Pasinocclus*, 1 carabid, 1 tettigoniid, at least 27 *Melanoplus*); wolf spider, 8 (67 in total; individuals: *Lycosa*).

SPECIAL PHASE STUDY 3—Southern Wis.

Late summer through early fall, 1930.
Representations in 10 pellets: cottontail, 6; meadow mouse, 2 (8 individuals); deer mouse, 2 (3 individuals); flying squirrel, 1; short-tailed shrew, 3; insect, 3 (probably 20 or more individuals, including *Pseudolucanus* and *Carabus*).

Late fall through early winter, 1930-32.
Representations in 35 pellets: cottontail, 17; Norway rat, 2; house mouse, 1; meadow mouse, 4; deer mouse, 9 (35 individuals); flying squirrel, 2; weasel (*Mustela frenata spadix*), 1; short-tailed shrew, 1; meadowlark, 1; robin, 1; bluejay, 1; young domestic chicken, 1; bob-white, 1; ruffed grouse, 4; insect, 1 (11 individuals: 10 *Harpalus*, 1 acridian).

SPECIAL PHASE STUDY 4—Southern and Central Iowa.

Early fall through early winter, 1932-35.
Representations in 25 pellets: cottontail (including 4 pellets with remains of young), 18; Norway rat, 3; meadow mouse, 3; deer mouse, 6 (24 individuals); mink, 1; short-tailed shrew, 1; shrew (*Sorex* sp.), 1 (2 individuals); mole, 1; fringillid, 1 (3 individuals); domestic chicken, 3; bob-white, 1; very small bird, 1; insect, 2 (19 individuals: 18 *Harpalus*, 1 acridian).

SPECIAL PHASE STUDY 5—Cloquet, Minn.

Winter, 1932-33, to April 20.
Representations in 21 pellets: cottontail, 1; snowshoe hare, 19; rabbit or hare (including 1 pellet with remains of young), 2; meadow mouse, 1 (2 individuals); northern flying squirrel (*Glaucomys sabrinus*), 1; chipmunk, 1; white-throated sparrow, 1.

Winter, 1933-34, to May 9.
Representations in 60 pellets from adult and young owls of 4 nests: cottontail, 7; snowshoe hare (including 2 pellets with remains of young), 50; young rabbit or hare, 1; meadow mouse, 5 (7 individuals); mouse, 1; swamp sparrow, 1; fringillid, 7 (9 individuals); kinglet, 1; brown creeper, 1; hairy woodpecker, 1; flicker, 2; solitary sandpiper (*Tringa solitaria*), 1; sora, 2; domestic chicken, 1; ruffed grouse, 2; hawk, possibly goshawk, 1; wild duck, 1; small bird, 1 (2 individuals); frog, 1; insect, 3 (3 individuals, including 1 dytiscid).

SPECIAL PHASE STUDY 6—E. Prairie du Sac, Wis.

Winter, 1936-37.
Representations in 51 pellets: cottontail, 35; Norway rat, 2; meadow mouse, 18 (32 individuals); deer mouse, 42 (84 individuals); short-tailed shrew, 2; mole, 2; fringillid, 2; downy woodpecker, 1; screech owl, 2; salamander, 2 (3 individuals).

* Collected by R. T. King and students.
SPECIAL PHASE STUDY 7—E. Prairie du Sac, Wis.

Winter, 1937-38.

Representations in 78 pellets: cottontail, 59; meadow mouse, 12 (21 individuals); deer mouse, 36 (61 individuals); mouse, 4; flying squirrel, 1; small shrew, 1; mole, 8; junco, 1 (3 individuals); fringillid, 3 (4 individuals); bluejay, 1; bob-white, 3; ruffed grouse, 2; salamander, 5; amphibian 1; insect, 2 (2 individuals: Melanoplus).

SPECIAL PHASE STUDY 8—N. W. Madison, Wis.

Winter, 1929-30, to April 19.

Representations in 30 pellets: cottontail, 1; Norway rat, 4; house mouse, 2 (3 individuals); meadow mouse 20 (43 individuals); deer mouse, 15 (52 individuals); mouse, 1; cricetine rodent, 3 (5 individuals); flying squirrel, 3; short-tailed shrew, 12 (18 individuals); fringillid, 2 (4 individuals, including 1 probable indigo bunting, Passerina cyanea); English sparrow, 1; bluejay, 1; salamander, 1.

SPECIAL PHASE STUDY 9—N. W. Madison, Wis.

Winter, 1929-30, to April 19.

Representations in 33 pellets: cottontail, 9; Norway rat, 13; meadow mouse, 15 (26 individuals); deer mouse, 26 (87 individuals); mouse, 2; cricetine rodent, 1; short-tailed shrew, 6 (8 individuals).

SPECIAL PHASE STUDY 10—Stoughton, Wis.

Winter, 1929-30, to April 12.

Representations in 21 pellets: cottontail, 5; Norway rat, 7; meadow mouse, 13 (34 individuals); deer mouse, 9 (23 individuals); short-tailed shrew, 1; song sparrow, 1; red-winged blackbird, 1; starling, 1; bluejay, 1; insect, 3 (3 individuals: 1 Hypera, 2 giant water bugs, either Benacus or Lethocerus).

SPECIAL PHASE STUDY 11—N. W. Emmetsburg, Iowa.

Fall, 1933, to March 16, 1934.

Representations in 32 pellets: cottontail (including 4 pellets with remains of young), 19; Norway rat, 3; house mouse, 1; muskrat, 6; meadow mouse, 2 (4 individuals); deer mouse, 5 (9 individuals); harvest mouse, 1; mouse, 1; Harris sparrow, 1; fringillid, 1; red-winged blackbird, 1; chickadee, 1; sapsucker (♀), 1; red-headed woodpecker, 1; flicker, 1; short-eared owl, 1; screech owl, 1; pheasant, 3; Hungarian partridge, 1; snake, 1; insect, 7 (16 individuals: 1 Phyllophaga, 1 Dytiscus, 1 dytiscid, 1 Anisodactylus, 9 Harpalus, 2 Pasimachus, 1 beetle); crayfish, 1.

SPECIAL PHASE STUDY 12—N. N. E. Prairie du Sac, Wis.

Fall, 1932, to April 27, 1933.

Representations in 50 pellets: cottontail, 33; jumping mouse, 2; meadow mouse, 10 (12 individuals); deer mouse, 23 (67 individuals); mole, 1; fringillid, 4 (6 individuals, including 2 juncos); thrushes (including 1 probable robin and 1 probable Hylocichla sp.), 3; coot, 4; bob-white, 5; insect, 1 (1 individual: cucujid).

SPECIAL PHASE STUDY 13—E. Prairie du Sac, Wis.

Winter, 1934-35.

Representations in 42 pellets: cottontail, 9; Norway rat, 3; meadow mouse, 33 (61 individuals); deer mouse, 27 (85 individuals); flying squirrel, 2; bob-white, 8.
SPECIAL PHASE STUDY 14—Fairfield, Iowa.
Fall, 1934, to March 4, 1935.
Representations in 85 pellets: cottontail, 52; house mouse, 2; meadow mouse, 10; deer mouse, 45 (117 individuals); mouse, 1; shrew (Sorex sp.), 6; fringillid, 3; grackle, 1; English sparrow, 1; yellow warbler (Dendroica aestiva), 1; red-bellied woodpecker, 2; short-eared owl, 2; screech owl, 1; mourning dove, 1; bob-white, 19; insect, 1 (3 individuals: 1 Geotrupes, 2 Canthon); crayfish, 2.

SPECIAL PHASE STUDY 15—Fairfield, Iowa.
Fall, 1934, to April 6, 1935.
Representations in 65 pellets: cottontail (including 5 pellets with remains of young), 55; Norway rat, 1; meadow mouse, 7 (9 individuals); deer mouse, 21 (63 individuals); mouse, 1; weasel (1 each of Mustela frenata spadix and M. rixosa), 2; shrew (Sorex sp.), 1; fringillid, 1; English sparrow, 1; robin, 1; flicker, 3; domestic pigeon, 2; bob-white, 4; small bird, 2; insect, 1 (individual: Harpales).

SPECIAL PHASE STUDY 16—Mud Lake,* Emmet County, Iowa.
Spring to May 3, 1934.
Representations in 14 pellets: cottontail (including 6 pellets with remains of young), 7; Norway rat, 1; house mouse, 1; meadow mouse, 2; deer mouse, 8 (14 individuals); harvest mouse, 1; fox squirrel, 1; short-tailed shrew, 1; grackle, 4 (5 individuals); meadowlark, 1; passerine bird, 2; domestic chicken, 1 (remains of adult and of 3 young of about 10 days); pheasant, 1; scaup (probably Nyroca affinis), 4; baldpate, 4; duck, 1; insect, 2 (3 individuals: 2 Canthon, 1 beetle).

SPECIAL PHASE STUDY 17—S. Madison, Wis.
Winter, 1931-32, to April 3.
Representations in 53 pellets: cottontail, 22; Norway rat, 4; meadow mouse, 9 (10 individuals); deer mouse, 14 (63 individuals); small bat, 1; short-tailed shrew, 1; fringillid, 2 (6 individuals, including 2 possible tree sparrows); kinglet, 1; robin, 2; pheasant, 1; bob-white, 1; bird, 1; salamander, 1; fish (13 individuals: 4 Lepomis, 6 Micropterus, 1 centrarchid and 2 Cyprinus).

SPECIAL PHASE STUDY 18—N. E. Ogden, Iowa.
Winter, 1933-34, to April.
Representations in 21 pellets: cottontail, 10; meadow mouse, 1 (2 individuals); deer mouse, 4 (5 individuals); weasel (Mustela frenata spadix), 1; shrew, 1; mole, 4; junco, 1; bluejay, 1; bob-white, 3; fish, 6 (9 + individuals: 1 Lepomis, 1 Semotilus, 2 Catostomus, 1 Ictiobus and at least 4 other fishes); crayfish, 1.

SPECIAL PHASE STUDY 19—S. W. Roxbury, Wis.
Winter, 1929-30, to April 12.
Representations in 40 pellets: cottontail, 37; Norway rat, 1; meadow mouse, 4; deer mouse, 5 (7 individuals); mouse, 1; chipmunk, 1; domestic pigeon, 1.

SPECIAL PHASE STUDY 20—City Waterworks Supply Grounds, Des Moines, Iowa.
Fall, winter and early spring, 1932-35.
Representations in 29 pellets: cottontail, 20; jumping mouse, 2; Norway rat, 1 (2 individuals); meadow mouse, 6 (7 individuals); deer mouse, 5 (14 individuals); short-tailed shrew, 1; shrew (Sorex sp.), 1 (2 individuals); red-winged blackbird, 2; domestic pigeon, 2.

* This is a different Mud Lake from the one north of Ruthven to which usual reference is made in this bulletin.