The barn owl in Michigan; its distribution, natural history and food habits.

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THE BARN OWL IN MICHIGAN

ITS DISTRIBUTION, NATURAL HISTORY AND FOOD HABITS

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SUMMARY

1. This investigation, concerned mainly with the food habits of East Lansing barn owls over a 3-year period covering both the high and low phases of a *Microtus* cycle, involved the examination of about 2,200 pellets (calculated) and the identification of 6,815 prey animals.

2. The American race of *Tyto alba pratincola* (Bonaparte) occurs from northern Central America north to the northern tier of states, and, sparingly, into southern Canada. In Michigan it is largely limited to the southern four tiers of counties, and is an irregular, but essentially permanent, resident throughout this range.

3. A map of the known breeding stations and other locality records, supplemented by a detailed list and brief history of the records, presents the Michigan distributional picture as completely as seems practicable.

4. An examination of banding records reveals that barn owls, though often year-round residents (adults?), also disperse widely at times (young?), travelling even from the northernmost to the southernmost states.

5. Barn owls display great adaptability in the selection of nesting sites, usually, but not without exceptions, using cavities or structures affording shelter from the elements. No nest is constructed other than the broken-down pellets and prey, but such a structure may then be used repeatedly.

6. Barn owls, peculiarly, breed at all seasons, but perhaps nestings are divisible into a spring and a late summer or fall brood; or, according to another interpretation, the birds may nest more or less continuously during periods of abundant prey and then cease to breed when the food supply fails.

7. The three complete clutches of eggs observed were of 7 eggs, a common number (the literature reports 4 to 12 eggs per clutch); the eggs were laid on alternate days (not irregularly, as sometimes reported); incubation apparently began with the first egg; and the incubation period for each of three marked eggs was about 30 days (21 to 24, or sometimes longer, cited by Forbush).

8. In spite of relatively large broods, and repeated nestings, barn owls are uncommon in the northern states. Known decimating factors include observed winter die-offs, persecution by uninformed farmers and hunters, and perhaps periodic failures in cyclic prey which may interrupt breeding.

9. Barn owls commonly accumulate large supplies of prey at the nesting site, perhaps chiefly in times of easy prey availability. In the fall of 1945, 189 mice and 1 shrew were discarded on the floor opposite the nest box, and during the spring incubation period, excess mice, up to a maximum of 80 at one time, were stored in this nest.

10. Inherent weaknesses in food-habits studies by pellet examinations do not strictly apply to barn owls, which are particularly favorable for pellet studies. Lost items, if any, would be soft-bodied invertebrates, cartilaginous prey, and perhaps nestling birds.

11. Vertebrate prey (rats and mice) fed to two captive barn owls was nearly 100 percent recoverable in pellets.

12. Two captive barn owls, on a rat and mouse diet, produced one pellet per day fairly regularly; another ate smaller meals at more frequent intervals and often produced two or three pellets per day. The rhythm of pellet production, and thus the consumptive capacity of barn owls, was not definitely determined, but it is felt that the two-pellet average cited by Guérin for European barn owls does not strictly apply to Michigan birds, and that the number varies with individual owls, hunting conditions, length of night, and other factors.

13. Examination of many hundreds of whole pellets indicates that they are composed of an average of close to three prey items (mice) per pellet, and that since smaller pellets are often extras, the daily quota of prey is more than three items, but probably less than the six assumed by followers of Guérin.

14. The dimensions of 254 year-round pellets varied from 28 by 17 mm. to 109 by 35 mm., averaging 53 by 30 mm., and varied in dry weight from 1.0 gram to 17.2 grams, averaging 6.8 grams. They contained from one to eight prey animals per pellet, with an average of 2.7.

15. Examination of 310 pellets from a 1945 spring nesting site yielded 725 (81.0 percent) meadow mice *(Microtus),* 93 other mice (10.3 percent), 54 shrews (6.0 percent), and 20 birds (2.2 percent),

the latter mainly English sparrows and starlings (16 out of 20). The 81 percent *Microtus* proved to be a decidedly average figure when compared to subsequent findings, and to the findings of other workers in nearby states.

16. In mid-July the spring nesting site was reoccupied and six young were raised, the young remaining in the barn till early December; then a 1946 spring brood was also raised, these leaving the barn in early June. This permitted an accurately dated month-by-month collection and analysis of pellets for an 11-month period. Monthly *Microtus* percentages rose to as high as 96.9 and averaged 92.5 percent for the year, reducing other items (shrews, other mice, and birds) to decidedly minor roles.

17. Study at this station was unfortunately terminated by the shooting of the female during the laying of a fourth consecutive clutch of eggs, so pellet collecting was shifted to the less satisfactory and much molested campus roost for completion of the 3-year study.

18. A 1945 spring-fall campus collection of 3,655 skulls yielded another decidedly average *Microtus* figure of 81.3 percent, but during the fall and winter months, the *Microtus* yield rose to 95.1 percent (for February 1946) corresponding to the winter peak cited for the other station. Thereafter *Microtus* percentages dropped gradually to a low of 57.6 percent for the 1946-47 winter period. Known trends in local populations seem to follow these trends revealed by the barn-owl diet.

19. Barn-owl populations may adjust themselves to prey levels, suffering a decline (by dying off or dispersing) when the food supply fails, and increasing (by rapid breeding) when prey availability is high.

20. Of the total of 6,815 prey animals identified at both stations, 5,791 or 85.0 percent were meadow mice, but this percentage may be a little high because more pellets were available during the peak of the *Microtus* cycle.

21. Deer mice of the genus *Peromyscus*, practically all *bairdii*, amounted to 4.5 percent of the diet (308 individuals) but rose to 21.4 percent during the spring of 1947, when *Microtus* was less abundant. The only other mice represented were *Zapus* (80 individuals, 1.2 percent), *Mus* (37, or 0.5 percent), *Synaptomys* (23, or 0.3 percent).

22. Three species of shrews were taken: 445 *Blarina* (6.5 percent), 28 *Sorex* (0.4 percent), and 4 *Cryptotis* (0.06 percent). *Blarina*, like *Peromyscus*, invariably rose when *Microtus* declined, and reached 20.2 percent when meadow mice were at their lowest point. In Ohio, Texas, and Europe, Insectivores apparently play a greater role than in Michigan.

23. Only 15 rats (0.2 percent), these mainly young, were taken, revealing, as do other Michigan, Ohio, and Wisconsin studies, that rats probably play an unimportant role in the barn-owl diet in these states.

24. Miscellaneous items included four star-nosed moles *(Condylura)* two prairie moles *(Scalopus)*, two juvenile cottontails *(Silvilagus)*, and a least weasel *(Mustela rixosa allegheniensis)*, the latter apparently the first record for this species in Ingham County.

25. Seventy-three birds (1.07 percent) were recovered, but 50 of these were English sparrows, 15 were starlings, and 2 were pigeon squabs, all introduced (nuisance) birds. The 6 native songbirds included 2 savannah sparrows, 1 song sparrow, and 3 unidentified passerines.

26. No trace of poultry or game birds was found among the 6,815 vertebrates identified, but there is the acknowledged possibility that downy nestlings might be completely digested and thus not be discovered in pellet examinations.

27. Clearly, the relatively small catch of insectivorous shrews (7.0 percent) is the only item on the negative side of the barn owls' economic ledger. It is hoped that the detailed and probably irrefutable data presented in this paper will provide a sound basis for the protective measures that Michigan barn owls seem to merit.

The Barn Owl in Michigan

Its Distribution, Natural History, and Food Habits

By GEORGE J. WALLACE

INTRODUCTION

At intervals during the past 3 years, particularly during the fall of 1946 and of 1947, the writer has been studying barn owls. The principal purpose of the investigation has been a study of the food habits of these birds at East Lansing, but this has been supplemented by assembling the available records of their distribution in Michigan, by some incidental observations on nesting habits, and, for comparative purposes, by an examination of the somewhat voluminous American literature on the food and feeding habits of barn owls and related predatory birds. It is hoped that these data will provide a sound basis for a critical evaluation of the economic status of the barn owl in Michigan.

For the local studies, two stations at East Lansing have been available: a small colony that in recent years has occupied various buildings and a conifer roost on the College campus, and another group that has repeatedly nested in a largely unused barn on Hagadorn Road, about 2 miles from the campus. From the campus roosts, occupied by a varying number of owls over a 3-year period, some 1,200 pellets containing 3,655 prey animals were collected, and from the Hagadorn Road barn, occupied by a pair of owls known to have raised three broods totaling 17 young in 1945 and 1946, about a thousand more pellets containing 3,160 prey animals were available, or a total from the two stations of a calculated 2,200 pellets, and 6,815 prey animals. The farm station on Hagadorn Road was followed closely during two of the three nesting periods, and is the basis for the detailed studies of pellets and prey, but the campus collections covered a longer period, and provided the necessary material during the low phase of the meadow-mouse cycle after the disappearance of the owls at the farm station.

ACKNOWLEDGMENTS

To several departmental staff members in Zoology I wish to express my appreciation for their interest, encouragement, and help in promoting this research: namely to H. R. Hunt, Head of the Department, who originally pointed out the opportunity for study afforded by the owls inhabiting the barn near his residence; to J. W. Stack, Director of the College Museum, for tracing some early museum records; to Don W. Hayne, whose concurrent interest in *Microtus* populations has provided useful comparative data; to B. T. Ostenson for help with some questionable mammalian skulls; to Robert C. Ball for assistance with the tables and graph; and to M. D. Pirnie and D. W. Hayne for a critical reading of the manuscript.

In the Bird Division of the Museum of Zoology at Ann Arbor, J. Van Tyne has kindly made their excellent skeleton collection, library facilities, and distributional files completely available, and G. M. Sutton has helped with some troublesome skulls. In the Mammals Division, L. R. Dice has offered helpful suggestions for separating the closely related species of *Peromyscus* by mandibular measurements, and Emmett Hooper has verified the identification of a series of small shrews.

PART I. DISTRIBUTION AND NATURAL HISTORY

SUMMARY OF DISTRIBUTIONAL STATUS

The American barn owl, *Tyto alba pratincola* (Bonaparte), one of the 34 known geographic races of *Tyto alba* (Peters, 1940) is widespread over southern portions of North America, from Central America north to the northern tier of states, and, sparingly, into southern Canada. Though the latitude of 41° (southern New England, north-central Ohio, northern California) was originally designated as the northern limit of its breeding range, there are now so many authentic outposts located farther north,[1] that the original designation has lost much of its validity. Well established in the central and southern states, particularly in parts of the southwest, the species fluctuates markedly in the north, probably in response both to climatic severity and to the cyclic nature of its prey, but it is generally conceded to be a permanent resident as far north as it breeds.

[1]Cayouette (1947) reports a barn owl nesting near Quebec (at 46°); in Michigan, the bird is considered a permanent resident up to 43°; and Cowan (1942) reports nesting in British Columbia at about 49°.

In Michigan, the barn owl is largely limited to the southern four tiers of counties, with a possibly semi-permanent northern extension in the Saginaw valley. Even in the inhabited counties, known stations of resident birds are few, in part no doubt because their secretive habits cause them to be overlooked, and in part because of the instability of a species near the northern limits of its range. Though the barn owl has definitely passed from the status of "rare curiosity" accorded it several decades ago, it nevertheless has not multiplied to the extent that its large broods of young and repeated nestings augur. A station or roost may be inhabited for several successive years, then abandoned for a similar period, perhaps because of the death of the adult occupants.

MICHIGAN LOCALITY RECORDS

The accompanying map (Fig. 1) illustrates, and the appended list gives detailed data for, known occurrences of the barn owl in Michigan. These are based on published records (many of which were obtained from the files of the University of Michigan Museum of Zoology, which were generously made available by Dr. Van Tyne), specimens in museums, and additional records that have come to my attention through correspondence or direct inquiry (as editor of "Seasonal Records" for the Michigan Audubon Society, I have been in contact with nearly all active ornithological observers in Michigan).

Unfortunately several factors prevent this distributional account from being a full picture of the bird in Michigan: a) the prevalent practice of uninformed hunters and farmers in ridding their premises of "vermin" interferes with the natural pattern of its distribution, b) collected specimens often become mantle pieces without reliable data as to their time and place of capture, and c) the secretive nocturnal habits of the birds, perhaps fortunately, permit them to go largely undetected in many communities. There obviously are, and have been, more barn owls in Michigan than the known records imply. Perhaps needless to say, I have made no concerted attempt to locate and verify old specimens, many of which are no longer available; other possible records have been rejected for lack of inclusive data. Barrows (1912) lists seven locality records (probably based largely on specimens reported to him in letters) for which I could find no supporting evidence. The accompanying map and list

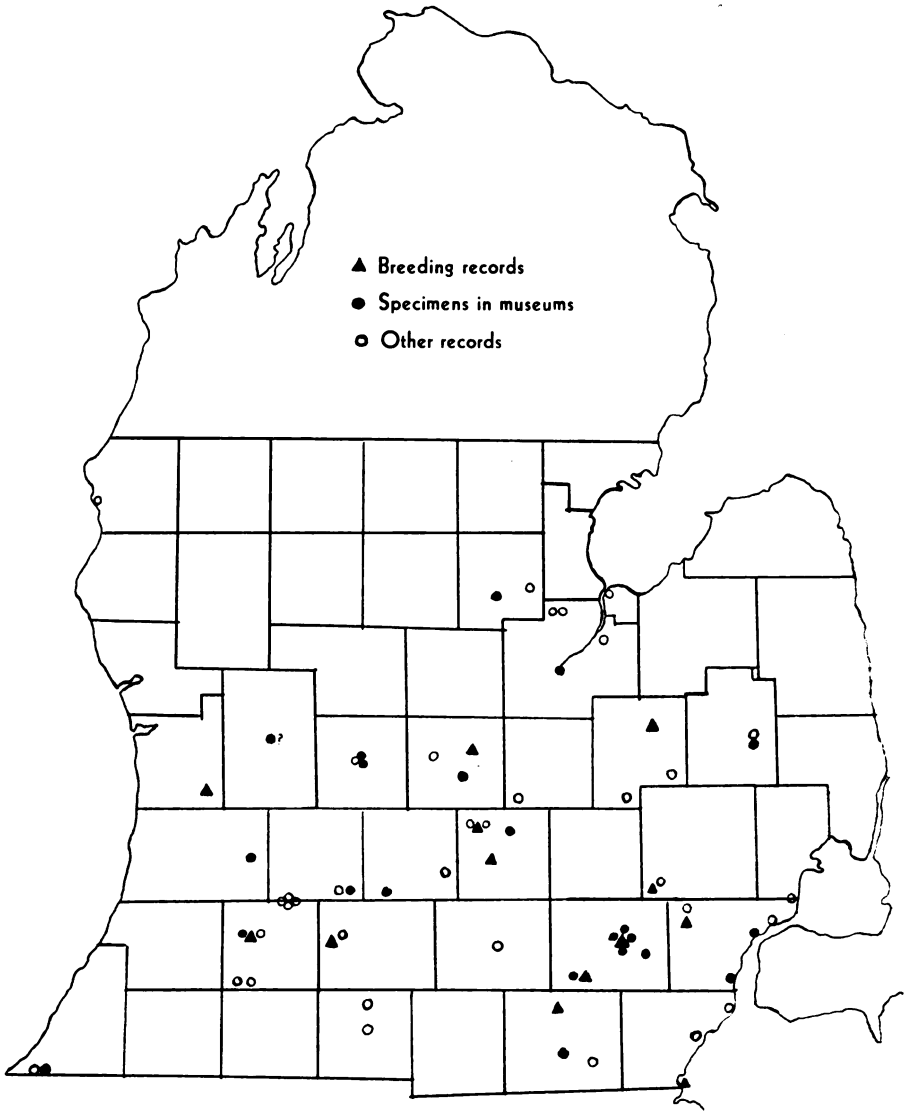

Fig. 1. Distribution of the barn owl in Michigan.

of records, however, present the distributional picture as completely as seems practicable.

A brief history and analysis of the Michigan records may serve a useful purpose here. The barn owl was considered extremely rare in early days (Gibbs, 1879; Cook, 1893), when it was known from only scanty records. The collection of a specimen in Genesee County

BREEDING RECORDS (CHRONOLOGICAL BY COUNTIES)

County	Town	Date	Other data	Authority
Washtenaw.	Ann Arbor.....	Spring, 1905 ..	Reported nesting.....	Swales, 1906
	Ann Arbor.....	1929-1944	At least 6 nestings....	Van Tyne; Moore, 1945
	Bridgewater.....	June 1936	4 young in pigeon box.	Hinshaw
Ingham.....	Mason.....	1906.....	Nest of "white owls".	Barrows, 1912
	East Lansing.....	1932; 1940-1946	At least 10 nestings...	Stack; Wallace
Oakland....	South Lyon.....	April 8, 1916...	First set of eggs.....	Hastings
Genesee.....	Geneseeville.....	Sept. 29, 1927..	4 nestlings banded....	East, 1930
Monroe.....	North Cape.....	June 27, 1937..	5 young in nest tree ..	Stophlet
Wayne.....	Plymouth.....	1938-1939.....	Nesting in barn.....	Van Coevering
Kalamazoo..	Kalamazoo.....	1943.....	5 young in silo.....	Fleugel
Clinton.....	St. Johns.....	Sept. 1945.....	5 young in silo.....	Kreag (Wallace, 1946)
Ottawa.....	Hudsonville.....	Oct. 1945.....	Photo of young in nest	East (Wallace, 1946)
Calhoun....	Battle Creek.....	Summer, 1946..	Raised young in hollow tree.	Walkinshaw
Lenawee....	Tipton.....	Summer, 1946..	5 young in church steeple.	Dyer (Black and Wallace, 1947)

OTHER RECORDS (ALPHABETICAL BY COUNTIES)

Allegan.....	Shelbyville.....	1914.....	No. 20981, G.R.P.M.*	DuMond
Barry.....	Johnstown.....	Sept. 21, 1904..	Captured alive, later mounted.	Barrows, 1904
	Johnstown.....	Sept. 29, 1938..	Speciman, K.M.N.H.* another in 1939.	Brigham
Bay.....	Oak Grove.....	Oct. 8, 1923..	Specimen.....	Empey
Berrien.....	Three Oaks.....	Nov. 20, 1929..	No. 61950,U.M.M.Z.*	Van Tyne
	Three Oaks.....	Oct. 1932.....	Mounted specimen...	Raz, 1935
Branch.....	Girard.....	Aug. 3, 1939..	Pole-trapped & banded	Martin
	Coldwater.....	May 1946.....	Wings nailed on barn.	Martin (Wallace, 1946)
Calhoun.....	Battle Creek.....	Apr. 23, 1934..	1 mounted for Cons. Dept.	Pirnie
Clinton.....	.....	Oct. 28, 1929..	No. 100861, G.R.P.M.	DuMond
	Fowler.....	Oct. 31, 1945..	Specimen taken.....	Empey
Eaton.....	Olivet.....	.....	Mount in museum....	Barrows, 1904
	Eaton Rapids.....	Apr. 3, 1946..	Banding recovery.....	Campbell
Genesee.....	Goodrich.....	About 1897....	Mounted specimen...	Barrows, 1912
	Fenton.....	May 24, 1932..	Banded, recovered near Ann Arbor.	Van Tyne
Ingham.....	Lansing.....	1869.....	No. 1602, M.A.C.* specimen lost.	Barrows, 1904
	Williamston.....	Sept. 20, 1906..	Specimen, M.S.C.*....	Stack
	East Lansing.....	1932-1947.....	Many records, no specimens.	
Ionia.....	Ionia.....	Mar. 30, 1946..	2 specimens in collection.	Zimmerman
	Ionia.....	July 16, 1947..	Injured bird captured.	Houghton (Lansing State Journal)
Jackson.....	Jackson.....	Dec. 1931.....	Christmas census.....	Wings

County	Town	Date	Other data	Authority
Kalamazoo..	.....	Between 1885-1898.	1 shot by Ben Syke...	Gibbs, 1898
	Kalamazoo.....	May 4, 1922..	No. 84227-U.M.M.Z..	Van Tyne
	Vicksburg.....	June 1925	Pair seen 13 times, nesting (?).	Bryens, 1926
	Augusta.....	Oct. 2, 1930..	No. 10096, G.R.P.M..	DuMond
	Kellogg Sanctuary.	Aug. 18-Oct. 9, 1933.	4 caught in pole traps.	Pirnie
	Schoolcraft.....	Mar. 11, 1947..	1 in barn (Bartels)....	Black & Wallace, 1947
Kent (?)....	.....	1893 (?), 1912..	2 Kent (?) Co. specimens, G.R.P.M.	DuMond
Lapeer.....	Imlay City.....	1944-1945.....	Adult seen; 1 shot....	Zimmerman
Lenawee....	.....	Sept. 10, 1889..	Specimen, M.S.C.....	Stack
	Near Blissfield....	Dec. 1945.....	Banding recovery.....	Campbell
Mason.....	Ludington.....	.....	Specimen.....	Wing
Midland....	Midland.....	Oct. 16, 1932..	Specimen.....	Empey
	.....	Nov. 12, 1938..	Specimen, K.M.N.H..	Brigham
Monroe.....	Pte. Mouillee.....	Oct. 29, 1901..	.....	Swales, 1905
	Monroe.....	May 31, 1907..	Caught in ice house...	Detroit *Free Press* photo
Oakland....	South Lyon.....	Sept. 18, 1904..	Male taken.....	Blain, 1904
Saginaw....	Saginaw.....	Oct. 2, 1904..	Shot from duck boat..	Barrows, 1904
	.....	Oct. 21, 1938..	Specimen, K.M.N.H..	Brigham
	Freeland.....	June 25, 1946..	Specimen taken.....	Empey
	Freeland.....	Feb. 1947.....	Injured bird found dead	Empey (Black & Wallace, 1947)
Shiawassee..	Woodhull.....	Oct. 4, 1919...	Specimen in Dunham collection.	Stack (Barrows)
Washtenaw.	Ann Arbor.....	Fall, 1905.....	Pair mounted by A.B. Covert.	Swales, 1906
	Ann Arbor.....	Oct. 23, 1932..	Banding recovery.....	Carstens
	Ann Arbor.....	1920-1943.....	12 specimens, U.M.M.Z.	Van Tyne
	Delhi.....	May 11, 1912..	No. 42589, U.M.M.Z.	Van Tyne
	Ypsilanti.....	Sept. 27, 1932..	No. 69824, U.M.M.Z.	Van Tyne
	York.....	Aug. 11, 1932..	No. 69177, U.M.M.Z.	Van Tyne
	Bridgewater.....	June 16, 1936..	No. 83489, U.M.M.Z.	Van Tyne
Wayne.....	Northville.....	Oct. 8, 1898..	One taken by A. Sheffield.	Purdy, 1899
	Gibraltor.....	Oct. 1901.....	No. 44317, U.M.M.Z.	Swales, 1905
	River Rouge.....	Aug. 19, 1905..	No. 816e, U.M.M.Z..	Van Tyne
	Greenfield.....	Oct. 1905.....	One collected.....	Swales, 1906
	Gratiot Ave.....	Dec. 10, 1908..	Taverner collection...	Swales, 1912

*Abbreviations: U.M.M.Z.—University of Michigan Museum of Zoology, Ann Arbor.
G.R.P.M.—Grand Rapids Public Museum, Grand Rapids.
M.A.C. (M.S.C.)—Michigan Agricultural (State) College, East Lansing.
K.M.N.H.—Kingman Museum of Natural History, Battle Creek.

(Barrows, 1912, Appendix I) in about 1897 apparently heralded an influx that resulted in the capture of at least 18 specimens in the ensuing decade. Then followed another decade or more of scarcity, with only about four specimens reported between 1909 and 1925. Thereafter, however, particularly in the 'thirties and 'forties, records became more numerous and more widely distributed, including those concerning nesting stations throughout the occupied areas.

The oldest record seems to be a Lansing specimen taken in 1869 and donated to Michigan Agricultural College (Catalogue No. 602)

by James Satterlee, but unfortunately the bird was lost track of prior to 1894 (Barrows, 1912, Appendix I). Another old specimen, taken in Lenawee County in September 1889, is also entered in the Michigan State College catalogue (Stack), and may be the Hudson (Lenawee County) bird mentioned by Barrows. Aside from a dateless Kalamazoo bird shot by Benjamin Syke sometime between 1885 and 1898 (Gibbs, 1898), and three records in the late 'seventies (Cook, 1893), there seem to be no other definite records until 1897, when the decade of influx began. The capture of at least 11 specimens in the southeastern corner of the state between 1897 and 1908 suggests an overflowing from that source, a movement thought to be associated with the clearing of the land (Van Tyne and Wood, unpublished), as suggested by Trautman (1940) for Ohio, and Cowan (1942) for British Columbia; but the invasion quickly spread north to Saginaw and west to Barry County, specimens being taken in both counties in 1904 (Barrows, 1904).

The first breeding records, unfortunately, are somewhat indefinite, one of the earliest based on the verbal report of a man who brought a pair of barn owls to A. B. Covert in 1905 to be mounted and said they had nested in a tree in his yard in Ann Arbor that spring (Swales, 1906). A subsequent report of a nest of "white owls" in Mason (Ingham County) in 1906, presumably refers to barn owls (Barrows, 1912). Even more vague, geographically at least, is a detailed nesting account, and a supporting photograph, by Gene Stratton Porter (1906) in the *Ladies Home Journal.* Her indefinite reference to "Michigan," the "Inland Route," and brooding young nearly 5° north of the northern limit of the species apparently prompted Barrows to place the record in Cheboygan County, but its authenticity seems open to question.

A more positive breeding record awaited the collection of a set of eggs by Walter Hastings at South Lyon, Oakland County, in 1916, the set now in safekeeping in the University of Michigan Museum of Zoology. Considerably later, on September 29, 1927, Ben East (1930) banded four nestlings from a nest near Geneseeville. Bryens (1926) suspected that a barn owl seen on 13 evenings in June 1925, at Vicksburg, Kalamazoo County, was nesting near by, though no nest was located. Since 1929, however, nesting discoveries have been more frequent, but highly irregular with respect to both time and place. In the last few years, 1944-46, 10 nesting records in 6 counties have

been reported, but apparently none of the known nesting sites was reoccupied in 1947, suggesting another period of decline perhaps inaugurated by the 1946-47 failure in the meadow-mouse population.

BANDING AND MIGRATION

Though barn owls are usually considered permanent residents in areas where they nest, there are many known migrations of banded birds. The probable explanation is that nesting adults tend to become sedentary, while their young disperse in all directions from the home site, especially southward in winter. Campbell and Van Camp (correspondence) have had 17 recoveries from 87 Ohio-banded barn owls: three went north, into Michigan and Ontario, one went east to Pennsylvania, the others (except those shot in the neighborhood where banded) went south, the farthest to Louisiana. One of Potter's (1926) New Jersey-banded fledglings was shot at Wilmington, North Carolina, 400 miles south of its birthplace. Another young bird (Ijams, 1924), released from short-term captivity at Knoxville, Tennessee, was shot 5 months later in southern Alabama, 350 miles south of the point of release. Bent (1938) adds that there are also known flights of banded birds from Wisconsin to Arkansas, from Illinois to Mississippi, from Ohio to Arkansas and Alabama, and from Pennsylvania to Georgia. In California, where migrations might be expected to be less pronounced, Sumner (1940) had 11 recoveries of 55 banded nestlings, 5 of them within 4 miles of their birthplace, the other 6 at greater distances (up to a maximum of 85 miles). The only recovery of my 11 banded nestlings in East Lansing was a bird reported (shot?) near the nesting site the month following its departure.

These data, plus uncited observations, indicate that barn owls may be year-round residents in a given area, or they may, on occasions at least, travel long distances.

NESTING NOTES

No attempt is made here to present a complete discussion of the nesting cycle. Incidental observations made at East Lansing are included, however, in part because a survey of the literature discloses that aside from Sumner's detailed papers on growth and development (1929, 1933a, 1933b), and the many records pertaining to nesting sites and the peculiarity of the breeding season, there appears, in this country at least, to be a dearth of information on the subject.

NESTING SITES

In adaptational response to man-made structures, barn owls have ventured far from their original nesting sites in hollow trees. Though they still use hollow trees on occasions, especially in river bottomlands (Poole, 1930, and others), their addiction to church steeples, towers of all kinds affording shelter, granaries, elevators and mills, unused attics, silos, and other farm buildings has long been known. In parts of the southwest they habitually nest and find shelter in holes and and crevices in cliffs; Dixon and Bond (1937) reported 300 domiciled along a 3-mile stretch in California. In other regions, as in Utah (Behle, 1941) and Illinois (Bellrose, 1936), the birds may resort to steep canyons and river banks. Sharp (1907) reports them nesting in California mineshafts, 65 feet below the surface, and even resorting to old crow nests.

Of the two nesting sites observed at East Lansing, one was quite typical, the other decidedly atypical; the former was in a box on a high platform in an old barn, the latter, on the bare open roof of Beaumont Tower on the Campus. Since barn owls build no nest other than a gradual accumulation of their broken-down pellets and debris, the latter site proved ill-fated, as the incubating bird apparently experienced difficulty in keeping her eggs beneath her. At least on July 11, 1946, when Dennis Murphy, who played the chimes in the tower, showed the author the would-be nest, three scattered eggs with dead embryos were found, together with one half-grown owlet in a corner and a loose flattened mass of pellet material which may have been the original point of deposition of the eggs. A similarly exposed but even more futile nesting site is reported from California (Bent, 1938), where a barn owl laid 24 eggs on the bare tin roof of a cupola. The eggs of course rolled hopelessly about on the smooth metal, and rotted from the reflected heat when the female abandoned attempts to cover them.

As already stated, barn owls do not construct a nest before egg laying, but during incubation, which seems to start with the deposition of the first egg, the female apparently deliberately dissects her regurgitated pellets and forms a nest of the dissociated materials. Since such a nesting site may be used repeatedly, subsequent nestings start with an already formed structure. Excess dead prey and uneaten pieces may also become incorporated in the nest structure, naturally giving the owls an unsavory reputation as housekeepers. Several

authors have remarked on the stench that may arise from an occupied cavity in a tree or poorly ventilated enclosure. During the East Lansing 1947 spring nesting (the only one followed through a complete nesting cycle), however, the incubating bird gradually assembled a fairly respectable nest of clean dry mouse fur which was not seriously soiled until near nest-leaving time. To visualize what seven young owls can do to a nest before the end of the season, however, requires little imagination.

NESTING SEASON

It has long been known, but not widely recognized, that barn owls are peculiarly irregular in their nesting periods. As early as 1895 (Bendire, 1895) winter young (with natal down) were twice reported from the famous Smithsonian Tower nesting site in Washington, D. C. J. J. Hickey told the author that Christmas census observers in New York could usually depend on finding young barn owls to count at some nesting site in the city.

A reasonably thorough, though not exhaustive, search of the available literature emphasizes not only the peculiarity of winter young, but also of nestings at all seasons. There are published records of downy young for every month of the year, and of nests with eggs for every month except January. No doubt the eggless January gap could be filled by further search. In Table 1 an attempt is made to portray the span of the nesting season in 10 selected eastern states. No particular effort was made to run down all the probable records in these states, however, and of course the span of time covered by eggs or young could be extended 2 or 3 months if the age of the young or the fate of the nest were known, but in most cases these data were not given in the published reports.

The records suggest indiscriminate and haphazard nesting, but perhaps they are divisible into a spring and a late summer or fall nesting (first and second broods?), with a great amount of overlap at different stations. Eggs for the spring nesting, for instance, may be laid by early February in Massachusetts (Eliot, 1934), or Michigan (Van Tyne, unpublished), or they may be delayed until March, April or May (many records). Second sets may be laid as early as June or July (East Lansing, Wallace), or delayed till fall. December egg records in Washington, D. C., and Florida, however, (and perhaps other states) are a little difficult to explain. Are they belated fall, or early spring, nestings?

TABLE 1—*Span of barn owl nesting activities in 10 eastern states*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Authority
Michigan			e---y	--y--	--y--	-y e	e--	-e-y-	--y--	--y--			Wallace
		e--	-y--	e--	--y--	-y			y	y			Van Tyne; Moore
Ohio				e					y	y	y		Bales; Earl
				-	---y						y		Goetz
Illinois						--e--	y----	y					Bellrose
					--y	e y--	--y						Hess; Fisher (W.L.
New York						-e--y	---y-	---y			--	---y-	Bedell; Hickey
					---y	-y		--y--	--y				Dutcher; Mitchell
Massachusetts	y	e		--e--	--y--	--y--	--y						Eliot
						y---	--y						Eliot
Pennsylvania	-y	e---	---		---	-y				--y			Harlow; Poole
			e ey	e e	y e				---e-	-			Leibelsperger; Reed
Washington, D. C.	-y---	--y		-e---	e--y-	--y--	--y				e--	-e--	Bendire; Fisher (A.K.
	y----	-y							e	----y	-----	-y	Bendire
South Carolina	-y--		e--	e---	--y				-e---	y----	-y---	-y	Pearson; Wayne
										-e---	-y		Cottam
Georgia			e---	e									Tompkins
Florida		e----	ye---	--e	--y--	-y		e					Howell; Chapman
								----e	-y---	-y---	--	-e-	Butler; Williams

e=eggs.
y=young.
Linked symbols (e--y) are for a continuous nesting; separated symbols (y y) for different nestings.

An alternative explanation, rapidly gaining favor with further study of population cycles, is that the owls may breed more or less continuously during the periods of abundant *Microtus* prey (for about 2 years), and then slow down or cease nesting during periods of rodent scarcity (roughly, for another 2 years). Guérin (1928) in France believes this may explain why his previously double-brooded barn owls failed to nest when their food supply declined. Some support for this view may be found in the East Lansing nestings, where, in 1945 and 1946, the birds raised three successive broods and started a fourth, almost without interruption. In the spring of 1945, according to the Nellers who owned the occupied barn, the owls raised

seven young which left the building in June. On October 3, the time of the author's first fall visit, there were seven more young of various ages in the nest, which, according to Sumner's growth data (1933a), probably hatched from eggs laid during the latter half of July, indicating about a month's interval between the two nestings. These fall young used the barn as headquarters until early December, then disappeared, and egg laying started again on March 1. Four young were raised from this third 7-egg nesting, and these left the barn in early June (they were there on June 5, the youngest not able to fly). On June 15 the laying of the fourth clutch began. Three eggs were laid; then events at the nest reached an unfortunate termination when a pigeon hunter shot the owls (ostensibly to protect the pigeons, with which the owls had associated apparently in almost perfect harmony for more than a year). As will be shown subsequently by data on food habits, these nestings were concurrent with a period of high meadow-mouse availability, when for a year's period, at least, more than 90 percent of the owls' diet was of this species.

EGGS AND INCUBATION

Various authors place the number of eggs per clutch for the barn owl from 4 or 5 to 8, or rarely up to 11, but, as suggested by the foregoing paragraph, 6 or 7 is a common number. A case was recently recorded (*Bulletin of New England Bird Life*, 1945, p. 141) where a nesting site on a water tower in Connecticut contained 6 eggs and 6 young at the same time, possibly the joint efforts of two females. My records of the laying of a 7-egg clutch, and of 3 eggs in another set, indicate laying on alternate days, a practice that receives added confirmation from the apparent ages of young in this and other nests. Others, however, report of eggs laid irregularly, with a gap of several days to a week between certain eggs. Though such irregularity may well occur, of course such an effect could be falsely produced (after hatching) by the failure of certain eggs to hatch, or by the disappearance of one or more young of intermediate age.

Incubation apparently starts with the deposition of the first egg, a supposition supported by repeatedly flushing a bird from an incomplete clutch of eggs, as well as by the staggered intervals at which the young hatch. Since, for practical purposes, the sexes are indistinguishable by plumage, it is not known how much, if at all, the male assists in incubating, but Merriam (1896) reported seeing a barn owl replace its mate in a nesting cavity in a tree. There are frequent

records of flushing two owls from a nesting site simultaneously, a condition usually interpreted as a case of the male merely sitting beside the female.

The incubation period for barn owls is not given in any of the original literature consulted, but Forbush cites "21 to 24 days (authors)," adding that it may sometimes be longer. At the 1946 spring nesting in Neller's barn, the author marked seven eggs whose approximate laying dates were known, but unfortunately three of the eggs did not hatch, and data for one of the others was not obtained. Egg 1, believed to have been laid on March 1 and hatched on March 30, gave an incubation period of 30 days, but there was a little uncertainty about both the laying and the hatching date. (One dry egg was in the nest on March 2, and three more on March 7. They were thus assumed to have been laid on alternate days, on March 1, 3, 5 and 7.) A second young was in the nest, dry, on April 3. If it hatched the preceding day, it may have been Egg 2 hatching on the 30th day, or Egg 3 hatching on the 28th day (it was marked 3, but as three eggs were marked on March 7, 2 and 3 may have been marked wrongly). Another egg was hatching on my April 7 visit—the chick could be heard peeping, even at a distance, within the pipped shell—but had not completely emerged at the time of my departure. The number on the shell was lost by heavy staining, but it may well have been the March 7 egg (Egg 4—the one marked 2 did not hatch), another approximately 30-day period.

Thus it appears that the incubation period for each of three eggs was about 30 days, but a possible weakness in these observations, in addition to the acknowledged uncertainty of exact laying and hatching dates, is the seemingly reasonable assumption that incubation is continuous from the laying of the first egg, as suggested both by the hatching sequence in this and other nests, and by flushing an apparently incubating bird on four different occasions from an incomplete clutch of eggs (March 2, 7, 10, 11). East (1930) describes an extraordinary case of barn owls incubating spoiled eggs for about 3 months, then pitching out the blackened eggs and starting with a fresh supply, which hatched in another month.

There are so many published notes on the behavior of young barn owls, both at the nest and in captivity, that it seems needless duplication to review the material here. For further details on the growth and development of barn owls, the reader is referred to Sumner's excellent studies (1929, 1933a, 1933b).

BREEDING RATE AND SURVIVAL

The apparently high potential breeding rate of the barn owl poses an interesting problem in relation to survival, where climatic or other factors may nullify an otherwise high productivity. It has been pointed out that barn owls lay large clutches of eggs, usually six or seven, sometimes more, and that they often appear to raise a second brood, though what appears to be a second brood could conceivably be merely a reoccupation of a favored nesting site by a new pair after it has been vacated by the first. A possible additional balancing factor is that the owls may reproduce rapidly when the food supply is abundant, but offset this by slackening efforts during a period of failure of the food supply.

Whether there are ample grounds for postulating a regulatory adjustment between the breeding rate and rodent fluctuations, there is strong evidence that severe winters cause high mortality. Errington (1931), in an analysis of Wisconsin barn-owl pellets, noted a winter decrease in pellet contents from three to six prey animals per pellet to only one, and in February found two dead owls following an unusually cold late January. A pronounced winter die-off of barn owls has also been reported by Speirs (1940) in Illinois, and by Baumgartner and Baumgartner (1944) in Oklahoma. In the former instance the die-off was due to forced exposure to cold; in the latter it was due to concurrent cold and failure of the staple food supply (cotton rats). Bond (1939) reports a 75-percent reduction in hawks and owls in California during a mouse decline that was accompanied by sub-zero temperatures. At this time he found eight dead barn owls under the roosting cliffs. Others have commented that, with a thinner covering of plumage than is characteristic of other owls, the barn owl is not able to withstand severe or prolonged cold. But how much a winter die-off, and consequent failure of the birds to increase more rapidly in northern parts of their range, is due to climatic severity and how much to fluctuations in their cyclic prey, is not clearly indicated by available data.

FOOD STORAGE AT THE NEST

A somewhat spectacular feature of considerable economic interest, related both to nesting and to the food supply and thus forming a connecting link between these nesting notes and the following section on food habits, is the owl's habit of taking food in excess of

immediate needs when the supply is abundant and storing up or discarding the surplus items at or near the nest. The various references in the literature that speak of miscellaneous prey items often found in or around the nest, however, hardly prepared the author for what occurred in Neller's barn. During the fall nesting, at the time of his first visit on October 3, he found an accumulation of 189 dead mice and 1 short-tailed shrew *(Blarina brevicauda kirtlandi)* on the floor opposite the nest box, under a favorite roost of one of the adults. The mice included 186 meadow mice *(Microtus pennsylvanicus pennsylvanicus),* 97.9 percent of the dead animals, and 1 deer mouse *(Peromyscus* sp.), 1 house mouse *(Mus musculus musculus)* and 1 unidentified mouse. Eighty-six of the 189 mice had been beheaded, but there were 9 detached skulls, perhaps belonging with the headless specimens. Many of the headless mice also lacked forelimbs, and in six only the hind quarters remained. Two of the skulls had no lower jaws. These data help to explain the mix-up that sometimes occurs in pellets, where the skeletal parts of the included prey do not check.

The mouse carcasses, littering perhaps 50 square feet of floor space, were stiff and dry, with no appreciable odor. The most apparent explanation is that the male (or non-incubating bird) accumulated the stock pile during the incubation period in late July and August, an explanation strongly supported by my observations the following spring, and by Guérin's (1928) observations in France.

The mouse-hoarding habit continued in the spring. On March 2 an owl was flushed from the nest box, which contained 1 egg and 13 mice, all *Microtus,* conveniently cached in the nest box around the egg. Five days later (March 7) there were 4 eggs and 64 mice, including 1 prairie deer mouse *(Peromyscus maniculatus bairdii),* in the box. On March 10, the mouse count was up to 80 and a sixth egg had been added. On March 16 the egg clutch of 7 was complete but the mice had declined to 45. Two deer mice *(bairdii)* had disappeared from the stock pile, but the appearance of a star-nosed mole *(Condylura cristata)* indicated some turnover in the larder. By March 23 the whole supply had vanished, for though 3 mice were in the box, they were obviously fresh replacements. In all cases the author left the mice in the nest to learn what the owls would do with them.

Both the origin and disappearance of the prey are something of a mystery. It is assumed that the male brought the mice to the incubating female, but his presence was never actually verified, and

it is not certain that the incubating bird was always the female, although she must have been associated with the nest during the 15-day egg-laying period, which was also a period of incubation. The rapid disappearance of the hoarded mice (curiously coincident with warmer weather) is even less satisfactorily explained. The 32 recoverable March pellets yielded only 50 mice for the whole month, whereas at least 80 disappeared between March 10 and 23, 45 of them between the 16th and 23rd. This is at the rate of more than 6 per day, or close to 200 for the month, compared with the 50 actually recovered. There was, however, some pellet loss from the incubating birds, whose pellets were dissected for nest material. Moreover, the off-the-nest bird may have eaten half of the supply without contributing to the retrieved pellets, though why he should feed on dead mice, if he did, when fresh-caught ones were apparently so readily procurable, is another problem. Finally, there is no real proof that the mice were consumed, though it is hard to imagine the owls carrying the dead animals away. During the previous summer the uneaten mice were dropped on the floor opposite the nest and left to rot. Though a few dropped mice were nearly always to be found about the barn floor, an abandoned supply was not found during the spring, either inside or outside the barn.

A further accumulation of mice accompanied hatching. On April 7, with 2 young hatched and a third struggling in a pipped egg, there were 32 *Microtus* plus a headless 10-day-old rabbit in the nest (the age of the latter was estimated by Robert Rafferty from hind-foot measurements). By April 13 there were 4 young, all that hatched, and 73 mice, including 2 *bairdii*. In another 7 days (April 20) only 4 mice were left in the box, although 9 others were found in various positions at the opposite end of the barn—a disappearance of at least 69 mice in 7 days (about 10 per day), with only 4 small young in the nest. Thereafter there were no surplus mice left lying around.

PART II. FOOD HABITS

SUMMARY OF ECONOMIC STATUS

Though it is not the intent of this paper to discuss the many papers or notes on barn-owl food studies in other regions, consultation with the available references on the subject permits a brief summary of economic relationships. Though prey species differ considerably in different regions, particularly in parts of the South and West, in most cases the diet consists largely of rodents, nearly always with a preponderance of the ones considered the worst enemies of farm crops in the region in question. Shrews and songbirds have been the only other consistent items in most studies—the only ones that could be considered on the negative side of the ledger—and songbirds, though consistent in the diet, have usually appeared in very small amounts. In the northern states in particular, the highly microtine diet of these owls has almost completely overshadowed other prey.

This apparent beneficial trend in barn-owl food preferences has been known to ornithologists for the past 50 years, but it seems not to have been duly impressed on the layman. Farmers and sportsmen in particular, the ones most directly concerned, have been slow to accept the facts, the former in the groundless apprehension that the owls might be a menace to poultry, the latter in the unsupported belief that predation by barn owls threatens game populations. This situation emphasizes the need for more effective education, supported by unquestionable data which this investigation aims to provide.

PELLET STUDIES

It is common knowledge that raptorial birds prey on other animals, usually smaller vertebrates, and that the less digestible portions of their victims—bones, fur, feathers, scales, and chitinous appendages—are periodically regurgitated in the form of pellets or castings. It is less commonly known that species differ widely in pellet-forming habits, that the degree of digestive action varies with the time the prey is retained in the stomach, and that the time materials are retained in the stomach and thus subjected to digestive action, varies with the bulk taken in. Hawks, with some exceptions, are poor pellet producers, Cooper's hawks and eagles, for instance, often plucking the flesh from their larger prey, and not eating pellet-forming materials. Brooks (1929), in particular, has raised objections to the standard prac-

tice of making food-habits studies by pellet analysis, citing among other things an eagle's habit of swallowing pellet-forming feathers and bones of grebes, while they commonly pluck only the flesh from duck carcasses. But these and other criticisms apply principally to certain hawks, much less to owls, and perhaps least of all to the barn owl, which is commonly accepted as a species to which pellet studies are particularly applicable.

PREY RECOVERY FROM PELLETS

Barn owls are known, not only from pellet studies, but from stomach examination and direct observation, to prey so largely on small vertebrates that are swallowed whole, or more rarely in sizable hunks, that the regurgitated dejecta give an unusually accurate picture of the prey consumed. Reed and Reed (1928) have shown that the 1-mm. diameter of the pyloric opening from the stomach to the duodenum (in the great horned owl) presents a mechanical bar to the further passage of coarse materials. The lack of free acidity in the stomach, as shown by fluoroscopic studies, prohibits any appreciable corrosive action, so that typically the bones, fur and feathers are ejected entire, even the broken ends of bones commonly showing little or no erosion. Only soft-bodied invertebrates (earthworms), or cartilaginous prey, and perhaps nestling birds (all rare items in a barn owl's diet) would escape detection. Insects, juvenile mice, and the smaller shrews are easily overlooked, however, and if retained for long in the stomach may be completely digested.

Proof of the complete or nearly complete recovery of vertebrate prey comes from experiments. In 1945 the writer kept a 2-month-old barn owl from October 22 to November 9. During the 18-day interval the bird was fed 66 mice (mainly laboratory stock and trapped escapees of the genus *Mus)* and 2 white rats, and the remains of exactly 66 mice and 2 rats were recovered from the pellets. In all cases except one, where there was some confusion in the recovered items, the exact number of animals fed during the night was represented in the following day's pellet. In most cases all of the larger bones were recovered, though the skulls were badly broken up, more so than in typical field pellets, and often were detectable only by toothed portions of the upper jaw.

Another young owl kept in semi-confinement for 66 days afforded no example of a vertebrate animal being eaten and not recovered, at

least in part, usually within 12 hours. Failure to recover certain bones is sometimes due to breakage of the structures, so that they are easily overlooked, sometimes due to chance location of a bone on the periphery of the pellet, so that it drops off, or more rarely items may actually become dissociated from the rest of the pellet in the stomach and retained long enough to be completely digested, or to be added to a subsequent pellet. Except during part of the nesting season, when the prey is apparently deliberately divided before consumption, field-collected pellets are usually complete with respect to skulls and correlated limb bones; 70 percent of 254 pellets examined for this feature were essentially complete.

RHYTHM OF EJECTION

Extensive studies have been made on this subject by several investigators, but the topic is still a controversial one. Banks (1884) and Errington (1938) have demonstrated that the great horned owl may eject pellets daily at times, or store up items for 2 or 3 days and then unload a casting of extraordinary dimensions. Chitty (1938) reports that the tawny owl in Europe ejects two pellets each night and none during the day, but his short-eared owls, in part diurnal feeders, cast frequent pellets, day or night, the number depending on the size and frequency of the meal. Sensenig (1945), experimenting with a barred owl at Ann Arbor, Michigan, usually got a daily pellet within 8 hours of the previous night's feeding, but reported that several times the owl expelled two or three at brief intervals.

With the European barn owl *(Tyto alba alba),* Ticehurst (1935) reported that small animals fed to a captive bird on several successive evenings produced a complete pellet ejected the following morning, and concluded that a single diurnal pellet following the night's feeding is the rule. But apparently the experiment was not varied by staggering meals, nor does hand-feeding an owl all it can eat at one time necessarily simulate feeding schedules of wild birds. Guérin (1928), after extensive studies in France with both captive and unconfined nesting birds, concluded that though a maximum of four pellets may rarely be obtained, the daily quota is usually two, a small "pelote nocturne" dropped on the foraging grounds (and thus not previously suspected) before the owl takes its second or morning meal, and a larger "pelote diurne" resulting from the morning meal and dropped at the diurnal roost (the pellet commonly recovered by collectors). The two-pellet rule, however, apparently presupposes

that the owls take an evening meal and do not feed again until near morning (observational proof of which is lacking for the American form) after ejecting the pellet from the evening's prey.

Results of experiments with the author's captive barn owls are not entirely in accord with the conclusions of either European worker, although, as Guérin maintains, work with captive birds is not a wholly safe criterion for judging wild birds. One owl regularly ejected a diurnal pellet containing remains of all the prey eaten during the night, regardless of the number of prey animals eaten, and regardless of the staggered hours at which feeding took place. During the 17 nights the bird ate from one to eight mice each night, and on two occasions ate a whole rat (not full size), followed several hours later by three mice, and in all cases except one a single pellet was recovered the following day, from 8 to nearly 24 hours after the first and sometimes only meal was eaten. Once an incomplete pellet was secured in the morning and the missing portion recovered at noon. It is not certain whether the fragment was overlooked in the morning, or whether it was actually dissociated in the owl's digestive tract and followed the main pellet several hours later. These results—a single, diurnal pellet—tend to support Ticehurst's (1935) conclusions, but the experiment was not carried on long enough to test the results of deliberately punctuated evening and morning meals. (The owl escaped from a poultry keeper to whom it was loaned for a rodent-control experiment.)

Another captive owl served largely to refute the results obtained with the first. Taken from the nest-site at about 1 month of age, when it fell from the nest and suffered a broken leg, this very tame young owl usually ate smaller meals, then would not eat again until relieved of the pellet-forming materials. The result was smaller pellets, more frequently ejected. From 43 nights' feedings (from one to several meals each night, or occasionally during the day) 74 pellets were secured, an average of 1.7 daily. A single pellet was produced 16 times, 2 pellets per day 23 times, and on four occasions, 3 pellets per day were produced.

A third owl, kept at the College animal house in a large outdoor cage permitting considerable freedom of movement, was not directly under my care, but during October 1947, at weekly intervals the author collected and counted the pellets. During the 31 days, the equivalent of about 33 pellets was obtained (with some uncertainty as to how the broken pieces should be counted). This roughly fol-

lowed the pattern of the first owl—a daily pellet, with apparently some extras of single skulls of the rats on which he was fed. The owl usually ate one medium-sized rat each night, but several times the skull pellet was separate from the body pellet. (Barn owls usually detach the head of a rat and eat it first.)

The time interval required for the production of pellets was studied only with the first two owls. With the first owl, which ate larger meals, the interval between feeding and pellet ejection varied from 8 to nearly 24 hours. It was usually around 12 hours, though I seldom was present at the time of ejection to ascertain the interval exactly. The second owl, which was observed more closely, ate smaller meals more frequently, and the interval varied from 5½ hours to 12 or more. Once, on a day of voluntary fasting, the interval was more than 21 hours; but, as Chitty (1938) found in carefully controlled experiments with short-eared owls in England, the time varied directly with the size (weight) and frequency of the meals. If the owl ate only one mouse or a small portion of a rat (as it frequently did), and did not feed again within 6 hours, a small pellet would be ejected before a second meal was eaten. With a larger meal (two or more mice or a small rat), the period for pellet formation would be prolonged to 8 to 12 hours or more. If a second meal, or even a third, was taken within a few hours of the first (less than 6 hours in these incomplete experiments) the residue from the first feeding was held down and combined with the subsequent meal or meals to form a single larger pellet. In the resulting pellet the separate meals were often distinguishable, the remains of the first meal being more thoroughly digested, those of later meals less digested, and the time for its inclusion in the pellet necessarily shortened. The sight of fresh food seemed to hasten the ejection of a pellet: often the owl would refuse food until the pellet from the previous meal was ejected (i.e., within certain limits pellets can be produced at will), and conversely the absence of food or hunger caused further retention and more complete digestion of the prey.

It is not certain how accurately experimental results with two captive owls apply to conditions in the field. It appears, however, that if a barn owl feeds at intervals during the night, a single pellet will be produced the following day. Similarly, if a large meal were eaten on a summer evening (after 8:00 p.m.) there would hardly be time to form and eject a pellet before daylight (5 a.m. or earlier), after which it would be too late to hunt. But if a small meal were

eaten in the early evening, and no food taken within a 6-hour period, a small pellet would be ejected before daylight and another meal could be taken, resulting in the "pluri-rejet quotidien" of Guérin. Obviously, too, there is considerable difference between a winter and a summer night, the increased hunting hours available in winter perhaps permitting an additional meal. Winter pellets were measurably smaller than those collected in the fall and spring (February pellets averaged 1.8 prey animals compared with 3.4 animals per pellet in October and May), but it is not certain whether the smaller winter pellets reflect more limited rations, maturity of the owls and consequent smaller food requirements compared to October and May young, or whether it means more and smaller pellets produced because of increased hunting time.

Theoretically, at 6-hour intervals, four daily ejections are possible. Guérin (1928) states that this is the maximum number obtained. However, except at nesting sites where a hoarded larder of mice permits daytime feeding, this hardly seems feasible for strictly night-hunting owls, and the author's captive bird could not be induced to eat frequently enough to produce more than three pellets per day, even with daytime feeding. During winter an owl might have a maximum of three ejections, by eating small meals at about 6 p.m., 12 p.m., and 6 a.m., or two ejections for the shorter summer nights, but whether owls commonly punctuate their meals thus or (as seems more likely) merely take what they can get whenever they can get it—which results in an unpredictable irregularity of pellet formation—is uncertain.

It is admittedly a little frustrating, in view of these somewhat extensive observations, not to have found an answer regarding the frequency of pellet ejection, which, if accurately known, would simplify the arithmetic for computing how much an owl eats daily, monthly, or annually. Some of the published records of the barn owl's consumptive capacity (i.e., Lord Lilford's 12 mice in an evening, and others) are based on maximum performance, rather than on long-time averages, and are thus misleading. The author's tentative conclusion is that the daily quota is more than the 3-prey-per-pellet average (since smaller pellets are often extras), but probably less than the 6-prey-per-day average assumed by Guérin.[1]

[1]It need not be inferred, here or elsewhere, that Guérin's conclusions are erroneous, but simply that they do not necessarily apply to the American barn owl, which is a different subspecies, lives on different prey (fewer shrews), and apparently casts larger (and probably fewer) pellets.

PELLET EXAMINATIONS

Table 2 presents some of the results of a detailed month-by-month analysis of 254 year-round pellets collected in the Hagadorn Road barn. These were weighed, measured, and each pellet separately analyzed as to number, identity, and completeness of representation of prey items. The table gives the monthly trends in pellet size, the maximum, minimum, and average weights and measurements for each month, and similar data for the contents.

Measurements accurately expressing size were difficult to take because of irregularities in shape, the principal distortions usually due to flattening or blunting of the pellets during their fall from high perches. Measurements given are the greatest length (occasionally discounting a protruding bone or wisp of fur) by a compromised diameter—i.e., the greatest diameter if the pellet was reasonably uniform in shape, but with certain adjustments for misshapen pellets and for pronounced projections of bones on the sides. Because of these dimensional inconsistencies, weights are probably a better criterion of size in pellets of similar age. Weights given are of dry pellets that had been stored in the laboratory from several months to a year (collected at intervals from October to June, examined the following October).

The smallest pellet for the year (a December ejection) measured 28 by 17 mm. and weighed only 1.0 gram, but there were 12 others of less than 2 grams weight. The smallest contained a single juvenile *Microtus*, badly disintegrated, as is typical of juvenile mice. Six other pellets, however, contained a single shrew *(Blarina)*, and 57 others contained one mouse.

The largest pellet (a November casting) measured 109 by 35 mm., weighed 17.2 grams, and contained seven *Microtus* and one *Blarina*. Six others were seven-mouse pellets.

The 254 pellets thus varied from 1.0 to 17.2 grams in dry weight, averaging 6.8 grams, varied from 28 by 17 mm. to 109 by 35 mm. in dimensions, averaging 53 by 30 mm., and contained from 1 to 8 prey animals, averaging 2.71. Possibly the prey contents are better expressions of pellet variations than are weights or measurements. The following summary lists the distribution of mice, and other occasional prey, in the 252 pellets examined for these features:

Pellets with 1 *Blarina* = 6 (1 other had 2 *Blarina)*

TABLE 2—*Monthly size trends in 254 barn owl pellets*

	Number of pellets*	Weight in grams			Dimensions in mm.			Contents of pellets								
								Maximum prey per pellet			Minimum prey per pellet			Average prey per pellet		Total prey
		Maximum	Minimum	Average	Maximum	Minimum	Average	M [1]	P [2]	B [3]	M [1]	P [2]	B [3]	Microtus	Total mice	
July-September...	20	11.4	1.4	6.0†	99 x 28	33 x 20	51 x 28	7	0	0	1	0	0	2.55	2.86	2.91
October.....	35	15.1	1.4	6.8	93 x 35	27 x 21	51 x 31	6	1	0	1	0	0	2.62	2.67	2.78
November.....	64	17.2	1.6	7.8	109 x 35	28 x 24	57 x 32	7	0	1	0	0	1	2.92	3.02	3.37
December.....	37	15.8	1.0	7.1	91 x 42	28 x 17	54 x 31	6	0	0	1	0	0	2.36	2.44	2.69
January.....	20	13.6	1.8	6.2	71 x 40	32 x 20	50 x 28	5	0	0	1	0	0	2.25	2.25	2.30
February.....	29	16.1	1.6	5.0	102 x 40	32 x 16	48 x 27	6	0	0	0	0	1	1.69	1.72	1.86
March.....	20	7.6	2.7	4.6	54 x 32	35 x 23	43 x 28	2	0	0	1	0	0	1.52	1.68	1.68
April.....	19	12.7	1.3	6.8	73 x 32	31 x 17	53 x 28	4	1	0	0	1	0	2.18	2.42	2.48
May.....	10	14.2	6.8	9.7	74 x 35	53 x 28	63 x 31	5	0	0	2	0	1	3.20	3.30	3.40
Total.....	254			6.76			53 x 30							2.44	2.54	2.71

*Larger number used to determine contents for some months (i.e.—22 for July-September lot, 55 for October, 65 for November, 39 for December, 20 for April)
†Attacked by dermestids and moths, probably reducing weight, but not affecting measurements or contents.

M [1] = Microtus
P [2] = Peromyscus
B [3] = Blarina
[4] = incomplete
[5] = juvenile
[6] = part of third

Pellets with 1 mouse = 57 (7 others included *Blarina* with a single mouse)
Pellets with 2 mice = 55 (7 others included other prey with 2 mice)
Pellets with 3 mice = 49 (6 others included other prey with 3 mice)
Pellets with 4 mice = 29 (6 others included a *Blarina* with 4 mice)
Pellets with 5 mice = 11 (1 other with an added *Blarina*)
Pellets with 6 mice = 8 (1 other with an added shrew)
Pellets with 7 mice = 6 (2 others with an added *Blarina*)

Many of the pellets were checked for completeness of individual animal parts, to find out, for instance, whether all of the bones of a mouse would be recovered in the same pellet, or scattered through several pellets, and how commonly animals were divided and the parts eaten at different feedings, as with the large prey of the great horned owl. Of 200 pellets checked for this feature, 71 (35.5 percent) were considered complete (that is, the proper number of apparently matching skulls and limb bones were present), 72 (36 percent) were essentially complete (one or more limb bones were lost or more probably overlooked), 45 (22.5 percent) were obviously incomplete (skull count and limb bones did not check). Twelve others (6 percent) were listed as questionable or unexplainable for one reason or another. Since many of the incomplete pellets were retrieved from the incubating or nesting birds, there is a strong probability of roost-collected pellets being complete as to associated parts. A pellet containing three *Microtus* skulls, for instance, usually yields six of all of the paired bones, if a careful search is conducted. The most elusive bones were the relatively short humeri, which are difficult to find if broken even once, and the pelves, which crush easily. Rats and starlings were the only prey animals that gave much evidence of division before consumption (that is, their parts were not all in the same pellet).

In spite of the usual complete representation of parts, peculiar anomalies occasionally occur, as a mouse with two left mandibles and no right, or one with an extra humerus or other limb bone (missing parts are to be expected, but extras are hard to explain except by dissociation in the stomach). Several examples of broken bones that

had subsequently healed were encountered, and one interesting case of malocclusion in a *Microtus* incisor was found.

These examinations indicate, perhaps not surprisingly, that small animals are usually consumed entire, their bodies digested and their remains ejected more or less together (at least 70 percent of the pellets being essentially complete), but that various exceptions and anomalies occur, particularly during the nesting season.

THE HAGADORN ROAD (NELLER'S BARN) STATION

HISTORY

This station was located in an upland farming area on Hagadorn Road, about 2 miles from the College campus. Around 1940, a pair of barn owls, perhaps originating from the campus stock, appropriated the top floor of a largely unused barn owned by the late Louis Neller. According to Mrs. Neller, the owls nested there regularly in the spring, usually appearing in March and leaving with their young in June. During the spring of 1945, the owls were said to have reared seven young in an open-top box on a platform near a high open window. Abundant evidence of this was found at the time of my first visit on July 7, for, though no owls were there at that time, the chaff-covered floor was littered with about 300 pellets, mostly of recent origin. The following paragraphs present the analysis of this collection.

THE 1945 SPRING COLLECTION

The accumulation of pellet material obtained from the floor of this barn on July 7 was assumed to be largely, if not entirely, from that spring's nesting, as the owls were said by Mrs. Neller not to have occupied the site since the previous spring. At the rate of outdoor weathering of pellets (Errington, 1940; Wilson, 1938), this 1945 spring collection would not have been contaminated by older materials, but the rate of indoor weathering under the conditions in this particular barn is not known. Sensenig (1945) states that pellets (from a barred owl on a laboratory *Peromyscus* diet) kept in dry storage disintegrate within a year, but Wilson (1938) states that under laboratory conditions barn-owl pellets seem to last indefinitely. Some of the pellets collected by the author were kept up to 2 years in the laboratory without complete disintegration, even when attacked by dermestids and moths, and a pellet placed on a beam in the barn in question, remained without appreciable disintegration from No-

vember 1945 to November 1946. The floor of the barn was not entirely weatherproof, however; broken windows permitted snow and rain to beat in, the roof leaked in places, and most of the floor was covered with chaff, all of which presumably hastened disintegration. Consequently it seems safe to assume that the bulk of the collection originated during the 1945 spring season, but that a few "oldish-looking" pellets and loose skulls may conceivably have survived from previous periods. The 310 pellets and 890 prey animals obtained from this family of two adults and seven young are closely comparable with those obtained from a family of the same size in the fall for a slightly longer period (335 pellets and 997 prey animals).

Table 3 presents the analysis of the 200 whole or essentially whole pellets examined, and of the remaining pieces and recoverable debris, computed by the Baumgartner (1944) formula to represent 110 pellets.

Baumgartner formula (modified):

$$\frac{\text{No. whole pellets (200)}}{\text{No. } \textit{Microtus} \text{ in whole pellets (468)}} = \frac{\text{No. of broken pellets } (x)}{\text{No. of } \textit{Microtus} \text{ in broken pellets (257)}}$$

$$x = 109.8$$

Since the items in this collection proved so closely comparable to those in subsequent examinations, discussion of the individual species and their significance may well be deferred until other tables are presented. The high incidence of the meadow mouse (81.0 percent) here shown proved to be a decidedly average figure, which rose 10 percent or more in the following year of high *Microtus* availability, and declined 10 to 20 percent when the meadow-mouse population was reduced. The scarcity of rats (0.1 percent) and house mice (0.8 percent) is readily apparent, although both were available in the immediate vicinity, suggesting, as others have observed. that the owls may go farther afield for their prey. The relatively small take of birds (2.2 percent), however, was largely of English sparrows and starlings (16 out of 20), which did live with the owls in the barn, although there is no certainty that this was their place of capture. Only four native songbirds (0.4 percent) appeared in the collecton—two savannah sparrows *(Passerculus sandwichensis),* an unidentified fringillid which may well have been another savannah sparrow, and an unidentified, non-fringillid passerine.

In comparing the prey from the 200 whole pellets with that from

TABLE 3—*Analysis of a 1945 spring collection of pellets found in Neller's barn*

Prey animals	In 200 whole pellets		In 110 broken pellets		Total	
	Number	Percent	Number	Percent	Number	Percent
Microtus	468	83.4	257	76.9	725	81.0
Peromyscus	30	5.3	33	9.9	63	7.0
Zapus	8	1.4	11	3.3	19	2.1
Mus	4	0.7	3	0.9	7	0.8
Synaptomys	3	0.5	1	0.3	4	0.4
Total mice	513	91.4	305	91.3	818	91.4
Blarina	30	5.3	15	4.5	45	5.0
Sorex	5	0.9	2	0.6	7	0.8
Cryptotis	1	0.2	1	0.3	2	0.2
Condylura	1	0.2	1	0.3	2	0.2
Rattus	—	—	1	0.3	1	0.1
BIRDS*	11	2.0	9	2.7	20*	2.2
Total prey	561	—	334	—	895	—

*English sparrow, 10 (1.1 percent), starling, 6 (0.7 percent), Savannah sparrow, 2 (0.2 percent), Unidentified, 2 (0.2 percent).
Average *Microtus* per pellet 2.34
Average mice per pellet 2.56
Average prey item per pellet 2.80

the pieces and debris (Table 3), there is a strong suggestion that pellets made of the smaller mice *(Peromyscus, Zapus* and *Mus)* break up more readily than the more compact pellets composed entirely or largely of *Microtus* remains. Though perhaps less evident, it is equally true that pellets of avian material may fall apart quite easily and the skulls become separated from other parts. Thus an analysis of selected samples of only the whole pellets, as has been made by some investigators, may not be a strictly accurate criterion of the actual prey.

MONTHLY TRENDS IN ONE YEAR'S PREY

Fortunately, and a little surprisingly, the owls returned in mid-July to this 1945 spring nesting site in Neller's barn, reared a late summer or fall brood, remained over winter, and re-nested in the spring (1946), thus permitting an accurately dated collection of pellets, usually from a known number of owls, over a period of nearly a year. A detailed chronology follows for these owls and their two broods of young during this period of continuous occupancy of the barn from mid-July 1945 to mid-June 1946. Table 4 presents, and the following chronology explains, the results of the pellet examination, including: (1) the monthly trends in prey, (2) the number of pellets

TABLE 4—*Monthly trends in one year's prey of the barn owl, July 1945 to June 1946*

Prey animals	July-Sept. 64 pellets 2 adults and 7 young*	October 126 pellets 2 adults and 5-7 young	November 145 pellets 4-5 owls	December 60 pellets 2-5 owls	January 28 pellets 1-2 owls	February 40 pellets 1-2 owls	March 32 pellets incubating female	April 120 pellets female and 4 young	May 84 pellets female and 3-4 young	June 6 pellets nest litter (100± pellets)	Totals 805 pellets
Microtus.....	160 (92.0%)	328 (92.4%)	422 (90.2%)	143 (88.3%)	63 (96.9%)	68 (89.5%)	47 (94.0%)	260 (95.2%)	268 (94.4%)	337 (93.6%)	2096 (92.5%)
Peromyscus..	6 (3.4%)	6 (1.7%)	7 (1.5%)	5 (3.1%)	1 (1.5%)	2 (2.6%)	3 (6.0%)	5 (1.8%)	7 (2.5%)	6 (1.7%)	48 (2.1%)
Synaptomys..	... .	... .	4 (0.8%)	1 (0.6%)	... .	... .	... .	3 (1.1%)	1 (0.4%)	1 (0.3%)	10 (0.4%)
Mus.....	... .	4 (1.1%)	1 (0.2%)	... .	... .	... .	... .	1 (0.4%)	... .	... .	6 (0.3%)
Zapus.....	3 (1.7%)	... .	... .	... .	... .	... .	... .	... .	... .	1 (0.3%)	4 (0.2%)
Total mice.	169 (97.1%)	338 (95.2%)	434 (92.7%)	149 (92.0%)	64 (98.4%)	70 (92.1%)	50 (100%)	269 (98.5%)	276 (97.3%)	345 (95.9%)	2164 (95.5%)
Rattus.....	1 (0.6%)	2 (0.6%)	1 (0.2%)	... .	... .	1 (1.3%)	... .	1 (0.4%)	... .	... .	6 (0.3%)
Blarina.....	2 (1.1%)	14† (3.9%)	33 (7.1%)	8 (4.9%)	1 (1.5%)	4 (5.3%)	... .	3 (1.1%)	8 (2.8%)	15 (4.2%)	88 (3.9%)
Cryptotis....	... .	1 (0.3%)	... .	1 (0.6%)	... .	... .	... .	... .	... .	... .	2 (0.1%)
Birds.....	2 (1.1%)	... .	... .	4 (2.5%)	... .	1 (1.3%)	... .	... .	... .	... .	7 (0.3%)
Total prey.	174 (100%)	355 (100%)	468 (100%)	162 (100%)	65 (100%)	76 (100%)	50 (100%)	273 (100%)	284 (100%)	360 (100%)	2267 (100%)

*Mainly from adults, young not contributing much till late September.
†All but 2 or 3 taken *after* October 22.
‡2 English sparrows, parts of 2 starlings, pieces of 2 pigeon squabs, and 1 song sparrow.

on which the observed trends are based, (3) the probable number of owls producing the pellets each month, and (4) the total prey animals and percentages.

July to September—Pertinent data for the initial stages of this interesting late summer-fall nesting are not available, as the barn was not visited between July 1 and October 3. On the former date there were no owls, for they had apparently vacated the barn with their spring young in June; on the latter date, there were seven more young in various stages of development in the nest. Since the oldest bird was probably 45-50 days old (Sumner, 1933, 1933a), it is inferred that the owls started laying near mid-July, laid the seven eggs over the latter half of the month (probably in 14 days), the young hatching over a similar spread of time during the latter half of August (see nesting data), to produce young from a little over 30 to little under 50 days of age in early October.

Pellet data for the late summer months are necessarily combined. The 64 pellets available for this period were mainly from the adults. The young, though hatching in August, probably do not form pellets very regularly during their first 2 or 3 weeks of nest life (Errington, 1932; Sumner, 1933), apparently digesting many of the bones to satisfy calcium requirements (Errington, 1932), a dietary feature lacking in adults (Reed and Reed, 1928). Thereafter, for about 4 to 6 weeks, the more regularly formed pellets are ejected into the nest and trampled under-foot. By late September, however, the older young may have cast some of their pellets over the nest box onto the platform and floor.

Pellet recovery from the adults is also incomplete. During incubation (at least a 42-day period from the laying of the first egg to the hatching of the last in a 7-egg nest) part of the pellets are dissected for nest material. Contributions from the non-incubating bird are uncertain, but floor pellets away from the nest were of course from off-nest birds. Altogether these losses—food of the early young, unrecovered material in trampled and dissected pellets, some probable ejections of the adults away from the barn—must deduct considerably from the total prey.

July-September prey in the 64 pellets (Table 2) totaled 174 vertebrate individuals, of which 160 (92.0 percent) were meadow mice *(Microtus pennsylvanicus pennsylvanicus)*. Two other species of mice, 6 deer mice *(Peromyscus* sp.) and 3 meadow jumping mice

(Zapus hudsonius hudsonius), boost the total mice to 169, or 97.1 percent. The remaining prey, 1 rat *(Rattus norvegicus)*, 2 short-tailed shrews *(Blarina brevicauda kirtlandi)* and 2 birds – an English sparrow *(Passer domesticus domesticus)* and a song sparrow *(Melospiza melodia euphonia)*–were decidedly minor items in the late summer bill of fare.

Not included in these totals is an even greater number of uneaten mice (189) that were brought in and discarded on the floor of the barn (see section on "Food Storage at the Nest").

October–Seven young were in the nest during the first part of the month, and five to six young were in and out of the nest on adjacent perches during the latter part of the month. One bird died about mid-month, apparently as a result of a back injury sustained in a fall from the nesting box on October 11 during a combat with another bird, which precipitated both of them to the floor in a clinch (young owls lie on their backs when disturbed and clutch blindly at anything in reach, including their nest sibs). Another of the young was taken home on October 22 for feeding experiments. Thus the 126 October pellets include those retrieved from the nest in the early part of the month (incomplete) and those recovered from the five or six owls in the barn after nest-leaving (probably complete); the contributions of the adults, as usual, are uncertain.

The 126 pellets contained 355 prey animals (2.78 vertebrate items per pellet), 328 or 92.4 percent of which were *Microtus*. The only significant species changes, in comparison with the July-September period, were the early (too early?) disappearance of jumping mice, which of course hibernate, and the rise in shrews toward the close of the month, all but 2 or 3 of the 14 (13.9 percent) being taken after October 22. Considering the large number of animals taken (355), the complete absence of birds is perhaps noteworthy, as is the paucity of rats (2) and house mice (4).

November–The number of owls inhabiting the barn through November in uncertain. Four were counted on three of the visits between October 31 and December 1, and five were seen on the latter date, but it was difficult to enter the upper story of the barn (via a stairway covered by a heavy trap door) and get a quick and accurate count of the owls as they hastily departed through the broken windows. From these observations, as well as from the pellet count (145 for the month), it seems probable that four or five owls roosted

more or less regularly by day in the barn (roughly a pellet per day per owl).

Pellets and prey reached a maximum in November. Pellet size, as based on weight, measurements, and prey contents, reached a maximum not again attained or rivaled until May, when the young of the spring brood were leaving the nest (Table 2). The 64 November pellets critically examined averaged 7.8 grams each, measured 57 by 32 mm. and contained 2.92 *Microtus*, or 3.37 prey items, per pellet. The largest (also the largest for the year) weighed 17.2 grams, was 109 by 35 mm., and contained 7 *Microtus* plus a shrew. Four other November pellets contained 7 *Microtus* each. This probably denotes large meals by hungry young, though this interpretation is not unquestionable.

The take of *Microtus* dropped 2 percent, owing to the apparently characteristic increased catch of shrews in the fall months. The 468 vertebrates taken included 422 *Microtus* (90.2 percent) and 33 *Blarina* (7.1 percent), with smaller numbers of deer mice (7, or 1.5 percent), bog lemmings—*Synaptomys cooperi cooperi*—(4, or 0.8 percent), a house mouse (1, or 0.2 percent), and a rat (1, or 0.2 percent).

December—The five owls counted in the barn on December 1 apparently declined to one or two for most of the month. The 60 pellets obtained suggest an average of two birds roosting in the barn, possibly the original pair, with their young dispersed. One of the October-banded young was reported recovered (shot?) nearby in early December.

Table 2 illustrates a general reduction in pellet size and contents for the month, the average weight dropping from 7.8 grams in November to 7.1 grams in December, and the average prey from 3.37 to 2.69. This suggests smaller meals, but whether this is due to more limited rations, to increased maturity and lowered food requirements of the owls, or to more frequent but smaller meals because of the increased hunting time in the longer winter nights, is not certain.

The December findings disclosed a drop in *Microtus* to 88.3 percent, the lowest for the year. A higher than average take of shrews (5.5 percent) and *Peromyscus* (3.1 percent), and a record take of birds (2.5 percent) made up the balance. The exact avian prey is a little dubious. One pellet contained a considerable part of a starling *(Sturnus vulgaris vulgaris)*, including the skull, while another pellet contained more starling parts, without a skull. Two other pellets

contained traces of pigeons *(Columbia livia).* Uneaten prey on the floor included parts of at least three starlings (three right wings, two left wings, one head and separate hindquarters, as well as a partly formed pellet of undigested feet and leg bones), and two pigeon squab wings of different sizes (98 and 113 mm., respectively, with the primaries not fully unsheathed. This uncertain evidence of a December kill for two pigeons (the birds may have been carrion) is my first and only record of barn owls utilizing the pigeons that nested throughout the year in the barn.

January—Two owls were in the barn on January 1, but only one on February 2, at the time of the author's next visit. The 28 pellets obtained point to the probability of only one resident owl during January, though other explanations are conceivable. The further reduction in pellet size (from 7.1 grams to 6.2 grams in weight, and from 2.69 to 2.30 average prey items) is evident from Table 2, and its possible explanation has been commented on in the December account.

Of the 65 prey animals found in the January pellets, all but two (a *Peromyscus* and a *Blarina)* were *Microtus,* the highest yield of meadow mice for the year (96.9 percent). The small number of pellets available, however, render these figures less significant, though the almost complete absence of other prey re-emphasizes the dependence of the owls on the *Microtus* population.

February—Again one owl is believed, on the basis of the single observation cited as well as the pellet number (40), to have roosted in the barn by day, though possibly a second owl (the male?) frequented the building part of the time. The 40 pellets collected were smaller than those for any previous month, averaging only 5.0 grams in weight, and containing only 1.69 *Microtus* (or 1.86 prey items) per pellet. This is further emphasized by the fact that 28 January pellets yielded 63 *Microtus,* while 40 February ones gave only 68 (5 additional mice for 12 additional pellets). The larger number of pellets for the month can be accounted for by their smaller size, which causes more frequent formation, or by some contributions from the second bird, which the March nesting proves existed.

Microtus representatives in the February prey dropped to 89.5 percent, a slightly smaller percentage than for any previous or subsequent month except December. Items making up the remaining

11.5 percent were two deer mice, one rat, four shrews, and an English sparrow.

March—March was a month of egg-laying, incubation, and food storage, features already commented on under "nesting notes." One egg and 13 mice were in the nest box with the incubating owl on March 2, and by March 16 the clutch of seven eggs was complete, with 45 mice and a star-nosed mole conveniently cached nearby, a decline from the 80 mice on hand on March 10. On March 31 the first chick was in the nest, probably hatching the previous day.

Coincident with this abundant larder of stored mice, March pellets reached their minimum in size and contents, averaging 4.6 grams in weight (compared to 7.8 in November) and 1.68 items per pellet (compared to 3.37 for November). A ready explanation for this is that the incubating bird probably ate smaller meals more frequently, even during the day. In that way several small pellets (up to a possible maximum of four) would be produced instead of one or two larger ones. Further evidence of casual snatches from the larder was found in the pellets examined. Of the 20 whole ones available for analysis, 10 were incomplete in skeletal materials (heads were eaten separately from the bodies).

Prey items derived from the few March pellets (32) are of special interest in that, for the first time, mice made up the full 100 percent (94 percent *Microtus* and 6 percent *Peromyscus*). The sample is small, but that it presents a nearly true picture is indicated by the appearance of only one other item (a star-nosed mole) among the hoarded mice at the nest during this month.

April—Hatching and mouse-hoarding continued through the first part of April. By April 13, the fourth and last chick had emerged (three eggs did not hatch), and the mouse count was up to 71, the maximum for the month. The mice rapidly declined, however, coincident with the growth of the owlets and warmer weather, and in 7 days all but four had disappeared.

The 120 pellets recorded for April are an approximation. Only 37 whole or nearly whole pellets were secured, but enough pieces, litter and loose skulls (some possibly leftovers from March) were salvaged from the nest to account for about 83 additional ones (on the basis of 2.2 *Microtus* per pellet, the average found for the 20 April pellets examined).

As might be expected from the account of stored mice, microtine contents in the pellets ran high. Of the 273 prey animals identified, 260 (95.2 percent) were *Microtus*, and 9 of the remaining 13 prey animals were of other species of mice (5 *Peromyscus*, 3 *Synaptomys*, and 1 *Mus*). One rat and 3 shrews (*Blarina*) made up the remainder. There were no avian victims during the spring months, March to June inclusive.

May—Four young were in the nest until May 9, when one jumped out and broke his leg.[1] The other three remained in the nest another week, but thereafter, for the rest of the month, took occasional excursions about the floor and occupied various perches in the barn.

Only 10 whole pellets were recovered for the month, but three boxes of litter from the nest gave supplementary information concerning the prey. The 10 pellets, however, included no small ones, so that they exceeded the November high in average weight and contents, perhaps not a true picture. Using the average *Microtus* content per pellet (3.2) to calculate the number of pellets that the litter would represent gives only 84, too low a number for three or four hungry young and their parents. After the young left the barn in early June, the equivalent of about 100 pellets (over 300 skulls) was found in the nest box. Many of these undoubtedly belonged in the May count, but some probably were left over from earlier months, particularly March, and possibly even from the preceding fall.

Prey representations in the May pellet material differed but slightly from previous months. Of the recovered animals 268 or 94.4 percent were *Microtus*, with enough other mice (7 *Peromyscus* and 1 *Synaptomys*) to raise the catch of mice to 97.3 percent. Eight shrews were the only other items. Inclusions in the June litter were very similar, the slightly higher percentage of shrews (4.2 percent) suggesting that possibly *Blarina* skulls drop out of pellets more readily than *Microtus*. One jumping mouse (*Zapus*) was recovered from the nest litter, the first occurrence of this species since September of the preceding year.

June—The three young left the barn sometime in early June. All three were present on June 5, one taking immediate exit through an open window, one remaining perched securely on a high hayfork carrier, the third running wildly about on the floor. On June 14, only

[1]This young bird, the subject of the feeding experiments described in the section on pellet studies, recovered from the broken limb, although the bones were out of alignment, and became a remarkably tame and docile pet, finally flying away on July 19.

one bird was seen (probably an adult), and on the following day there was a fresh egg in the nest box with an adult owl in attendance, the beginning of a fourth consecutive nesting within a 16-month period. Two more eggs were laid, apparently on alternate days, and then the owls disappeared. An empty cartridge on the floor under the nest suggested the explanation, and later a nearby resident admitted he had shot the owls on the grounds that they were eating the pigeons, beside which they had nested without apparent conflict for several years.

Summary for the Year—Although discussion of the individual prey items utilized by the owls in this particular year may best be deferred to a later section, a brief analysis of the principal trend may serve a useful purpose here. The outstanding feature, obviously, is the surprisingly high incidence of *Microtus* in the diet, which for the monthly periods varied from a low of 88.3 percent (higher than most averages) in December to a high of 96.9 percent in January, averaging 92.5 percent for the whole year. This is higher than any known published figure, and suggests, as later events seemed to confirm, that the period coincided with the probable peak of the *Microtus* cycle. In subsequent analyses, at another station, the *Microtus* catch dropped to as low as 57 percent for the lowest period. Reports of local mammalogists and some trapping reveal an abundance of mice during the winter of 1945-46, with a decline apparently setting in gradually during the summer and fall of 1946[1] (see Fig. 2).

With so high an incidence of meadow mice, other mice were relatively unimportant. *Peromyscus*, apparently all *bairdii* (48, or 2.1 percent), was the only species that amounted to more than 1 percent. The three remaining species (bog lemming, house mouse and jumping mouse) altogether amounted to only 0.9 percent, though the latter of course were not available during the winter. Rats were likewise notably few (6, or 0.3 percent).

Shrews were the only other items of importance and these – 88 *Blarina* and 2 *Cryptotis*, together amounting to 4 percent – were taken less frequently than in other periods, or in other studies. The take of birds (7, or 0.3 percent) included only one native songbird (a song sparrow) among the 2,267 prey items.

[1]D. L. Allen (verbally) reported an abundance of *Microtus* at the Rose Lake Wildlife Experiment Station during the winter of 1945-46; his statement probably was based on J. P. Linduska's unpublished trapping data. D. W. Hayne found *Microtus* disappearing during May 1946, on one College Farm plot but not on another, while on a third area they were still numerous in October. In the spring of 1947 the mice were at a low level in all the areas inspected. His data suggest sudden local declines, and gradual failure over wider areas.

It was hoped that a year of close observation of this nature would be an accurate criterion for measuring the total prey for the period, but it now appears that there are so many unrecovered items – from the food of the young, pellets of the non-incubating bird, those lost on nocturnal forays – that the figures obtained are considerably less than the total consumption. Identified items, however, total 2,267 vertebrate prey animals for the adult owls (probably one pair) and their two broods of six and four fledged young for the period from mid-July 1945 to mid-June 1946.

THE CAMPUS STATION

HISTORY

It is not known when barn owls first became a part of the campus avifauna. They apparently were not resident here at the time of the publication of Barrow's "*Michigan Bird Life*" (1912). During the next 2 decades, definite records also seem to be lacking, until in 1932 Professor J. W. Stack banded a young bird caught in Demonstration Hall. Since then, sight records have been frequent enough to suggest that the owls have probably been essentially permanent though perhaps irregular residents about the campus.

A favorite roost, continuously occupied during at least the past 3 years, has been the dense grove of planted conifers adjacent to the stadium. Other birds, presumably strays from this colony, have taken up their (usually) solitary abode in various campus buildings, such as the Horse Barn and a silo at the Beef Barn. In the summer of 1946, as already noted, a pair nested, with only partial success, on the open roof of Beaumont Tower.

The chief source of pellets, however, has been the conifer grove near the stadium. This productive roost was first disclosed to the author by Fred Hall, a forestry student, in the spring of 1945 (April 14). At that time the ground beneath some of the trees was littered with an amazing display of pellets. Largely out of curiosity, he and the author and Dale Zimmerman of Imlay City picked up a sample sackful of perhaps a hundred or more pellets, and Mr. Zimmerman took them home. Nothing further was done about the matter until September, when the author returned and gathered up all the available material, including hundreds of weathered skulls from which the binding material had long since dissolved away.

It is assumed that this was largely the summer's accumulation of material, with many of the free skulls dating back into spring or even

earlier (the owls had obviously wintered there). Even under the protective canopy of dense evergreens, which prolongs the resistance of pellets to weathering (Errington, 1940; Wilson, 1938), whole pellets or pieces of pellets probably did not date back earlier than midsummer, but there is no reason to suppose that the free skulls were not much older. As can be seen from Table 5, this summer collection was a large one, comprising 1,357 skulls, and perhaps denoting the daily roost of a good-sized family of owls, although their spring nesting site, if they had one, was not known that year.

Thereafter monthly collections were made through fall and winter, up into April 1946, when the findings became so unreliable, owing to the irregular habits of the owls, that only occasional collections were made. This was perhaps caused by the large influx of students on the campus who may have disturbed the birds. Including these unavoidably meagre 1946-47 samples, however, the station afforded material over nearly a 3-year period, apparently covering both a high and a low in the *Microtus* cycle.

ANALYSIS OF COLLECTIONS

Table 5 presents the analysis of these periodical collections from the campus stations (including 175 skulls from Beaumont Tower for July 1946, and 89 skulls from the Beef Barn silo for August 1946), for the period from the spring of 1945 through October 1947. The graph

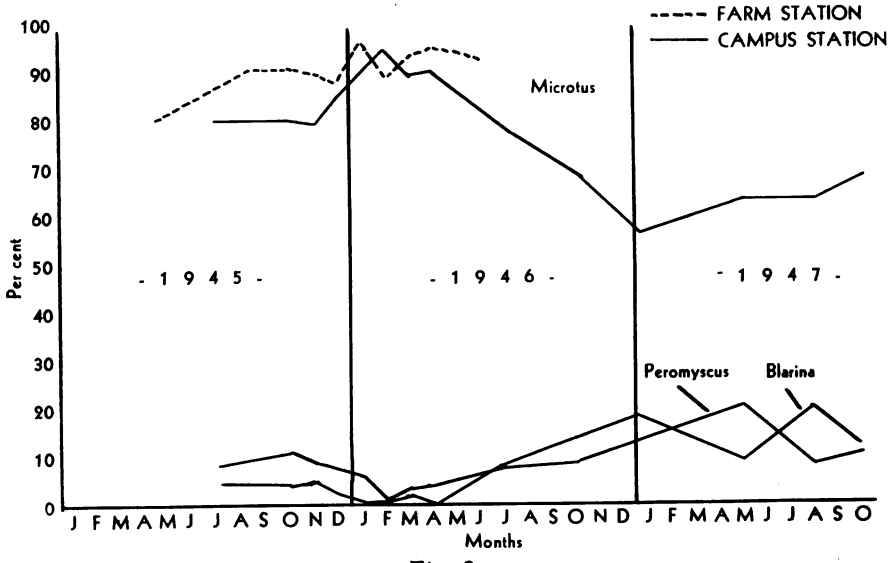

Fig. 2.

TABLE 5--*Fluctuations in the catch of prey species by barn owls on M.S.C. campus, 1945-47*

	Microtus		*Peromyscus*		*Zapus*	*Mus*		*Synaptomys*	*Blarina*		Other Shrews	Moles	Rats	Miscellaneous	Birds		Total
	Number	Percent	Number	Percent	Number Percent	Number	Percent	Number Percent	Number	Percent	Number Percent	Number Percent	Number Percent	Number Percent	Number	Percent	
Summer 1945	1107	(81.5)	65	(4.9)	26 (1.9)	8	(0.6)	5 (0.4)	117	(8.6)	8 (0.6)	3 (0.2)	1 (0.1)	2 (0.1)	15	(1.1)	1357
October 1945	232	(75.8)	14	(4.6)	11 (3.6)	3	(1.0)	.....	37	(12.1)	1 (0.3)	.....	1 (0.3)	.....	7	(2.3)	306
November 1945	251	(80.0)	17	(5.3)	.....	3	(0.9)	2 (0.6)	30	(9.3)	4 (1.2)	.....	3 (0.9)	.....	3	(0.9)	323
December 1945	169	(86.2)	7	(3.6)	.....	3	(1.5)	.....	17	(8.7)	.....	.....	.....	.....	.....		196
January 1946	147	(92.0)	2	(1.2)	.....	.....		.....	9	(6.0)	1 (0.6)	.....	.....	.....	1	(0.6)	160
February 1946	176	(95.1)	3	(1.6)	.....	1	(0.5)	.....	3	(1.6)	2 (1.1)	.....	.....	.....	.....		185
March 1946	180	(90.4)	8	(4.0)	1 (0.5)	1	(0.5)	.....	6	(3.0)	.....	.....	.....	.....	3	(1.5)	199
April 1946	117	(91.4)	5	(3.9)	.....	.....		2 (1.6)	1	(0.8)	1 (0.8)	.....	.....	.....	2	(1.6)	128
May-September 1946	367	(79.1)	35	(7.6)	12 (2.6)	1	(0.2)	.....	39	(8.4)	4 (2.0)	1 (0.5)	2 (0.4)	.....	3	(1.5)	464
October-November 1946	60	(69.0)	8	(9.2)	2 (2.3)	.....		.....	13	(14.9)	.....	.....	.....	.....	4	(4.6)	87
Nov. 15-February 1947	57	(57.6)	14	(14.1)	1 (1.0)	1	(1.0)	.....	18	(18.2)	2 (2.0)	.....	1 (1.0)	.....	5	(5.1)	99
March-July 1947	27	(64.3)	9	(21.4)	2 (4.8)	.....		.....	4	(9.5)	.....	.....	.....	.....	.....		42
August-September 1947	37	(63.8)	5	(8.6)	2 (3.4)	1	(1.7)	.....	12	(20.7)	.....	.....	.....	.....	1	(1.7)	58
October 1947	33	(68.7)	5	(10.4)	.....	2	(4.2)	.....	6	(12.5)	.....	.....	.....	.....	2	(4.2)	48
Totals	2970		197		57	24		9	312		23	4	8	2	46		3652

(Fig. 2) illustrates the fluctuations in the *Microtus* catch, and the compensatory upward trend in shrews *(Blarina)* and deer mice *(Peromyscus)*. Of particular interest in this graph is the conspicuous decline in *Microtus* from a peak of 95.1 percent in February 1946, to a low of 57.6 percent the following winter (November 15 through February 1947), in apparent correlation with the actual trend in the local meadow-mouse cycle. An unavoidable weakness in these data, however, is the meagreness of the collections during the final phase of the study, and, disturbingly enough, a barred owl *(Strix varia varia)* was found on the area 2 months after the last collection was made. Fortunately a barn owl was seen at the roost at the time of the last two collections.

DISCUSSION OF PREY SPECIES

Microtus—In all of the preceding tables and accounts, as well as in the table of summaries for both stations for the whole period (Table 6), the important role of the meadow mouse *(Microtus pennsylvanicus pennsylvanicus)*[1] is obvious at a glance. In the campus collection of 3,655 skulls, collected over a 3-year period covering both a high and a low of the *Microtus* cycle, 2,970 or 81.3 percent were this species. In the collection from Neller's barn, comprising 3,160 prey animals taken mainly during a high *Microtus* year, meadow mice averaged 89.3 percent—or a combined total from the two stations of 5,791 mice of this species, averaging 85.0 percent. Since most of the Neller's barn collections, and a major portion of the campus materials, were taken during a period of high *Microtus* availability, it is evident that these percentages are a little high.

Studies by other investigators in the Great Lakes States disclose similar, though usually lower, percentages. An Ann Arbor collection of 619 barn-owl pellets examined by Wilson (1938), yielded 1,887 *Microtus* (90.6 percent), likewise an unusually high figure. However, Wilson states that he selected only well-formed pellets of mammalian remains (his chief interest was in a comparative study of pellet form and sizes), which might result in a disproportionate loss of small skulls—particularly of *Peromyscus, Zapus* and *Mus*—and of birds, raising his percentage of *Microtus* unduly. The only other Michigan figures available are those of Moore's (1945) examination of 91 pellets from an Ann Arbor spring nesting site in 1944. These gave 82.1 per-

[1]All of the toothed skulls were checked with a hand lens for possible examples of *Microtus ochrogaster*, a more western form known to occur in southwestern Michigan, but none was found.

cent meadow mice, closely comparable to my 1945 spring nesting collection (81.0 percent) before *Microtus* took a sudden upward sweep (Fig. 2).

The only really large-scale study for another northern state is that of Stupka's (1931) in Ohio, the results briefly published in mimeographed form. Stupka's figures, based on a total of 8,151 skulls from three regions in Ohio gave 79.7 percent *Microtus* for a Columbus (campus) collection, 80.4 percent for Buckeye Lake (see also Trautman, 1940), and 76.8 percent for a Toledo lot. Errington's (1932) analysis of a smaller Wisconsin collection (319 pellets, 893 skulls) gave a typical 83.1 percent *Microtus*. A recent Indiana study (Kirkpatrick and Conway, 1947), however, is not strictly in agreement with other northern states, for *M. ochrogaster* predominated over *M. pennsylvanicus* and the two together constituted only 56.2 percent of the barn owl's diet.

The figures from East Lansing, with supporting data from Ann Arbor, Ohio, and Wisconsin, suggest that in ordinary times close to 80 percent of the barn owl's diet is of *Microtus*, and that during periods of abundance of these rodents, the catch may rise to 90 percent or more, or drop correspondingly during periods of low availability.

This highly microtine diet of the owls leaves little doubt as to their general beneficial influence, but how effective the *Microtus* removal is from an agricultural standpoint is unknown. Elton *et al* (Chitty, 1938) have estimated that during an outbreak of voles on the Scottish border, 8 resident short-eared owls removed only .02–0.5 percent of the vole population per night, making little or no impression on the total, but subsequent failure of the voles by epidemic disease caused a sharp decline in the owls to a single resident pair. On the other hand, Russian investigators, Kalabukhov and Raevskii (Errington, 1946), by recovering banded mice from pellets of predatory birds, calculated that 1.5 percent of the local population of mice was removed every day, and another worker, Klinov, describes a situation where an initial population of 58 rodents per acre was reduced to about 9 per acre in a month. Obviously there are too many uncertainties concerning predator-prey relationships to justify conclusions here. Errington's detailed recent paper (1946) discloses some of the complexities involved. Further studies of barn owl prey might well attempt to measure the effectiveness of the removal of the prey by the predators.

Other Mice—Four other species of mice, comprising 451 individuals (6.6 percent of the total prey), bring the total catch of mice to 6,242 animals or 91.6 percent. Of these, only deer mice of the genus *Peromyscus* appear to be of more than incidental occurrence in the diet. Though the *Peromyscus* totaled only 308 individuals (4.5 percent), they were taken at all seasons of the year, and during the period of microtine scarcity, they rose to a temporary high of 21.4 percent for the period of March-July 1947, when the catch of meadow mice had dropped to 64.3 percent. Thus *Peromyscus* shares with *Blarina* the shift in predation when *Microtus* declines.

Since the occipital region of a *Peromyscus* skull in pellets is invariably crushed or entirely lacking, specific identifications by the standard skull measurements is not possible. The following listing, however, gives measurements for 159 unbroken right mandibles (the left was used in known pairs when the right was damaged), the measurements taken to the nearest 0.5 mm. from the tip of the condyle to the end of the incisor:

Length in mm.	Number of Mandibles
12	3
12.5	5
13	16
13.5	27
14	47
14.5	32
15	26
15.5	1
16	2

According to Dice's extensive measurements of *Peromyscus* mandibular variations (Dice, 1932, 1937), all but three of the jaws are typical of the prairie deer mouse *(Peromyscus maniculatus bairdii)*. One (15.5 mm.) is somewhat intermediate, and the two 16-mm. mandibles may well be the larger woodland form *(Peromyscus leucopus noveboracensis)*. This is as might perhaps be expected, since barn owls hunt mainly, if not entirely, in *bairdii* habitats in open terrain. The four whole specimens brought by owls to the nesting site in 1946 were definitely *bairdii*.

The remaining mice included 80 meadow jumping mice *(Zapus hudsonius hudsonius)*, 1.2 percent of the total prey; but the catch of this species rose, perhaps accidentally, to 3.6 percent for October,

1945 (before the *Microtus* decline), and to 4 percent for the summer of 1947, when *Microtus* was still relatively scarce after the previous winter's slump. This hibernating form was, of course, not available during the winter of 1946-47 when the *Microtus* supply was limited. Its earliest occurrence was in a March 1946 pellet (presumably late March), and it was usually absent from November collections; one recovered after November 15 in 1947 may have been overlooked in picking up the October pellets. All the available upper jaws were carefully checked for *Napaeozapus,* the more northern form, but none was found.

The limited occurrence of the house mouse *(Mus musculus musculus),* only 37 individuals (0.5 percent) among the 6,815 prey animals, is perhaps a little surprising. The majority of these (24) were in the campus collection, where a genetical laboratory using mice of this genus may have made some escapees available and may thus have influenced the catch. Wilson (1938) and Moore (1945) found no house-mouse remains in the Ann Arbor pellets. The species was also poorly represented (less than 1 percent) in Stupka's extensive collections in Ohio. The chief exception to this prevailing observation is a small collection of 54 pellets from Philo, Illinois, in which Cahn and Kemp (1930) found 42 percent house mice and only 14 percent *Microtus,* a peculiar reversal of the usual picture. House mice ran comparatively high (24 percent) in Fisher's (1896) Smithsonian Tower pellets in Washington, D. C. Available hunting grounds undoubtedly influence selection; even barn owls in buildings often go far afield for their prey.

The only other mouse species found in the East Lansing prey was the bog lemming *(Synaptomys cooperi cooperi).* There were 23 of these (0.3 percent), sparingly spread over all seasons at both stations. Their scarcity, rather than implying local rarity, may merely indicate that barn owls do not hunt in *Synaptomys* habitats regularly. Long-eared owls nesting in tamarack swamps (author's unpublished data) take a heavier toll of bog lemmings.

Table 6 lists three unidentified mice. These were the toothless palates of *Peromyscus, Zapus,* or *Mus.* Originally a fairly large category of "questionable *Microtus*" was included in the data. In these individuals, the second and third diagnostic upper molars commonly used to identify *Pitymys* were lacking, but since none of the latter was found, the questioned items were finally included with *Microtus.* Failure to find any *Pitymys,* which occurs locally, was a little pro-

TABLE 6—*Barn owl prey at East Lansing, Michigan, 1945-47*

Prey animals	Campus		Farm		Total	
	Number	Percent	Number	Percent	Number	Percent
Microtus	2,970	81.26	2,821	89.27	5,791	84.97
Peromyscus	197	5.39	111	3.51	308	4.52
Zapus	57	1.56	23	0.73	80	1.17
Mus	24	0.66	13	0.41	37	0.54
Synaptomys	9	0.24	14	0.44	23	0.34
Unidentified	3	0.08	—	—	3	0.04
Total mice	3,260	89.19	2,982	94.37	6,242	91.59
Blarina	312	8.56	133	4.21	445	6.53
Sorex	21	0.57	7	0.22	28	0.41
Cryptotis	2	0.05	2	0.06	4	0.06
Rattus	8	0.22	7	0.22	15	0.22
Condylura	2	0.05	2	0.06	4	0.06
Scalopus	2	0.05	—	—	2	0.03
Mustela	1	0.03	—	—	1	0.01
Sylvilagus	1	0.03	—	—	1	0.01
Total mammals	3,609	98.74	3,133	99.15	6,742	98.93
Birds	46	1.26	27	0.85	73	1.07
Total prey	3,655	—	3,160	—	6,815	—

voking, since it signifies that more than 5,000 hand-lens examinations of microtine molars were absolutely futile. The apparent absence of this species is partially explained by its relative scarcity in the region (Burt, 1946), by its subterranean habits, which gives it some immunity, and by its preference for heavier cover than is characteristic of *Microtus*. Pine mice were also lacking in Wilson's (1938) and Moore's (1945) Ann Arbor examinations, and in Errington's (1932) Wisconsin pellets, but Stupka (1931) listed 35 pine mice in his Buckeye Lake collection of 5,137 skulls (none from Columbus or Toledo), and Fisher (1896) found 4 in his Smithsonian collection of 1,821 skulls.

Rats—Ever since A. K. Fisher's studies (1893, 1896) of the owls inhabiting the Smithsonian Tower in Washington, D. C., barn owls have been popularly supposed to live on rats and mice, though actually only 20 rats (7 percent) were recorded at that station. No published studies in the northern states have disclosed more than incidental preying on the Norway rat *(Rattus norvegicus)*. Fifteen rats (0.22 percent) were taken during the period covered by this paper, these mainly young animals. Rats inhabited the poultry houses be-

side the barn occupied by the owls, but the birds apparently went farther afield for their prey. Captive barn owls seemed unable, or at least reluctant, to handle full-grown live white rats, and had obvious difficulties dissecting the tough rodents. One owl worked for 2 hours beheading a large tethered specimen. Rats were absent from the Ann Arbor studies quoted above, and were decidedly minor items in Ohio (0.68 to 1.62 percent at three stations) and Wisconsin (0.9 percent), but in the southern states cotton rats and rice rats may figure more prominently in the diet, even being a leading or staple item in some cases (Baumgartners, 1944).

Shrews—The only non-rodentia appearing in significant numbers in the prey were shrews, the second most important item. These totaled 477 individuals (7.0 percent of the total prey) and included three species: 445 short-tailed shrews *(Blarina brevicauda kirtlandi)*, 28 masked shrews *(Sorex cinereus cinereus)*, and 4 least shrews *(Cryptotis parva)*.

In addition to occupying second place in the total count, shrews are the first items to jump into prominence when *Microtus* becomes less available. Table 5 and Fig. 2 illustrate this interrelationship between *Blarina* and *Microtus*, where any drop in the latter is compensated for, in part at least, by an increased take of shrews. Thus, *Blarina* rose to 18.2 percent when the *Microtus* figure dropped to its lowest point (57.6 percent), and stood at 20.7 percent during the late summer and fall. A slight upward trend in *Blarina* seems characteristic of the late summer or fall months, regardless of the trend of the *Microtus* cycle, and is presumably to be explained as the surplus of the summer's crop of young seeking new quarters, and becoming temporarily more vulnerable to predation.

There are indications, from other investigations, that shrews may at times become even more prominent than my results imply. In Williams County, Ohio, a small collection of 118 skulls from barn-owl pellets yielded 22.9 percent least shrews *(Cryptotis parva)* and 62.6 percent *Microtus*, while another collection of 77 skulls from Paulding County gave 22.1 percent least shrews and 48.1 percent *Microtus*, the further drop in meadow mice due to increased take of *Peromyscus* (Price, 1942). Davis (1938), in Texas, records a sudden switch from the usual barn-owl diet of rodents to a 41 percent take of *Cryptotis*, and suggests that mammalian remains in owl pellets may be a reliable criterion for measuring local outbreaks of small mammals.

Though it is not the intent of this paper to make a comparison with European studies, it is interesting to note that shrews play a much more important role in the diet of the European barn owl *(Tyto alba alba)* than is usual with the American form. Altum, in a study of 703 pellets (2,551 skulls), found 62.01 percent Insectivores, and Lataste, in 2,995 skulls, obtained 64 percent, where as Guérin's figures, based on an amazing total of 12,292 skulls over a longer span of time ranged from 15 to 49 percent, averaging 26.01 percent (Guérin, 1928).

Miscellaneous Prey—Among the other mammalian items, perhaps to be placed in the category of curiosities, that were found in the barn-owl diet at East Lansing, were four star-nosed moles *(Condylura cristata)* and two prairie moles *(Scalopus aquaticus machrinus)*. The campus collection included one skull of a young cottontail *(Silvilagus floridanus mearnsi)* and one of a least weasel *(Mustela rixosa allegheniensis)*. The latter is of additional interest because it appears to be the first record of this species for Ingham County, although it has been recorded for adjacent counties (Burt, 1946). Another star-nosed mole, and a second young cottontail (hardly larger than a full-grown mouse) appeared in the stored prey at the 1946 spring nesting site in Neller's barn, but failed to be recovered in the pellets for that month.

Mammals not found in the East Lansing prey, but recorded for other regions in Michigan and Ohio include a red squirrel *(Sciurus hudsonicus loquax)* at Ann Arbor (Wilson, 1938), and 56 bats in the Buckeye Lake pellets collected in the attic of a deserted schoolhouse inhabited by bats (Stupka, 1931). Fifty-three of the bats were little browns *(Myotis lucifugus lucifugus)* and three were big browns *(Eptesicus fuscus fuscus)*. Strangely, no ground squirrels *(Citellus)* have been found in any of the studies in the Great Lakes States, although they appear frequently in western reports.

Four crayfish claws *(Cambarus)* appeared in my campus material, but as it was not certain that they belonged with the barn owl pellets, they are not included in the tables. They may have been deposited by crows which also frequented the grove.

No positive identifications of insects were made in my pellet analyses, the few traces detected not being separable with certainty from the remains of dermestids and moths commonly associated with old pellets, or from the stomach contents of other prey. The author's

captive owl ate a few large earthworms, but would not eat June beetles. Insect remains seem to be found only rarely in barn-owl castings, with an exception perhaps in the not uncommon occurrence of Jerusalem crickets in California pellets. Their presence in stomach contents (Fisher, 1896) suggests that they do not persist well in pellets.

Birds—The data on birds furnish some interesting and perhaps unexpected features, particularly in view of the popular conception of the relationship between owls and other birds. A total of 73 birds (1.07 percent of the total prey) appeared in the East Lansing pellets, 46 in the campus collection, and 27 from Neller's barn. Of these, 50 were English sparrows *(Passer domesticus domesticus),* 15 were starlings *(Sturnus vulgaris vulgaris),* and 2 were pigeon squabs *(Columbia livia),* all commonly regarded as injurious or undesirable birds. Only six (0.08 percent) were native songbirds.

The following table (Table 7) summarizes this avian prey:

TABLE 7—*Birds found in 2,200 East Lansing barn-owl pellets*

Species	Number	Percent of bird catch	Percent of total prey
English sparrow	50	68.5	0.73
Starling	15	20.5	0.22
Rock dove	2	2.7	0.03
Savannah sparrow	2	2.7	0.03
Song sparrow	1	1.4	0.01
Unidentified passerines	3	4.1	0.04
Totals	73	100	1.07

From Table 7, it is evident that the total take of all birds is small (1.07 percent) and that most of these (67 out of 73, or 91.7 percent) are introduced (nuisance) birds. All but one of the campus avian victims were English sparrows or starlings, but the Hagadorn Road station included three native sparrows and two unidentified passerines.

There are indications (see Table 5) that in times of *Microtus* scarcity some attention may be diverted to birds. The catch of English sparrows and starlings on the campus rose to about 5 percent during the low phase of the meadow-mouse cycle. Errington (1932b) remarks that barn owls in Wisconsin failed to adapt themselves to

abundantly available avian prey when the *Microtus* supply gave out. In Ohio, Stupka (1931) found larger numbers and a greater variety (11 or more species) of birds, but the percentage was still low (1.07 to 2.04 percent at three stations).

Published exceptions to an almost strictly non-avian diet are found in some Carolina studies (Cotton and Nelson, 1937; Townsend, 1926), where rails and marsh birds figured prominently; in a few of the many western studies (Alcorn, 1942; Bond, 1939), where Brewer's blackbird seems to have borne the brunt of minor avian attacks; and in two extraordinary cases in the Pacific Northwest (Bonnot, 1928; Howell, 1920), where barn owls were found to be preying, at least temporarily, almost exclusively on an island population of petrels *(Oceanodroma leucorhoa beali).*

As already noted, the relationship between barn owls and pigeons, which frequently share the same shelter, is peculiar. In Neller's barn, pigeons nested at all seasons of the year in close proximity to the owls; one of the dove nests, in fact, was in a box on which the owl box rested, so that the young of both species were reared simultaneously within a few inches of each other (the box partitions between) without apparent harm to the pigeon squabs. The single exception to this apparently harmonious, or perhaps indifferent, relationship, was the finding, in December 1945, of two pigeon squab wings on the barn floor and two pigeon bills and a few bones in the pellets for that month, substantial evidence that parts of two young pigeons were eaten, though not absolute proof that they were killed by the owls. A number of observers have reported the seemingly friendly relationship between owls and doves in barns, belfries, and towers; but that this may not always prevail is suggested by observations by Jeanne Moore in Ann Arbor. During a 1944 spring nesting in the Engineering Tower (Moore, 1945), there seemed to be no conflicts between the two species, but on a subsequent visit in 1947 Miss Moore says that the owls appeared to have turned on the pigeons and slaughtered them.

Farmers are ever under the apprehension that all owls are a potential if not actual threat to domestic poultry, and barn owls are often shot (legally in Michigan) by farmers and hunters, the former probably in the earnest conviction that they are safeguarding their poultry, the latter usually for something to shoot at. Among the 6,815

prey animals now identified by the writer, there has been no suggestion of either domestic poultry or game birds. Only two instances of attacks on poultry have come to his attention: in a table compiled by Hawbecker (1945) for California, one *Gallus domesticus* was listed, without any data on the nature of the unusual incident; and Fisher (1896) found remains of poultry in one stomach, but none in pellets. Stupka (1931) found three bob-whites among his Ohio avian victims.

It is not meant to imply here that young chicks might not be vulnerable to barn owls in certain situations, but of course barn owls hunt at night, when poultry is in roosting quarters, and it is doubtful if grown chickens are in any danger. There is also the possibility that the soft bones and down of very young chickens, if eaten, would be completely digested, without detectable representations in the regurgitated pellet. Glading, Tillotson and Sellick (1943) have shown by experiment, as others have suspected, that juvenile birds may at times be so completely digested that telltale evidence is not always recoverable in the pellets.

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