

A LIFE-HISTORY STUDY OF THE TUFTED TITMOUSE,
PARUS BICOLOR LINNAEUS

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
William P. Pielou
1957

This is to certify that the
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 A Life-History Study of the Tufted
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presented by
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has been accepted towards fulfillment
 of the requirements for
Ph. D. degree in Zoology

George J. Wallace
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A LIFE-HISTORY STUDY OF THE TUFTED TITMOUSE,
Parus bicolor Linnaeus

By

William Percival Pielou

AN ABSTRACT

Submitted to the School of Graduate Studies of Michigan
State University of Agriculture and Applied Science
in partial fulfillment of the requirements
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DOCTOR OF PHILOSOPHY

Department of Zoology

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Approved George J. Wallace

A life-history study of the Tufted Titmouse, Parus bicolor, was the object of investigation from September 1953 to September 1955. The study is presented in two parts: (1) classification, nomenclature, and distribution; (2) observations on the annual cycle. The information in Part I was based on a review of the literature and extensive correspondence. The mapping of the distribution of the Tufted Titmouse in Michigan is based in part on the author's own observations but mainly on correspondence with ornithologists throughout the state.

The data presented in Part II were gained largely from field observations in three woodlots on the property of Michigan State University, East Lansing, Michigan. This was the principal objective of the research and included a study of: (1) the nesting cycle, from the time of pairing and separation of birds from the winter flocks to the dispersal of juveniles and formation of the fall flocks; (2) ecological relationships; (3) flock composition and behavior; (4) voice; (5) roosting; (6) food and feeding habits, based on stomach analyses and field observations.

Nesting Cycle. Pair formation, and separation of birds from the winter flocks, occurred in late March and early April. Nest construction, which was the duty of the female, began

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several days after pairing. Territory establishment seemed to coincide with nest construction. The male defended the territory until the young left the nest.

All nests were located in abandoned woodpecker holes or natural cavities in living deciduous trees. The average height of twenty nests was 38.5 feet. The loosely constructed nests all contained dried grass, moss, and hair, and often other miscellaneous items.

First eggs were laid from May 4 to May 11, and the eggs were deposited at the rate of one a day until the full complement of five or six was reached. Copulation was observed only during this period. Incubation was performed solely by the female and she was fed during both her attentive and inattentive periods by the male. Incubation lasted approximately thirteen days.

Hatching brought about a shift of the male's feeding attention from his mate to the young. The rate of feeding the young by both parents gradually increased until the young left the nest, fifteen days after hatching.

The young remained with their parents at least several days and in some cases the family group formed the nucleus of fall flocks.

Flocking. Flocks of titmice and associated species began forming as early as August. The size of the flock was variable

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but averaged seven birds. During their feeding excursions in the fall the titmouse groups were enlarged with migrant birds, especially warblers.

Voice. Of its variable repertoire the Tufted Titmouse's most commonly heard and characteristic song is the "peto, peto" expression. In addition it has a location note, alarm note, recognition note, hissing note, invitational note, begging note, and distress note.

Roosting. Roosting occurred in evergreen and deciduous trees and the birds roosted wherever they happened to be at sundown during the fall and winter. During the nesting cycle the female slept in the nest cavity while the male roosted nearby.

Food and Feeding Habits. Tufted Titmice consume two-thirds animal matter and one-third vegetable matter annually. Food was secured from the ground litter to the uppermost twigs of the tallest trees. Insects were gleaned mostly from the bark and leaves but hawking of insects was noted on one occasion.

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Introduction

The Tufted Titmouse, Parus bicolor Linnaeus, was selected as the subject for this investigation because of its permanent-resident status locally; because of its comparative tameness and availability for study; and because, despite the fact that it is a common bird, many aspects of its life history have not been recorded.

The chief purposes of the research were to learn more about the life history of the Tufted Titmouse in Michigan and to assemble all available data, both new and old, about its habits. The new facts about its habits were gained through a field study of its annual cycle in lower Michigan.

The material is presented in two parts: (1) classification, nomenclature, and distribution; and (2) the annual cycle in Michigan. The material included in Part I is a summary of the information obtained by a review of the literature and by correspondence with selected members of various state ornithological societies and other individuals. The events in the annual cycle are presented in the following order: pair formation and the coincident dispersal of the winter flocks, the nesting cycle, dispersal of juveniles, mortality, voice, flocking, roosting, and feeding.

Field observations were mainly limited to a two-year period, from September 1953 to September 1955. Additional

information on nesting habits is included from observations made during the spring of 1956. The study was conducted in three East Lansing woodlots belonging to Michigan State University. Titmice were banded from September to April during the study period. As part of the food-habits study, I examined the stomach contents of five adults.

Acknowledgments

The completion of this study was partially dependent upon information obtained from other individuals. Correspondence regarding observations in other Michigan localities was very helpful, and I am grateful to everyone who took time to answer letters and to offer information and suggestions.

Acknowledgments are due first to Dr. George J. Wallace, chairman of my guidance committee, for his advice during the study and for his constructive criticism in the preparation of the manuscript. The other members of the guidance committee, Dr. Walter F. Morofsky, Dr. William B. Drew, and Dr. Henrik J. Stafseth, have been helpful in reading and criticizing the manuscript.

Acknowledgments would be remiss without due credit to my wife, for her constant help and encouragement throughout this investigation.

PART I

CLASSIFICATION, NOMENCLATURE, and DISTRIBUTION

Classification

The Tufted Titmouse is a member of the Family Paridae, which consists of titmice, verdins, and bushtits. Each of these groups constitutes a separate subfamily: Parinae, titmice; Remizinae, verdins; and Psaltriparinae, bushtits. The Subfamily Parinae now contains only the one genus, Parus, which includes all chickadees and titmice. The 7 species of chickadees in North America currently include 30 subspecies (Fifth A.O.U. Check-list of North American Birds, 1957:382-393). Although three of the titmouse species are polytypic, Parus bicolor is monotypic, containing only one described form.

Nomenclature

Nomenclatural History. The genus Parus was established by Linnaeus (Systema Naturae, ed. X, i, 1758:189). In the 12th edition, vol. I, of his Systema Naturae, 1766, he refers to specimen 340 as Parus bicolor. Its designation was based on neither a specimen nor a description, but on a painting by Mark Catesby (1731) of the Crested Titmouse, Parus cristatus (Allen, 1951:466).

In 1829 Kaup suggested the generic name Lophophanes for the crested titmice, type Parus cristatus. Thus it is that Bonaparte's List of the Birds of Europe, 1842, gives Lophophanes and Parus as the generic names of the crested titmice and chickadees respectively (Baird, 1875:88). In 1850, Cabanis suggested the new genus Baeolophus for the American crested titmice (type, Parus bicolor, L.). In this same year Reichenbach suggested the genus Penthestes for the chickadees (type, Parus lugubris, Temminck). Baird (1858), disagreeing with Cabanis's suggestion that our genus of tufted titmice was distinct from the European crested titmice, continued to use Lophophanes for the crested titmice and Parus for the chickadees. The First and Second A.O.U. Check-lists, 1886 and 1895, list the genera Parus and Lophophanes. In the 12th A.O.U. Supplement (1903:357-359) the genus Lophophanes, Kaup, was changed to Baeolophus, Cabanis.

Ridgway (1904) recommended the splitting of the original genus Parus into the following genera: Lophophanes for the crested titmice of Europe, Baeolophus for the crested species of the Nearctic region, and another genus (Penthestes) for the chickadees. In 1908 the A.O.U. Check-list Committee acted on Ridgway's recommendation and re-established Reichenbach's generic name of Penthestes for the chickadees (14th Supplement, 1908:386-387).

The Third A.O.U. Check-list (1910:347-352) lists the genus Baeolophus, Cabanis, for our crested titmice, and Penthestes, Reichenbach, for our chickadees. This nomenclature was continued in the Fourth Edition in 1931. Hellmayr suggested uniting all the Parinae into the single genus Parus and does so in his Catalogue of Birds of the Americas (1934:70). The A.O.U. Check-list Committee--in the 19th Supplement, 1944--acted on Hellmayr's suggestion and united Penthestes and Baeolophus into the single genus Parus. Thus the original name of Parus bicolor, Linnaeus, for the Tufted Titmouse, is reinstated.

Common Names. The English name for the Latin generic name Parus is "titmouse." The specific name, bicolor, means "of two colors." The most widely used common name for this species is Tufted Titmouse, often shortened to Tufted Tit. Other names, sometimes still encountered in older works, are Crested Titmouse, Top-knot bird, Black-fronted Titmouse, Tomtit, Peter-bird, Sugar bird, Tufted Chickadee, Peto-bird, Crested Tomtit, and Tip-top.

Distribution in North America

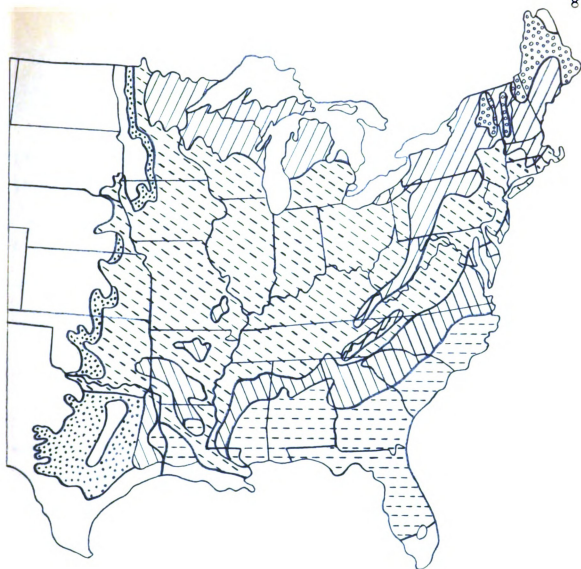
Geographical Distribution. Since the Tufted Titmouse is essentially non-migratory, its winter range and breeding range are practically identical. In distribution it is limited to the eastern half of the United States (See Fig.1). The political limits to the north are the southeastern corner of South Dakota, the southern part of Minnesota and Wisconsin, the lower half of the lower peninsula of Michigan, the lower half of New York State, and the western part of Connecticut. The eastern boundary is the Atlantic coast, from Connecticut to Florida. The southern limit extends west from Florida along the Gulf coast to the eastern half of Texas. The western extension is to the eastern part of Nebraska and Kansas, and the eastern half of Oklahoma and Texas. The usual breeding range is slightly less extensive and within these limits it is a common resident except along the Appalachian ridge, where its numbers decrease with altitude. The occasional nesting records that have been reported outside of the established breeding range are indicated on the accompanying map (Fig. 1).

Ecological Distribution. It is well established that the distribution of any organism depends on the interaction of many factors--climatic, physiographic, and biotic--and the Tufted Titmouse is no exception. Its range is directly



DISTRIBUTION OF THE TUFTED TITMOUSE
Compiled from data supplied by the Patuxent
Research Refuge, Laurel, Maryland.

Figure 1



Legend

	Deciduous Forest		Coniferous Forest
	Oak-Pine Subclimax		Coniferous-Deciduous Forests Ecotone
	Pine Subclimax		Grassland
	Deciduous Forest-Grassland Ecotone		

MAJOR BIOTIC COMMUNITIES OF EASTERN UNITED STATES
Compiled from F. A. Pitelka (1941:114)

Figure 2

affected by climate, which in turn influences distribution through its effect on plant life.

Vegetation is of prime importance in supplying such essentials as nest material, nest sites, food, and cover. There is a definite correlation between the distribution of the deciduous forests in North America and the range of the Tufted Titmouse. Fitelka (1941) states that it occurs in deciduous forest growths ranking from mid-seral to climax stages, occurring most frequently, however, in mature flood-plain forests. A comparison of Figure 1, showing the distribution of the Tufted Titmouse, and Figure 2, showing the distribution of the principal vegetation types of North America, reveals this close correlation. The apparent extension of the range of this species into the grasslands of Oklahoma, Kansas, Nebraska, and southern South Dakota, is explained by the presence of bottomland woodlands along waterways and plantings about farms.

Another biotic factor which is probably of some influence in the distribution of the Tufted Titmouse is its association with other hole-nesting species that excavate their own nest cavities. Because the titmouse does not have a bill adapted for digging into wood it must rely on old woodpecker holes or decayed knot-holes for nest sites. Since these are usually plentiful in fairly mature stands of deciduous trees, titmice do not ordinarily have difficulty locating suitable nest cavities.

Distribution and Status in Michigan

Historical Background. The first records of the Tufted Titmouse in Michigan were reported toward the end of the last century. Wood (1921:594) reported a personal sight record on October 7, 1878, in the vicinity of Ann Arbor, Washtenaw County. The first record of a specimen was from Detroit, Wayne County, collected by E. E. Campbell on December 7, 1878. Other specimens were collected by B. F. Sykes at Almira, Van Buren County, on May 12, 1880, and by J. E. Nichols at Lansing, Ingham County, in September, 1881. On October 5, 1886, N. A. Wood collected three specimens at Ann Arbor. Two specimens were taken by S. E. White in June, 1891, in Kent County--the northernmost station up to that time. A. J. Cook (1893:126) lists the Tufted Titmouse as a common winter bird in the more southern parts of the state and comments that it is a summer resident in the northern counties of Indiana. At the time of his writing there were apparently no nesting reports for the state. The first breeding record was reported by F. M. Kidd on May 13, 1898, at which time he collected a set of eggs on Belle Isle, Wayne County (Wood, 1951). By the turn of the century this species was observed frequently as a winter bird in the lower tier of counties but had not yet become a permanent resident in the state.

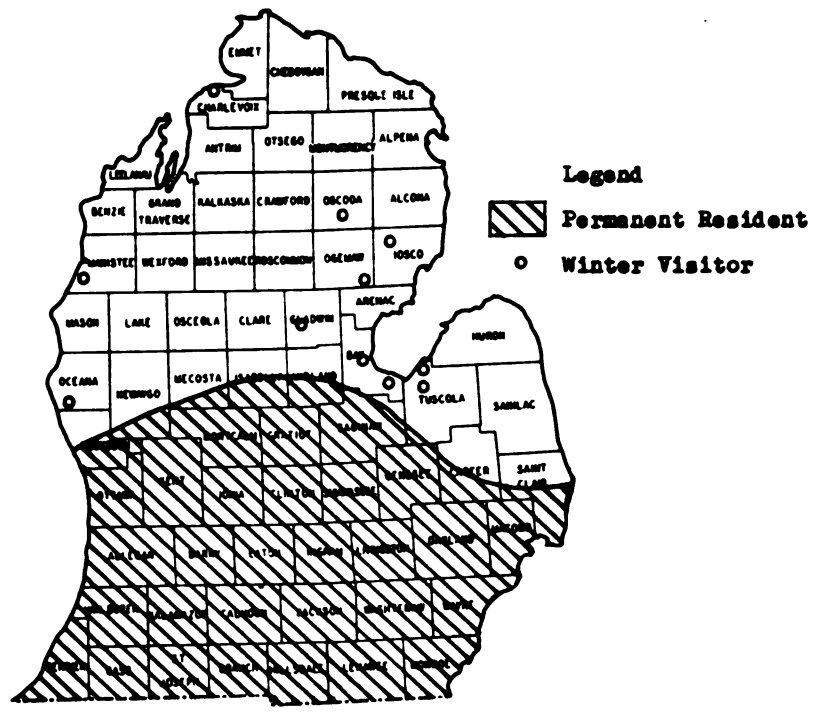
During the first 25 years of this century the Tufted Titmouse gradually established itself as a permanent resident in the southern counties. In 1908, A. D. Tinker reported a breeding record a few miles west of Ann Arbor. In 1916 another nesting record was reported by F. A. Stuart from Calhoun County and A. D. Tinker reported another Washtenaw County breeding record in June, 1918.

Current Distribution. During the last 30 years the Tufted Titmouse has become firmly established as a breeding bird in the southern counties of the lower peninsula, has increased in numbers, and is gradually extending its range northward. The northernmost nest records are from Brook Township, Newago County; Alma, Gratiot County; and Imlay City, Lapeer County. The species has been observed throughout most of the year at Mt. Pleasant, Isabella County, and at Midland, Midland County, but no actual nest records have been reported up to 1957. Winter records of this bird in areas north of its breeding range have been reported from Stony Lake, Oceana Co.; Manistee, Manistee Co.; Gladwin, Gladwin Co.; Mio, Oscoda Co.; Loon Lake, Iosco Co.; Prescott, Ogemaw Co.; Bay City, Bay Co.; Sebawaing, Tuscola Co.; and Charlevoix, Charlevoix Co. The latter record--the most northern one yet reported--was of a bird photographed by J. J. Fessenden on January 7, 1937. This is certainly an

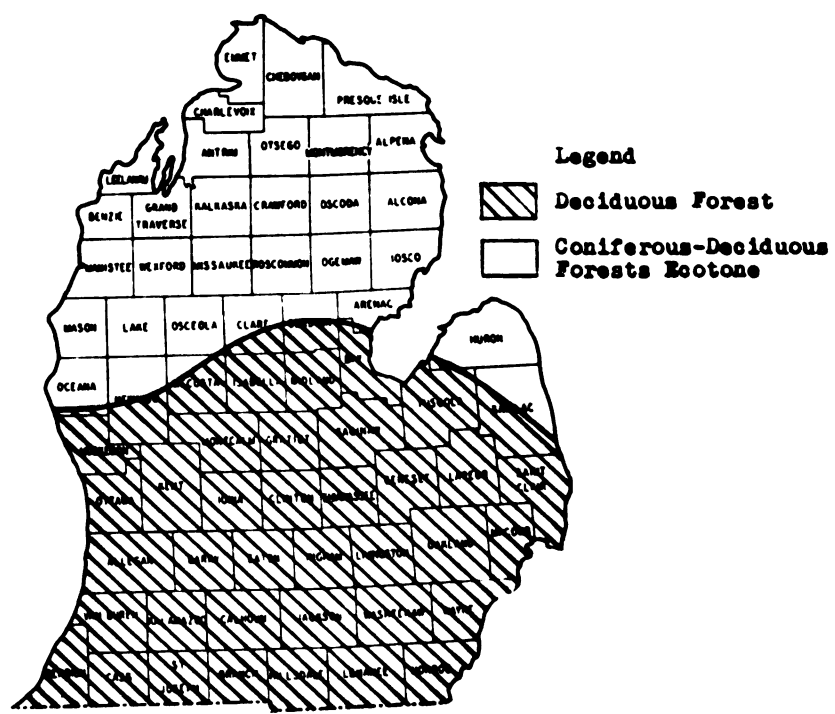
unusual record because the Tufted Titmouse has not been reported from Charlevoix in any year since.

Nest records indicate that the present breeding range of the Tufted Titmouse extends northward into Michigan as far as an imaginary line running from Muskegon across the state through Alma, Saginaw, Inlay City, and Port Huron. Since it has been reported in almost every month of the year in Mt. Pleasant, Isabella Co., and in Midland, Midland Co., it is reasonable to assume that it breeds in those areas, even though no nests have been reported. North of the breeding range its status is that of an occasional winter visitant. The limits of the range of the Tufted Titmouse in Michigan are indicated on the accompanying map (Fig. 3).

A comparison of Figure 3 and Figure 4 reveals the close correlation between the range of the Tufted Titmouse and the distribution of the deciduous forest in Michigan. The deciduous forest is found in the lower half of the lower peninsula. The remainder of the state is somewhat ecotonal, being bounded by the Canadian coniferous forest to the north, and by the deciduous forest to the south. The dependency of this species on deciduous trees is explained by its need for nest sites. Old woodpecker holes and decayed knot-holes are usually not found in conifers.



The Distribution of the
Tufted Titmouse in Michigan
Figure 3



The Biotic Communities of the
Lower Peninsula of Michigan
Figure 4

Extension of Range

The Tufted Titmouse has been gradually extending its range northward in other states as well as in Michigan. There are many reports of the first appearance and the subsequent establishment of these birds in regions beyond their regular breeding range. The following examples of this extension are typical of the situation all along its northern limits.

In Minnesota the first specimen was taken in 1920, and by 1932 titmice were breeding in the southeastern part of the state. Numerous sight records have been reported recently from several localities north of the Minneapolis-St. Paul area. A titmouse was banded at St. Cloud in November, 1953--the northernmost record at that time.

In Connecticut there has been a gradual increase in sight records since 1934. The first breeding was noted at Westport in 1949. L. Griscom (1954), reporting for the New England area, states that the Tufted Titmouse is slowly spreading northward into western Massachusetts and Vermont but that there are no nesting records north of Connecticut.

Although it is easy to cite examples of the northward extension of the range of the Tufted Titmouse, identifying the causes is more difficult. The environmental changes that have resulted in conditions favorable for this expansion

have been occurring over a long period of time. Apparently these changes have been unusually favorable during the past few decades. Such factors as the availability of suitable nest sites, food, predators, and competition with other species of similar habits influence extension of the range. Climatic factors, acting directly on the species, or indirectly through their influence on plant succession, must be considered also.

In the last few decades the climate has been gradually changing in the area marking the northern limit of the range of the Tufted Titmouse. In Michigan, for example, the average temperature has increased slightly since the turn of the century. Baten and Eichmeier (1956) state that the average monthly temperatures for the last 27 years of this century were higher than those for the first 27 years. The most pronounced change was recorded for the months of January and February. The mean temperatures of these months increased one and three degrees respectively. The fact that these two months are often the most difficult for bird life makes these slight changes significant.

This gradual temperature change, especially during the winter months, could affect the expansion of the range of the Tufted Titmouse in two ways. First, the warmer winter temperatures would increase the chances for survival, causing an increase in the breeding population. This

subsequent increase in the population beyond the nest-carrying capacity in a given region could induce movement into new localities. Second, if the birds found suitable habitat in the new area, they might become established as permanent residents, though only if the winter temperatures were favorable.

The records indicate that the Tufted Titmouse generally appears first in areas north of its breeding range during the winter months. After its initial appearance it gradually becomes established as a breeding bird. This behavioral pattern lends support to the possibility that winter temperatures are an important ecological factor in the spread of this species.

Vegetation should also be considered as a possible environmental factor. The range of the Tufted Titmouse parallels the distribution of the deciduous forests in eastern North America and experimental evidence indicates that these forests are spreading northward. In Michigan, Parmalee (1947) indicates a possible series of floral changes that have occurred in the southern part of the state since the period of glaciation. The most recent stage cited by him is characterized by a return to mesophytic conditions. The increase in mesic sites and the drying up of hygric sites has resulted in an invasion of mesophytic plants, primarily beech and maple. This change in

vegetation has been due mainly to the result of combined climatic and edaphic changes. These deciduous woodlands, that have invaded previous xeric and hygric sites, are now providing suitable habitat for a whole new association of animals, including the Tufted Titmouse. Its establishment in these deciduous woodlands, however, did not occur until there was a sufficient number of old trees in which other hole-nesting species could excavate cavities. This nest-site requirement is probably one reason why the northward spread of the Tufted Titmouse has lagged behind the similar movement of other cavity-nesting birds.

Several other species of birds parallel the Tufted Titmouse in extending their northern limits. Included in this movement are three warblers--Prothonotary, Blue-winged, and Cerulean--as well as the Bewick's Wren, the Carolina Wren, the Blue-gray Gnatcatcher, the Red-bellied Woodpecker, the Red-shouldered Hawk, and the Cardinal. The range extension of the latter bird, as well as that of the Tufted Titmouse, has especially come to the attention of individuals who maintain feeding stations. Consequently, the literature contains more references on these species than on the others.

Part II

Observations on the Annual Cycle

Introduction

A field study of the annual cycle of the Tufted Titmouse at East Lansing was the main objective of this part of the research. As mentioned previously, the observations were largely limited to a two-year period--September, 1953, to September, 1955. Some information on nesting habits during 1956 is also included. The investigation was carried on with equal intensity throughout the study period. The observations on the various aspects of the life of the titmouse included a survey of associated plants and animals.

Materials and Methods

Banding. In a study of this nature it was necessary to be able to identify individual birds. For this purpose numbered aluminum bands and painted aluminum bands (size 1B), furnished by the Fish and Wildlife Service, were used. The red, yellow, and green bands, together with the numbered band, were arranged in various combinations on either one or both tarsi. For example, individual R-YGA was banded on the right tarsus with yellow, green, and aluminum bands.

No difficulty was experienced in seeing the colors at a distance of 75 feet. Distances greater than this made accurate identification questionable.

Twenty-nine birds were marked: ten adults during the fall and spring of 1953-'54, nine nestlings in the summer of 1954, and ten individuals during the fall and spring of 1954-'55.

Painting. An adult male (A194151) from Nest RC1 was marked with white "Duco" enamel so that his relationship to his mate, nestlings, and other birds could be followed. Approximately five millimeters at the tip of the tail was painted and allowed to dry before releasing the bird. Although his mate and other individuals regarded him with curiosity at first, they soon seemed to accept this alteration of his appearance and no adverse reactions were noted.

Trapping. The method of trapping was modified several times, until one was finally found which produced the best results. Conventional government sparrow traps placed on the ground were used at first--with very poor results. Even when placed on tables, which were constructed and arranged to prevent mammalian predation, these traps were not adequate for trapping titmice, as they soon found their way out of these funnel traps. As a possible remedy I constructed Potter treadle traps and Chardonneret swinging treadle traps. These also were relatively unsuccessful

because many other woodland birds were trapped. A finely woven bird trapping net, suspended between two trees so that the birds would fly into it on their way to or from the feeding table also proved fruitless.

I finally resorted to the use of hand-operated spring traps, a method which was very time consuming but which yielded the best results. The construction of the traps was based on the pattern of the Higgins model, as described by Lincoln (1947:35). A picture of one of them is presented on Plate II, Fig. B. They were made of one-quarter inch square wire mesh netting and the dimensions were 46X56X18 centimeters. The large entrance doors were placed opposite each other and a long elastic band, connected to the inside of the doors, supplied the spring action. The doors were released by pulling a string attached to a heavy piece of wire, which extended over the top of the trap and held down the trigger wires from each door. An observation blind was unnecessary because I was able to conceal myself behind trees and shrubs, some 50 to 75 feet away from the trap.

Feeding stations were maintained for two weeks preceding banding operations so that the birds would get accustomed to coming to the trapping site. The feeding stations were covered platforms suspended from trees.

Banding was carried out in each of the three campus

woodlots. As much consistency as possible was maintained in the time of banding, usually early morning and late afternoon. Birds were trapped on alternate days and were given free access to the baited traps at other times. The traps were visited just before dark to make sure no bird had accidentally become entangled in the wire mesh.

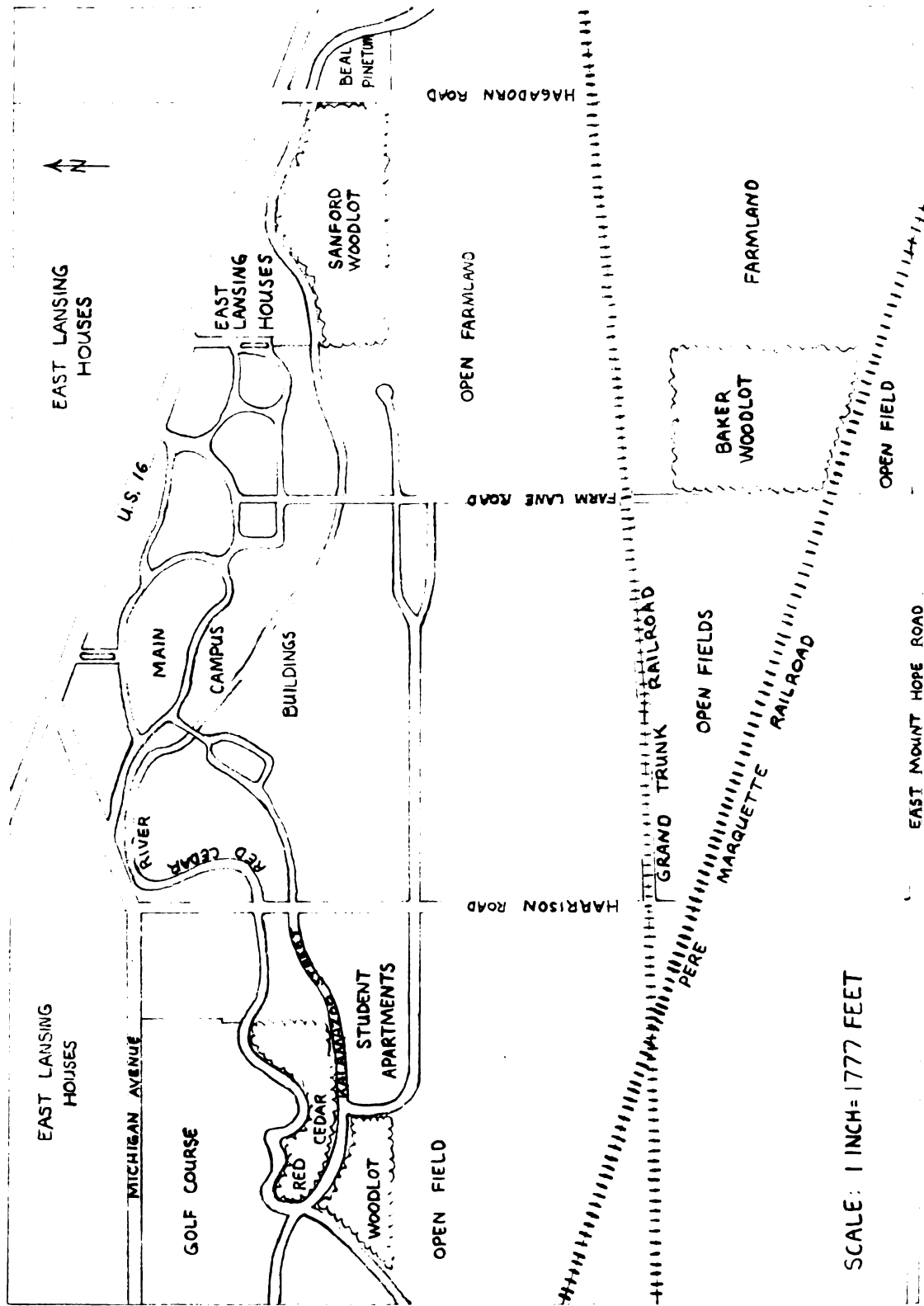
The Study Area

The woodlots involved in this study are located at Michigan State University, East Lansing, Township 4N, Ingham County, Michigan. The three areas are known as the Sanford, Red Cedar, and Baker woodlots. Their location and approximate size is indicated on the accompanying map (Fig. 5).

Sanford Woodlot. This is a 54-acre stand of relatively mature deciduous trees, with Fagus grandifolia and Acer saccharum being the primary dominants. The secondary dominants include Fraxinus americana, Tilia americana, Quercus rubra var. borealis, Ulmus americana, and Ulmus fulva.

The ground floor is gently rolling, with a gradual drop in relief from the south side toward the river. Some of the small depressions contain shallow water part of the year.

The woodlot is the site of numerous activities, including the harvesting of maple sugar. Many departments of the university use it for class field trips and for individual research.



Campus and Associated Woodlots, E. Lansing, Michigan
Michigan State University, E. Lansing, Michigan
Figure 5

Red Cedar Woodlot. This 35.9 acre stand of relatively mature deciduous trees is bisected by Kalamazoo Street. The land is generally low, rising a little over ten feet above water level. Several depressions contain shallow water most of the year and during the spring intermittent streams flow through the area.

The dominant trees are Ulmus americana and the soft maples, Acer rubrum and Acer saccharinum. Secondary dominants include Fagus grandifolia, Fraxinus americana, Quercus rubra var. borealis, and the hard maples, Acer saccharum and Acer nigrum.

This woodlot is maintained chiefly for class use and research. Because selective cutting has not been practiced in recent years there is a pronounced absence of small trees and shrubs except in the openings.

Baker Woodlot. This 72-acre mixed deciduous association contains such dominants as Fagus grandifolia, Acer saccharum, Acer rubrum, Quercus rubra var. borealis, and Prunus serotina. Associates occurring less frequently are Tilia americana, Ulmus americana, Fraxinus americana, and Carya cordiformis.

The area is generally level but does contain three shallow depressions which are filled with water most of the year.

Since this woodlot likewise had not been subjected to selective cutting at the time of this study, there was a general absence of shrubs and small trees. Although one large concentration of Acer saccharum is used for maple sugar harvesting the main use for this woodland is for class field trips and research.

Climate and Weather. The records of the East Lansing Weather Bureau (1941) supplied the following information on climate and weather.

The average temperature for the coldest month, January, is 22.9°F., while the average temperature for the warmest month, July, is 71.1°F., with a maximum of 102°F. and a minimum of -26°F. The average date of the last killing frost in spring is May 5 and the average date of the first killing frost in fall is October 10. These average frost dates encompass a growing season of 158 days. The average annual precipitation is 30.52 inches. Rainfall is fairly evenly distributed throughout the growing season with occasional thunderstorms in the summer. Snowfall is moderate, rarely exceeding ten inches, and the ground is seldom continuously covered for long periods. The prevailing winds are moderate and westerly. The winter months are characterized by much cloudiness, while spring has a variation of cloudy and clear days, and the summer often has many long periods of uninterrupted sunshine.

The first signs of spring may appear as early as late February or early March, but spring does not usually become established until the middle of March. This season is characterized by high winds, cloudiness, and temperatures ranging close to freezing. Both day and night temperatures rise during spring, so that by the nesting period in May and June the night readings range from 40° to 50°F., while

those during the day range from 60° to 85°F. A summary of the weather conditions during the winter months and during the months of nesting is given in Table III. Temperatures and other data in the study area were assumed to be comparable to those at the Lansing weather station.

The Population at Beginning of Study

The Tufted Titmouse occupies the woodlots throughout the year, but there is a seasonal as well as an annual fluctuation in the population. Numbers are greatest and most variable in late summer and fall. The fall population in the three woodlots in 1953 was approximately 34, as compared with 18 during the following nesting season. Most of the breeding birds were present in the fall flocks, but many of the winter residents left the area in the spring, one of them moving as far as three-quarters of a mile. Similar seasonal shifts have been reported for the Black-capped Chickadee, by Odum (1941) at Rensselaerville, New York; by Wallace (1941) at Lenox, Massachusetts; and by Butts (1931) at Ithaca, New York.

Fair Formation

Time of Occurrence. Fair formation in most passerine birds is usually preceded by the establishment of a breeding territory by the male. My observations indicate that it

usually occurs earlier in the Tufted Titmouse. Only one of the seven pairs, in which I was reasonably certain of the time of pairing and of territory establishment, was formed after territorialism was evident.

Pairing and the dispersal of the newly formed pairs from the winter flocks occurred gradually during the period from March 21 to April 12. In 1954 the first indication of pair formation was evident on March 25 and the last semblance of a flock (three apparently unmated birds) was seen on April 10. During the spring of 1955 pairing first became evident on March 21 and continued until April 12. After this date the only birds seen were mated pairs or single unmated wanderers. Prior to the dispersal of the winter flocks there was movement of individuals from one group to another and new birds occasionally appeared. Similar early spring wandering has been reported for the Black-capped Chickadee (Butts, 1931; Bowditch, 1938; Odum, 1941). Gillespie (1930) recorded the same behavior for the Tufted Titmouse at Glenolden, Pennsylvania.

Courtship and Mating. During the period of pair formation there was no evidence of courtship. The feeding of the begging female by the male, which was the only observed indication of courtship, did not occur until the birds were examining possible nest sites. The male also fed the female during nest construction, egg laying, and

incubation. Approximately two weeks elapsed between the first sign of definite pairing and courtship feeding. Sixteen days elapsed between the formation of Pair S1 and the first record of the begging-feeding behavior. It was noted on two different occasions, occurring first while the pair was examining possible nest sites.

Copulation was witnessed three times during egg laying. Whether copulation occurred during pair formation as well as after nest construction was not determined.

Behavior of Newly Paired Birds. In one case (Pair S4) the newly paired birds remained within the area where mating occurred. Other birds were found nesting in areas quite distant from the one in which pair formation took place. In a few cases the birds were already constructing nests or incubating before the pair was located so that the relationship between the place of pairing and the place of nesting could not be determined.

The newly paired birds remained closely associated throughout the day. Their daily activities consisted of feeding, resting, preening, and exploring for prospective nest sites. During their movements through the woods the birds usually maintained close contact with each other. They frequently uttered a soft "tseep" note, which seemed to act as a means of communication between them. When they became separated the "tsicka-dee-dee" call was used to

locate the mate. On April 15, 1954, when a Red-shouldered Hawk (Buteo lineatus) flew over Sanford Woodlot, male 146205 emitted a loud, explosive "tsicka-dee-dee." This note apparently acted as a warning to the other birds because they suddenly became quiet and remained that way until the hawk left. Vocal display and chasing resulted whenever another titmouse approached a pair of titmice. Both of the mated birds uttered the "peto, peto" notes, repeated in rapid succession, and on three occasions when chasing ensued, they both took part in the pursuit. After several minutes of calling and chasing, the intruder departed and the pair resumed its activities. This defense of a mate prior to the establishment of a nesting territory has been referred to by Noble (1939) as defense of "sexual territory."

Permanence of Mating. In several species of Paridae the mates maintain an attachment for each other beyond the breeding season. Steinfatt (1938) found that Marsh Tits (Parus palustris) in East Prussia wander about in winter in pairs and that the Crested Tit (Parus cristatus) and the Willow Tit (Parus atricapillus) also are permanent residents and mate permanently. In 14 years of banding Great Tits (Parus major) at Budapest Wurga (1939) did not record any change of mates from season to season, and Kenrick (1940) found that Blue Tits (Parus caeruleus) in England usually retained the same mates.

In the North American Paridae, Price (1936) and Dixon (1949) state that the Plain Titmouse (Parus inornatus) in California is usually seen in pairs throughout the year and keeps the same mate from year to year. Nice (1933) reports a case of a pair of Carolina Chickadees (Parus carolinensis) which remained associated three winters and two summers in Ohio. Baldwin (1934) also noted several pairs of Carolina Chickadees which remained mated for two or more seasons in Massachusetts. In the Tufted Titmouse Middleton (1949) reports a male that was mated to one female for three successive years and then to another female for three more consecutive years. His observations were made at a nest box in Norristown, Pennsylvania.

In a two-year study little can be determined regarding permanency of mating, but male 146205 and female 146207 were known to be mated for two successive years. In three other banded pairs either the male or female was replaced by another mate the following season.

Territory

Establishment. The Tufted Titmouse territory serves as a nesting and feeding area for the adults and later as a feeding place for their young. The newly mated birds wander about for several days before claiming a territory. Even though Pair S1 was established by April 8, there was

no indication of territoriality until April 25, after the pair had been investigating possible nest sites. Territorialism was most evident at the beginning of nest construction for other pairs as well. Perhaps the selection of a suitable nest cavity induces the establishment of a territory. It may or may not coincide with the area where pair formation occurred or with the winter range. One member (146214) of a flock moved three-quarters of a mile from the winter range to nest.

Defense. Territorial defense was observed several times during the nesting season. The male assumed the leading role but he was occasionally assisted by the female. Defensive behavior did not seem to be as elaborate as Nice (1937) describes for the Song Sparrow. Of the five types of behavior she attributes to the Song Sparrow, I noted only the following two for the Tufted Titmouse. (1) The challenge: When the territory was invaded the male challenged the invader with loud "peto, peto" calls. The intruder responded with similar notes but left the area upon the approach of the defender. (2) The chase: In a few instances the intruder did not retire immediately and a chase ensued. On two occasions (Pairs S3 and RC1) the defending male was joined by his mate. While chasing the intruder from their territory the mated birds scolded continuously. Actual

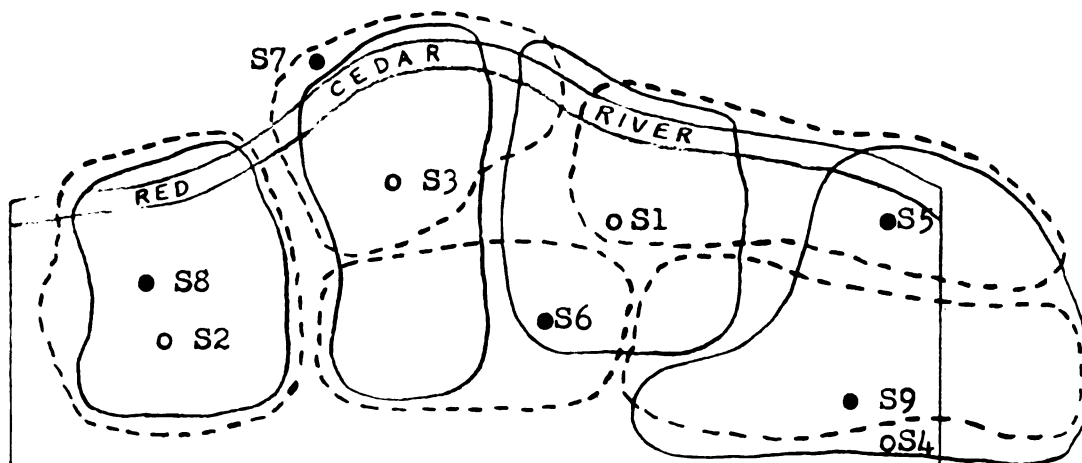
fighting was not observed and the only other belligerent behavior that was noted was the increased erection of the crest feathers during scolding.

The vocal activity of the mated birds diminished noticeably after establishment of the territory. It is this reduction in vocalization that makes the detection of nesting birds difficult. The literature contains numerous reports that the birds either "disappear" during nesting or that they are extremely "shy." Most of the singing during the nesting period was done either by unmated birds or by males having territorial disputes.

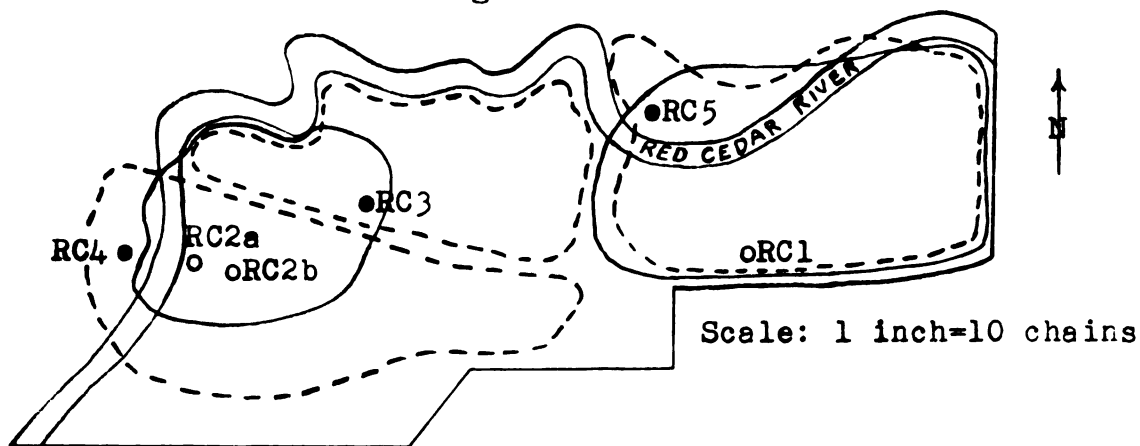
Defense of the territorial boundary against another species was not recorded, and I witnessed a dispute with another species only once. When a female Cowbird (Molothrus ater) ventured close to the titmouse nest hole, she was immediately chased by the male titmouse.

The territory was maintained until the young left the nest, but it was defended most frequently during the early part of the nesting period, when territories were being established and the birds were still quite unsettled. Defense was recorded once after hatching, when the young were ten days old. The decline in aggressiveness after hatching may be attributed to the fact that the males were busy securing food for the young. Protection of the territory evidently becomes very weak or stops entirely during the fledging period, as other titmouse families wandered through occupied territories without challenge.

Size of Territory. The territories established by 14 pairs of Tufted Titmice in the Sanford and Red Cedar Woodlots are indicated in Figures 6 and 7.



Territories of the Tufted Titmouse in Sanford Woodlot
Figure 6



Territories of the Tufted Titmouse in Red Cedar Woodlot
Figure 7

- Legend
- 1954
 - 1955
 - Nest, 1954
 - Nest, 1955

The solid and broken lines, for 1954 and 1955 respectively, outline the maximum area used and defended by each pair during the early part of nesting. The numbers indicate the pair which occupied the territory and the dots and circles mark the location of the nest. Although the use of lines gives the impression of definite limitations, rigid boundaries were apparent only where territories came into contact. At other points the territorial boundary seemed to fluctuate, especially as the nesting season progressed. Overlapping of territories was not apparent. The territories were determined early in the breeding season, during the last week of April and the first week of May. The singing birds were heard from the same localities and pairs were seen in the same area each day.

The size of the territories, calculated with a planimeter, ranged from 7.8 acres (3.2 hectares) to 13.9 acres (5.6 hectares), with an average of 10.4 acres (4.2 hectares). These dimensions are comparable to those reported for other Paridae. Dixon (1949) reported an average of 6.3 acres (2.6 hectares) per pair for the Plain Titmouse at Berkeley, California. Odum (1941) calculated an average of 13.2 acres (5.3 hectares) per pair for the Black-capped Chickadee at Rensselaerville, New York.

Although the diagrams indicate the size of the territories at the beginning of the nesting period, the defended

area diminished as the nesting period progressed. During nest building, egg laying, and incubation, the birds ranged widely over their territory, but they limited themselves to an area closer to the nest after the young had hatched. The distance traveled for gathering food gradually decreased with the development of the young. Butts (1931) and Odum (1941) noted this same behavior in the Black-capped Chickadee.

Habitat. The titmouse territories included two types of habitat. The territory of pair RC4 consisted of a stand of young aspen, willow, ash, and maple. The territories of all other pairs were located within mature (climax) stands of beech, maple, elm, oak, and ash. Abandoned fields, farmlands, and pine plantings adjacent to the woodlots were utilized in winter but were not used appreciably during the nesting season so that territories were essentially restricted to deciduous woodlands. Titmouse territories extended vertically into all of the various nesting societies--ground nesting society, low shrub society, high shrub society, and the upper canopy society.

Population Density. The number of pairs of titmice in the Sanford and Red Cedar Woodlots averaged 7 pairs per 89 acres--adjusted to include areas immediately adjacent to the woodlots that were parts of territories. This density would mean one pair per 12.7 acres (5.1 hectares) of

suitable habitat--excluding roads and open water. Comparing the territorial boundaries with the vegetation in the woodlots indicated that little suitable habitat was left unoccupied.

There is a close correlation between the density found in this study and the densities reported by others. Twomey (1945) found an average of 13.3 acres (5.4. hectares) per pair in a two-year study of an elm-maple forest in east-central Illinois. Williams (1936) calculated an average of 9.3 acres (3.7 hectares) per pair over a four-year period in a beech-maple forest near Cleveland, Ohio.

The Nest

Nest-Site Selection. Nest-site selection began several days after pair formation. In 1954 the birds were seen examining cavities from April 1 to April 13, while in 1955, due to a delayed spring, this activity extended from April 9 to April 20. A pair of titmice searched for possible nest sites together but the female did most of the inspection of the cavities while the male waited on a perch a few feet away. The nests were located by watching either the movements of both birds together or an individual carrying building material. They were made either in old abandoned woodpecker holes or in natural cavities.

Of the 20 nests in the study area, 9 were in American elms; 10 in red maples; and one in a beech. Although the nest sites were limited to these three trees, titmice were seen inspecting prospective locations in other trees. The height of the nest hole above ground ranged from 18 to 66 feet, with an average of 38.5 feet. The reported extremes in nest height range from less than one foot (nest in a fence post that extended one foot below ground level) to 97 feet (Bent, 1946). Cairns (1889) reported an average height of 35 feet, based on data from over one hundred nests.

In addition to the trees mentioned above, Tufted Titmice have been reported nesting in the following: Pine; cypress; white, red, blue, and scrub oaks; dogwood; birch; apple; tupelo; sycamore; hemlock; mulberry; sugar maple; yellow and black locust; white ash; and chestnut. Wayne (1910) reported an unsuccessful attempt to build a nest in Spanish moss (Tillandsia usneoides). In addition to such natural sites the Tufted Titmouse sometimes uses bird houses and abandoned woodpecker cavities in fence posts.

None of my banded titmice reused the nest site that they occupied the previous year. McLaughlin (1888) reported a similar lack of reuse, but Bent (1946:396) states that "they will continue to use the same cavity for years, if unmolested."

Nest Construction. The female did the actual nest building, although both birds carried material. Even in this latter activity the female was the more active of the pair. Often the male simply accompanied his mate to and from the nest hole. When the female entered the nest cavity the male remained outside, calling softly or waiting in silence. During the period of nest construction the female often begged for food and was fed by the male.

Once started, nest building progressed rapidly until the nest was completed. The birds were just as active in the afternoon as in the morning. During the morning of the second day of construction at Nest S1, the female, accompanied by the male, made 8 trips to the nest in a period of 40 minutes. This same pair made 20 trips in a two-hour period during the afternoon of the third day of building. Sometimes they flew directly to the nest while at other times they lingered along the way.

The average length of time required for the construction of seven nests was four days. All nests under study (with the exception of a second nest completed on June 7) were completed by the middle of May, the latest on May 16.

After the nesting season four nests were collected for examination. All contained dried grass, moss, and hair; two contained pieces of string, dried leaves, and strips of bark; and one contained four white chicken feathers. While

nest composition presumably varied with the availability of materials, there was a definite preference for dried grass, green moss, hair and other soft materials. The hair was from raccoon, opossum, dog, fox squirrel, and red squirrel. Other sources of hair that have been reported are rabbit, horse, cattle, cat, mice, woodchuck, and man.

The sizes and shapes of the nests were quite variable, depending on the character of the cavity, which in one case was so deep it necessitated a large amount of loose material to fill the extra space. The depth of the cavities ranged from 21.2 cm. to 27.5 cm. The depth of the nests ranged from 13.7 cm. to 20.0 cm., while the outside diameter ranged from 10.0 cm. to 12.5 cm. The inside diameter of the hair-lined cup was difficult to measure because of its irregularity but was approximately 7.5 cm. The depth of the depression in which the eggs were laid averaged 3.9 cm. The distance from the top of the nest to the entrance averaged 8.42 cm., and the diameter of the opening ranged from 4.4 cm. to 5.6 cm. The specific dimensions for each nest are presented in Table V.

Nesting Associates. The 29 species of birds found nesting in the study area are given in List II of the Appendix. None of the titmouse nests contained Cowbird eggs, even though Cowbirds were present in the area. Friedmann (1938) reports five records of titmouse nests being parasitized by Cowbirds.

Egg Laying

Deposition of Eggs. In this latitude the eggs of the Tufted Titmouse are laid in May. The dates of first eggs ranged from May 4 to May 11 in this study. Information from four nests indicated that egg laying occurred early in the morning and that the eggs were laid at the rate of one a day. The female partially or completely covered the first few eggs with nest material. Sets of 5 eggs were found in Nests RC1, RC2b, and S10, whereas Nest RC6 contained 6 eggs. Bent (1946) mentions that the number may vary from 4-8, with 5 or 6 being the most common.

Description of Eggs. The eggs examined were generally ovate, with some having an elongate-ovate shape. The ground color was pure white or creamy white and the surface was dull and speckled. I noticed no variation in the color of the spots on the eggs in a given set but there was variation between sets. The specks on the eggs were hazel in Nest S10; dark hazel in Nest RC1; chestnut in Nest RC2b; and light hazel in Nest RC6. The distribution of the spots varied in each set of eggs, being concentrated at the large end on 5 eggs and evenly distributed on 16 others. Egg measurements were not attempted because of the difficulty in removing the eggs. Bent (1946) lists the average dimensions of 50 eggs as 18.4 by 14.1 mm. The extremes in length were

20.7 mm. and 16.8 mm., while the extremes in diameter were 14.7 mm. and 12.7 mm.

Behavior During Egg Laying. The sexes remained closely associated during the egg-laying period. A pair spent most of its time ranging over the territory, carrying on the usual daily activities of feeding, preening, and resting. The female occasionally begged successfully but this behavior was more evident during incubation. During the day the birds spent little time near the nest, sometimes not returning for three hours. The female roosted at night in the nest hole, as she had done during nest building. Incubation apparently did not begin until all the eggs in a set were laid because hatching was more or less simultaneous.

Copulation was observed three times during the egg-laying period, once for each of the following: Pair S1 - 9:30 A.M., May 3, 1954; Pair RC1 - 10:20 A.M., May 5, 1954; and Pair S10 - 2:10 P.M., May 8, 1956. The copulatory behavior was similar on all three occasions, but the post-copulatory actions of the male were most unusual in two cases. The following is a summarized account of the behavior recorded for Pair RC1 on May 5, 1954.

(10:15 A.M.) Female (146203) perched 15 feet up in elm tree 10 feet away, twittering and vibrating wings rapidly, head extended forward, crest depressed.

(10:17) Male (A194151) flew into same tree and almost immediately flew to perch next to female. Female continued to twitter and flutter wings. Male attempted to mount female. Male resumed perch

next to mate, while she continued displaying. First attempt apparently unsuccessful.

(10:20 A.M.) Male attempted mounting again. Female flew away immediately after the act to a nearby tree where she began preening and arranging her feathers, no longer displaying. Apparently copulation was successful this time. Male remained perched on limb where copulation had occurred. His body was pressed close to the limb so that his legs were concealed. Head and tail were extended in line with the body, eyes gradually closed. He remained in this horizontal position on the branch for a few seconds and then began to tip slowly backward on the limb. His body continued to rotate slowly backward and downward until it was suspended beneath the limb. With eyes still closed in this stuporous state the male then fell toward the ground. After falling about eight feet he suddenly revived and flew off into some nearby bushes. He remained there resting and preening for a few seconds before flying into the woods out of sight.

(10:23:30) Female flew off in same direction.

This same behavior was noted for the male (146205) of Pair S1 on May 3, 1954, but no such actions were displayed during the copulation of Pair S10 on May 8, 1956. Immediately after copulation the two birds flew into a nearby tree and began preening.

Incubation

Role of Sexes. During the incubation period a total of 42 hours was spent at four nests. Incubation was undoubtedly the duty of the female, for I never saw a male stay in the nest cavity for more than a few seconds. Incubation by the male at night was not observed and the males examined did not reveal a brood patch. The time of

the appearance of the female's brood patch was not determined but it was still present when the young left the nest.

Bent (1946) mentions that incubating and brooding are performed mainly by the female. Price (1936) and Dixon (1949) state that incubation is the duty of the female in the Plain Titmouse. Odum (1941) found no evidence that the male Black-capped Chickadee takes part in incubation at any time.

Behavior During Incubation. The period of incubation was characterized by alternating periods of attentiveness and inattentiveness. During the attentive periods the female was fed by the male, who announced his approach to the nest with a low whistled "tuee, tuee." On some occasions the female was fed on the nest, while at other times her mate perched near the nest hole and called the female off the nest. Regardless of the place of feeding the male announced his arrival with a call, corresponding to the "signal song" used by the male Song Sparrow (Nice, 1937), Hooded Warbler (Odum, 1931), Black-throated Green Warbler (Pitelka, 1940), Black-capped Chickadee (Odum, 1941) and others. Whether the female titmouse always responded vocally to her mate's call was questionable, but on three occasions she emitted a soft twitter before receiving food from him. When fed in the nest cavity the female continued incubating

and did not come up to the opening. The male perched on the edge of the hole and thrust his head down into the cavity, leaving only the lower surface of his tail visible. Usually the female remained on the nest if she had been there only a few minutes, but if she had been incubating for several minutes, she left the nest just after being fed.

Two incubating females made hissing sounds when I approached. At other times they either remained quiet or flushed immediately. This hissing defense also has been reported for the Blue Titmouse and Great Titmouse (Armstrong, 1947), and for the Black-capped Chickadee (Odum, 1941).

During the inattentive periods the female usually begged for food in the presence of the male. He fed his mate at intervals and she also fed herself. Occasionally the male accompanied the female to within a few feet of the nest but usually she returned alone. During the return to the nest, which was quite direct, neither bird emitted any vocal sounds. Between his feeding visits to the nest the male moved leisurely about the territory, feeding and resting. He sang occasionally but generally singing diminished during incubation.

Table IV summarizes data gained from 24 hours of observation during incubation at four nests. The observations at a given nest were not made continuously but in

one to three-hour periods at different times of the day during the latter half of the incubation period. The average attentive period was 25.8 minutes and the average inattentive period was 8.9 minutes. The number of times the male fed the female on the nest during each attentive period averaged 1.5. In 64 percent of the cases when the female left the nest she did so in response to the call of her mate. There was no pronounced difference in the behavior of the birds at different times of the day.

These findings are similar to those recorded for other Parinae. In the Plain Titmouse Dixon (1949) recorded an average of 8.5 minutes for the inattentive period and 28.5 minutes for the attentive period; Steinfatt (1938) recorded a female Marsh Tit averaging 37.09 minutes on and 7.9 minutes off the nest during an all day observation; and Odum (1941) recorded an average of 7.2 minutes for the inattentive period and 24 minutes for the attentive period in the Black-capped Chickadee.

Incubation Period. The incubation period was established with reasonable accuracy in four nests. The time between the laying of the last egg and its hatching averaged 13 days and 3 hours, as determined by marked eggs.

The incubation periods for other Parinae are somewhat longer than that determined for the Tufted Titmouse. Dixon (1949) recorded 16 days for the Plain Titmouse; Odum (1941)

gives the incubation period of the Black-capped Chickadee as 13 days; and Witherby, et al (1938) state that incubation in the Coal-tit (Parus ater) requires from 14-16 days, while it lasts 13 to 14 days in most other European Parinae.

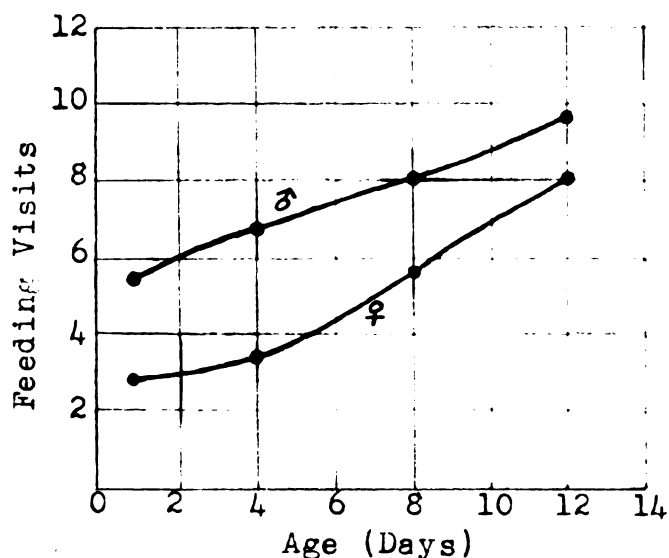
Hatching. All 5 eggs in Nest RC1 hatched within 10 hours; 4 of the 5 eggs (one infertile) in Nest RC2b hatched within 18 hours; and 5 of the 6 eggs (one infertile) in Nest RC6 hatched within 20 hours. The last two records included hours of darkness. The egg shells were carried a considerable distance away from the nest and I could not see whether they were eaten or simply discarded.

Care of the Young

Brooding and Feeding. The behavior of the adults during the first week after hatching was quite similar to that during incubation, but now the male directed his feeding to the young instead of to his mate, and the female fed the young when returning from her inattentive periods. During the first few days after hatching the brooding periods of the female were approximately of the same length as her attentive periods during incubation but gradually decreased as the development of the young progressed. The male transferred food to the brooding female but whether she swallowed

it or fed the young could not be observed. As development of the nestlings progressed the begging behavior of the female subsided until both parents were directing their feeding to the young.

Data on the feeding rate were recorded at three nests, when the young were one, four, eight, and twelve days old (Fig. 8 and Table VI).



Average Hourly Rate of Feeding Nestlings
(based on data from three nests)

Figure 8

During the first four days the male fed the young approximately twice as often as the female, who spent about two-thirds of the time brooding. At 8 days the male still fed more often than the female, but at 12 days the sexes were feeding at about the same rate and the female was not

brooding during the day. The number of feedings per hour per pair increased from 8 when the young were one day old to 17.7 when the nestlings were 12 days old.

The behavior pattern changed during the last few days of nest life. The male no longer announced his arrival at the nest and he discontinued feeding the female entirely, both at the nest and away from it. Vocal activity diminished and brooding by the female ceased almost entirely, except during cold and wet periods and at night.

Nest Sanitation. Nest sanitation appeared to be the duty of the male at first, but as nest life progressed he was assisted by the female. The fecal sacs were removed after feeding the young and were carried a considerable distance from the nest so that I was not able to determine whether they were discarded or eaten. Dixon (1949) mentions that the male Plain Titmouse sometimes swallows the fecal sacs.

Length of Nest Life. The young left the nest 15 days and 17 hours after hatching (average of four nests). This figure compares favorably with the 15 to 16-day period given by Bent (1946). The Plain Titmouse remains for a somewhat longer period, given as three weeks by Dixon (1949). Odum (1941) recorded 16 days for the Black-capped Chickadee.

Development of Nestlings

Nestlings were removed from Nests RC2b and RC6 at regular intervals for examination. To facilitate removing the young the entrance into the nest cavity was enlarged with a small keyhole saw and the removable piece of wood then held in place with a leather strap. Examination of the nestlings was done as quickly as possible to minimize disturbance. Consequently, information on the development of nestlings is limited to notes on external appearance and behavior.

External Appearance. The first day after hatching the young were almost entirely naked, pink, blind, and helpless. The mouth and abdomen were large and the limbs were small in comparison to the rest of the body. Natal down appeared in six small tufts, two each on the capital, humeral, and spinal tracts. The number of feathers per tuft varied but was less than 14. On the fourth day the eyes were partly open and the feather tracts were more distinct. At eight days the eyes were completely open, the gray feathers of the juvenal plumage were developing on the back, and the flanks were tinged with rusty brown. The remiges were in the pin-feather stage. By ten days the body was nearly covered with contour feathers although apteria still showed and the remiges were

partly sheathed. At 14 days the nestlings were well feathered and closely resembled the adults, except for the shorter primaries and rectrices, and the yellow rictus of the mouth.

Behavior. The behavior of the nestlings paralleled morphological and physiological changes. On the first day they responded to stimuli either by opening their mouths for food or by squirming. Sense of fear was absent and did not appear until the fourth day. From the age of eight days the nestlings made hissing sounds, somewhat similar to the reaction of an incubating female when the nest was disturbed. The young were quite active at all ages, the amount of activity increasing with age.

Number of Broods. One brood is usual for the Tufted Titmouse. There were no second broods during this study and the literature revealed only two records of double broods, one from Ohio and one from Virginia. The other resident Paridae, the Black-capped Chickadee, occasionally raises two broods. Steinfatt (1938) reports that among European Paridae the migratory species raise two broods and the resident species one.

Postnest Life

Nest Leaving. Of the seven nests in which the time of departure was recorded, the young titmice left four of them in the morning and three of them in the afternoon. Apparently they do not leave until they are capable of climbing up to the exit, at which time they are ready to fly.

Fortunately I was present when the brood left Nest RC1--one of the two nests in which the young were banded. From my vantage point I could see that the young were becoming restless, repeatedly coming up to the entrance hole. At 9:15 A.M. on June 5, 1954, three of the young left the nest in rapid succession. They flew into some bushes 50 feet from the nest. The other two departed at 10:35 and joined the rest of the family. While the young were leaving the nest both parents flew about excitedly, frequently emitting the soft "tsick-adee-dee" call note. Soon after all the fledglings had left the nest the family began to move through the trees away from the nesting site, with the parent birds in the lead. While the young were being fed by one parent the other parent flew to a new location about 50 feet away, and began calling softly, using the "peto" song. The rest of the group then joined him. This procession continued until 11:30 A.M., at which time the family was 75 yards from the nest cavity. During their movements through the trees and while being fed, the young voiced an

anxious "seep, seep." The parents usually foraged a few feet away, although they occasionally traveled 50 yards from the young. At the end of their first day out of the nest the fledglings were found with their parents in a bladdernut (Staphylea trifolia) thicket, close to the spot where I had last seen them that morning. I presumed that they roosted in the thicket, as they remained in it and were quiet when darkness ended observations at 8:15 P.M.

Dispersal of Young. On their second day out of Nest RC1 the young titmice were quite inactive, remaining almost stationary in the foliage while waiting for their parents to feed them. Feeding was occasionally interrupted by a short flight to a new location. Five days after leaving the nest the young were first seen feeding themselves. By June 26 the calls of the young closely resembled those of the adults and by July 3, at six weeks of age, the fledglings were definitely foraging for themselves and no begging was noted. At this time there were only four young, individual 146212 having disappeared. This family of six was still intact on July 10, but on August 7 two more of the young (146211 and 146214) had disappeared. One of them (146211) was discovered almost a quarter of a mile away in a flock of unbanded titmice.

The postnest history of another family (Nest RC2b) is summarized in the following paragraph.

- July 10--Four young fledged at 1 P.M.
- July 14--Family seen at north end of territory.
- July 17--Attempt to locate birds failed.
- July 24--Parents and three young feeding in northeastern part of territory, fourth young (146218) not present in study area and was never seen again.
- August 14--Female parent and two of her young (146216 and 146219) in flock with three unbanded birds. This was the first indication of a flock consisting of more than just a family group.
- October 9--Female parent and her two remaining young came to the feeding shelf with two unbanded birds.

Of the nine young banded from these two nests, only two were present in the breeding area the next year. One of these (146213) had replaced the lost mate of a banded resident, while the other (146217) was mated to an unbanded individual of unknown origin. One of the young (146216) from Nest RC2b nested three-quarters of a mile from the study area.

Van Tyne (1948) has suggested that family ties remain strong and that the family group forms the basis for fall and winter flocks. The data gathered in this study support this view since two of the fall flocks in 1954 contained parent birds and some of their young.

Nesting Mortality and Longevity

Nesting Mortality. Because of the inaccessibility of many of the nests, the information on nesting success is based on four accessible ones. All of these were successful in that at least one young left the nest. Nineteen fledglings from 21 eggs was a nesting success of 90 percent.

Nice (1937), summarizing data on nesting success, gives the average for hole-nesting passerines as 65 percent. In nesting boxes in Holland 61 to 76 percent of the titmice eggs produced young that left the nest. The higher percentage of nesting success in this study may be due to the limited number of nests.

Thus the 12 birds which were present at the beginning of the breeding season (1954) in the Sanford and Red Cedar Woodlots produced 28 young, a percentage increase of 233. Since two adults were lost the fall population was not more than 38 birds. This total, compared with the number present at the beginning of the season, represents a three-fold increase from April to August.

This summer increase is comparable to the average found in a 14-year study of the House Wren (Kendeigh, 1937), where the average number of adults nesting on 15 acres was 19.7 and the number of young produced was 56, or a percentage increase of 284.

Longevity. The longest age record revealed in this study was at least 3 years and 11 months. This male bird (A194151), banded by J. V. Lund on October 23, 1951, was last seen on May 20, 1955. The oldest bird reported in the literature was a male of at least 7 years and 4 months (Middleton, 1949). During his long life this unusual male had three mates and raised 47 young in the same nest box. The oldest Tufted Titmouse that nested in natural cavities was one of 5 years and 11 months (Laskey, 1943).

Predators. Mammalian predators present in the study area were the Raccoon, Red Squirrel, and Fox Squirrel. Avian predators were the Red-shouldered Hawk, Red-tailed Hawk, Sharp-shinned Hawk, and Great Horned Owl. These, however, are potential predators only, as I had no actual records of loss from these animals.

Flocking

After the post-nuptial molt in July or August the titmice assembled in small flocks and remained together until pair formation separated them in late March or early April.

Formation. On August 14, 1954, my first flock that was not strictly a family group was observed. It consisted of the female from Pair RC2b, two of her young, and three unbanded juveniles. On September 4, 1954, another flock

in the same woodlot consisted of both parents from Pair RCl, two of their young, and two unbanded birds. This evidence indicates that the family group may form the nucleus of the flock. These findings agree with those of Van Tyne (1948), who mentions that young from different nests continued to accompany their parents to his feeding station from the time of fledging until as late as January 10.

Size and Composition. The determination of the size of a flock, as well as the recognition of its individuals, was especially difficult in the woods. A flock crossing an opening afforded the best opportunity for recording numbers and composition. Two or more birds seen together were considered a flock. The occasional single birds encountered during the fall and winter are not included in the summarization of the data on the size of flocks presented in Table XI.

The large postnesting population in September consisted of a greater number of flocks than during the following winter months. The decrease in the population by January resulted in fewer flocks but the average number of birds per flock was only slightly smaller than it was during the fall months. For example, 14 separate groups were recorded on September 25, 1954, while 5 were noted on January 8, 1955. The average number of birds per flock was 9 and 6, respectively.

The behavior of SF3 (flock number 3, Sanford Woodlot) was typical of the instability of the titmice flocks. On November 17, 1954, SF3 consisted of six birds. Two days later one of the individuals (146207) was noticed in another flock, while the size of SF3 had increased to eight birds with the addition of three new members. On November 22 the composition of the flock was again different. Individual 146207 had returned to it while two other members (146205 and 146208) had joined other flocks, thereby reducing the size of SF3 to seven birds. Similar shifts in other groups indicated that the titmouse flocks were loose aggregations, varying in both size and composition.

Associates. Other species were often seen accompanying the titmouse flocks. If these other birds remained with the titmice as the group moved from place to place they were considered members of the flock but if they did not remain with the titmice they were considered independent. Various associations with the Tufted Titmouse were noted, although they were somewhat temporary.

In the fall, transient warblers and Ruby-crowned Kinglets formed temporary flocks with the titmice. In September the loose aggregations of warblers and titmice were commonly seen feeding in the tree tops. The Tufted Titmice were the noisiest of the group and were undoubtedly the leaders since the warblers followed them in their

movements. Mayfield (1937) reports a similar observation in Tennessee where Carolina Chickadees and titmice share in the leadership of mixed autumnal flocks. The species of warblers most commonly associated with the Tufted Titmouse were the Magnolia, Black-throated Green, Blackburnian, Canada, Black-and-White, Bay-breasted, Chestnut-sided, and the Redstart. Myrtle Warblers, which passed through after the first wave of warblers, did not mix with the titmice flocks but remained in their own small groups. The Ruby-crowned Kinglets, passing through in October and November, replaced the warblers in the flocks of Tufted Titmice and their behavior was similar to that of the warblers.

During the winter months Black-capped Chickadees were the most common and most permanent associates in the flocks of Tufted Titmice but Hairy Woodpeckers, Downy Woodpeckers, and White-breasted Nuthatches were seen in temporary association with the titmice.

Roosting Habits

Since the roosting habits of the Tufted Titmouse were slightly different in the winter than in the breeding season, they will be described separately.

Fall and Winter. During the fall and winter months most of the titmice roosted in tall evergreens or in cavities. Three were found in cavities, two in old woodpecker holes

and one in a decayed knot-hole. None of these cavities was used for nesting the following year. By using a ladder I was able to look into the knot-hole without alarming the sleeping bird. It was in a squatting position on the floor of the cavity and appeared to be a ball of gray fluff, with its head thrust under the scapulars. The tail was raised against the side of the cavity.

Bent (1946) mentions that Dickey reported titmice roosting in woodpecker holes and natural cavities in Pennsylvania and West Virginia. Huey (1927) reported a case of a titmouse roosting on a twig surrounded by the leaves of a broadleaf tree. It is possible that such a roost surrounded by dense foliage may have afforded concealment and shelter similar to a cavity.

The places of roosting reported for other Parinae are about the same as those of the Tufted Titmouse. Odum (1942) mentions the use of natural cavities, old woodpecker holes, and hemlock shelters by the Black-capped Chickadee. Williams (1941) found Chestnut-backed Chickadees (Parus rufescens) roosting singly under eaves of houses and in vines, and quoted Bassett as reporting a Mountain Chickadee (Parus gambeli) roosting in an old Robin's nest. Mogall (1939) found that Great Tits and Blue Tits commonly roosted singly in nesting boxes during the winter, and Dixon (1949) reported the use of cavities by the Plain Titmouse.

Breeding Season. With the breakup of the winter flock and the pairing of birds in March and April the winter roosting sites were abandoned. Until the nesting site was selected a pair seemed to sleep wherever it was convenient. In one instance I noted that the birds of a pair (S5) did not roost close together. The male (146223) sought shelter in a spruce tree while his mate remained active. She later went to roost in a spruce tree in the same area but about 75 feet from the male.

Not until the nest was completed did the female begin sleeping on it, but from that time until the young left the nest she used it regularly. The male roosted in trees in the general vicinity of the nest. After the young had fledged the family group roosted wherever they happened to be at sunset.

Time of Roosting. During the fall and winter of 1954-'55 the roosting time of a flock of titmice in Sanford Woodlot was recorded. This was assumed to be the time when the last call was heard, by which time most of the birds were settled.

The fall and winter roosting times in relation to sunset are summarized in Table I, page 60, while Table II presents the roosting times recorded for Pairs S5 and S9 during the nesting season of 1955. The "+" before a number means minutes after sunset that the birds went to roost, while the "-" indicates minutes before sunset.

Table I

60

Time of Roosting during Fall and Winter

Weather	Months				
	October	November	December	January	February
Clear					
No. observ.	3	1	0	1	1
Average	+13.3	+10	---	-15	-19
Partly cloudy					
No. observ.	0	2	2	1	1
Average	---	+4	+3	-18	-25
Overcast or snowing					
No. observ.	2	1	2	1	2
Average	+3	-2	-8	-29	-36
Total No. observ.	5	4	4	3	4
Average	+9.2	+8	-2.5	-20.7	-29
Variation	+2 to -16	-2 to +10	-10 to +4	-29 to -15	-40 to -19

Table II

Time of Roosting during Nesting

Date	Male	Female	Condition
April 15	-46	-48	Pair S5, both in evergreens
April 28	-34	-38	Pair S9, both in evergreens
May 7	-30	-32	Pair S5, both in evergreens, nest construction
* May 10	-25	-35	Pair S5, egg laying
* May 15	-42	-56	Pair S9, incubation
* May 17	-20	-32	Pair S5, incubation
* May 20	?	-30	Pair S9, incubation
* May 24	-18	-30	Pair S5, incubation
* May 30	-16	-22	Pair S9, feeding young
* June 5	-17	-20	Pair S5, feeding young
* June 9	?	-17	Pair S9, feeding young
* June 15	-16	-18	Pair S5, feeding young

* Female roosting in cavity, male elsewhere.

Although the number of observations was limited in both sets of data, certain behavioral patterns are evident. The birds usually went to roost earlier in January and February than in October and November. Birds roosted earlier on overcast days than on partly cloudy or clear days (Fig. 9). Individual birds tended to retire later before nesting began than after. Once the female began using the nest cavity for roosting she usually retired before her mate.

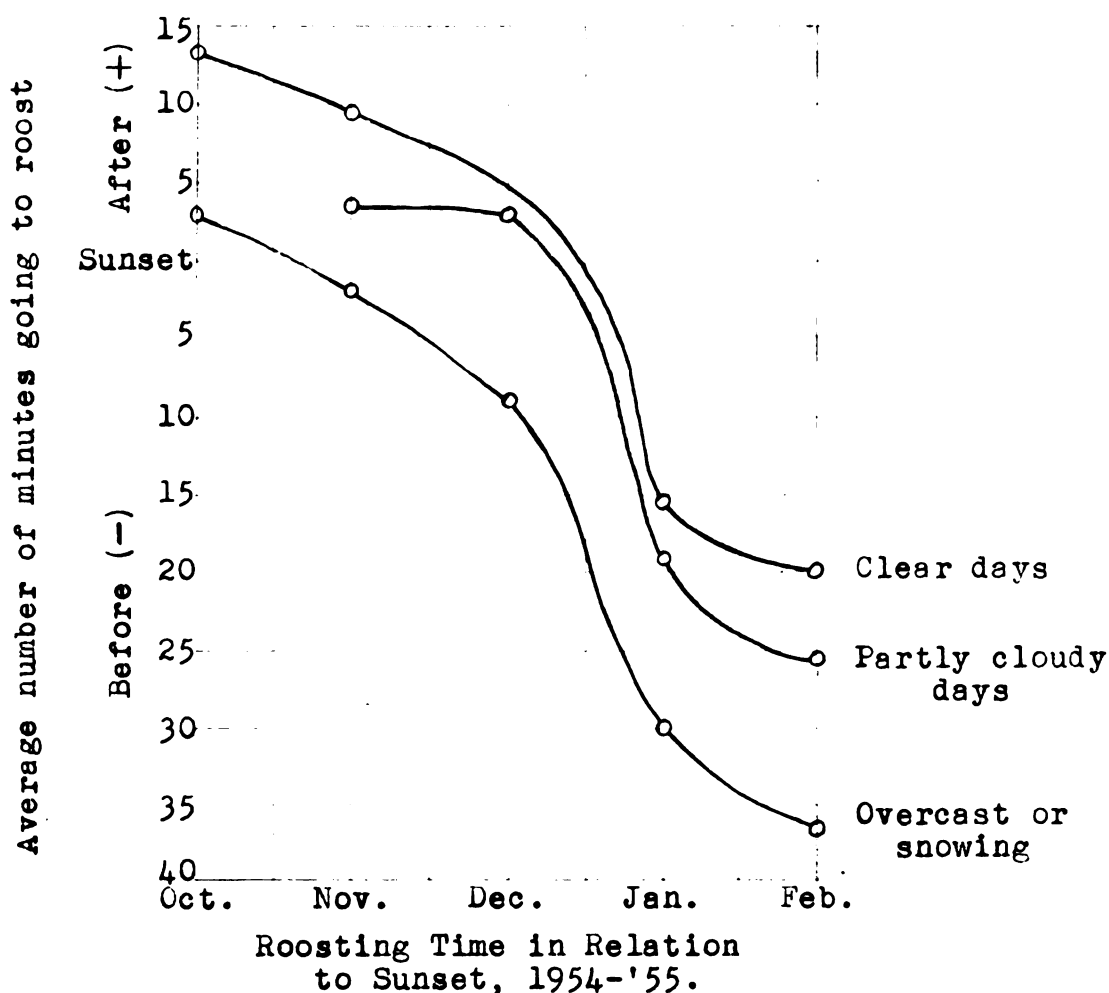


Figure 9

The literature reports similar findings for several other species. The seasonal variation in roosting time has been recorded for the European Tree Creeper (Certhia familiaris britannica)(Rankin and Rankin, 1940); Chestnut-backed Chickadee and Bewick's Wren (Thryomanes bewicki)(Williams, 1941); and the Black-capped Chickadee (Odum, 1942). Williams and Odum found a similar sex difference in the roosting of Chestnut-backed and Black-capped Chickadees, respectively--the female roosting earlier and rising later than the male.

During the winter of 1954-'55 observations were made on the time of leaving the roost in relation to sunrise. The average of three records in November, 1954, was 6 minutes before sunrise, while the average of three observations in January, 1955, was 14 minutes before sunrise. My observations indicate that the Tufted Titmouse goes to roost early and rises late. The continued activity of other woodland birds after titmice had retired, and first singing in the morning, before they had left their shelters, was also noted. In November, 1954, they spent approximately 14 hours on the roost; in January, 1955, about 15 hours. Long roosting times have also been reported for other species of the genus Parus.

Voice

The vocabulary of the Tufted Titmouse consists of a great number of notes used in various combinations. The following list includes only those which I have been able to relate to a specific function, i.e., they were given in a particular situation and frequently produced definite observable responses.

"Peto" Song. This is a high-pitched, clearly whistled phrase, usually repeated two to four times. It has various translations, the most common of which are "peto, peto, peto" and "peter, peter, peter." The accent falls on the first syllable when the song is uttered slowly and on the last when singing is rapid, but in either case the first syllable of each phrase is higher in pitch. This song was heard in all months of the year, becoming almost monotonous in the spring. It was uttered by both sexes but more frequently and more loudly by the male, especially during courtship and defense of territory.

Location Note. This note was given by both sexes throughout the year but most frequently during the fall and winter flocking periods. It sounded like a dry, scratchy "tsicka-dee-dee." This note seemed to be used for re-establishing contact with other members of the flock or for re-establishing contact with the other member of a feeding

pair. A similar note has been recorded for the Plain Titmouse (Dixon, 1949) and is similar to the "chick-a-dee-dee-dee" of the Black-capped and Carolina Chickadees. When this note is given by the Tufted Titmouse it is louder, hoarser, and more slurred than it is in these other species.

Alarm Note. When alarmed at close quarters, such as while feeding on the ground or during banding operations, the birds gave a short, explosive "chit, chit" or "tsicka-dee-dee." After dashing to cover or after being released from the trap, this alarm note was often followed by the harsh scolding note--a loud, rapidly given "tsicka-dee-dee-dee," with the emphasis on the "dee" part of the note. This expression was often given when my presence was detected or when a predator was sighted. It was also given by titmice in nearby trees during banding operations.

Recognition Note. While foraging together the members of a pair frequently gave soft lisping notes which may be transcribed as "tsip, tsip" or "tseep, tseep." This note was heard throughout the year from both sexes but it was heard most frequently when a pair was feeding. They rarely used this note during brooding or during exceptionally cold weather when they were more stationary.

Hissing Note. This sound, sometimes accompanied by puffing, is probably more the result of a forced expiration than a true vocal utterance. It was given by incubating

and brooding females, and by the young in the nest. According to Bent (1946) it is a characteristic defensive behavior in several species of the genus Parus.

Invitational Note. On several occasions females gave an invitational or begging display which consisted of the soft, high-pitched, rapidly uttered notes "tsee, tsee, tsee" and the simultaneous quivering of her wings. On two occasions this behavior preceded and accompanied copulation.

Begging Note. This note was quite similar to the invitational note except that it was much louder. It was given by the female when begging food from the male, and also by the young from the time they left the nest until they were independent. The begging note was accompanied by wing quivering in both the adult female and the young.

Distress Note. The shrill, high-pitched "see, see, see" was given by adults and nestlings while they were being banded. The distress notes usually elicited a scolding response both from other titmice in the vicinity and from the parents of the nestlings being banded.

Many of the above notes of the Tufted Titmouse are not described in the literature, but similar notes have been reported for other members of the genus Parus. Odum (1942) describes 16 different notes for the Black-capped Chickadee, while Dixon (1949) describes 13 functionally different notes for the southwestern Plain Titmouse. This great variation

in vocalization is characteristic of other strongly social species. Davis (1940) lists 13 notes for the highly gregarious Smooth-billed Ani (Crotophaga ani), and Erickson (1938) lists more than a dozen notes for the Wren-tit (Chamaea fasciata). On the other hand, Hann (1937) lists but five call notes for the Ovenbird (Seiurus eurocapillus), a generally non-social species.

Food and Feeding Habits

Feeding is one of the principal diurnal activities of titmice, especially during the cold fall and winter months, when nearly all their time is spent in seeking food.

Food. According to Beal (1941) the food of the Tufted Titmouse, as revealed by the analysis of 186 stomachs obtained at all season, consists of 66.57 percent animal matter and 33.43 percent vegetable matter. Table X summarizes the results of the stomach analyses. One item, caterpillars, formed more than half the animal food, and together with wasps, formed more than half the total food. These were torn into small pieces before being swallowed, thus making identification difficult. Coleoptera made up 7.06 percent of the titmouse diet and more than two-thirds of these were snout beetles or weevils. The cotton boll weevil was found in four stomachs.

Beal mentions that ants were found only occasionally but other hymenopterous insects--bees, wasps, and sawfly larvae--were eaten extensively (12.5 percent). Hemiptera, principally pentatomids, and Homoptera (membracids and coccids) were eaten to a moderate extent (4.03 percent) in 7 of the 12 months. A single fly was found in a stomach collected in January. The only traces of orthopterous insects (0.42 percent) were eggs of katydids, egg cases of cockroaches, and a jaw and ovipositor thought to be those of a grasshopper. Spiders and a few snails made up the remainder of the animal food.

Beal's analysis of the vegetable matter consumed indicated that fruit was eaten to a moderate extent (5.15 percent), mostly in midsummer, and included raspberries, blackberries, strawberries, elderberries, hackberries, blueberries, huckleberries, and mulberries. Seeds of various kinds--sumac, poison ivy, and bayberry--totaled 4.07 percent. Broken seeds and mast formed more than two-thirds of the vegetable matter. Mast amounted to 23.4 percent of the total year-round food, comprising 95 percent of the food eaten in November, 50.42 percent in January, and 55.97 percent in February. Mast was also the principal form of vegetable matter consumed from August to March.

In this study specimens were not deliberately collected for stomach analyses, but five adult Tufted Titmice, which had been killed accidentally, were examined. The results of these examinations are presented in Table IX.

In no instance was food found in any part of the digestive tract except the gizzard. Because the food was so finely divided a stomach was often recorded as containing only one insect when it doubtless contained parts of more than one.

Feeding Habits. Tufted Titmice were very versatile in seeking food, foraging from the ground to the tops of trees in a variety of habitats, although they generally fed at low or at intermediate levels in trees and shrubs. Several distinctly different habits associated with feeding were recorded.

Most of the insect food eaten during the spring, summer, and autumn months was taken from broadleaf and coniferous foliage, mainly from the former. The birds often tore open the cases of leaf-rolling larvae and on two occasions the forest tent caterpillar (Malacosoma americana) was taken. During the spring months opening buds were frequently examined, probably for insects. Inspection of the bark of limbs and twigs occurred throughout the year but it was especially prevalent during the winter months. Tufted Titmice were often seen hanging upside down at the

ends of twigs in their search for food. In addition to gleaning small insects from the bark of twigs and limbs, the birds captured moths from the tree trunks. The wings of moths were removed and only the soft body eaten. Bent (1946) reported titmice eating small white grubs contained in an oak apple, and Trautman (1940) noted a titmouse eating the pupal contents of a cecropia moth (Samia cecropia) cocoon.

Seeds and fruit were eaten mostly in the fall and winter months. On one occasion a small winter flock was noted feeding in a hemlock on the campus. The birds hung upside down on the cones while carefully removing their seeds. Beechnuts were also consumed during the winter months. No storing of naturally occurring seeds was observed, but on November 20, 1954, one particular individual (146203) stored at least 20 sunflower seeds in the bark of a black cherry tree, located a short distance from a feeding station. This storage of items from feeding stands is a commonly observed practice. Titmice were seen eating the fruit of the following trees, shrubs, and vines: choke-cherry, stag-horn sumac, wild crab-apple, Virginia creeper, and flowering dogwood.

Tufted Titmice spent considerable time searching for food in the ground litter. After locating an edible item they would carry it to a nearby perch before consuming it.

This habit prevailed also at the feeding tray where the most common practice was to hold the seed against the perch with their feet, while they deftly and quickly removed the seed coat.

Hawking insects is apparently not a regular habit in titmice. In the literature I found only one observation, that of Dickey (Bent, 1946), of hawking a moth or butterfly. I witnessed this behavior once. At 4:30 P.M. on August 27, 1955, I saw a titmouse that was perched 15 feet from the ground in the edge of a red maple tree suddenly fly straight out about 8 feet to capture a cabbage butterfly (Pieris rapae). The bird returned immediately to its perch where it removed the wings before consuming the soft body of the insect. Although I waited for a possible repeat performance the bird soon flew out of sight.

Tufted Titmice bathed and drank in the small woodland pools. They also used artificial bird baths for drinking and bathing. On five different occasions I watched titmice drink water from melting snow on trees. While clinging to the underside of a limb they reached up and drank drops of water as they formed.

SUMMARY

A life-history study of the Tufted Titmouse, Parus bicolor, was the object of this investigation from September 1953 to September 1955. The study included a review of the classification and nomenclature of this species, an analysis of its past and present distribution, and its annual cycle in Michigan. The latter was the principal objective of the research.

The Tufted Titmouse is a monotypic species of the family Paridae and is indigenous to North America. The scientific name, Parus bicolor, was established by Linnaeus in 1758. The generic name was changed several times but was re-established in 1944. The English name for the Latin generic name, Parus, is "titmouse," and the specific name, bicolor, means "of two colors."

The Tufted Titmouse is a non-migratory species whose range covers most of the eastern half of the United States. The political limits to the north are the southern portions of the northern tier of states from Minnesota to New York, and southern New England. The southern limit extends along the Gulf coast from Florida to the eastern half of Texas. The western extension closely parallels the 99th meridian. This distribution coincides very closely with the distribution of the eastern deciduous forests.

In Michigan the northern limit of the breeding range extends to a line running roughly from Muskegon across the state through Mt. Pleasant and Midland to Port Huron.

During the past 25 years the Tufted Titmouse has been gradually spreading northward in all the states along the northern limits of its range. This extension may be due to a number of factors. The gradual rise in temperature, especially during the critical winter months, is suggested as a possible contributing factor. Evidence of vegetational succession is also presented, especially as it relates to the availability of suitable nesting sites.

Studies on the annual cycle were conducted in three woodlots at Michigan State University, East Lansing. The woodlots consist of a mixed deciduous tree association, tending toward the beech-maple climax stage of succession.

Numbered aluminum bands and colored aluminum bands were used in various combinations for the identification of adults and young.

The hand-operated Higgins trap proved to be the most successful of the several trapping methods attempted.

At the beginning of the study, in the fall of 1953, there was a population of approximately 34 titmice in the three study areas. This number dwindled to 18 by the spring of 1954.

Pairing and the gradual break-up of the winter flocks occurred during the period from March 25 to April 12. The newly paired birds wandered about for several days before investigating possible nest sites.

The establishment of territory, which seemed to coincide with nest building, was principally for feeding and nesting. Territories varied from 7.8 to 13.9 acres, averaging 10.4 acres (4.2 hectares). Defense was mainly the duty of the male although the female sometimes assisted in banishing an intruder. The size of territory and the vigor of its defense decreased as nesting progressed.

The titmice did not excavate their nest sites but used natural cavities or abandoned woodpecker holes. Nests were found in elm, maple, and beech trees, but of course a much greater variety of nest sites has been reported in the literature, including bird boxes. The height of the 20 nests ranged from 18 to 66 feet, with an average of 38.5 feet. Nest construction was the duty of the female, although the male accompanied his mate and occasionally carried building material. Building of the nest averaged four days. All nests were loosely constructed and all contained dried grass, moss, and hair. Additional items in some nests were strips of bark, dead leaves, string, and paper. The hair formed the shallow cup in which the eggs were laid.

The dates of first eggs ranged from May 4 to May 11 and they were laid at the rate of one a day until the full complement of five or six was deposited. The eggs were white, unevenly marked with brown specks. Copulation was observed only during the egg-laying period.

Incubation was by the female. The male fed his mate both on the nest and away from it. Attentive periods averaged 25.8 minutes, inattentive periods 8.9 minutes. The incubation period in four nests averaged 13 days and 3 hours.

After hatching the young were fed by both parents but mainly by the male during early nestling life. The male now ignored the begging of his mate and concentrated on feeding the young. The total number of feedings per hour by both parents increased from 8, when the young were one day old, to 17.7, when they were 12 days old. By the time the young were ready to leave the nest they closely resembled the adults, except for their fluffier plumage, shorter primaries and rectrices, and the yellow rictus of the mouth. The young left the nest 15 days and 17 hours after hatching (average of four nests).

After fledging, the young followed their parents for several days or longer. In some cases at least, the young remained with their parents through the remainder of the summer, so that the family formed the nucleus of fall flocks. This was possible in this species since only one brood was raised.

Nesting success in four nests was 90 percent and there was a three-fold increase in the summer population. The longest age record in this study was at least 3 years and 11 months.

The flocks of titmice and associated species began to form in August. They assembled gradually and changed considerably during the fall and winter months. Some of the flocks were started by family groups, while others were mixed associations including young from several nests. The size of the flocks was quite variable but averaged seven birds. During the fall and spring the size of the titmouse flocks increased with the addition of migrants, especially warblers.

During the fall and winter the birds roosted wherever they happened to be at sundown. Roosting was in conifers as well as in deciduous trees and shrubs. The birds generally went to roost much earlier, in relation to sunset, during January and February than in October and November. They also retired much earlier during the nesting season than they did at other times of the year. Data on the time of leaving the roost, in relation to sunrise, indicate that Tufted Titmice, compared to most other species, go to roost early and rise late. In November, 1954, approximately 14 hours was spent on the roost, while in January, 1955, the time was extended

to 15 hours. During the breeding season the female slept in the nest cavity, the male nearby. On days of inclement weather and general cloudiness the birds went to roost earlier than on days of fair weather.

The songs and calls of the Tufted Titmouse were many and varied. The most common song of "peto, peto" was given by both sexes throughout the year, but less frequently during the nesting season. In addition to this song I discerned a location note, recognition note, alarm note, hissing note, invitational note, begging note, and distress note. Some of these are basically similar but have distinct variations associated with various types of behavior.

The food of the Tufted Titmouse, based on the analysis of 186 stomachs by Beal (1941), consists of two-thirds animal matter and one-third vegetable matter. The territory for securing food extends vertically from the ground litter to the uppermost twigs of the tallest trees. Most insect food is gleaned from bark and leaves, but the hawking of a butterfly was noted on one occasion.

APPENDIX

Table III

Average Weather Conditions at East Lansing, Michigan
for the months from December to June, 1953-'54 and 1954-'55*

	Temperature (Degrees F.)			Precipitation (Total Inches)		Wind (M.P.H.)		Sunshine (Per cent)
	Max.	Min.	Av.	Water	Snow	Max.	Av.	
1953								
December	38	25.2	31.6	1.48	7.5	45	15.1	29
1954								
January	30.4	15.9	23.2	1.61	12.1	47	13.2	30
February	38.5	24.3	31.4	4.21	13.3	35	14.2	43
March	38.9	22.5	30.7	3.25	13.8	50	15.2	55
April	59.6	37.3	48.5	2.75	0.1	42	13.8	44
May	64.5	41.5	53.0	1.14	0.3	40	11.5	60
June	80.3	59.2	69.8	4.07	0	51	8.5	64
December	33.6	22.4	28.0	2.71	10.9	17	5.3	26
1955								
January	30.6	18.5	24.6	1.47	5.2	18	6.3	41
February	34.1	19.0	26.6	1.89	13.4	16	5.8	51
March	43.5	25.1	34.3	2.97	8.5	29	7.2	67
April	65.7	43.3	54.5	1.56	T	23	6.7	78
May	73.0	49.0	61.0	1.53	0	18	5.2	60
June	78.9	56.4	67.7	3.81	0	22	4.0	59

* Data from the U.S. Department of Commerce, Weather Bureau,
Local Climatological Data

Table IV

Summary of Incubation Behavior

Pair No.	Attentive Period				No. of times ♀ leaves nest		Inattentive Period		
	Number of Observ.*	Length (minutes)		No. of times ♂ feeds ♀ during one period	When ♂ calls	Of her own accord	Number of Observ.	Length (minutes)	
		Aver.	Var.					Aver.	Var.
RC1	8	24.0	8-34	1.1	7	3	10	7.5	4.4-10.1
RC2b	7	26.7	10-41	1.7	5	3	8	8.7	3.3-18.3
S1	14	25.0	6-52	1.9	9	7	16	10.5	2.5-24.3
S3	10	27.5	9-48	1.4	8	4	12	8.7	3.6-18.4
Totals	39	25.8	6-52	1.5	30	17	46	8.9	2.5-24.3

* Observations made during latter half of incubation.

Table V
Dimensions of Nest Cavities and Nests

Nest Cavity	N E S T						
	RC1	RC2a	RC6	S10	Aver.	Max.	Min.
Opening (diameter)	4.4*	5.0	5.6	5.3	5.07	5.6	4.4
Depth	21.2	27.5	25.0	22.5	24.05	27.5	21.2
Diameter (smallest)	10.0	11.2	12.5	11.2	12.5	12.5	10.0
Nest							
Depth							
Outer	13.7	20.0	15.0	15.6	16.1	20.0	13.7
Inner cup	3.7	3.1	4.4	4.4	3.9	4.4	3.1
Edge of nest to outer edge of entrance	7.5	8.7	10.0	9.5	8.42	10.0	7.5
Diameter							
Outside	10.0	11.2	12.5	11.8	11.22	12.5	10.0
Inner cup	6.9	7.5	8.7	8.1	7.5	8.7	6.9

* Figures in centimeters.

Table VI
Hourly Rate of Feeding Nestlings

	Age (Days)							
	1		4		8		12	
	♂	♀	♂	♀	♂	♀	♂	♀
Sex								
Pair No.								
RC1	5	3	7	4	9	6	11	8
RC2b	5	2	6	4	7	6	8	9
RC6	6	3	7	2	8	5	10	7
Totals	16	8	20	10	24	17	29	24
Average	5.3	2.7	6.7	3.3	8	5.7	9.7	8
Per pair	8		10		13.7		17.7	

Table VII

Location of Nest Sites

Species of Tree	N E S T										Totals	Percent	Average	Maximum	Minimum											
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	B1	B2	B3	RC1	RC2a	RC2b	RC3	RC4	RC5	RC6						
<u>Ulmus americana</u>	X					X		X	X	X		X				X		X		X		9	45			
<u>Acer rubrum</u>		X	X		X		X				X		X	X	X		X				X	10	50			
<u>Fagus grandifolia</u>				X																		1	5			
Part of Tree																										
Side limb	X	X		X		X	X	X	X	X		X		X	X	X	X	X	X			15	75			
Junction of main trunk and side limb			X		X						X		X								X	5	25			
Nature of Cavity																										
Old Woodpecker hole						X			X							X	X					4	20			
Decay cavity	X	X	X	X	X		X	X		X	X	X	X	X	X			X	X	X	X	16	80			
Height above ground*	66	58	42	38	32	57	31	45	28	21	54	40	34	25	45	20	25	58	33	18		385	66	18		
Location of opening relative to tree	E	S	N	S	E	N	E	N	W	N	W	S	E	S	N	S	W	S	E	S	N					
Direction of opening	N	W	S	E	E	S	S	S	E	W	W	S	N	N	W	W	E	E	E	E						
Distance from nearest Tufted Titmouse nest*	7462	922	462	922	528	782	594	594	528	772	626	772	626	584	650	584	594	594	594	646		763	484	62		

* Figures refer to number of feet.

Table VIII

Materials Used in Nest Building

	N E S T			
	RC1	RC2a	RC6	S10
Plant				
Grass	60*	70	65	55
Moss	23	16	17	20
Bark (<u>Populus</u> sp.)		2	1	
Leaves				
Deciduous			2	3
Evergreen				2
Total	83	88	85	80
Animal				
Hair	16	10	14	20
Feathers		1		
Total	16	11	14	20
Miscellaneous				
String	1	1		
Paper			1	
Total	1	1	1	

* Figures indicate percentage by volume relationships.

Table IX

Stomach Analyses of Five Tufted Titmice

	Date of collection				
	1/1/'54	2/4/'54	3/10/'54	12/30/'54	1/8/'55
Animal					
Insects					
Lepidoptera (larvae)	5 *	3	3	6	2
Coleoptera					
Adults	2	2	10	2	4
Larvae	3			2	
Spiders				2	2
Miscellaneous			30		
Total	10	5	43	12	8
Vegetable					
Seeds	10	8		10	5
Mast (incl. broken seeds)	60	59	42	51	62
Moss	5	10	2	6	5
Miscellaneous (leaves, bud scales, fruit pulp)	5	10	5	6	10
Total	80	87	49	73	82
Grit	10	8	8	15	10

* Figures indicate percentage by volume relationships.

Table X

Summary of Food Items from Stomachs
of 186 Tufted Titmice (Beal, 1941)

Animal	Percent	Vegetable	Percent
Lepidoptera (caterpillars)	38.31	Fruit (wild and cultiv.)	5.15
Hymenoptera (bees, wasps, sawfly larvae)	12.50	Seeds	4.07
Coleoptera (beetles)	7.06	Mast	24.21
Hemiptera	4.03		
Orthoptera (eggs)	.42		
Misc. (snails, spiders)	4.25		
Total (Animal)	66.47	Vegetable	33.43

Table XI

Size of Flocks of Tufted Titmice

Year Month	Number of Observations		Average number of birds per flock		Variation in size	
	'53-'54	'54-'55	'53-'54	'54-'55	'53-'54	'54-'55
Sept.	34	30	10	9	2-12	2-13
Nov.	20	18	8	8	2-14	2-15
Jan.	16	15	6	5	2-15	2-14

List I

Non-Avian Vertebrate Associates of the Tufted Titmouse (observed in the woodlots)

Mammals

Opossum, Didelphis virginiana
Masked Shrew, Sorex cinereus
Short-tailed Shrew, Blarina brevicauda
Raccoon, Procyon lotor
Long-tailed Weasel, Mustela frenata
Striped Ground Squirrel, Citellus tridecemlineatus
Eastern Chipmunk, Tamias striatus
Red Squirrel, Tamiasciurus hudsonicus
Fox Squirrel, Sciurus niger
Prairie Deer Mouse, Peromyscus maniculatus bairdii
White-footed Mouse, Peromyscus leucopus
Meadow Vole, Microtus pennsylvanicus
House Rat, Rattus norvegicus
Cottontail, Sylvilagus floridanus

Amphibians

Spotted Salamander, Ambystoma maculatum
Jefferson's Salamander, Ambystoma jeffersonianum
Red-backed Salamander, Plethodon cinereus
Tree Toad, Hyla versicolor
Swamp Cricket Frog, Pseudacris triseriata
Leopard Frog, Rana pipiens
Eastern Wood Frog, Rana sylvatica

Reptiles

Garter Snake, Thamnophis sirtalis
Painted Turtle, Chrysemys picta

List II

Birds Observed in the Study Area from September '53 to September '55

Common Name	Scientific Name*	Transient		Resident		
		Feeding	Resting	Breeding	Feeding	Resting
Wood Duck	<u>Aix sponsa</u>			X		
Red-shouldered Hawk	<u>Buteo lineatus</u>					X
Red-tailed Hawk	<u>Buteo jamaicensis</u>					X
Sharp-shinned Hawk	<u>Accipiter striatus</u>				X	
Ring-necked Pheasant	<u>Phasianus colchicus</u>					X
Killdeer	<u>Charadrius vociferus</u>					X
Spotted Sandpiper	<u>Actitis macularia</u>				X	
Mourning Dove	<u>Zenaidura macroura</u>			X		
Yellow-billed Cuckoo	<u>Coccyzus americanus</u>					X
Great Horned Owl	<u>Bubo virginianus</u>					X
Common Nighthawk	<u>Chordeiles minor</u>					X
Chimney Swift	<u>Chaetura pelagica</u>				X	
Ruby-throated Hummingbird	<u>Archilochus colubris</u>				X	
Belted Kingfisher	<u>Megasceryle alcyon</u>			X		
Yellow-shafted Flicker	<u>Colaptes auratus</u>			X		
Red-bellied Woodpecker	<u>Centurus carolinus</u>				X	
Red-headed Woodpecker	<u>Melanerpes erythrocephalus</u>			X	X	
Yellow-bellied Sapsucker	<u>Sphyrapicus varius</u>				X	
Hairy Woodpecker	<u>Dendrocopus villosus</u>			X		
Downy Woodpecker	<u>Dendrocopus pubescens</u>			X		
Eastern Kingbird	<u>Tyrannus tyrannus</u>					X

* A.O.U. Check-list of North American Birds, 5th ed., 1957.

List II (continued)

Common Name	Scientific Name	Transient		Resident			
		Feeding	Resting	Feeding	Resting	Feeding	Flew over
Great Crested Flycatcher	<u>Myiarchus crinitus</u> .						
Eastern Phoebe	<u>Sayornis phoebe</u> .						
Eastern Wood Pewee	<u>Contopus virens</u> .						
Horned Lark	<u>Eremophila alpestris</u>						
Tree Swallow	<u>Iridoprocne bicolor</u> .						
Purple Martin	<u>Fregata subis</u> .						
Blue Jay	<u>Cyanocitta cristata</u> .						
Common Crow	<u>Corvus brachyrhynchos</u>						
Black-capped Chickadee	<u>Parus atricapillus</u> .						
Tufted Titmouse	<u>Parus bicolor</u> .						
White-breasted Nuthatch	<u>Sitta carolinensis</u> .						
Brown Creeper	<u>Certhia familiaris</u> .						
House Wren	<u>Troglodytes aedon</u> .						
Winter Wren	<u>Troglodytes troglodytes</u>						
Catbird	<u>Dumetella carolinensis</u> .						
Brown Thrasher	<u>Toxostoma rufum</u> .						
Robin	<u>Turdus migratorius</u> .						
Wood Thrush	<u>Hylocichla ustellina</u>						
Hermit Thrush	<u>Hylocichla guttata</u> .						
Veery	<u>Hylocichla fuscescens</u> .						
Eastern Bluebird	<u>Sialia sialis</u> .						
Blue-Gray Gnatcatcher	<u>Polioptila caerulea</u> .						

List II (continued)

Common Name	Scientific Name	Transient		Resident			
		Feeding	Resting	Breeding	Feeding	Resting	Flew over
Golden-crowned Kinglet	<u>Regulus satrapa</u>						
Ruby-crowned Kinglet	<u>Regulus calendula</u>						
Cedar Waxwing	<u>Bombycilla cedrorum</u>	X					
Starling	<u>Sturnus vulgaris</u>	X		X			
Yellow-throated Vireo	<u>Vireo flavifrons</u>				X		
Red-eyed Vireo	<u>Vireo olivaceus</u>						
Warbling Vireo	<u>Vireo gilvus</u>						
Black-and-White Warbler	<u>Mniotilta varia</u>	X					
Golden-winged Warbler	<u>Vermivora chrysoptera</u>	X					
Tennessee Warbler	<u>Vermivora peregrina</u>	X					
Nashville Warbler	<u>Vermivora ruficapilla</u>	X					
Parula Warbler	<u>Parula americana</u>	X					
Yellow Warbler	<u>Dendroica petechia</u>			X			
Magnolia Warbler	<u>Dendroica magnolia</u>	X					
Cape May Warbler	<u>Dendroica tigrina</u>	X					
Black-throated Blue Warbler	<u>Dendroica caerulescens</u>		X				
Myrtle Warbler	<u>Dendroica coronata</u>	X					
Black-throated Green Warbler	<u>Dendroica virens</u>		X				
Cerulean Warbler	<u>Dendroica cerulea</u>		X				
Blackburnian Warbler	<u>Dendroica fusca</u>		X				
Chestnut-sided Warbler	<u>Dendroica pensylvanica</u>		X				
Bay-breasted Warbler	<u>Dendroica castanea</u>	X					

List II (continued)

Common Name	Scientific Name	Transient		Resident			
		Feeding	Resting	Breeding	Feeding	Resting	Flew over
Blackpoll Warbler	<u>Dendroica striata</u>						
Palm Warbler	<u>Dendroica palmarum</u>		X X				
Ovenbird	<u>Seiurus aurocapillus</u>			X			
Yellowthroat	<u>Geothlypis trichas</u>		X X				
Mourning Warbler	<u>Oporornis philadelphia</u>						
Canada Warbler	<u>Wilsonia canadensis</u>						
American Redstart	<u>Setophaga ruticilla</u>	X X					
House Sparrow	<u>Passer domesticus</u>			X			
Eastern Meadowlark	<u>Sturnella magna</u>						
Red-winged Blackbird	<u>Agelaius phoeniceus</u>						
Baltimore Oriole	<u>Icterus galbula</u>			X			X X
Bronzed Grackle	<u>Quiscalus quiscula versicolor</u>				X		
Brown-headed Cowbird	<u>Molothrus ater</u>			X			
Scarlet Tanager	<u>Piranga olivacea</u>			X		X	
Cardinal	<u>Richmondia cardinalis</u>			X			
Rose-breasted Grosbeak	<u>Phœucticus ludovicianus</u>					X	
Indigo Bunting	<u>Passerina cyanea</u>			X			
Purple Finch	<u>Carpodacus purpureus</u>				X		
American Goldfinch	<u>Spinus tristis</u>			X X			
Rufous-sided Towhee	<u>Pipilo erythrophthalmus</u>			X			
Vesper Sparrow	<u>Poœcetes gramineus</u>						
Slate-colored Junco	<u>Junco hyemalis</u>	X					

List II (continued)

Common Name	Scientific Name	Transient		Resident			
		Feeding	Resting	Breeding	Feeding	Resting	Flow over
Chipping Sparrow	<u>Spizella passerina</u>			X	X		
Field Sparrow	<u>Spizella pusilla</u>						
White-crowned Sparrow	<u>Zonotrichia leucophrys</u>	X					
White-throated Sparrow	<u>Zonotrichia albicollis</u>	X					
Fox Sparrow	<u>Passerella iliaca</u>	X					
Song Sparrow	<u>Melospiza melodia</u>			X			

PLATE I

Fig. A. Sanford Woodlot as it appears from the south,
beyond an open field. June 18, 1955.

Fig. B. Sanford Woodlot, viewed from within. June 18,
1955.

PLATE I



Fig. A



Fig. B

PLATE II

Fig. A. Sanford Woodlot as it appears during the winter. February 19, 1955.

Fig. B. Trapping Station. Note the large doors on the sides of this Higgins trap. The written authority for the operation of the banding station in the campus woodlots is posted on the tree to the left. February 19, 1955.

PLATE II



Fig. A



Fig. B

PLATE III

Fig. A. Nest cavity of Pair S6 in Sanford Woodlot.
The nest site is located 57 feet from the ground in an
American elm tree. February 19, 1955.

Fig. B. Nest cavity of Pair RC2a in Red Cedar Woodlot.
Close-up view was taken through a 60mm. spotting scope.
The cavity is 45 feet from the ground. February 19, 1955.

PLATE III



Fig. A



Fig. B

PLATE IV

Nest cavity of Pair S4 in Sanford Woodlot. The nest site is located in a limb extending over Hagadorn Road. Beal Pinetum is evident in the background. February 19, 1955.

PLATE IV



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