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A COMPARATIVE ETHOECOLOGICAL STUDY OF THE CAROLINA CHICKADEE (*Parus carolinensis*) AND TUFTED TITMOUSE (*Parus bicolor*) IN CENTRAL OKLAHOMA

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CHAPTER I

INTRODUCTION

Behavior, in its simplest terms, can be defined as what an organism does. Having studied and described the manner in which an animal acts, however, the ethologist then attempts to determine how its behavior is adaptive in helping the animal fit its environment. He also attempts to determine the origin of specific behavior patterns in evolutionary history, and to determine the relationship between the animal's behavior and its anatomy, physiology, and genetic makeup. The ethologist's task is difficult and complex because an animal's behavior is the result of the sum total of all bodily activities.

An animal is an integral part of its environment. It has been adapted in the course of evolution to react to the stimuli of its surroundings in a manner that enables both the individual and the species to survive. To remove an animal from its environment is to isolate it from the stimuli which elicit its behavior and for which its behavior is adapted. In the sterile environment of a laboratory cage the animal is forced to adjust to a stimulus-poor environment which in no way resembles its natural surroundings. In so doing its behavior often becomes distorted and perverted and is of little value to the ethologist in his attempt to understand the animal's behavior in terms of evolution or ecology, unless previous studies of the animal's behavior in a natural environment are available to act as a control. Because of a lack of such studies on the two species being investigated, this study was conducted entirely in the field and every effort was made to avoid interference with the animal's normal routine.

The goal of this investigation was to make a comparative study of two closely related species of animals, preferably of the same genus. Its purpose was to determine how the two species have diverged behaviorally and how such divergence is ecologically adaptive in permitting them to coexist within the same range. Particular emphasis was placed on activities where competition could occur such as in the selection of foraging zones, nest-sites and roost-sites, and in activities where similarities in behavior could lead to interference between the two species as in vocalizations and displays. In many respects the goal was too ambitious to be fulfilled in a study of such short duration, and it was often not possible to go beyond the descriptive phase.

The Carolina Chickadee and Tufted Titmouse were suggested as study animals by Dr. George Miksch Sutton. They were finally selected because of their permanent-resident status locally, and because they are easily captured and can be approached and observed at close range without undue interruption of their normal activities.

Study Area

The study area, known as the Oliver Wildlife Preserve, is located on the south edge of Norman, Oklahoma, on the fourth and highest level of the South Canadian River floodplain. This level lies several feet below the surrounding plain, which is Permian red bed in origin and is believed by Hefley (1937) to be a true river terrace. The area is approximately sixty-three acres in size. The preserve is bounded on the west by a secondary road, on the north and south by cultivated fields, and on the east by a cultivated field and a woodland grazed by cattle.

The western half of the preserve is poorly drained and often holds standing water during the fall, winter, and spring. During 1968-69 up to a foot of water remained in this area from mid-October until early June. No further accumulation occurred during the remainder of 1969 because of the small amount of rainfall.

Penfound (1948) found the dominant trees in the preserve to be American elm (Ulmus americana) and green ash (Fraxinus lanceolata). Because of the presence of a few large cottonwood (Populus deltoides) and black willow (Salix nigra) trees he suggested that a cottonwood-willow forest was the immediate predecessor of the elm-ash community.

Rice and Penfound (1956) found only one dominant, green ash, with American elm, persimmon (Diospyros virginiana), and cottonwood as important secondary species. Minor species, in order of descending importance, were hackberry (Celtis laevigata), burr oak (Quercus macrocarpa), pecan (Carya illinoensis), black willow, box elder (Acer negundo), catalpa (Catalpa speciosa), hawthorn (Crataegus viridis), chittamwood (Bumelia lanuginosa), and Kentucky coffee tree (Gymnocladus dioica). The total importance percentage of these nine species was about the same as that of any one of the major secondary species. In addition to the trees listed above a few large black walnut trees (Juglans nigra) are presently found on the northern edge of the preserve.

The 1956 study indicated that the number of dead trees per acre was about three times that of saplings and found that the area had been deteriorating since 1948. This was attributed to the continuing death of trees due to drought and the very small number of saplings, probably resulting from heavy overgrazing.

Cattle were removed from the preserve in 1961, and since then a large number of saplings have sprung up. In some parts of the woods the sapling and young tree growth is so thick that walking is difficult. They range in height from about fifteen feet to a foot above ground level.

The large cottonwood trees are slowly disappearing and are not being replaced by saplings. A large number of dead trees are still standing in the area, and the ground is littered with dead and decaying trees.

Local Climate and Weather*

While some influence is exerted at times by warm, moist air currents from the Gulf of Mexico, the climate of Norman, Oklahoma falls mainly under continental controls characteristic of the Great Plains Region. As a result of the continental effect, pronounced daily and seasonal temperature changes, as well as considerable variation in seasonal and annual precipitation occur.

The normal annual temperature is approximately 60° F. During an average year there will be 76 days with a maximum temperature of 90° F. or higher. During the colder season, an average of 81 days will have temperatures of 32° or lower, but only one winter in three has temperatures of zero or lower.

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*All information supplied by the records of the Oklahoma City Weather Bureau (1969).

The average length of the growing season is 223 days, with a range of 180 to 251 days. The average date of last freeze in spring is March 28, and the average date of first freeze in fall is November 7.

The average annual precipitation is 31.52 inches. Seasonal distribution is normally as follows: 13 percent in winter, 33 percent in spring, 31 percent in summer, and 23 percent in fall. Snowfall averages less than 10 inches per year and seldom remains on the ground long.

Prevailing winds are southerly except in January and February when northerly breezes predominate. Wind speed averages 12 m.p.h. in summer and 15 m.p.h. in spring.

Methods

Quadrat markers. The study area was staked out in sixty-three one acre squares. Movements of flocks and individual animals were plotted on maps of the area showing the location of all important landmarks as well as the location of each of the steel marker stakes and feeders. Roost-sites, nest-sites, the location of boundary disputes and copulations were also plotted. Winter ranges and breeding territories were then determined from the maps.

Feeders. Seven small feeder platforms were positioned throughout the study area. Each platform contained a four inch diameter seed cup and a small suet basket. Individual feeders were filled only a few days each month to prevent a possible increase in the population size of the two species. A feeder was filled one or two days prior to a trapping operation to assure that it would be in use.

A commercial mixture of seeds was first used at the feeders, but this attracted too many bird species. When it was noted that the chickadees and titmice fed primarily on the sunflower seeds in the mixture, these were used exclusively. This eliminated all but a few of the bird species which had been visiting the feeders.

Suet (beef kidney fat) was used when a banding operation or several successive days of observation at a feeder were planned. This was necessary because even if the seed cup was filled several times a day all of the seeds were removed by the birds in a few hours. The suet, however, lasted several days, and it was not necessary to repeatedly fill the seed cup.

Banding. It is important in a study of this type to be able to identify individual animals. Colored celluloid rings were used to mark individual birds. A numbered Fish and Wildlife Service aluminum band was placed on the leg not color ringed.

Small colored plastic flyers attached to the celluloid rings were also tried. These were more readily observed than the rings but proved unsatisfactory because male birds pulled them off quickly. Female birds usually tolerated them for several months, but eventually they too pulled them off leaving only the celluloid ring.

In the course of the study 76 chickadees and 57 titmice were color banded. All adult birds of both species were color marked during the two nesting seasons, but during the non-breeding season unbanded birds were occasionally observed in the study area.

Trapping. Birds were trapped as they came to feed in mist nets placed in front of the feeders. The trapping method worked quite satisfactorily throughout the study. Some birds, having been caught once, would evade the net. Others were recaptured several times.

Study Period. The birds were followed through two complete annual cycles from early spring 1968 to early spring 1970. Approximately 1200 hours were spent observing them in the field.

CHAPTER II

OBSERVATIONS ON THE ANNUAL CYCLE

Territory

Flock Dispersal. Early singing by the males of both species began during the first week of January in 1969. Through January and early February singing and other territorial behavior waned on cold days and increased on warm afternoons. Flocking was observed on cold, overcast days and in early morning. On warm days during the last week of January paired birds became conspicuous and chases and supplanting attacks among members of the winter flocks were observed frequently. Such attacks took place without strict regard for boundaries. The break-up of the flocks was gradual, lasting from the first week of January until early March. By this time most of the birds unable to withstand the attacks of the alpha male had left the woods, and only pairs which would later defend a territory and nest remained. In each instance, these were the dominant male of the winter flock and his mate. The area utilized by the alpha male and his mate was the same as the winter range of their flock. The male simply drove away the remainder of the flock. Since his dominance was already well established, prolonged fighting was not necessary to accomplish this and was not characteristic of this period. He also prevented interlopers from other flocks from settling in the area. Whereas chickadees and titmice earlier were members of well-coordinated flocks and responded to each other's calls, they now began to ignore each other.

Formation of Territorial Boundaries. The second phase, following dispersal of the winter flock, was the delineation of territorial boundaries between pairs remaining in the woods. The most noticeable difference between the territory and winter range was the sharp delineation of the boundaries during nest-building. Throughout March the pairs traveled about foraging, investigating cavities, and beginning nest construction. During this period males defended their mates against intruders, but territorial boundaries were still fluid.

Territories, in the classical sense of a defended area, were not in evidence until after selection of a nest site. Once a site was selected prolonged and aggressive disputes were observed between neighboring pairs as common boundaries were delimited. Earliest building in 1969 by a chickadee pair was 17 March (CP6A). Latest date for a first nest-building attempt was 2 April. Nest-building by a titmouse pair in 1969 was first observed on 29 March (TP3A), and latest first attempt was 13 April (TP6A).

The territorial boundaries were determined to some extent by the location of the nest site. This was most readily observed when the nest site was located at the edge of the area utilized by the pair and during renesting attempts. The male attempted to extend his area to include the nest site and its immediate surroundings. If he was successful the nest site was utilized; if not, it was abandoned and a new site selected. The following two examples will serve to illustrate this.

> Titmouse pair 4 (TP4) was observed investigating a cavity on 21 March at the edge of the area it utilized following dispersal of the flock. Following selection of the site prolonged chasing and fighting were observed between this pair and adjacent pair TP5. Six days later TP4 was investigating cavities deeper within its own area and was not observed again at the contested nest site. On 3 April TP5 was observed investigating the contested cavity, and the female began constructing a nest on 5 April. The TP4 nest was located two hundred and fifteen feet west of the cavity, and the final boundary was approximately equidistant between the two nests.
>
> On 18 March chickadee pair 10 (CP10) was observed inspecting a tree cavity near the edge of its utilized area. Excavation was begun on 20 March. On 21 March CP11 was observed investigating a cavity one hundred and fifty feet southwest of the CP10 nest site. Excavation began on 25 March. On 26 March chasing and supplanting attacks were observed between the two males but no actual fighting. The CP10 pair abandoned its nest site shortly thereafter, and CP11 extended its boundary to include it.

Common territorial boundaries were very sharp as indicated by repeated chases and fights from the same tree. Boundaries were less sharp where uncontested.

Territory Following Nest-Building. In his study of the breeding territory in Black-capped Chickadees (Parus atricapillus) Stefanski (1967) found that "only in the nest-building stage were enough boundary disputes noted to determine a territory as a defended area." He felt that territories measured in stages other than nest-building represented utilized rather than defended areas. During egg-laying and incubation the space utilized decreased, and territorial contests were infrequent and short. The utilized area increased during the nestling stage but remained only a small fraction of the area defended during nest-building. The territory disintegrated during the fledgling stage, and aggressive behavior occurred only when broods accidentally met while foraging. In his review of territory in the Paridae, Gibb (1956) also stated that territorial activity is strongest just before the eggs are laid and wanes during the remainder of the breeding season.

In general, my observations on the Carolina Chickadee and Tufted Titmouse agree with the findings discussed above. During the prenesting stage disputes between males involved defense of mates, during nest-building defense of nest site and territory, and following fledging defense of brood. After the nest-building stage singing and territorial disputes decreased markedly and only a small portion of the original territory was utilized. This utilized area, however, was not as compact as Stefanski (1967) found for the Black-capped Chickadee. Rather, both species continued to utilize favorite foraging areas throughout the original territory and occasionally visited foraging grounds inside the territories of neighboring pairs. Thus, while only a small portion of the territory was utilized, this portion was dispersed rather than compact. Distinct airway "paths" were used in flying to and from these areas and the nest. During the last week of nestling life, however, and earlier during periods of rapid feeding (just before and after roosting, etc.), most foraging took place near the nest.

Function. During the most critical phase of nesting, the nestling stage, only a small fraction of the original territory was utilized. The large territory, then, was not required for feeding the young. It did, however, serve at least two vital functions--it regulated population density and insulated the pairs against intraspecific interference during the incubation and nestling stages. My discussion will deal with the latter of these two.

During the prenesting stage the two members of a pair traveled together. When incubation began, however, the birds were separated, the female remaining on the nest and the male roaming the territory. This condition prevailed until nearly the last week of nest life. It thus became important to the success of the nest that the activities of the two adults be coordinated. This coordination was achieved through the use of calls, and almost all vocalizations after egg-laying were communications between mates.

The large territory prevented interference between pairs by insulating them from each other's calls.

This insulation appeared to be necessary because the birds of both species were apparently unable to recognize the call notes of particular individuals and responded to calls given by any member of their species. The female, for example, could be called off the nest by a crude imitation of the male's signal song or by recorded calls of another male. Likewise, the male could be brought to the nest or made to answer by an imitation of the female's location note. In one instance, I led a male titmouse (he had just accompanied the incubating female to the nest) for over a hundred yards by walking a short distance ahead and whistling the location note (peet). Each time I whistled he would fly to me and perch, then look about as if searching for his mate. On another occasion, when I whistled the same note near a titmouse nest the brooding female came to the opening and perched outside, and the male flew to the nest (without food). The confusion and hazard to the success of the nest which would result if the female was repeatedly called from the nest by stray calls, or if she was unable to locate her mate upon leaving the nest, can easily be imagined.

The birds responded not only to the call itself, but also to the location of the call. If one member of the pair was foraging alone near its boundary, it would not respond to an imitation or recording of a particular call note which originated within the adjacent territory, even if the call was given only a short distance away. It responded immediately, however, to calls much further away which originated within its own territory.

The large area defended during nest-building insured a lack of interference between the communication of neighboring pairs, and the shrinking of the utilized area following nest-building provided further insulation. Following fledging the family group traveled together, and there was no longer any need for such insulation. Consequently, defense was transferred from the nest-site and territory to the family group.

Interference from intruding calls may also be important in the conditioning of the nestlings to the calls of the adults. The young birds seemed to learn to associate the calls of their parents with food brought to the nest. This will be discussed in greater detail later.

Size. The average size of the eight titmouse territories as determined by boundary disputes during nest building was 9.3 acres (3.8 hectares), ranging from 6.5-10.4 acres (2.6-4.2 hectares). Average size of six chickadee territories determined in the same manner, was 8.1 acres (3.3 hectares), ranging from 5.8-10 acres (2.3-4 hectares).

Following the break-up of the family group in late summer and early fall, the resident pair confined its activities to the boundaries of the breeding-season territory. Since the resident male titmouse dominated and led the other members of the flock (of both species), the flock as a whole moved within the boundaries of his breeding-season territory. During warm afternoons when the flock was more dispersed, first-year birds wandered more widely and were often observed at considerable distances from their winter range. Such birds often joined other flocks, particularly birds lower in the social hierarchy. If the alpha-male titmouse disappeared during the non-breeding season he was replaced, and the new despot, having traveled in the flock and learned its boundaries, also stayed within the original boundaries. This caused the breeding territories to remain remarkably similar during the two years, even when the resident male disappeared and was replaced. It also caused the breeding territory of the alpha chickadee and titmouse males of any given flock to have similar boundaries. The actual boundaries differed slightly because of changes caused by nest-site selection as was discussed earlier. Likewise, the number of winter flocks equaled the number of breeding pairs in the spring.

Chasing and Fighting. The titmouse territories did not appear to extend to the ground except at the nest. Territorial disputes often ended abruptly when the intruder(s) flew to the ground or to a perch several feet above ground and became silent. Often the intruders began to forage in the leaf litter. On these occasions the resident male continued calling for several minutes but made no attempt to chase the intruder.

Chickadees foraged in saplings and the crowns of taller trees during nest-building and were not found on the ground except when females were gathering nesting materials. Consequently, it was difficult to determine whether or not their territory extended to the ground. All observed conflicts started above ten feet except in the immediate vicinity of the nest, but no bird was ever observed flying to the ground during a dispute.

In both species the male assumed the leading role in territorial defense. Auditory, rather than visual stimuli, initiated territorial conflicts. A silent intruder was safe from attack. When an intruder sang the resident male immediately challenged it with loud general call notes and short, loud portions of the song. The intruder either answered with similar calls or retired. If he stood his ground a chase developed which was characterized by short flights from perch to perch (circular chases), supplanting attacks, rapidly uttered high-frequency calls, and loud aggressive call notes. Such conflicts were often preceded by the resident male crouching close to the limb with his body horizontal, crest depressed, head and tail extended forming a straight plane across the back, and rapid wing fluttering. This display was usually accompanied by a high-frequency call and was given at close range when the intruder did not flee. It was apparently elicited by both visual and auditory stimuli. My own whistles elicited it at close range as did the sight of another titmouse following a challenge by the male.

During conflicts the female was usually present but limited her participation to singing and calling. Her presence seemed to be important as no prolonged conflicts were observed in either species in her absence except in the immediate vicinity of the nest. In prolonged chases the male frequently flew to the female, perched near her briefly, then, as if reassured by her presence, rejoined the chase.

Actual fighting was rare and was observed only at the boundary between two territories during nest-building and egg-laying. More often the conflict was simply a series of supplanting attacks and chases. The two males perched near each other and each attempted to force the other to flee. When one flew the other pursued. Both species used similar movements and calls in attempting to supplant another of its own species. The first was the wing-flutter display described above. At close range the crest feathers raised and the body swung from side to side on the perch while the feet remained in place. A quick wing snap or tail flick was also observed on occasion, as the two birds faced each other. If neither flew one or both shifted its perch or moved along the limb toward the other until he flew, then gave chase. At the next perch the process was repeated. Such encounters often lasted up to thirty minutes and were repeated several times a day. The encounters ended when one of the combatants dropped to the ground (titmouse) or flew away.

Pair Formation

Pair formation in both species occurred prior to the establishment of a breeding territory by the male and may have occurred as early as late summer of the preceding year. No obvious courtship rituals were observed, and pair formation may be a gradual process. All observed pairs except two (both titmice) were from the same winter flock. Baldwin (1935) observed a tendency for Black-capped Chickadee mates to keep together during the non-breeding season. Odum (1941a) observed no such tendency in the same species. A definite tendency for mated birds to keep together during the non-breeding season was observed in this study in both the chickadee and titmouse. The following observations were made of several pairs.

> TP3. The male titmouse (blue flyer) first appeared as a hatching-year bird in the area of nest TP2A in late June 1968, before the young had fledged, and became a member of the flock made up primarily of the TP2-family group. The TP3 female (blue L) was first observed in the area during the second week in July. She was an adult bird and had been the mate of a male

(red L) in an adjacent area. In early November blue-flyer male and blue-L female were repeatedly seen together as they foraged or fed alone at the feeders. They continued to be observed together throughout the winter when the flock was not compact. On 19 November I recorded in my field notebook "blue flyer and blue L appear to be paired." When the resident male (white L) disappeared from the woods in late September blue flyer became the dominant bird in the flock. From early January until after the breeding season the male was observed accompanying the female to her roost. During the 1969 breeding season the pair successfully nested.

TP4. The male (red L) was mated to the blue-L female discussed above during the 1968 breeding season. As early as 5 November the male was observed traveling with another bird, purple L. On warm afternoons in early November the two would spend hours alone carrying seeds from the feeder or foraging together. They remained together throughout the winter although during cold weather they appeared to be nothing more than members of the same flock. They successfully nested during the breeding season in 1969.

CP6. During the 1968 breeding season the female chickadee (red R) was mated to orange-R male. He disappeared early in July. The male (blue L) was banded as a hatching-year bird on 8 July at the local feeder. In early November red-R female and blue-L male were observed traveling with a third chickadee, particularly on warm afternoons. Shortly thereafter the third chickadee disappeared and the two birds traveled alone. During cold weather it was impossible to note any tendency by them to keep together in the flock. In early January of 1969, the male was observed accompanying the female to her roost site before entering his own forty feet away.

TP6. The female (white flyer) traveled in a different flock than the male until the first week in January. At this time the pair was traveling together. The male's flock was not observed closely during the winter, but it was noted that two titmice disappeared from the flock prior to January. The male could have been mated earlier and lost his mate.

TP7. The female of this pair spent the winter in an adjacent flock and was not observed with the male until 14 January. Following this first observation the two birds were often seen together, and in the spring they nested successfully in the same area.

Several of the above pairs were described as traveling together in early November. However, they could have been doing so prior to this. It was difficult to observe color bands and individual birds while the foliage was still out. Also, the large size of the flocks in late summer and early fall made the following of individual birds difficult. Dixon (1949) suggested that pair formation in the plain titmouse (Parus ornatus) may occur in immature birds following the break-up of family groups in late summer. The same may be true of both mature and immature birds in both these species.

Permanence of Mating. It is impossible to determine the permanence of mating in a two-year study. There are several brief reviews of mating permanence among the Paridae (Brewer, 1961; Odum, 1941a; Pielou, 1957; Hinde, 1952). The general consensus seems to be that if both members of the pair survive they remain mated for more than one season and may pair for life.

No pair of chickadees or titmice remained paired during the two years of this study, either because of the disappearance of one or both of the mates or because of divorce. Only one case of divorce was noted.

The Nest

Nest-Site Selection

Male and Female Roles. In both species the male took the lead in searching for and investigating prospective nest cavities. Pielou (1957) stated for the Tufted Titmouse that the pair searched together, but the female did most of the inspection of prospective nest sites while the male waited on a perch a few feet away. This is the reverse of what I found. Dixon (1949) stated that nest-site selection in the Plain Titmouse was an activity characteristic of the female alone. The Nethersole-Thomsons (1943) found that in the Great Tit (Parus major) and Blue Tit (Parus caeruleus) the male "suggested" several possible sites to the female who chose one of them. Stokes (1960) stated that in the Blue Tit the male took the lead in investigating cavities. Hinde (1952) indicated that in the Marsh Tit (Parus palustris) the male inspected while the female waited nearby.

Nest-site inspection was observed from late March to the middle of April except for pairs seeking a cavity for a renesting attempt later in the breeding season. The earliest date pairs were observed investigating was 21 March during the 1969 breeding season (both chickadees and titmice).

When inspecting a cavity the female perched silently near the opening while the male entered. After being inside for a minute or more he would come to the opening and perch near the female. If he then flew the female followed. Often, however, he sang briefly either with his head out of the opening or after perching beside the female. Following the song the female usually entered the cavity briefly. The brief song may have been an attempt by the male to indicate possession of the nest site, or it may have been an invitation to the female to enter the cavity. Later in the nesting cycle the female often refused to enter the nest following a disturbance until the male had entered, come out, and whistled a brief song.

Many visits were made to the prospective nest site following the first, and each was similar to that described above except that the female spent a relatively greater time in the cavity than on earlier visits. If the female made the final selection of the actual nest site she selected only from among cavities the male had led her to and inspected first.

Following selection of a nest site the male and female occasionally entered the cavity together. I observed this twice in one titmouse pair and once in a chickadee pair. Stokes (1960) states that pairs of Blue Tits often stay together for considerable periods inside the nest cavity prior to nest-building but to my knowledge this has never before been reported for American Paridae.

Comparison of Species. Because of the large number of dead trees and sizeable populations of woodpeckers, a large number of tree cavities, both natural and woodpecker excavated, existed in the study area. Birds whose first nests were destroyed seemed to have little difficulty in finding a new nest site for a second or third nesting attempt. It is assumed, therefore, that the nesting cavities represented in Table 1 were not chosen of necessity as might be the case in marginal habitats.

No competition for nest sites was observed between the two species. The titmouse, being the larger bird, requires a larger cavity. The titmouse nest cavities studied were in all respects significantly larger than those chosen by chickadee pairs. In addition, the titmouse pairs chose a different type of cavity than the chickadee pairs. Six of the seven titmouse nests studied were located in natural decay cavities. The one woodpecker cavity utilized by a titmouse pair was a large cavity such as a Red-bellied Woodpecker (Centurus carolinus) makes.

Of the ten chickadee nest cavities studied only three were natural decay cavities and these were considerably smaller than those chosen by titmouse pairs. Six of the chickadee cavities were small woodpecker cavities such as a Downy Woodpecker (Dendrocopos pubescens) makes. Several of the six cavities appeared to have been enlarged slightly at nest level by the female chickadee.

Titmouse nests ranged from 4.3-16.1 meters above ground with an average of 10.2 meters. The chickadee nests ranged from 0.6-12.4 meters with an average height of 4.0 meters. The difference between the two means is significant. Seven of the chickadee nests were in small dead tree stubs. The natural cavities utilized by the titmice tended to be in the crowns of larger trees. This may account for the difference in height between the two groups of nests.

The size of the nest opening is usually a good measure of the overall cavity size. The chickadee pairs chose cavities with a small opening (2.5-4.7 cm) relative to their body size. Titmouse pairs, on the other hand, chose cavities with large openings relative to their body size (6.0-12.7). This may be due in part to their selection of natural cavities, which usually have large openings. The ranges of opening sizes between the two species did not overlap.

The marked difference in the size of nest cavities chosen by the two species precludes competition between them for nest sites.

Excavation

No titmouse was ever observed excavating or enlarging a nest cavity, and none of the seven titmouse cavities I examined showed any evidence of excavation. Dixon (1955), however, reports the enlargement of a nest cavity by a female Plain Titmouse, and it may be that in marginal habitats, where suitable nest cavities are scarce, the Tufted Titmouse also excavates to some extent.

The earliest date excavation was observed at a chickadee nest was 11 March during the 1969 breeding season. It was observed at five chickadee nests in all. One cavity was dug entirely by the female chickadee in a rotten post

TABLE 1

COMPARISON OF NEST CAVITIES

	Nest	Cavity Type	Height (M)	Opening Size	Depth	Width of Cavity		Tree Species
						At Opening	At Nest	
TITMOUSE	TP2A	N*	4.3	7.6-9.5	20.4	10.2		*Fraxinus pennsylvanica*
	TP3A	N	8.7	7.6	84	10.5-7.6	8.9-9.5	*Fraxinus pennsylvanica*
	TP4A	W**	5.3	6	26	10.5-8.9	12.1-8.9	*Ulmus americana*
	TP4B	N	14.3	7.6	33	7.6	7.6	*Fraxinus pennsylvanica*
	TP6A	N	9.6	6.1-5.7	22.3	15.2-12.7	10.1-8.9	*Ulmus americana*
	TP6B	N	13	7.6-8.9	30.2	7.6	8.9	*Salix nigra*
	TP7A	N	16.1	10.5-12.7	22.3	15.2-12.7	10.1-8.9	*Ulmus americana*
	TP6B	N	13	7.6-8.9	30.2	7.6	8.9	*Salix nigra*
	TP7A	N	16.1	10.5-12.7	43	5.1-9	10.2	*Fraxinus pennsylvanica*
	Mean		10.2	7.9	37	9.3	9.3	
CHICKADEE	CP3A	W	3.7	2.5	15.2		4.8	*Ulmus americana*
	CP3B	N	4.3	5		5.0-7.6		*Ulmus americana*
	CP3C	E***	.9	2.5	9	7.4-5.6		Fence Post
	CP5A	N	.6	4.4		4.4		Fence Post
	CP6A	N	12.4	3.1	66	3.1	4.9	*Fraxinus pennsylvanica*
	CP7A	W	4.9	4.1	10.9	5.4	7.3-8.3	*Fraxinus pennsylvanica*
	CP7B	W	3.2	4.4	11.7	4.4-7.9	7.3	*Fraxinus pennsylvanica*
	CP8B	W	2.5	4.7-3.5	12.3	6	8.0-8.9	*Salix nigra*
	CP11A	W	2.3	3.2-4.4	12	5.1-5.7	5.4-5.6	*Fraxinus pennsylvanica*
	CP12A	W	5.5	3.8-4.4	18	5.4	6.4	*Fraxinus pennsylvanica*
	Mean		4.0	3.8	19.4	5.4	6.5	
	P value		$.01 > P > 0.001$	$P < 0.001$,	$0.20 > P > 0.10$+	$P < 0.001$	$0.01 > P > 0.001$	

*N = natural decay cavity
**W = woodpecker cavity
***E = cavity excavated by female chickadee
\+ If depth of CP6A cavity is excluded the difference is significant ($P < 0.05$).

without a hard shell. The following discussion then, applies only to the Carolina Chickadee.

In every instance where excavation was observed the interior of the nest limb or stem was very rotten and soft, and in some instances the outer shell was also soft. Only females were observed excavating at all five chickadee nests; however, Brewer (1961) reported that he observed both members of Carolina Chickadee pairs excavating, and Odum (1941b) and Brewer (*op. cit.*) state that both members of Black-capped Chickadee (*Parus atricapillus*) pairs excavate.

Of the remaining five chickadee nests which were observed, four were in old woodpecker nest or roost cavities. The last was a natural-decay cavity and no excavation took place.

Drury (1958) and Brewer (*op. cit.*) report that excavation is a necessary part of the chickadee nesting cycle. This is not the case for Tufted Titmice and may not be true for the Carolina Chickadee. Nest CP6A was a natural-decay cavity which showed no evidence of excavation. Nevertheless, this chickadee pair successfully completed the nesting cycle.

Construction

The female alone constructed the nest in both species. She also gathered the materials and carried them to the nest cavity. The male usually accompanied her and perched nearby while she gathered materials. When she flew to the nest, he followed and perched outside the cavity. At times the female was unaccompanied by the male as she collected material and carried it to the nest.

Much of the nesting material was collected from the ground. After picking up a quantity of material, the female usually flew up to a low perch and compacted it by pressing the sides of her bill along the perch limb. She then either collected more and repeated the compacting process or flew to the nest. A large quantity of material was carried to the nest on each visit. Strips of bark were collected from dead trees or limbs either on the ground or still standing. The soft inner bark was stripped away at a spot where the bark was hanging loose. The outer dead bark of Red Cedar (_Juniperus virginiana_) was also stripped away in a similar manner.

The nests were built to conform with the walls of the cavity and were tightly woven. The typical chickadee nest was constructed almost entirely of green moss, fine strips of bark, and hair and feathers. The moss was always on the outside of the nest against the cavity walls and was sparse except for a dense plug sometimes placed at the bottom. The remainder of the nest consisted of densely woven bark shreds, hair, and a few small feathers. The percentage of hair and bark used was quite variable and ranged from mostly bark with a small amount of hair to a nest constructed entirely of hair. The availability of materials may have determined the actual composition.

The titmouse nests were less densely woven and were composed of coarser materials. The same materials were used as in the chickadee nests, but all of the titmouse nests observed contained only a small amount of hair and were constructed primarily of bark fibers. Two of the nests contained shed snake skin in addition to the other materials.

Once started, nest construction progressed rapidly in both species until the nest was completed (3-5 days). Egg-laying began upon completion of the nest, but the female continued to carry materials at infrequent intervals into the nest cavity until hatching. This often occurred following a disturbance at the nest but was also observed when the nest was undisturbed. Often, while I worked to cut an opening in a nest cavity following egg-laying the female (both species) collected nest materials which she sometimes carried into the nest when I finished. This seemed to be a displacement activity caused by the disturbance of the nesting routine. At other times the female entered after I finished, carried out small pieces of wood caused by the sawing, and carried back nest materials.

Renesting

When a nest of either species was destroyed, the pair immediately began searching for a new nest site. Renesting was observed closely in two different pairs of each species.

In all four instances the clutch size was smaller in the second or third nest than in previous nesting attempts.

There are certain disadvantages to a renesting attempt as compared with a successful first nest. The clutch size is smaller, as indicated, and considerable energy is required of the female in excavating, building, and egg-laying and of the male in feeding the female and nestlings. Furthermore, changing the nest site often involves changes in the territorial boundary which lead to prolonged boundary disputes. Also, in the later stages of a renesting attempt, young birds from successful first nests invade the area utilized for nesting and foraging. These young birds beg from the adults (and are often fed), perch on the nest opening and peer inside, and invade the family group following fledging.

An unusual case of the latter occurred at TP6B. The largest nestling, red-white R, fledged at 09:45 and flew to a perch near the nest. At 09:50 a young titmouse from an adjacent area, earlier observed begging from the male and following him to the nest, perched beside red-white R and began to wing flutter and give a high-frequency call. At 10:15 the same bird again perched beside red-white R, began to call and wing flutter with crest depressed, then mounted the fledgling. Red-white R was barely able to maintain its perch under the weight of the older bird. The intruder remained near the fledgling throughout the day repeatedly mounting him, at times knocking him from his perch. Red-white R had disappeared by the following day and was presumably dead.

The male often chased such intruders when they were at the nest site, but no male was ever observed fighting with one. Following fledging he also chased them from the family group, but they returned and seemed impervious to his attacks.

There is some evidence to indicate that young birds from late nests ranked lower in the social hierarchy of the winter flock. This was probably due to their interaction with more mature hatching-year birds following fledging and to their submission to such birds during conflict situations. This was a decided disadvantage to young from late nests, as they were forced from the area by dominant birds following flock dispersal in the spring and had to search elsewhere for a suitable breeding territory.

Double Broods

Despite close observation no evidence for more than one successful brood was found for either species. The literature also contains no good evidence for a successful second brood in these two species. In some instances where double-broodedness is suggested the lateness of the season and small clutch size indicate a renesting attempt rather than a second brood. Odum (1941b; 1942c) reports six cases of second broods by Black-capped Chickadee pairs, and Kluyver (1961) reports one second brood in the same species.

Disappearance of One Adult

At only one nest (TP6B) did one of the adults disappear during nesting. The female disappeared when the young were ten days old. The male continued feeding the young at about the same frequency as both adults did earlier and increased the frequency as the young grew older. All five birds fledged successfully.

Copulation

Copulation in chickadee pairs was observed eight times. Three of these occurred during nest-building, three during egg-laying, and two at an undetermined stage of nesting. All but one of the eight copulations occurred before noon, and this occurred at fifty minutes past noon. Seven of the eight occurred within fifty feet of the nest. The following is a summarized account of the behavior recorded for pair CP6 on 25 March 1969, and is typical of the behavior observed in all of the eight chickadee mountings.

> Pair approached nest from west at 11:35 hours and female entered. She came out after brief stay inside and flew to male foraging in elm nearby, perching about 15 feet from him. She began to wing flutter and call <u>tsweedle</u> <u>dee</u>--crest feathers depressed, head extended forward, and tail held level with body forming a straight plane across head, back, and tail. Male immediately flew to her and perched about one foot away facing her. He began to wing flutter, whereupon she immediately increased speed of her own flutter. Male continued to flutter, turned his left side to her, then turned to face her and approached within inches. She called <u>tsweedle</u> <u>dee</u> loudly twice, whereupon male flew around her right side, mounted calling <u>tsi</u> <u>tsi</u> <u>tsi</u> loudly, then flew to an adjacent tree. From beginning to end lasted about 15 sec. Female continued wing

> flutter for 4-6 sec., then flew to ground and began collecting nesting material which she carried to nest.

I again observed this pair copulating on 27 March. They were foraging and making their way toward the nest. While still several hundred feet from the nest the female began to wing flutter near the male, but he was unresponsive. When the pair was about thirty feet from the nest, she began to wing flutter weakly while foraging. She then faced the male (ten feet away) and fluttered more rapidly, giving the same call as above and assuming the same posture. He flew to her, perched about a foot away, and fluttering his wings, moved toward her. Without pausing he flew around her right side and mounted. She continued to wing flutter briefly after he flew. The entire sequence was shorter than the one observed earlier, the precopulatory behavior becoming shorter and less rigid as egg-laying progresses. This was noted in other pairs as well and may be the result of an increase in the sexual drive of one or both birds.

Several variations were noted in the precopulatory behavior of various pairs. One male responded to the female's postures and calls by perching in front of her facing away and wing fluttering. He turned, paused briefly, then mounted. In another instance the male perched behind the female prior to mounting. On one occasion a pair was observed copulating while the female was carrying a large amount of nesting material.

In two instances precopulatory behavior was observed following the completion of egg-laying. In both instances the wing flutter of the female was very weak. When the male attempted to mount, the female moved but did not fly. She may have been begging food rather than initiating copulation.

In every instance where copulation was observed, it was initiated by the female. This appears to be true also of the two copulations witnessed by Brewer (1961). In several instances a male was observed to fly to the female and begin wing fluttering in front of her. In none of these did she respond except by moving or flying away.

Apparently the male will respond to any female that initiates precopulatory behavior. The following account is from an observation on 3 April, 1968.

> Unbanded chickadee perched about 30 feet high calling <u>chicka</u> <u>dee</u> <u>dee</u> <u>dee</u> loudly. Resident male flew to and perched in adjacent tree. Unbanded bird immediately began to wing flutter, whereupon male flew to, perched facing, and also began to wing flutter. Just as it appeared male would mount, his mate dived at unbanded bird and missed hitting it by inches. Intruder immediately flew pursued by female.

The wing flutter observed prior to copulation is not an up and down motion, as it first appears, but a back and forth motion. The wings move rapidly out from the body, then close with very little, if any, extension of the primaries. The carpal joint is held close to the body and during rapid fluttering the wings are horizontal. Copulation apparently ensues only when both birds flutter.

Copulation by a titmouse pair was observed only once, and it occurred during nest-building at 10:05 on 25 April 1969, as follows.

> Female entered nest carrying material. Male accompanied and perched nearby. She came out and flew about one hundred and fifty feet north. Male followed and perched nearby. Female began to wing flutter (body straight across head, back, and tail; crest depressed). Male approached and also began to wing flutter, paused briefly before her, and mounted. Male then flew and female began to forage.

No calls were heard, but I was standing a considerable distance from the pair. There seemed to be no significant difference between this titmouse copulation and those I observed in chickadee pairs. Descriptions in the literature (Pielou, 1957; Offutt, 1965) of titmouse behavior during copulation is also very similar. The post-copulatory behavior of the male as observed by Pielou (op. cit.) on two occasions (body pressed close to limb, eyes gradually closed, head and tail extended in line with body, rotation of body backwards until suspended beneath limb, and fall toward ground) was not observed in any chickadee male following copulation or in the one titmouse male.

Egg-Laying

The eggs were laid one-a-day in both species and were covered with a flap of nest material until the set neared completion. The flap was constructed of materials similar to those found in the nest. The flap completely concealed the eggs and probably also served to insulate them so that development was not initiated by the female's roosting in the cavity.

The pair spent very little time at the nest during egg-laying, sometimes not returning for several hours. In early morning the female often made several trips into the nest with nest materials, presumably repairing the flap following the laying of an egg.

Incubation

Incubation in both species began following the laying of the last or next to the last egg, and continued until hatching, twelve to thirteen days later. The female alone incubated. She did not sit directly on the eggs but stood on the sides of the nest and crouched over them. The male's role during incubation was to feed the female on and off the nest.

The behavior of male and female birds near the nest site continually changed as the nesting cycle progressed. During the winter male chickadees and titmice dominated the females. This continued through nest-site selection as the male led the female about; however, attacks and threats were no longer observed between mates. Following nest-site selection and the beginning of nest building the female became the controlling influence at the nest site, and the male approached it cautiously.

All of the activities of the pair centered about the nest site following its selection and the female took the leading role in all activities concerned with the nest. Her activities dominated and controlled the male's, thereby coordinating the activities of both mates and focusing their combined energies upon the nesting attempt. Since the female was more directly associated with the nest, she was in the best position to perform this vital function. The female's dominance at the nest site continued until the end of the nestling stage but weakened in the last week before fledging and disappeared following fledging.

As the male approached to feed the female during incubation, he perched several times in the last forty or fifty feet to the nest and last perched on a limb very close to the nest opening. This same perch was used in each approach. Here he signaled his presence with a soft version of the whistled song. If the female did not immediately come out of the nest cavity, he flew to the opening and leaned inside to feed her.

If the female was chased from the nest, she usually flew to a perch from ten to thirty feet away and, after remaining silent for up to a minute, began to call rapidly using the "scolding" calls characteristic of each species. She then usually flew away for a short time and returned to enter the nest. If she had just entered the nest when it was disturbed, she often remained nearby, calling and flying about excitedly. When the disturbance was removed, the calls gradually decreased in intensity, speed, and duration, and finally she became silent. After a short interval of silence she entered the nest. In no instance was a bird observed to enter the nest while in an aggressive state. In some cases she remained outside until the male entered first, but this behavior was more typical of the brooding and nestling stages.

Average chickadee attentive periods (sum of twenty-four hours observation on five nests) were thirty-four minutes long, ranging from twelve to fifty-eight minutes. Inattentive periods averaged thirteen minutes, ranging from two to fifty-seven minutes long. Average titmouse attentive periods (sum of seventeen hours observation on four nests) were twenty-nine minutes long, ranging from seventeen to seventy-two minutes. Attentive periods were longer in the morning than in the afternoon and longer on cold days than on warm. The reverse was true of inattentive periods.

During inattentive periods the female usually begged for food when the male was present, but she also foraged for herself. Begging was first noted in both species during nest-building. When begging the female assumed a posture similar to that observed during pre-copulatory behavior--crown feathers depressed, body low, head and tail extended, wing fluttering--and gave the begging call. The male continued to feed the female until after hatching. During brooding his feeding activities were gradually transferred to the nestlings.

Acceptance of Foreign Eggs. On 15 April 1969, at one chickadee nest (CP11A) I replaced the original six eggs with six titmouse eggs from TP4A. The female chickadee was in the tenth day of incubation and the titmouse female in the second. The female chickadee immediately accepted the eggs even though they were nearly twice the size of her own. The eggs completely filled the small nest, but the female covered them all by opening her wings as far as the cavity permitted. She continued to incubate until 27 April when five of the six titmouse eggs hatched. The sixth egg was infertile. When the eggs hatched the female had been incubating for twenty-two days. Odum (1942b) recorded a Carolina Chickadee incubating infertile eggs for at least twenty-four days before abandoning them.

Five of the six chickadee eggs which were removed from CP11A were transferred to TP4A at 1800 hours, the sixth being broken in the process. The transfer required only a few minutes. The female titmouse quickly entered the nest and was still inside at sunset. At 08:00 hours the next morning, however, the eggs were cold and the titmouse pair were investigating tree cavities. Apparently the small size of the chickadee eggs failed to satisfy the female titmouse.

Snake Display

During excavation, nest-building, egg-laying, incubation, and brooding the entrance of foreign objects into the nest cavity often elicited from the female the so-called snake display first described in detail by Pickens (1928). Both the Carolina Chickadee and Tufted Titmouse gave this display.

Most of my observations on the display occurred during incubation and brooding. When sitting in the nest, the female usually sat at right angles to the nest opening above her. When a foreign object entered the opening, she drew her head back until it was pointing directly up at the opening and turned it slightly to face the object. As her head was drawing back she opened her bill wide. Pointing her bill directly at the object she suddenly lunged at it, giving a hissing sound and snapping her wings open and closed rapidly. At the same time her head moved forward and down until it touched the nest or wall of the cavity. The rapid opening and closing of the wings caused a snapping sound which was probably caused by their contact with the walls of the cavity. The wings opened only a short distance before snapping shut. During the display her tail was fanned as much as the cavity permitted. If the object remained she repeated the display. When the object was thrust far enough into the cavity, she lunged at it and grasped it in her bill. In one instance when I pushed a metal tape measure into a titmouse nest, the incubating female gave the display and held on to the tape so tightly that I lifted her halfway out of the cavity before she released it.

At one chickadee and one titmouse nest a block of wood was removed from the back of the cavity and a glass plate inserted over the opening. The glass was covered with black roofing paper when no observations were being made at the nest. When a blade of grass was thrust through the chickadee nest opening, the female repeatedly gave the snake display at it, despite the fact that I was standing in full view at the back of the nest. Even when I tapped on the glass and tried to divert her attention away from the blade of grass, she continued to display at it rather than me.

Bent (1946) reported eliciting the display from a female Carolina Chickadee by tapping on the cavity wall of the nest, and Burleigh (1930) reported the same for the Chestnut-backed Chickadee (Parus rufescens). I was unable to elicit it in this manner.

The name "snake display" was derived from the hissing call given when the bird lunges. Sibley (1955) felt that the display is an example of behavioral Batesian mimicry.

The greatest value of the display is probably in startling predators entering the nest cavity into fleeing. The display is also given outside the nest, and here a potential predator could hardly be fooled into mistaking the bird for a snake. The literature contains no accounts of the display being given outside the nest, but I have evoked it in captured birds by holding them by the feet with one hand and slowly moving an outstretched finger toward their bill with the other. The display was identical to the one given in the nest cavity, and I have elicited it in both chickadees and titmice. The opening of the wings only a short way by hand-held birds indicates that when given in the nest the wings are not restricted by the walls of the cavity. Not all birds gave the display when so handled, and chickadees gave it more readily than titmice. No known male of either species ever gave it under these conditions, and only the less aggressive birds gave it when so handled. The more aggressive birds thrashed about and attempted to fly when held only by the feet, and since titmice were somewhat more aggressive than chickadees when hand held, it was more difficult to elicit it from them.

The snake display has been observed in the Carolina Chickadee (Pickens, 1928; Bent, 1946; Brewer, 1961), Black-capped Chickadee (Dilger, in Sibley 1955; Griffee, in Bent, *loc. cit.*), Chestnut-backed Chickadee (Burleigh, 1930), and the Plain Titmouse (Allen, 1943; Dixon, 1949; Sibley, 1955). It seems likely that all species of American Paridae give the display.

Among European titmice it has been reported for the Great Tit and Blue Tit (Hinde, 1952; Jourdain, 1929) as well as the Coal Tit (*Parus ater*) (Jourdain, *op. cit.*) and Marsh Tit (Hinde, *op. cit.*). Hinde's description of the display in the Great Tit, Blue Tit, and Marsh Tit seems to be very similar to the display given by American Paridae.

Nestling Stage

Following hatching of the eggs the male began to enter the nest to feed the young and no longer fed the female away from the nest. He did transfer food to her while she was brooding, but whether she gave it to the young or ate it herself was not determined. During brooding the male accompanied the female back to the nest following inattentive periods and entered first to feed the young. The female then entered, usually with food, and resumed brooding. Brooding was discontinued during the second week of nestling life, but the female continued to roost in the nest cavity until the young were about ten days old.

It was probably the size of the nestlings that caused the female to cease brooding and roosting at the nest. At CP11A where the female chickadee successfully hatched six titmouse eggs, the female ceased brooding and roosting at the nest within three days following hatching. The six large titmice left little room in the cavity for her just as six young chickadees at a later age would have done. As a result of the early cessation of brooding all but one of the nestlings died in the next several days.

The female's dominance at the nest site waned quickly following the cessation of brooding. She still approached the nest more directly than the male, and he continued to signal his approach throughout the nestling period, but when the pair arrived at the nest site together, the male usually entered first while the female perched nearby. Simultaneous arrival at the nest was often accompanied by mutual wing fluttering and the giving of a high-frequency call before one of the pair entered.

Both species tolerated considerable interference at the nest and quickly adapted to an observer or to changes in the nest cavity. At CP11A and TP6B, where I had inserted a plate of glass in the cavity wall, a blind was built at the back of the nest in order to observe the nestlings. In both cases the female entered the cavity with food, but upon reaching down to feed them, saw me through the glass and backed toward the opening until no longer able to see me. After repeating this up and down movement several times both birds solved the problem in the same way. They turned in the cavity and backed down toward the nestlings, then twisted their head down, quickly fed one of the nestlings, and scampered out of the nest. The males simply fled upon seeing me. This continued for several visits, but within an hour both the males and females were feeding the young with impunity. Even when the blind was removed and the nest interior was brightly lit, the adults continued to feed the young.

During egg laying, incubation, and the nestling stage nest stubs were sometimes lowered several feet and the adults quickly found them. Their habit of perching on a particular limb near the nest opening before flying to it became so strong that after a nest was lowered they often perched, then flew directly toward the spot where the opening had been and hovered in mid air looking for it.

The movement of a nest cavity from a great height or to another location had to be made after the nestlings were begging loudly or the adults were unable to locate it.

When carrying food to the nest the adults usually perched on the opening rim and looked down into the cavity. Young nestlings often appeared to be unaware of the adults' presence. If the young did not beg, the adult remained at the opening and gave the nest call. The note immediately evoked begging by the nestlings (even in newborn birds), and the adult then entered and fed one of them.

The nestlings, at least during early nest life, responded entirely to sounds. When very young they begged at any sound in the cavity or at loud sounds nearby. Later they began to discriminate between various sounds and begged only at appropriate ones. Whistles, hisses, thumps, or scratching on the cavity wall, loud calls of any species of bird, and, strangely enough, blowing on their body caused nestlings several days of age or younger to beg. As they approached ten days of age, they became more discriminate. Thumping no longer elicited enthusiastic begging, but scratching sounds on the cavity wall, such as the adults made upon entering, did, as did any sound produced by the adults upon entering or approaching the nest. Chickadee nestlings at CP3C, for example, at eleven days of age begged immediately when one of the adults perched on the barbed wire attached to the nest post. They had apparently learned that the squeaking of the wire was always followed by a feeding. After ten days of age the nestlings began to respond discriminately to the calls or song of their parents outside.

When feeding a nestling the adults held onto the cavity walls above the nest, reached down, and placed the food deep into its gape. If, after a few seconds, the gape remained open and the tiniest part of the food was still visible, the parent bird pulled it back out and gave it to another nestling. This was repeated until one of the nestlings swallowed it completely. After feeding one of the young the adult usually paused briefly as if expecting a fecal sac. If none was forthcoming it left the nest. The nestlings did not defecate after each feeding. When they did defecate, however, it was always immediately after being fed. Upon swallowing the food the bird struggled to the top of the pile of nestlings, braced itself on its legs and wingtips, and thrust its rear end up into the air. Its body became stiff and trembled as the fecal sac was forced out. The adult took the sac in its bill before it was completely extruded, then either ate it or carried it out of the nest.

Beating of the wings, as in flying, was induced even in birds only a few days old by holding them in the hand, then rapidly lowering them. At ten days of age they could balance on a perch fairly well but could not fly yet except to break their fall to the ground. During the remainder of their nest life they developed the ability to fly short distances.

Fledging

Fledging was observed at three titmouse nests, but similar efforts to observe a chickadee brood fledge were unsuccessful. Consequently, what follows will deal with nest-leaving in the Tufted Titmouse.

TP2A was the first nest at which fledging was observed. It occurred on 24 June 1968, about one hour before sunset. In colorbanding the nestlings four days prior to fledging, a difference in general body size (see Table 2) as well as a difference in behavior was noted between the three birds. The largest, Orange-Pea L, pecked at my hand while being banded and tried vigorously to escape. It was also able to maintain its balance on a small limb. The two smaller nestlings were more docile while being handled, and while they were able to cling to the same limb, they could not balance on it and slowly slid down the side of the limb until they were hanging to its side with their head pressed against their feet. The order of fledging followed the size order; the largest bird fledged first (Time 0), the second largest next, fifty seconds later, and the smallest last, three minutes after the first. The first bird fledged at 19:12.

In order to determine whether size differences among nestmates influences the fledging order, a greater effort was made to observe fledging during the 1969 breeding season. I was successful at two titmouse nests, TP3A and TP4B. When I arrived at TP3A on the afternoon of fledging (14:10), the two largest birds had already left the nest. The remaining four birds each fledged according to their relative sizes, the largest bird remaining in the nest at any given time being the next to fledge.

At TP4B I observed the whole process. Again, the largest bird fledged first (11:55) followed by the next largest, etc., until all four had fledged.

<u>Cause of Size Differences</u>. As has been indicated, the female lays one egg a day until the clutch is completed and covers the eggs with nest material until incubation begins. The female begins roosting in the cavity following nest-site selection and continues to do so until the young are quite large. Thus, even though the eggs may be covered and are presumably somewhat insulated from the female's body heat, development of early eggs may be initiated prior to the beginning of incubation. The fact that the eggs hatch at different times seems to indicate this. In TP3A, the only nest where hatching was observed, a period greater than twenty-four hours separated the hatching of the first and last egg. Laskey (1957) found that the hatching of seven eggs in a Tufted Titmouse nest required about twenty-four

hours, and Pielou (1957) found that the eggs in three nests required from ten to twenty hours to hatch.

Gibb (1950) stated for the Great Tit that late-hatched young suffer from a lack of food, lack of brooding, or both. Thus the original size difference caused by different hatching times may later be accentuated by competition for food among the nestlings and by the different lengths of time they are brooded by the female.

Initiation. Pielou (1957) stated that Tufted Titmice young do not leave the nest normally until they are capable of climbing up to the cavity entrance at which time they are ready to fly. Dixon (1949) made the same statement about Plain Titmice young. Actually, Tufted Titmice young are capable of climbing up to the cavity entrance several days before they fledge, and for this reason great care must be taken in handling the young at this time or they will fledge early (see Forced Early Fledging).

What actually initiates fledging then? During the last two days of nest life the young titmice at TP6B became very restless. They called loudly for no apparent reason, preened, and jostled each other about. This restlessness may help initiate fledging.

A second possible factor is the size of the nestlings. Just prior to fledging there is a great deal of crowding in the nest, particularly in larger broods. This often results in two or three birds sitting atop the others

TABLE 2

FLEDGING ORDER IN RELATION TO SIZE AT THREE TITMOUSE NESTS

Nest	Individuals	Wing Length (mm)	Fledging Order and Time
TP2A*	Orange-Pea L	52	0
	Orange-Purple L	50	50 sec
	Orange-Red L	46	3 min
TP3A*	Orange-Pink R	57	0 ?
	Red-Pea R	56	0 ?
	2 Purple R	54	2.5-4.5 hrs**
	2 Blue R	51	14.5 hrs
	2 Yellow R	49	15 hrs
	Blue-White L	47	16.5 hrs
TP4B*	Orange-Pea R	51	0
	Yellow-Blue R	50	70 sec
	2 Pink L	45	43 min
	2 White L	39	47 min

*TP2A - measured 4 days before fledging
TP3A - measured 2 and 3 days before fledging
TP4B - measured 5 days before fledging
**Time of my arrival at nest

and causes considerable agitation when food is brought to the nest.

Calling by the adult birds near the nest may also influence fledging. As mentioned earlier, the male always announces his approach to the nest with a soft version of the whistled song. On occasions the female signals her approach in the same way. After ten days of age the young beg immediately upon hearing the approach signal or its louder version used in singing and seem to have become conditioned to it. Associating the song with food may cause them to attempt to move toward the source of the song, fledging in the process. The male uses this call in leading the family group following fledging, and they respond to it by flying toward its source.

Another possibility is that the birds attempt to follow one of the adults out of the nest. Following is often observed just after fledging when the young are fed. Likewise, after fledging the young often rush several feet at one of the adults in an attempt to get food, and if not fed will often try to follow the adult when it flies. In each instance where fledging was observed, it occurred immediately after a visit by one of the adults.

One, or perhaps all of these, may play a role in initiating fledging. Individual nestlings also seem to influence each other during fledging. At TP2A, for example, despite their size differences, all three nestlings fledged within a three-minute period (Table 2). This seems to indicate that the fledging of the first bird influenced the fledging of the remaining two. There may also be a relationship between the size difference of individuals and the time interval between their fledging. In TP2A, for example, there was a one millimeter wing-length difference between the two largest birds, and they fledged within fifty seconds of each other, whereas the second and third birds differed in wing length by four millimeters and fledged over two minutes apart. Likewise, at TP4B a one-millimeter wing-length difference separated the first bird to fledge and the second, and the time interval between their leaving the nest was seventy seconds. The second and third birds differed by five millimeters, and the time difference between their fledging was correspondingly longer (42 min.). The short time interval separating the fledging of the first two birds indicates that the second was in some way influenced by the first. Each bird in turn may influence the next. In nest TP4B the last bird to fledge (2 White L) was barely able to maintain its perch on the rim of the opening and could fly only to the ground. After observing it on the ground for nearly an hour, I placed it on a tree limb where it remained until fed by the female. When she flew away, it attempted to follow and again flew to the ground. Obviously this bird was not yet ready to fledge. The fact that it did fledge indicates that it was influenced by the fledging of its nest mates.

A similar thing occurred with the runt at TP3B (Blue-white L). It came to the entrance and rather than flying began climbing up the tree stem until it was perched about fifteen feet above the nest opening where it stayed for the remainder of the day.

Social Implications of Fledging Order. In all three titmouse nests the largest bird fledged first, followed in order by the next largest, etc., until all had fledged. Of the TP2A fledglings all three birds remained within the original area of their parents' territory until early November, during which time the largest, Orange-Pea L, consistently dominated Orange-Purple L and Orange-Red L at the feeders. Likewise, Orange-Purple L consistently supplanted Orange-Red L so that the social status of the three birds within the flock appeared to show a direct relationship to their relative sizes as nestlings and to their fledging order. The two smaller birds disappeared from the study area in November while Orange-Pea L moved to an adjacent flock within the woods and upon the disappearance of the alpha male became the dominant bird. In 1969 he successfully defended the area during the breeding season.

Of the TP3A nestlings, only Orange-Pink R (presumably a male) remained by late September. His father dominated the flock, and he was second in the social hierarchy. The other five birds from this nest had all disappeared from the study area by this time.

Gibb (1950) noted a severe competition for food among brood members in the Great Titmouse. He further noted that the smallest die first when food is scarce and that even when few die late-hatched birds leave the nest at a disadvantage. A social hierarchy, then, appears to exist within the nest and is directly related to the size and maturity of individual nestlings--the largest dominating, followed by the next largest, etc. The larger size of more mature birds gives them an advantage in competing for food and nest space over smaller birds. Dominance, or subordination, results from competition with more (or less) mature birds, at a time in life when behavioral plasticity is at its peak. The relative standing of siblings is then carried over into post-nest life.

Other factors intervene, however, to make the picture more complex. First, male birds always dominate female birds in the winter flocks. At TP2A the first bird to fledge was a male, but whether males generally fledge before females was not determined. Secondly, during post-nest life the young birds compete not only with siblings but also with birds from other nests. Of the TP4B nestlings only 2 Pink L remained by early November, and its behavior indicated that it was a female. The two larger birds from the nest may have been taken by a predator or may have been forced from the area by one or both of the two immature birds which invaded the family group on the day of fledging. The two intruders became members of the winter flock and both dominated 2 Pink L at the feeders.

Behavior of Young and Adults. The behavior of the young titmice during fledging was similar at all three nests. The young bird would climb to the opening and peer out sometimes backing down into the nest a short distance and remaining there until one of the adults arrived with food. After being fed the young bird would again climb to the opening, perch briefly with its crest raised, and fly a short distance to a perch at about the same height as the nest opening. At TP2A the young birds hopped out on a limb a few inches under the nest opening and moved out along it before flying. The first bird remained on the limb until the second hopped out onto it, and the second did the same until the third hopped out. All three birds flew in the direction of the adults and perched in the same tree about twenty feet from the nest.

At TP3A the birds likewise all flew in the same general direction upon leaving the nest except for the last which climbed the nest tree. At TP4B the first two birds both flew about fifteen feet toward the adults, as did the last two, but the adults had moved during the interval between the fledging of the second and third birds, and the first two fledglings had followed them. In flying from the nest the young birds often had difficulty gaining a perch and would hover briefly before perching. In one instance the bird clung upside down to a leaf, then struggled up to the limb. In all cases the young birds began to beg immediately after gaining a perch.

The adults fly about rapidly calling <u>dee</u> <u>dee</u> <u>dee</u> during the fledging of the first bird and begin feeding it immediately. Thereafter they resume foraging activity and continue taking food to the remaining nestlings as well as feeding the fledged birds. The female generally makes a greater number of visits to the nest after fledging begins, but the male also continues to visit it. The adults make several visits to the nest following fledging of the last bird but do not enter. They perch on the nest opening and peer inside, probably giving the nest call, but getting no response they fly away. At TP6B the widower male was still flying to the nest over one hour after the last bird had fledged.

<u>Forced Early Fledging</u>. As indicated earlier, the legs and feet of young chickadee and titmouse nestlings are well developed, and the birds are capable of balancing on a perch two or three days prior to fledging. Such birds will fledge readily if the nest is disturbed. On 6 May 1968, for example, I found three young titmice on the ground about fifteen feet from their nest. The birds attempted to fly when chased or held but were unable to do so except to break their fall to the ground. They were able to perch without difficulty and could hop along the ground. Apparently they

had been forced to fledge early, perhaps by a predator. At TP6B I removed the young tits to measure them, and when I placed them back in the nest the largest bird immediately ran the twelve inches up to the opening and flew. I was sitting behind the cavity, and the bird moved so quickly that it had fledged before I could place my hand over the opening. The remainder of the brood fledged over twenty-four hours later when a Black Rat snake (Elaphe obsoleta) began to enter the cavity.

When forced early fledglings were threatened while on the ground, they invariably hid under the nearest log, root, stone, etc., and became silent. They often remained hidden and silent for a considerable time. I searched for one young chickadee, forced to fledge early by flooding of the cavity, for over an hour before finding it under a large root. Such young birds did not move about but after a time often climbed a small sapling and remained perched until they were capable of flying.

Post-Nest Life

In both species the adult male led the family group following fledging. Their movements were restricted to the area defended during nest-building. During the first day after fledging the young did not move about much and often spent several hours perched in the same tree. The adults foraged nearby and did not often move far from the young. At night the whole family roosted near the top of whatever tree the young happened to be in near sundown.

Young birds seemed to lack sight recognition of their parents at the time of fledging. At TP2A a young titmouse was observed to beg from, and be fed by, an adult Red-bellied Woodpecker (Curry, 1969) within less than an hour after fledging. Young birds of both species also begged from immature birds which invaded the family group.

Most of the signals which passed between adults and nestlings were auditory, such as the nest call which initiated begging and the approach signal of the male. The use of visual signals would be difficult inside the dark nest cavity. Under such conditions the nestling's view of its parents is quite restricted, particularly since the adult bird blocks the only source of available light upon entering the cavity. Fledglings still depend upon auditory stimuli, but come to rely more and more on visual stimuli.

The world of a nestling Tufted Titmouse or Carolina Chickadee appears to be composed of the inside of its nesting cavity, its parents' calls near the nest, and the sight (limited) and feel of nest mates and of its parents as they feed or incubate. Very little else of the "outside" world filters into their stimulus-poor world. Even sounds from outside must be almost meaningless to the nestlings unless coupled with some stimulus inside the nesting cavity. Such conditions could lead, immediately after fledging, to poor sight recognition of parental birds and to begging if the fledgling is presented with the nestlings' normal stimulus, an insect larva dangling from a bill. Upon entering the stimulus rich "outside" world for the first time and being "bombarded" with previously unexperienced stimuli, the fledgling must have great latitude for quickly learning appropriate reactions to given stimuli, coupled with either inborn, stereotyped responses, or responses learned while in the nest. No doubt the fledgling quickly adapts to the broader spectrum of stimuli available in his new environment and learns to respond to a much larger part of the total spectrum of stimuli emitted by the parent birds. Visual stimuli, in particular, become increasingly important following fledging, and it may be that sight recognition of parental birds is learned after the young leave the nest.

The adults were very aggressive following fledging of the young and often engaged in prolonged conflicts with neighboring pairs. These conflicts were similar to earlier territorial disputes, but were in defense of the family group rather than a territorial boundary. During this time it was possible to elicit a threat display from parent chickadees by "squeaking" near the family group. When the squeaking began, one or both of the adults would fly toward the source of the sound and perch nearby. The wings opened slowly until they were outstretched and the tail was fanned. The bird then slowly waved his wings back and forth over the back. The head and tail were extended forming a straight plane across the head, back, and tail. The bird often lost his balance while doing this and fell nearly to the ground before flying. At other times he displayed, then glided directly at the source of the sound with wings outstretched and tail spread, and veered away when close. The birds often gave the same call given by the female during the snake display. Females also displayed in response to squeaking near the nest during the nestling stage, and, in one instance, at a wren when it perched near the nest.

Odum (1941b) observed a similar display in Black-capped Chickadee parents when he captured their young and they squealed loudly. He found that squeaking on the back of his hand got the same result and described the display as "injury feigning." It seems to be a threat display rather than injury feigning, however, as the birds fly directly at the source of the sound and do not attempt to lead the intruder away but rather to force it to flee. This seemed to be the case when the chickadee female displayed at a wren, and, in fact, the wren did fly. It may also serve to distract the intruder from the nest or young.

The display appeared to be the result of a strong conflict between the desire to flee and a desire to protect the young. The bird opened its wings as if to fly, then waved them impotently as if paralyzed, often falling in the process.

The display was observed only once in a titmouse. It was given by an unmated male early in the breeding season. The bird was singing from a high perch when I approached. He flew down and perched about six-feet high, gave the display, and fell to the ground where he alighted, then flew away. Laskey (1957) has also reported the display by a Tufted Titmouse when its mate was captured during the nesting season. Dr. George M. Sutton (1969, pers. comm.) has observed the display by Tufted Titmice in response to squeaking at all times of the year.

The legs and feet of young birds were well developed by the time they left the nest, but the bill was poorly developed as was the birds' ability to use it. Strong legs and feet are necessary to the survival of the young birds as they must be able to cling to branches swaying in the wind and maintain a perch throughout the day and night. Just how well the legs, feet, and ability to balance are developed in the young was earlier indicated in the case of the TP6A fledgling which was able to maintain its perch with another young bird on its back.

The bill, on the other hand, was little used immediately after fledging as all food was swallowed whole when received from the adults. For about a week the young kept up a continuous begging call and stayed in a compact group. In the second week after nest-leaving, they made attempts to forage for themselves and began to hold food against the branch with their feet and hammer on it as adult birds do. Their handling of food was clumsy and continued to be so for several weeks. At the feeders they lost many more seeds than they succeeded in opening.

Within a month after fledging, the young became very aggressive toward each other and were frequently observed chasing and even fighting. At this time they began to wander away from the family group, some disappearing from the study area and others moving into adjacent areas. The adults, and sometimes one or two of the young, remained and formed the nucleus of the winter flock which increased in size as other immature birds joined it.

Winter Flocks

Formation

In 1968 and 1969 recognizable flocks of both species were first observed during the first week of July. These were small, unmixed flocks made up of immature birds. Small groups of two or three immature birds of the same species were observed earlier than this when they invaded the territories of nesting pairs, but these groups seemed to lack cohesion or direction. The summer flock of immature birds traveled widely without strict regard for boundaries, and flock size and individual composition changed from day to day. Throughout August and September the many small groups consolidated around the resident pair and sometimes one or two of its young, and chickadee and titmouse flocks united to form a single mixed flock, which will be referred to here as the winter flock. Once formed the winter flocks were remarkably constant in individual composition, the same birds apparently remaining together throughout the winter if they survived.

Spacial Arrangement

When foraging, the flocks had a three dimensional character. Titmice were usually foraging in or near the ground, with some chickadees foraging in saplings and others in all levels of the crowns of taller trees. The birds were usually scattered over an area from one-half to one acre in size. When so arranged the flocks were extremely difficult to approach and seemed to provide a good early warning system against the approach at any level of potential predators.

When the flocks were compact and undisturbed, the individuals were usually quiet, uttering only the soft contact note with an occasional subdued general call note. Calls increased in frequency, duration, and volume as the flocks spread out, with chickadees usually being more vocal than titmice and calling more regularly. Even when the flocks were spread out, occasional brief quiet periods occurred.

Behavior at Feeders

When approaching a feeder, members of the mixed flock were very noisy, usually giving the general call note characteristic of each species. The birds all perched near the feeder and each bird called at least once before flying to it.

This continued for a short time as individual birds returned for another seed, but after five or ten minutes the birds usually approached silently unless a conflict developed.

The birds carried only one sunflower seed at a time from the feeder and ate it on a perch nearby. When eating a sunflower seed (or any other large food item), both the chickadee and titmouse held it against the perch limb by placing one foot over each end. They then hammered on it several times, pulled apart the seed coat, and ate the kernel. After eating a seed the bird would fly to the feeder and take another.

After eating several seeds both the chickadees and titmice began to carry away seeds and hide them. The titmice hid most seeds in the leaf litter or in dead trees on the ground. They carefully searched for a hiding place and often moved leaves aside to place the seed deep in the litter. Less often, the titmice hid seeds in crevices in the bark of a standing tree or in the soft pulp of a dead limb. When so doing, they placed the seed in the crevice and hammered on it several times to drive it in.

Chickadees were only rarely observed hiding seeds in the leaf litter. They usually hid seeds in upright trees, either in crevices in the bark or in dead limbs. They also searched carefully for a hiding place and then hammered the seed into position.

Occasionally individuals of both species removed the seed coat and hid only the kernel. No explanation was determined for this behavior except that perhaps it is a compromise between eating the seed and hiding it, indicating an equilibrium between the strengths of the two drives.

Seeds were hidden from a few feet to a hundred feet or more from the feeder, with most being hidden somewhere between these two distances. The birds would fly in all directions when hiding seeds, but some locations received more attention than others. Titmice, for example, often utilized a tangle of fallen trees as a "favorite" hiding spot. Members of flocks from another winter range invariably carried seeds in the direction of their own range when the resident flock was present at the feeder but moved around in all directions when they were alone. The birds often seemed to be following each other as they all carried seeds in one direction for a time, then shifted to a new direction. The dominant birds seemed to lead in this activity.

The birds of both species remained at the feeder as long as the cup held seeds and some birds hid many more seeds than they ate. Brief inactive periods occurred when the cup was kept filled for several hours, but the birds quickly returned. When only suet was available, they visited only occasionally for brief periods. Both species preferred sunflower seeds to suet.

Whether these two species routinely hid food obtained naturally was not determined, but both species were often observed flying to and from natural feeding areas in the same manner as they did at the feeders. One male titmouse was observed hiding the posterior portion of a ground skink (Scincella lateralis) in a crack in a dead limb about fourteen feet above ground level after it had eaten the anterior part of the animal. Odum (1942a) observed Black-capped Chickadees hiding hemlock seeds in the loose bark of trees.

It would be difficult to determine whether the birds remember where individual seeds are hidden. The hiding grounds were favorite foraging areas, however, and many of the hidden seeds were recovered and eaten. The finding of seeds was probably made easier by the birds' habit of hiding them in zones normally utilized for foraging.

The two species were most active at the feeders during the winter, less active during autumn and spring, and least active during late spring and summer.

Flock Size

There were approximately six flocks within the study area during the winters of 1968-1969 and 1969-1970. At least one other flock was occasionally observed at the eastern edge of the area, but since the greater part of their range was outside the study area they were not studied extensively and are excluded from this report.

As Tables 3 and 4 show the size of the mixed flocks gradually decreased as winter progressed. It was usually not possible to determine the fate of birds which disappeared. However, during January and February, as territorial behavior increased, subordinate birds of both species were often observed at feeders distant to their winter range and were presumably being forced out of the study area. No such movement was observed during late fall and early winter and presumably most of the birds which disappeared at this time were winter casualties.

Chickadees outnumbered titmice in most flocks throughout the winter.

Social Behavior

The chickadee-titmouse mixed flocks were remarkably cohesive social units. Whereas other species, such as Downy Woodpeckers and White-breasted Nuthatches, occasionally formed temporary associations with the flocks, the chickadee-titmouse associations were permanent and lasted throughout the winter. The two species responded to each other's call notes and the flock traveled as a unit. Also, members of both species respected the same boundary lines. It also appeared that the members of the two species recognized each other as individuals since certain titmice and chickadees were often seen traveling together on warm afternoons when the flock was scattered.

TABLE 3

SIZE OF MIXED FLOCKS IN 1968-1969 AS DETERMINED AT FEEDERS

Flock	Species	Sept.-Oct.		Nov.-Dec.		Jan.-Feb.	
1	T*	5	13***	3	9	3	6
	C**	8		6		3	
2	T	3	8	3	7	2	6
	C	5		4		4	
3	T	3	7	2	5	1	3
	C	4		3		2	
4	T	3	11	3	10	3	8
	C	8		7		5	
5	T	3	8	2	7	2	5
	C	5		5		3	
6	T	6	11	5	10	1	4
	C	5		5		3	
Mean	T	4	10	3	8	2	5
	C	6		5		3	

*Titmouse
**Chickadee
***Total

TABLE 4

SIZE OF MIXED FLOCKS IN 1969-1970 AS DETERMINED AT FEEDERS

Flock	Species	Sept.-Oct.		Nov.-Dec.		Jan.-Feb.	
1	T*	8	17***	3	12	1	6
	C**	9		9		5	
2	T	7	13	4	9	1	5
	C	6		5		4	
3	T	3	15	2	9	1	6
	C	12		7		5	
4	T	8	16	5	14	2	6
	C	8		8		4	
5	T	6	11	6	11	1	4
	C	5		5		3	
6	T	4	8	4	8	2	5
	C	4		4		3	
Mean	T	6	13	4	10	1	5
	C	7		6		4	

*Titmouse
**Chickadee
***Total

The leader of the mixed flock appeared to be the alpha titmouse male. He led the group as they moved from place to place. This was particularly evident when the flock moved quickly from one area to another, as when flying to a feeder or "favorite" foraging site. During these movements the alpha male titmouse always led, followed in turn by the subordinate titmice, the alpha chickadee, and finally the subordinate chickadees.

On several occasions the alpha male titmouse was observed to call the flock together when they were scattered. The following example is typical.

> 30 January 1969. 08:35. Flock 4. Red-dk blue L tit (alpha male) perched alone at top of a large elm tree. No other chickadees or titmice in evidence. Tit began to give rally call. During next two minutes while he continued to call, the flock of chickadees and titmice converged on his position from different directions and perched in the same tree. At 08:40 red-dk blue L tit left his perch, and followed by the flock, flew to the local feeder.

The two species also responded to each other's alarm, distress, warning, and aggressive calls. Birds giving the distress or warning call when being banded usually attracted birds of both species which perched nearby and gave warning and scolding notes. When a hawk approached the flock or flew over it, a warning call from either species caused the whole flock to fly to cover and freeze. They held this position until the dominant birds resumed activity. The following example of a male titmouse's response to a chickadee alarm call will illustrate.

> 10 December 1968. 10:45. Flock 1. Flock scattered over about 1/2 acre foraging quietly. Blue flyer tit (alpha male) foraging silently in leaf litter at periphery of flock for past five minutes about 15 feet from my position. A chickadee on the other side of flock gave an alarm call followed by scolding notes. Pale blue flyer tit immediately flew up from ground and perched about 6 feet high in a cedar tree. Tit facing calling chickadees (several calling now); crest depressed, feathers of neck all erected giving body a fluffy round appearance. Bird completely still and silent. He held this posture until chickadees' calls returned to slow general call notes (2-3 min.) then began to slowly look about. After preening briefly he resumed foraging in leaf litter.

Chickadees were observed giving similar responses to titmouse warning or aggressive calls, and their defensive posture in such situations was identical to that described above for the titmouse.

Dominance-Subordination Relationships. All data on intraflock and interflock dominance-subordination relationships was gathered at the feeders, which were so constructed as to allow only one bird at a time to take a seed. Criteria used to determine dominance or subordination were the same as Dixon's (1965) for the Mountain Chickadee: (1) supplanting attacks in which one individual displaced another from the feeder or its perch, or (2) chasing of an individual from the vicinity of the food, (3) retention of its perch by a bird despite an attempted supplanting, (4) withdrawal upon detection of an approaching individual several yards distant, and (5) obvious waiting by one individual until another had taken a seed and left. Tables 5 through 13 show the results of all observed intraflock encounters for flock numbers 3, 4, and 6.

Several tendencies can be noted from the data in the tables. In each flock the resident males of both species were the alpha bird of their species, in what was essentially a unilateral hierarchy. If the alpha bird survived, he and his mate held and defended the area of the winter range during the breeding season. This was true also of other flocks not represented in the tables. The alpha male was easily determined in all flocks because of his confident and frequent activity at the feeders.

In all instances where the sex of the birds was known or later learned, males were dominant over females. However, since subordinate males were forced from the area during the breeding season, their sexes remained unknown. Dixon (1965) found that in flocks of the Mountain Chickadee females sometimes held positions higher in the hierarchy than males. He also found that the mate of the alpha male ranked second in the hierarchy when the male was present. I did not find this to be the case with the Carolina Chickadee or Tufted Titmouse.

Mature birds usually dominated immature birds, particularly during late summer and early fall. Immature male birds, however, in several instances reversed the dominance of mature females during the winter.

TABLE 5

INTRAFLOCK ENCOUNTERS OF FLOCK 3 TITMICE DURING WINTER 1968-1969*

	15M	14U	16F	Total
15M**	-/-	21	8	29
14U	---	-/-	14	14
16F**	---	---	-/-	0
				28

*The Number of Encounters Won by Individuals at the Left can be Read in Horizontal columns.

**Mated

TABLE 6

INTRAFLOCK ENCOUNTERS OF FLOCK 4 TITMICE DURING WINTER 1968-1969

	23M	46U	40U	54F	Total
23M*	-/-	6	2	10	18
46U	---	-/-	4	7	11
40U	---	---	-/-	5	5
54F*	---	---	---	-/-	0
					34

*Mated

Dixon (1963) noted that beta male Carolina Chickadees often shared a portion of the winter range with the alpha male during the breeding season. Odum (1941a) found the same for the Black-capped Chickadee. No such

TABLE 7

INTRAFLOCK ENCOUNTERS OF FLOCK 3 CHICKADEES DURING WINTER 1968-1969

	7M	9U	20U	1F	Total
7M*	-/-	27	16	37	80
9U	---	-/-	10	17	27
20U	---	---	-/-	11	11
1F*	---	---	---	-/-	0
					118

*Mates

TABLE 8

INTRAFLOCK ENCOUNTERS OF FLOCK 3 TITMICE DURING WINTER 1969-1970

	10M	52M	49U	Total
10M	-/-	31	19	50
52M	---	-/-	16	16
49U	---	1	-/-	1
				67

division of the winter range into breeding territories was observed in this study.

In several instances, two feeders were located within the winter range of a flock, usually one being near the boundary. No difference in the social standing of any bird was noted at different feeders within the same range. Dixon (1965) found this to be true also of the Mountain Chickadee.

TABLE 9

INTRAFLOCK ENCOUNTERS OF FLOCK 4 TITMICE DURING WINTER 1969-1970

	23M	46U	40U	54F	Total
23M*	-/-	6	2	10	18
46U	---	---	4	7	11
40U	---	---	-/-	5	5
54F*	---	---	---	-/-	0
					34

*Mated

TABLE 10

INTRAFLOCK ENCOUNTERS OF FLOCK 6 TITMICE DURING WINTER 1969-1970

	26M	45U	47U	57F	Total
26M*	-/-	22	8	32	62
45U	---	-/-	17	6	23
47U	---	---	-/-	10	10
57F*	---	---	---	-/-	0
					95

On occasions a flock or some of its members would visit a feeder outside its own range. The meeting of two flocks at a feeder or while foraging was always accompanied by aggressive behavior. Chasing, supplanting attacks, and loud, rapidly uttered aggressive calls were observed on such occasions. The outcome of interflock encounters was

TABLE 11

INTRAFLOCK ENCOUNTERS OF FLOCK 3 CHICKADEES DURING WINTER 1969-1970

	7M	73U	75U	1F	Total
7M*	-/-	18	12	12	42
73U	---	-/-	6	13	19
75U	---	---	-/-	4	4
1F	---	---	---	-/-	0
					65

*Mated

TABLE 12

INTRAFLOCK ENCOUNTERS OF FLOCK 4 CHICKADEES DURING WINTER 1969-1970

	54M	67U	31F	61U	Total
54M	-/-	24	26	16	66
67U	---	-/-	18	11	29
31F*	---	---	-/-	9	9
61U	---	---	---	-/-	0
					104

*Resident female

dependent on the site of the encounters, as Dixon (1965) found for the Mountain Chickadee. Each flock gained the advantage when within its own range. Reverses were noted at the feeders between alpha individuals of both species, the outcome of an encounter being determined by the site of the

TABLE 13

INTRAFLOCK ENCOUNTERS OF FLOCK 6 CHICKADEES DURING WINTER 1969-1970

	24M	56M	71U	26F	69F	57U	Total
24M*	---	8	13	12	2	6	41
56M**	---	-/-	6	9	5	2	22
71U	---	---	---	---	8	7	15
26F*	---	---	---	---	3	5	8
69F**	---	---	---	---	-/-	4	4
57U	---	---	2	2	---	-/-	2
							92

*Mated
**Mated

feeder. At the feeder within the winter range of flock 3, for example, both the alpha and beta titmouse supplanted the alpha titmouse of flock 6 when this flock approached the feeder. The alpha male chickadee of flock 3 also supplanted the alpha male chickadee of flock 6 on the same occasions. When flock 3 visited the feeder within the winter range of flock 6, the outcome of encounters between the same individuals was reversed. No interflock encounters were observed between titmouse individuals of less than beta rank or chickadee individuals of less than alpha rank. It appeared that subordinate individuals avoided such encounters.

The behavior of dominant and subordinate birds at the feeders was quite different. In general, dominant birds were far more "confident" in approaching a feeder and in taking seeds. They were the first to feed when the flock approached, and they returned for seeds more frequently than subordinate birds and hid many more seeds than they ate. They usually flew directly to the cup and carefully selected a seed, often rejecting several in the process. Dominant birds often tore open and ate seeds while perched on the feeder even though other birds were perched nearby awaiting an opportunity to take a seed.

Subordinate birds always approached a feeder cautiously, perching several times in the approach and remaining perched nearby until the feeder was clear of other birds. When perched on the feeder they looked about for other birds, quickly took a seed, and flew. Subordinate birds never ate seeds at the feeder unless they were completely alone. When other birds were present, they made a relatively small number of trips to the seed cup and were often chased before taking a seed. Consequently, they usually ate more seeds than they hid.

Often, several birds would arrive at a feeder simultaneously and perch nearby. When this happened, the individuals flew to the seed cup in the order of their social standing--titmice before chickadees, the highest bird first, etc. If one flew out of turn, it was usually supplanted.

Birds at the bottom of the social hierarchy were very wary at the feeders and avoided encounters as much as possible. They did so by finding seeds on the ground under the feeder; by waiting, often for many minutes, until no other bird was nearby; or, by avoiding the feeder altogether and foraging nearby. Because they avoided encounters, it was often not possible to place them precisely in the flock hierarchy.

A subordinate bird looked about nervously for other birds when perched on the feeder. Seeing none, it would lean down into the cup for a seed, but upon reaching the point where its outside vision was blocked by the cup it would sometimes raise up again and look about. This up and down movement sometimes lasted as long as a minute, with the bird finally flying away without a seed or feeding briefly at the suet bin where its vision was not restricted.

At one feeder the four-inch seed cup was replaced with a ten-inch skillet. Even with the larger receptacle, however, only one bird at a time took a seed. If a subordinate bird of either species was perched inside or on the rim of the skillet when a dominant bird flew in, the subordinate bird often turned so as to be facing directly away from the dominant one. With crown feathers erect, it remained in this position until the dominant bird had selected a seed and flown. It then turned and took a seed. This face-away appeared to be a true submissive posture, as the birds are most vulnerable to attack from behind. On occasions even the alpha male titmouse was startled into flight when a chickadee or another titmouse unexpectedly landed in the skillet behind him. Dominant birds did not attempt to supplant a subordinate which was faced away.

Winter Roosting

Roost-Site Selection. All individuals of both species whose roost-sites were located roosted singly in tree cavities during the fall, winter, and early spring. This may have been due in part to the large number of both natural and woodpecker excavated cavities available in the study area and to the absence of large evergreen trees. Odum (1942a) found that Black-capped Chickadees roosted more often in dense conifer branches than in cavities during the fall and winter. The Plain Titmouse roosts in both natural cavities and dense foliage (Dixon, 1949). Williams (1942) found five Chestnut-backed Chickadees roosting under the eaves of buildings. Pielou (1957) found Tufted Titmice roosting in tall evergreens and tree cavities, and Bent (1946) quotes Dickey as saying that they roost in woodpecker holes and natural cavities.

One of the goals of this study was to determine whether the two species compete for roost sites. In an attempt to resolve this question thirteen chickadee and twelve titmouse roost cavities were measured. The results of these measurements are given in Tables 14 and 15. Four measurements were taken on each cavity as follows; diameter of entrance hole, width of cavity at entrance hole, depth of cavity from lower rim of entrance hole, and height of cavity (lower rim of entrance hole to ground level). In addition, the cavity was recorded as either a natural decay cavity or a woodpecker cavity.

The roost cavities of the Tufted Titmouse were significantly larger with respect to all four of the measurements than the cavities of the Carolina Chickadee. The difference in height between the two groups of cavities was not significant. Of the twelve titmouse cavities ten were natural decay cavities and two were large woodpecker cavities such as a Red-bellied Woodpecker makes. Only three of the thirteen chickadee roost cavities were natural decay cavities, and these were significantly smaller than the natural cavities utilized by the titmouse. The remaining ten were small woodpecker cavities such as a Downy Woodpecker makes. Both of the two species utilized specific tree species for roosting in about the same frequency.

All of the roost cavities of both species contained fecal droppings to a greater or lesser extent depending upon the length of time they had been utilized.

The choice of different sized cavities by the two species precludes competition for roost-sites. Also, the titmice chose primarily natural cavities (83 percent), whereas the chickadees chose principally holes dug by small woodpeckers (77 percent).

TABLE 14

ROOST CAVITIES OF THE CAROLINA CHICKADEE

Sex	Cavity Type	Cavity Dimensions (cm) Entrance	Width	Depth	Height	Tree Species
U*	W**	3.7-4.5	4.0-5.5	3.5	3.8	*Bumelia lanuginosa*
U	N***	3.0-3.5	3.0-3.5	27.7	3.7	*Quercus macrocarpa*
U	W	3.8	5.1	6.4	6.7	*Quercus macrocarpa*
F	W	4.5	4.1	17	14.6	*Quercus macrocarpa*
U	W	3.8-7.6	3.8-4.8	16.3	7.5	*Quercus macrocarpa*
U	W	3.8	3.8-7.6	12.6	6.2	*Quercus macrocarpa*
U	W	3.8	3.8-5.7	16.2	4	*Fraxinus pennsylvanica*
U	W	4.1-4.4	4.4-7.6	15	2.7	*Fraxinus pennsylvanica*
U	W	3.8-6.4	5.0	14	3.8	*Fraxinus pennsylvanica*
U	N	3.5-5.0	3.5-5.0	50.8	4.6	*Ulmus americana*
U	W	3.8	4.8	14	8	*Fraxinus pennsylvanica*
U	W	3.5	4.8	20	11.6	*Juglans nigra*
U	N	5.7-6.4	5.6-6.4	16.3	1.3	----------------------
Mean		4.3	4.8	17.7	6.0	

*Sex unknown

**Woodpecker cavity

***Natural cavity

TABLE 15

ROOST CAVITIES OF THE TUFTED TITMOUSE

		Cavity Dimensions (cm)				
Sex	Cavity Type	Entrance	Width	Depth	Height	Tree Species
M	N*	4.7-9.0	6.5-10.1	52	8.5	*Ulmus americana*
M	N	10	10	43	4	*Quercus macrocarpa*
M	N	5.5-15	5-7	15	4	*Quercus macrocarpa*
M	W**	5.1	10.1	56	3.7	----------------------
F	N	9	9	28	8	*Ulmus americana*
F	N	6.4	6.4	90.6	5.8	*Ulmus americana*
M	N	6.4-12.7	6.4-12.7	23	8.9	*Ulmus americana*
M	N	4.5-9	8.3-16.2	16	6.4	*Juglans nigra*
U	N	6.4-6.7	12	22	1.6	----------------------
M	N	7-9	7-9	68	7	*Juglans nigra*
M	N	12.7-7.6	7.6	30	11.3	*Fraxinus pennsylvanica*
M	W	5.1-4.2	9	18.7	3.9	*Quercus macrocarpa*
Mean		7.8	9.0	38.5	6.1	

*Natural cavity

**Woodpecker cavity

TABLE 16

ROOST CAVITIES OF THE DOWNY WOODPECKER

Sex	Cavity Type	Cavity Dimensions (cm) Entrance	Width	Depth	Height	Tree Species
F	W	3.8	8.2	14.6	1.7	*Salix nigra*
F	W	5.1-4.8	5.1-6.3	17.5	6.7	*Ulmus americana*
F	W	4.1	5.4	18.1	4.8	*Fraxinus pennsylvanica*
M	W	3.8	7.1	16.2	2	*Salix nigra*
F	W	3.2	7.1	15.2	1.8	*Ulmus americana*
Mean		4.0	6.7	16.3	3.4	

The ten chickadee cavities which appeared to have been dug by Downy Woodpeckers were compared with five cavities in which these woodpeckers were observed to roost (Table 16). The only dimension found to be significantly different between the two groups was the width of the cavity at the opening. The small number of downy cavities represented may account for this difference.

Individuals were not observed investigating potential roost cavities until just before roosting time. In several instances, a cavity of one of the two species had to be removed before it could be measured. Members of both species reacted similarly on such occasions. They arrived at the roost-site at the normal roosting time. Upon finding the cavity gone, they perched nearby and called for several minutes and often flew several times to where the cavity had been. In several instances the birds hovered in mid-air before the spot where the opening to the cavity had been. After several minutes they began to inspect cavities nearby (usually in the same or adjacent trees), then flew to another cavity some distance away and either entered it, or examined it and flew to another. In one instance a male titmouse spent the night deep in the foliage of a cedar tree, and in two instances a titmouse utilized a cavity formed by loose bark hanging under a dead limb when their cavities were removed. One chickadee investigated six cavities scattered over two acres in a ten minute period before selecting a new roost cavity. Often, cavities selected under such circumstances were replaced in later days by more substantial ones, but these also appeared to have been selected at roosting time rather than through the day. The birds apparently knew the location of many different potential roost cavities within their winter range, however, as evidenced by their direct flight to them when their own was destroyed.

Roosting Time. The data presented in Table 17 represents observed roosting times for each of the two species from November through March. A wide variation in the roosting times of individuals of both species was noted. Often, after a bird had entered its roost cavity others of its species would be heard calling. The last call heard from these late roosting birds was also recorded. Thus, the data may be biased in favor of late roosting birds. Individuals were found to be rather consistent in their roosting time in relation to others of their species. Some consistently roosted early and others late.

Even though the data are scanty, several trends are noticeable. Birds of both species roosted earlier in relation to sunset on cloudy days than on clear days. The average chickadee roosting time was earliest in November, became increasingly later through December and January, and was somewhat earlier in February. In March the average roosting time was later in relation to sunset than it had been at any time throughout the winter.

TABLE 17

FALL AND WINTER ROOSTING TIME OF THE CAROLINA CHICKADEE AND TUFTED TITMOUSE 1969-1970

	Weather	November	December	January	February	March
C	Clear					
H	No. Obs.*	10	5	6	12	4
I	Average	-7.8**	-5.3	-5.3	-12.1	-4.5
C	Range	-34 to -9	-3 to -11	+2 to -12	+3 to -25	-3 to -9
K						
A	Cloudy	----				
D	No. Obs.	----	----	4	2	7
E	Average	----	----	-21.5	-21	-37.1
E	Range	----	----	-15 to -29	-21 to -21	-30 to -40
	Clear					
T	No. Obs.	14	----	6	4	8
I	Average	-17.2	----	-20.3	-13.3	-29.1
T	Range	+7 to -34	----	-16 to -29	-1 to -23	-18 to -49
M						
O	Cloudy					
U	No. Obs.	----	----	3	5	6
S	Average	----	----	-28.3	-41.8	-29.1
E	Range	----	----	-27 to -29	-41 to -45	-20 to -74

*Observations

**- Represents minutes before sunset
\+ Represents minutes after sunset

The titmouse data indicate a tendency toward earlier roosting from November through January and a relatively later roosting time in February. In March the roosting times were earlier than those recorded through the winter. Because of the large variation in individual roosting times, the data for both species are probably insufficient to accurately represent a true average of roosting times.

A few roost-leaving times were recorded in January and February. Four observed times in January for the titmouse averaged 8.5 minutes before sunrise, and five observed times in February averaged 9.6 minutes before sunrise. The average of five chickadee roost-leaving times in January was 17.8 minutes before sunrise, and the average of seven times in February was 9.9 minutes before sunrise. Individuals of both species left the roost under lower light intensities than they entered it.

Roosting Behavior. In flock 1, in which roosting was observed most frequently, the flock approached a specific feeding area approximately 5 to 10 minutes before roosting. In approaching the area, the alpha male titmouse led, followed in turn by the subordinate titmice, the dominant chickadee, and the subordinate chickadees. Members of both species were relatively quiet in approaching the area but became very vocal upon entering it and continued to be so for several minutes. After foraging quietly for a few minutes, individuals would begin to leave the area and fly to their roosts. The order in which individuals left was fairly consistent from night to night. This same foraging area was used prior to roosting for two winters. A smaller number of observations on two other flocks indicated similar behavior in that the flock always flew to a specific foraging area before the individuals began flying to their respective roosts.

A definite tendency was noted for individuals of the same flock to roost in the same section of their winter range. Odum (1942a) noted a similar tendency in Black-capped Chickadee flocks as did Hinde (1952) in flocks of the Great Titmouse. In flock 1 three chickadees and three titmice roosted in an area 50 feet square during 1969-1970. One of the chickadees and a titmouse roosted in the same tree stub only a foot away from each other. This section of the woods was approximately 200 feet away from the pre-roosting foraging area. Three other chickadees roosted less than 100 feet from the others. In flock 6 three titmice and four chickadees roosted in an area less than one-half acre in size. This area was less than 100 feet from the pre-roosting foraging area.

After settling down in the pre-roosting foraging area, the birds were usually quiet until they went to roost. The only calls heard as they foraged and when they flew to the roost cavity was the soft contact note. In flying to the roost, the birds of both species usually perched several times. Some birds then flew directly into the roost cavity while others made a last perch near the entrance first.

On one occasion a titmouse and a chickadee roost cavity were examined 20 minutes after sunset. At both roosts the birds flew out when the cavity wall was touched. They were silent and flew to a nearby tree. Both of the birds roosted at a new site the following evening. Williams (1941) found that Chestnut-backed Chickadees also abandoned their roost-sites when they were disturbed during the night.

When individuals of either species approached to find an observer near the roost-site, they gave loud scolding notes. Often they flew away and returned a few minutes later. As darkness approached, they gradually inched closer to the roost cavity, and finally, at about 15 minutes past sunset, either entered the cavity or flew away to another roost. Individuals approaching a recently selected roost-site were particularly sensitive to the presence of an observer. A female titmouse flew out of a roost cavity 38 feet high, which she was using for the first time, when I walked under it. Birds using older roost-sites often entered when I was standing very close. Also, birds of both species were less sensitive to an observer on the ground than to one in an adjacent tree near the level of the roost cavity.

Upon leaving the roost in the morning, individuals of both species pearched nearby and gave a subdued general call note once or twice before flying to the same foraging area utilized prior to roosting. Here they called loudly. These calls apparently acted as a signal for individuals to reform into the flock. Following the break-up of the winter flocks, males usually sang upon leaving the roost instead of giving the general call note.

CHAPTER III

VOCALIZATIONS

The following discussion is based on Odum's (1942a) analysis of vocalizations of the Black-capped Chickadee. It does not include all of the sixteen different vocalizations he recognized and adds at least one he did not recognize. The vocabulary of the Carolina Chickadee and Tufted Titmouse consists of a large number of notes used in various combinations, depending upon the situation in which the bird is involved. Many variations of the calls listed below are heard, but they are excluded because no definite function could be attached to them.

Chickadee

Whistled song. The whistled song is a high-pitched clear whistle of four notes which is usually transliterated as fee-bee, fee-bay. In field notes I always write the song with the symbol  . As the symbol indicates, the second note is lower than the first, the third slightly higher than the first, and the last between the first and second. Both sexes give the song, but it is louder and more frequent in the male.

The song is heard infrequently throughout the year but most often during the nesting season. When heard during the winter it is usually hoarse and incomplete and lacks the thin clear tone of the nesting season song. During the nesting season it is heard most frequently from males unaccompanied by their mates.

Variations of the song include both two- and three-note songs which omit the last, or last two, notes. Immature birds were heard giving the song in July and August, but it was usually hoarse and imperfect or was interspersed into long, formless, calls not characteristic of mature individuals of the species.

The call functions to advertise the male's territory prior to and during nest-building and to apprise the female of his whereabouts. The female uses it to determine the position of the male and to inform him of her position. Male chickadees do not utilize regular singing posts but sing as they forage, and then usually only when the female is not present or when the male is leading the female about. Following nest-building, most songs seem to be communications between mates. The male uses it, for example, to reassure the female following a disturbance at the nest. After fledging, the male leads the family group about with the song. Whether it plays a role in pair formation or not was not determined.

Signal song. The signal song is a soft version of the regular song, often with the last note omitted. The male, and rarely the female, gives the call when approaching the nest, usually from a "favorite" perch near the nest opening.

General call note. The familiar chick-a-dee-dee-dee call is heard with numerous variations throughout the year in a wide variety of situations. In winter foraging birds give the call slowly at intervals, and it seems to function in announcing their position to the other members of the flock. During the nesting season, it is used to announce the bird's position to its mate and to reunite them when they become separated while foraging. When greater distances separate the pair, the whistled song is used for this purpose. Several variations of the call are discussed below.

Scolding note. The scolding note is similar to the general call note, but it is longer, more emphatic, and uttered more rapidly. Emphasis is placed on the dee portion and this part of the call is repeated many times, as chick-a dee-dee-dee-dee----. It can be heard during boundary disputes; when an observer approaches a nest, roost site, winter flock, etc.; and when potential enemies (owls, snakes, etc.) are sighted. At times the dee dee portion becomes lower and even more emphatic, sounding like a deep beep beep----.

Other aggressive notes. Sometimes, during aggressive encounters, the first part of the general call note is repeated loudly as chit-chit----. At other times it is replaced by a high-pitched whistle, similar to the warning note, followed by dee-dee----. The call is given rapidly as the bird darts at the intruder. If the intruder threatens, the dee-dee part is omitted and only the high-pitched whistle is given.

Other calls heard in aggressive encounters are squee-gee and tsweedle-dee. Brewer (1961) calls the latter deedle-up and thinks it equivalent to the dominance note described by Odum for the Black-capped Chickadee. The tsweedle-dee call is also given by the female while wing fluttering during precopulatory behavior and by both sexes when they arrive at the nest together and mutual wing fluttering is observed.

Alarm note. This is a short, explosive chick-a-dee or chit-chit, the latter sounding like a stuttering of the first part of the former. It is given when the bird is surprised at close quarters by another bird, a potential predator, or an observer. It was most often heard when a flock was surprised while foraging, when a bird was approached from behind by another at the feeder, and when birds flew out of the nest cavity to find an observer nearby.

Warning note. The warning note sounds like a very high-pitched tsee repeated a variable number of times, and it is often followed by scolding or other aggressive notes. It is given in potentially dangerous situations, as when a hawk flies over or an observer approaches or handles the young.

A typical progression of calls, i.e., when an observer approaches a nest or feeder, would be: _tsee_ _tsee_ ----, _tsee_-_tsee_-_tsee_-_dee_-_dee_---, _tsee_-_dee_-_dee_-_dee_---, _chick_-_a_-_dee_-_dee_-_dee_---. Upon first sighting the danger, the bird gives a warning note. As the bird adjusts to the observer, the warning note is gradually transformed into the scolding note and the scolding note into the general call note. After several minutes the bird resumes normal activity. The bird's emotional state as reflected by its calls changes from "fear" to aggression. As the aggression wanes the calls decrease in intensity, speed, and duration until the bird becomes silent.

Distress call. The distress call resembles a loud squeal. It was most often heard when immature birds were being banded. Most adult birds were silent when handled, but some gave the call.

Begging note. Brewer (1961) represents the begging note phonetically as _che_-_che_-_weweweup_. It is quite variable and difficult to transliterate but sounds like a modified general call note. The female uses the note to beg from the male both on and off the nest. Very young nestlings give a fairly high-pitched note sounding like _tseep_, _tseep_,---.

As they grow older, the note becomes lower in pitch and sounds like che-up or che-up-che. Begging by the female and fledglings is often accompanied by wing fluttering.

Recognition or contact note. A thin, weak tsip is heard at all times of the year in both sexes. It is uttered by birds in the flock while foraging and by mated pairs. It is also often given by individual birds as they fly to their roost cavities. The note is soft and can be heard only at close range. It apparently serves to keep individuals in contact with each other.

Hissing note. An explosive hissing note is given by the female during the snake display. I feel that it is a true vocal effort, rather than a forced expiration of air as described by Odum (1942a).

Nest note. This single-syllable call sounds like a low speep or dee pronounced clearly and deliberately. Sometimes it is repeated twice in quick succession, but each monosyllable is very distinct. It is given by adult birds at the nest opening when they enter with food and functions to announce their presence to the nestlings. The male also announces his presence to the female during incubation or brooding with the note.

It immediately evokes begging, even in newborn birds, and the adult then enters and feeds them. It sounds quite loud inside the cavity but cannot be heard from outside for more than a few feet. To my knowledge the note has never been described in the literature.

Titmouse

Whistled song. The songs of the male Tufted Titmouse are of at least four different types. The first is the familiar peto, peto song, sometimes described as peter, peter. The first syllable is accented when the song is uttered slowly and the last is accented when uttered rapidly. In both instances the first syllable is higher in pitch than the last, and the song sounds similar to the first two notes of the chickadee phoebe song but is lower and louder. It was heard most frequently during the early stages of the breeding season, reaching a peak during nest building. Both sexes give the call infrequently throughout the year, but it is louder and more frequent in the male. The note is usually repeated three to four times.

A second song heard as frequently as the peto song is one which I describe as here kitty kitty kitty. It is similar to the peto song, except for the first phrase which is higher in pitch than the last three or four phrases. Also, the first syllable of the last three or four phrases is not higher in pitch than the last syllable as in the peto song. Most often the first phrase is omitted, except when the bird first starts singing.

A third song, heard less often than the first two, is peet-peet-peet, each phrase being repeated two to four times. It is sometimes slurred, sounding like peety-peety-peety. The song appears to be the same as the first syllable of the peto song.

The above three songs are heard interchangeably. A singing male shifts from one to the other, and as far as I could determine, all serve the same function--advertisement of territory to other males and long-range communication between mates.

The last song is longer than the first three and is more difficult to describe. It sounds something like peet-whee-whee-whee-whee and was heard most frequently during January and February, at times becoming monotonous. It was uttered less rapidly than the other songs and was given only by male birds.

Titmice males spent greater time singing than chickadee males, and had regular singing posts prior to and during nest building. The male usually started singing low in a tree and worked up to the top, always staying within the foliage. Following the beginning of incubation, singing decreased, and most of the songs heard seemed to be communications between mates. Following fledging, the male led the family group about with one of the first three songs described above.

During July and August young titmice began making attempts to sing. As with young chickadees, the songs were long and formless but were interspersed with snatches of recognizable song.

Signal song. The signal song is a soft version of the whistled song which is given by the male, and rarely the female, in approaching the nest. It is usually given from a "favorite" perch near the nest opening. The kitty-kitty-kitty song is generally used, being given only once or twice. The call is very subdued and seems displaced. At times, even though I was watching the bird, I thought the call was coming from a different location. It functions to announce the male's presence to the female during incubation and brooding and to the young during the nestling stage.

General call note. This call sounds like tsicka-dee and corresponds to the chick-a-dee-dee of the Carolina Chickadee; however, it is lower in pitch and more deliberate than the chickadee call. It seems to serve the same function in both species. The first phrase of the call is often omitted. Like the chickadee note it has several variations, some of which are discussed below.

Scolding note. The scolding note is similar to the general call note but it is longer, more emphatic, and uttered more rapidly. The dee dee phrases are emphasized and repeated many times, receiving more or less emphasis depending on the situation. It was heard in situations similar to those discussed for the chickadee. The intensity, speed, and duration of the call increase when the bird is more aggressive. At high intensity the first phrase of the call is a very high-pitched whistle similar to the warning note but louder. A typical progression of calls when the bird is disturbed or threatened is: tsee-tsee-tsee---, tsee-tsee-dee-dee---, tsicka-dee-dee---, dee-dee---, dee-dee. As with the chickadee the warning note is gradually transformed into the scolding note, the scolding note into the general call note, and finally, as the aggression wanes, the bird becomes silent and resumes its normal activity.

Alarm note. An explosive tsicka-dee-dee or tsickt, tsickt is usually given when the bird is alarmed at close quarters. After flying up and away from the source of the disturbance the bird usually gives harsh scolding notes.

Warning note. The warning note is a very high-pitched tsee, tsee or see, see which is often followed by scolding notes. It is given in situations similar to those described for the chickadee.

Distress call. A loud squeal was usually given by both mature and immature birds when they were hand held. The warning note was given when I approached a netted bird and was interspersed with the distress call when the bird was being handled.

Begging note. Very young birds in the nest give a single syllable begging call which sounds like tseep, tseep. During the last week of nest life it becomes tseep-up, the last phrase being repeated from one to three times. The latter call is given by the young following fledging and by the female. The female was also heard giving a loud high-pitched call sounding like tseep when begging from the male. Wing fluttering accompanied the begging note in both the female and young.

Recognition or contact note. Both sexes give a soft tsip throughout the year while foraging. It was heard in the same situations as the corresponding note in the chickadee and appears to serve the same function.

Hissing note. The note given by female titmice during the snake display is very similar to the same note given by female chickadees.

Nest note. As with the chickadee, adult titmice give a soft but deliberate speep or dee call at the nest cavity entrance to alert the young to their presence.

Rally note. The rally note is a one syllable peet which sounds identical to the same note used in singing. The note is repeated only once or twice when used as a rally call. During the non-breeding season it was heard only from the alpha titmouse male of the flock. When he gave the call, the mixed flock of titmice and chickadees immediately converged on him.

During the breeding season both members of the pair gave the call. The female gave it, for example, upon leaving the nest, and the male would fly to her. Often, after the male escorted the female back to the nest, he gave the call several times as if searching for his mate. The call is easily imitated and is discussed further in the sections on the breeding season and winter flocks.

Dominance note. A loud note sounding like squiss is often given by aggressive males, and the note is usually followed by aggressive behavior. It was most often heard at the feeders when more than one bird attempted to feed. A dominant bird often caused a subordinate bird to flee simply by giving the note. It was also heard during supplanting attacks and territorial disputes.

CHAPTER IV

FORAGING BEHAVIOR

Methods

The procedure used to quantify the foraging zones utilized by each species and to represent these zones pictorially is similar to that used by Stallcup (1968). When a member of one of the two species was observed in the act of foraging, the length of time it spent in a specific zone was timed with a stopwatch. In this manner, samples of the length of time each species was observed foraging in certain zones of the environment were collected. Twelve specific zones were recognized, and, for ease of notation in the field, each was given a number as in Figure 1. Time measurements were recorded in units of five minutes. A five-minute period equaled one unit, two and a half minutes equaled one-half unit, etc. Field timing measurements were rounded off and recorded to the nearest half unit. Observations of less than one minute duration were discarded.

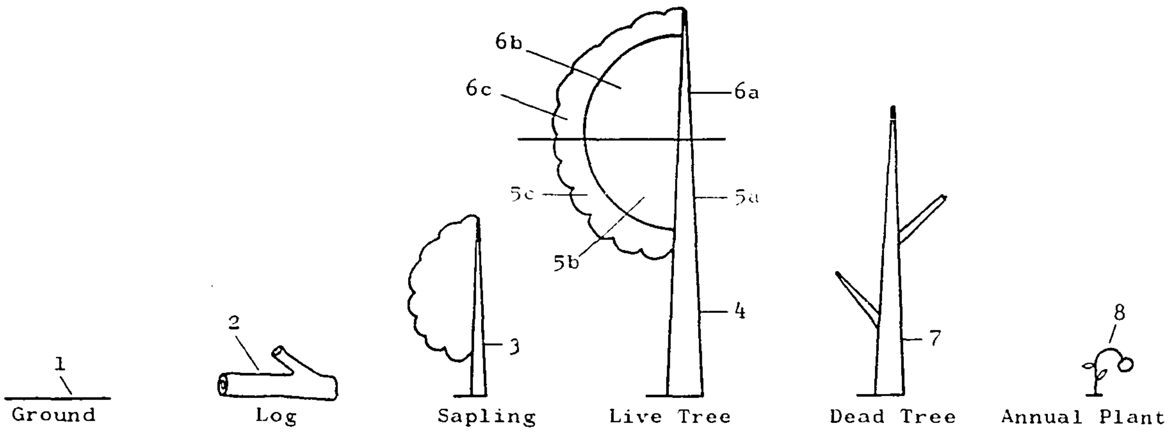
This method was used because both the chickadee and titmouse have the habit of carrying food items found in one zone to another zone to eat them. Foraging birds were,

Fig. 1. Pictorial representation of foraging zones. Classification of zones is as follows:

1. Ground
2. Log or branch on ground
3. Live sapling

4-6. Large living tree
    - 4 Main stem below branches
    - 5a Main stem at lower half of crown
    - 5b Interior of lower half of crown
    - 5c Periphery of lower half of crown
    - 6a Main stem at upper half of crown
    - 6b Interior upper half of crown
    - 6c Periphery upper half of crown

7. Standing dead tree
8. Standing annual plant


6b
6c
6a
5c
5a
5b
4
2
1
3
7
8
Ground
Log
Sapling
Live Tree
Dead Tree
Annual Plant

therefore, often seen in almost all of the twelve zones, and data which were collected by simply noting the position of foraging birds indicated no clear preference for specific zones.

The foraging behavior of both species changed with the seasons. The most obvious changes occurred in April when the vegetation leafed out and in late October when the growing season ended. For this reason, timing records taken from April through October were analyzed independently of those taken from November through March.

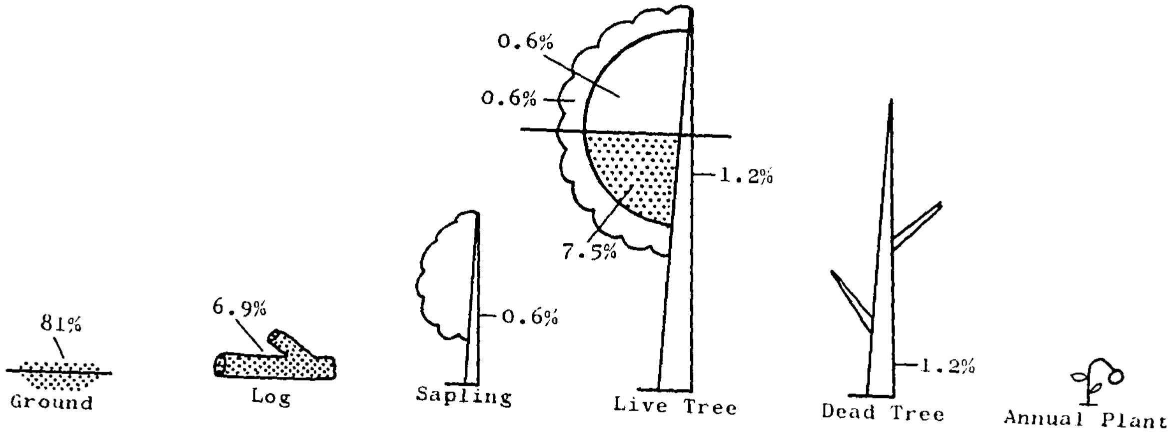
Results

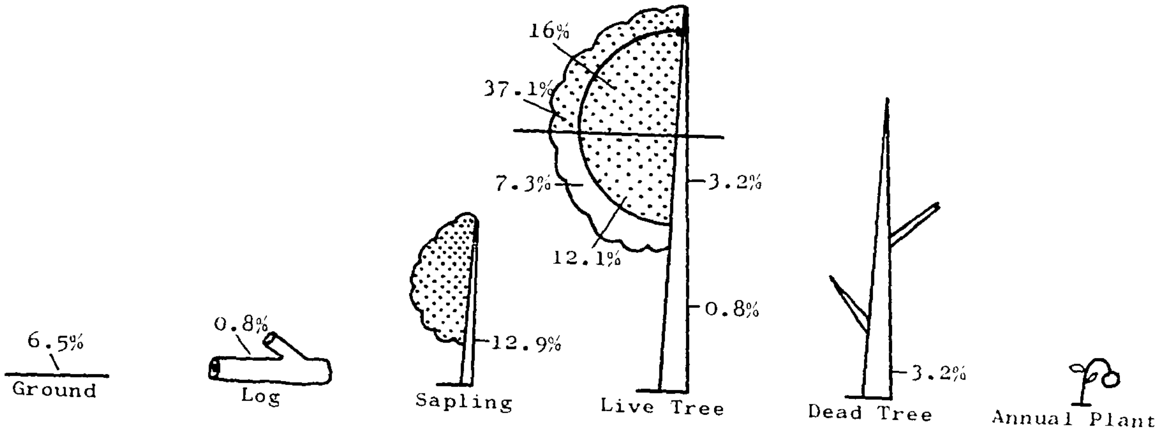
Titmouse. During the period from November through March the major foraging zone of the Tufted Titmouse was ground litter. Secondary zones were the interior of the lower crowns of large trees and decaying logs or branches on the ground (Fig. 2).

When foraging in leaf litter, a titmouse hopped along the ground and searched the litter visually. Upon finding a spot to its liking, it picked up dead leaves with its bill and threw them to the side with a quick snap of the head. Birds also often searched the litter from above by perching on the side of a very small sapling and peering down at it. They perched up to a foot high and flew from sapling to sapling until something in the litter attracted them, whereupon they alighted and began to dig. When food was found, it was carried to a low perch and torn apart and eaten.

Fig. 2. Foraging zones utilized by the Tufted Titmouse during the nongrowing season (November-March). The percent of the total length of time titmice were observed in each zone is shown. The three zones most frequently foraged are stippled and are referred to in the text as major foraging zones.

Fig. 3. Foraging zones utilized by the Tufted Titmouse during the growing season (April-October). Explanation as in Figure 2.


0.6%
0.6%
1.2%
7.5%
81%
6.9%
0.6%
1.2%
Ground
Log
Sapling
Live Tree
Dead Tree
Annual Plant


16%
37.1%
7.3%
3.2%
12.1%
0.8%
6.5%
0.8%
12.9%
3.2%
Ground
Log
Sapling
Live Tree
Dead Tree
Annual Plant

Individual birds moved slowly when foraging in this zone and were often observed on the ground for twenty minutes or more.

As they moved along the ground, birds often stopped and searched fallen logs or branches for food (Zone 2). They searched in crevices in the bark, behind loose bark, in cracks in the wood, and in decaying wood.

The only zone above the ground used extensively from November through March was 5b, the interior lower crown of living trees. When foraging in this zone, birds carefully searched the bark of larger limbs. Small decaying limb stubs were also examined. The birds moved quickly from place to place and from tree to tree when foraging above ground.

From April through October the titmice spent most foraging time on leaf surfaces, and the number of major zones utilized increased from three to four (Fig. 3). The zone in which most time was spent was the upper periphery of living tree crowns (6c). Here they foraged on the leaves, often hanging upside down while doing so. They also foraged extensively in the interior of crowns (5b and 6b) where they searched both leaf and limb surfaces for food. When flying to a tree, they usually perched near the stem and moved out along the branches, searching for food as they moved. Considerable time was also spent searching the foliage of large saplings in Zone 3c.

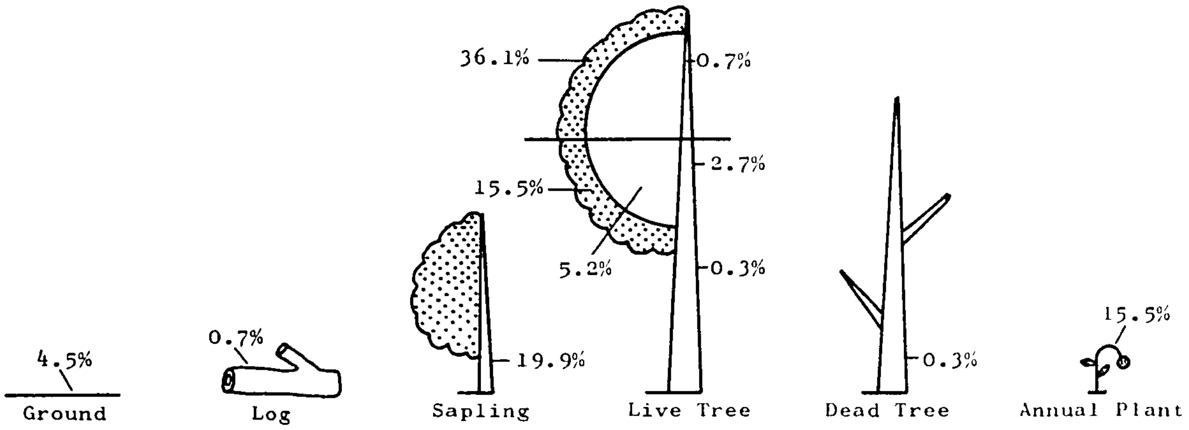
Very little of the total foraging time was spent in the leaf litter (Zone 1) during this period. Over 90 percent of the timing observations for this zone represented in Figure 3 were recorded in early April before the transition was made to leaf surfaces. There is a possibility of bias here, however, because the thick understory in full leaf made observation of birds on the ground extremely difficult.

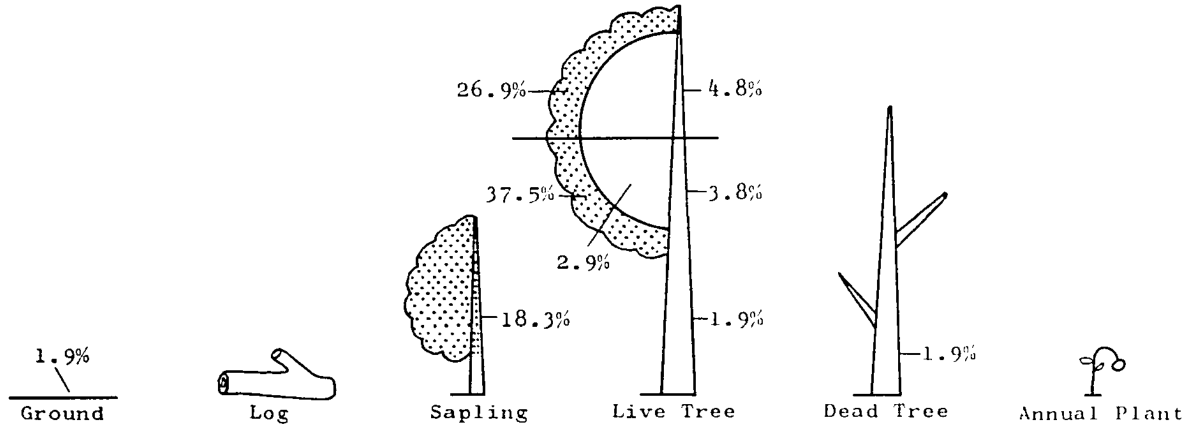
Chickadees. During the period from November to March, four major foraging zones were utilized (Fig. 4). The zone utilized most frequently was the periphery of upper living tree crowns (6c). Here the birds searched small twigs and were often seen tearing open the buds, causing small pieces to fall to the ground. The same was true of their behavior when foraging in saplings (Zone 3). Whether they were searching for insects or actually eating the buds was not determined. They also searched the main stem of saplings on occasion and could be seen hammering on the bark.

Annual herbaceous plants were foraged most often in late autumn and early winter. The plant foraged most extensively was the giant ragweed (*Ambrosia trifida*). The birds would cling upside down to the dead plants and remove the fruits. These were then carried one at a time to a nearby perch in a tree or sapling where they were torn open and the contents eaten. Birds were also occasionally observed eating the fruits of poison ivy (*Rhus radicans*).

Fig. 4. Foraging zones utilized by the Carolina Chickadee from November through March. Explanation as in Figure 2.

Fig. 5. Foraging zones utilized by the Carolina Chickadee from April through October. Explanation as in Figure 2.


36.1%
0.7%
2.7%
15.5%
5.2%
0.3%
4.5%
0.7%
19.9%
0.3%
15.5%
Ground
Log
Sapling
Live Tree
Dead Tree
Annual Plant


26.9%
4.8%
37.5%
3.8%
2.9%
18.3%
1.9%
1.9%
1.9%
Ground
Log
Sapling
Live Tree
Dead Tree
Annual Plant

Primary foraging zones from April through November (Fig. 5) were the periphery of live tree crowns (Zones 5c and 6c) and saplings (Zone 3). The most extensive foraging in these zones was on leaf surfaces.

Chickadees were more often observed clinging upside down to leaves or twigs than titmice and seemed to be more agile. More time was spent in the periphery of the lower half of the crown than in the upper, and birds usually flew directly to the periphery of the crown rather than to a large branch in the interior, as titmice were usually observed to do. Upon finding a large food item the chickadees always carried it to a larger branch before tearing it apart and eating it. When foraging on a tree, most birds started low and moved upward.

Overlap in foraging zones. There was no overlap in the major foraging zones utilized by the two species from November through March. From April through October an overlap occurred in Zones 3 and 6c. Even here, however, competition may be limited by the taking of different types and sizes of food (see section on Food Taken at Nest) and by differences in foraging behavior. The chickadees appeared to forage more on the leaves of the smallest twigs at the periphery of the crown. Even when they foraged deeper inside the crown, they tended to restrict their activity to the terminal leaves of the smaller twigs and branchlets and branches. Also, even though the populations of both species reached a peak in mid-summer, the abundance of food at this time would tend to lessen the effects of overlap in foraging zones.

Tree species foraged. Table 18 compares the percent of total observed foraging time spent in nine tree species. Both species of birds foraged extensively in American elm trees during the growing and non-growing seasons. No clear-cut difference between the two species is apparent, except for the extensive use of persimmon (Diospyros virginiana) during the winter by the Carolina Chickadee and lack of use of the same tree by the Tufted Titmouse.

Food

Titmouse. Specimens were not collected for stomach analysis in this study. Beal et al. (1916) examined the contents of 186 Tufted Titmouse stomachs obtained at all seasons and found that it consisted of 66.57 percent animal matter and 33.43 percent vegetable matter. One item, caterpillars, formed more than half the animal food (38.31 percent of yearly food) and were eaten in every month but November. Hymenopterous insects were eaten extensively (12.5 percent), most of these being bees, wasps, and sawfly larvae. Ants were found only occasionally. Beetles made up 7.06 percent of the yearly diet. Hemiptera, primarily stinkbugs, and Homoptera, principally tree-hoppers and scales, were eaten moderately in seven of the twelve months (4.03 percent). The only dipterous insect found was a single fly from a

TABLE 18

TREE SPECIES UTILIZED IN FORAGING

Species	Chickadee-Percent Total Time		Titmouse-Percent Total Time	
	Nov.-March	April-Oct.	Nov.-March	April-Oct.
Ulmus americana	40.6	31.4	28.6	42
Fraxinus pennsylvanica	12.9	15.1	7.1	17.3
Quercus macrocarpa	5.2	2.3	14.3	17.3
Celtis laevigata	10.3	15.1	7.1	7.4
Carya illinoensis	6.5	14	14.3	4.9
Juniperus virginiana	3.8	4.7	----	----
Populus deltoides	.6	11.6	21.4	7.4
Diospyros virginiana	19.4	3.5	----	----
Juglans nigra	.6	2.3	7.1	3.7

stomach taken in January. Eggs of katydids, egg cases of cockroaches, and a jaw and ovipositor thought to belong to a grasshopper were the only remains of orthopterous insects found (0.42 percent). Spiders and a few snails made up the remainder of the animal food (4.25 percent).

Other animal food reported in the literature includes bagworms (Thyridopteryx) (Harford, 1966), dead titmouse flesh (Stewart, 1955), the contents of a Cecropia Moth cocoon (Hyalophora cecropia) (Trautman, 1940), and forest tent caterpillars (Malacosma americana) (Pielou, 1957). In addition, I observed a male titmouse eat the anterior half of a Brown Skink (Scincella laterale).

Beal et al. (1916) found that broken seeds and mast formed more than two-thirds of the vegetable matter in the titmouse diet. Mast, amounting to 23.4 percent of the total year-round food, comprised 95 percent of the food eaten in November, 50.42 percent in January, 55.97 percent in February, and was the principal vegetable food eaten from August to March. The mast was composed largely of acorns but chinquapins and beechnuts were also included. The seeds of sumac, poison ivy, and bayberry were found (4.07 percent). Fruit was eaten to some extent (5.15 percent), mostly in midsummer. The remains of raspberries, blackberries, strawberries, elderberries, hackberries, blueberries, huckleberries, and mulberries were identified.

Other vegetable food reported in the literature includes cultivated grains (Trautman, 1940); the fruit of choke-cherry, staghorn sumac, wild crab-apple, Virginia creeper, and flowering dogwood (Pielou, 1957); beechnuts (Pielou, 1957); cultivated grapes (Blincoe, 1923); wild cherries and service-berries (Dickey, in Bent, 1946); and hemlock seeds (Pielou, 1957).

Chickadee. Beal et al. (1916) examined 210 stomachs of the Carolina Chickadee. The food consisted of 71.94 percent animal matter and 28.06 percent vegetable matter. Caterpillars formed 44.2 percent of the yearly food. The month of greatest consumption was October (78.1 percent) and of least consumption December (11.74 percent). Spiders were eaten in every month and made up 10.9 percent of the yearly food. Bees and wasps were taken regularly (4.48 percent). Hemipterous and homopterous insects were taken in the greatest numbers from April to July and averaged 15.13 percent for these months but only 5.68 percent for the whole year. This item of food included stinkbugs, shield bugs, leaf-hoppers, tree-hoppers, plant lice, and scales. Beetles, being rather terrestrial in habit, formed only 3.67 percent of the yearly food, and ants formed only 0.36 percent. No adult dipterous insects were found, but the eggs of a crane fly were found in one stomach.

The vegetable food consisted chiefly of fruit and seeds. Blackberries or raspberries, blueberries, and unidentified fruit pulp constituted 2.17 percent of the yearly food. Seeds of poison ivy (10.07 percent) were utilized in the colder months, but only the waxy coating was eaten. Other unidentifiable seeds made up 12.38 percent of the yearly food.

In the current study chickadees were observed to spend considerable time in late March and early April foraging on American Elm fruits. The birds pulled the fruits free one at a time, hammered on them, and apparently ate the contents. In late spring the birds also picked galls from hackberry leaves and ate the small white larvae (Psyllidae).

Brewer (1963) listed the most important insect families in the diet of the Carolina Chickadee as Tettigoniidae, Pentatomidae, Membracidae, Cicadellidae, Coccidae, Aphididae, Chrysomelidae, Curculionidae, Phalaenidae, Olethreutidae, Geometridae, and Lasiocampidae. He also stated that spiders are taken regularly.

Comparison of Food Carried to Nest. Food carried to the nest by parent birds during the nestling stage was collected at one chickadee and one titmouse nest.

At the chickadee nest (CP12a), food was collected from the fifth to the eleventh day of nestling life. The manner of collection was simply to remove the food from the nestlings' gape before it could be swallowed. This was relatively easy with the young nestlings, but became increasingly difficult as they grew older. When food could no longer be taken in this manner, a tally was kept of foods brought to the nestlings using the following classification: Lepidoptera larvae and pupae, Hymenoptera, and Spiders (Araneida). Twenty-eight individual specimens were collected and identified. Twenty-six were Lepidoptera larvae of the five families listed in Table 19, one was a spider, and one was the abdomen of an adult wasp. Percentages of families represented are not given because the selection was not random. Instead, an effort was made to collect specimens which appeared to be different from those already collected. Also, spiders were very difficult to remove from the gape before they were swallowed as were small larvae.

TABLE 19

FOOD COLLECTED OR OBSERVED AT CHICKADEE NEST CP12A

Order	Families Represented	Collected or Observed
Lepidoptera larvae - 74 % pupae - 4.3 %	Pieridae Nymphalidae Hesperiidae Libytheidae Geometridae	37
Hymenoptera adult - 4.3 %	Vespidae	2
Araneida 17 %	Dysderidae	8

Caterpillars were by far the most common food, making up 78.3 percent of the total food. Spiders were second with 17 percent, and wasps last with 4.3 percent.

At the titmouse nest (TP6b) the young were collared with pipe-cleaning wires for short periods each day from the tenth to the fifteenth day of nestling life. As at the chickadee nest, caterpillars made up the bulk of the food (92%) (Table 20). Sixty-four percent of these were of the family Noctuidae and all of the noctuids were the large, darkly colored, larvae of underwing moths (Catocala). One beetle larva (Carabidae), one spider (Oxyopidae), and a spider egg sac were also collected. In addition, several small pieces of old land snail shells were collected on two occasions.

No increase in food size was noted as the young grew larger at either nest. The caterpillars taken often had their heads snipped off and were occasionally torn in two. Nevertheless, the mean length of individual food items collected at the titmouse nest (35 mm.) was about double that of the items collected at the chickadee nest (17.6 mm.). These two means are based on actual measurements of all items collected without any attempt to estimate the sizes of individuals before they were torn apart. The difference between the two means is highly significant ($P < 0.001$).

It would not be justifiable to draw conclusions on the basis of the collections from these two nests. It was

TABLE 20

FOOD COLLECTED AT TITMOUSE NEST TP6B

Order	Family	No. Collected	% Total
Lepidoptera 92 %	Noctuidae	16	64
	Sphingidae	3	12
	Nymphalidae	2	8
	Satyridae	1	4
	Libytheidae	1	4
Coleoptera 4 %	Carabidae	1	4
Araneida 4 %	Oxyopidae	1	4

Additional - Small pieces of old land snail shell--
2 occasions

Spider egg sac - 1 occasion

obvious, however, even through a spotting telescope, that food brought to the observed titmouse nests was generally larger than that brought to the chickadee nests which had been similarly observed.

Water. Both species obtained water principally from natural cavities in the stems of living trees. These cavities held water for long periods of time, and birds of both species were observed drinking from the same "favorite" cavities throughout the year. They were also occasionally observed drinking or bathing in small ground pools or potholes.

CHAPTER V

DISCUSSION

The fact that the Carolina Chickadee and Tufted Titmouse coexist in a stabilized sympatric association over much of their range indicates that they are ecologically compatible. MacArthur (1958) suggests that such associations exist only where interspecific differentiation results in each species limiting its own population growth more than it limits the population growth of the other species. The results of the present study indicate a segregation of ecological niches between the two species which is the result of behavioral divergence.

The most obvious difference between members of the two species is the disparity in size. The weight of the Tufted Titmouse is approximately twice that of the Carolina Chickadee, and the size difference between these two species is the largest found among American Paridae (Dixon, 1961). The behavioral divergence which allows them to exist sympatrically seems to be based in large measure on this size difference.

Differentiation of foraging behavior has been found to be the major factor permitting different animal species to coexist in the same environment (Lack, 1954). Food becomes a critical factor during the winter months because of the short period of daylight and the cold temperatures. Also, the food supply probably diminishes as winter progresses because it is not replaced as it is eaten. The size of the populations of both species diminished progressively during the winter. Throughout this critical period the foraging zones of the two species were segregated more widely than at any other period in the year. The Titmouse foraged primarily in leaf litter on the ground while the chickadee foraged principally on bark surfaces.

During the growing season, when insect food was abundant, both the chickadee and titmouse foraged on leaf surfaces. The smaller and more agile chickadee appeared to take smaller food items and to glean them from the leaves of smaller twigs and branchlets than the titmouse. The segregation of foraging zones was less clear-cut during this period but interspecific competition appeared to be minimal as evidenced by the lack of mutually exclusive breeding territories.

Although members of both species nest and roost in tree cavities, no interspecific competition was observed for nest- or roost-sites because the two species chose different sized cavities. The disparity in body size appears to be partially responsible for the difference in cavity selection.

The vocalizations of the two species, while very similar in some respects, are sufficiently distinct to be distinguished by an observer. Species and sex recognition by members of both species seemed to be made on the basis of vocalizations. They responded to each others calls during the winter but no interference was noted during the breeding season and in no instance was interspecific territorialism observed.

The data on winter roosting times indicate that the titmouse goes to roost earlier and leaves the roost later throughout the winter than the chickadee. This too may be the result of the size difference between the two species. The titmouse being the larger bird would lose heat less rapidly through the day and during the long cold night, and would therefore not require as long a feeding period during the day.

CHAPTER VI

SUMMARY

The purpose of the study was to determine how the Carolina Chickadee and Tufted Titmouse have diverged behaviorally and how this behavioral divergence is ecologically adaptive in permitting them to coexist in a stabilized sympatric association. Special attention was given to activities where interspecific competition could occur, such as in foraging and roost-site and nest-site selection, and in activities where similarities in behavior could lead to interference, such as in vocalizations and postures.

The study area, known as the Oliver Wildlife Preserve, is located on the southern edge of Norman, Oklahoma, on the fourth and highest level of the South Canadian River Floodplain. This green ash forest is approximately 63 acres in size.

The study was conducted from 1968 to 1970 and included two complete annual cycles. Over 1200 hours were spent in the field during the course of the study.

The study area was staked out in quadrats one acre in size. The movements of flocks and individuals were plotted on maps of the area as were roost-sites, nest-sites, territorial boundaries, etc.

Seven small feeders were positioned throughout the study area. These were filled only a few days each month. Birds were netted as they came to feed and were then color banded. The feeders were so constructed that only one bird at a time could feed. The social hierarchy of winter flocks was determined by recording the outcome of encounters between individuals at the feeders.

The foraging zones utilized by each species were quantified by observing individuals in the act of foraging and timing their activities in specific zones. In this manner, samples of the length of time each species was observed foraging in certain zones were collected. Records were also kept of the vegetation being foraged. Twelve specific zones were recognized. Because of changes in foraging behavior, data collected during the growing season was treated separately from that collected during the nongrowing season. Food brought to the nest by adult birds was collected by collaring the nestlings. No birds were collected for stomach analysis.

Roost-site and nest-site selection by the two species were compared by noting the size, height, type, position, etc., of cavities selected by individual birds of both species.

The two species nested simultaneously. The titmice chose significantly larger and higher nest cavities than the chickadees, and chose primarily natural cavities. The chickadees chose primarily small woodpecker cavities, such as a Downy Woodpecker makes. No interspecific territorialism was noted between the two species. The male of both species took the lead in nest-site selection. The female alone excavated, constructed the nest, and incubated.

The fledging order of Tufted Titmice young followed their size order. The largest fledged first followed by the next largest, etc. The relative social standing of the siblings appeared to follow the same order.

During the late summer the two species formed mixed flocks which were remarkably cohesive social units. The leader of the mixed flock was the alpha titmouse (male). Individuals of the two species responded to each others calls, and the flock moved as a unit. Once formed, the individual composition of a flock was stable. The flocks decreased in size throughout the winter, however, as individuals disappeared (presumably winter casualties).

Titmice were always dominant over chickadees, males were usually dominant over females (intraspecifically), and mature birds dominated immature birds. The resident male was the alpha individual of his species in what was essentially a unilateral hierarchy.

The male-female standing was reversed during the early stages of nesting, and the females' behavior dominated the males'. During the last week of nest life the male gradually reasserted his dominance over the female.

Breeding territories for both species ranged from 6-10 acres in size, and the territories of the two species were superimposed. Territorial defense reached a peak during nest-building and declined thereafter. The area utilized by the pair also decreased following nest-building causing neighboring territories to shrink away from each other.

One of the primary functions of the large territory is to prevent interference between the activities of neighboring pairs. This is essential because the birds of both species respond to the calls of any member of their species or to crude imitations of their specific calls. Therefore, unless insulated from the calls of neighboring pairs, the members of a pair would have difficulty coordinating their separate activities, and the success of the nest would be in jeopardy. The large territory defended during nest-building and the shrinking of the utilized area thereafter provide this insulation.

The resident male titmouse remained within the boundaries of his previous breeding territory throughout the winter. Since he was its leader, the mixed flock also traveled within these boundaries. The meeting of two flocks was accompanied by increased vocalizations and by chasing and supplanting attacks. Prior to the breeding season, the alpha male of both species chased all subordinate birds but his mate from the area of the winter range and members of the two species began to ignore each others calls.

The breeding season territory had essentially the same boundaries as the winter range. No division of the winter range into breeding territories was observed. Because his dominance was well established, this period was not characterized by long chases or fighting. The next phase, during which neighboring pairs delineated their common boundaries, was marked with long vocal duels, chasing, supplanting attacks, and occasional fighting.

During the nongrowing season, the two species foraged in widely separated zones of the environment. The titmouse foraged primarily in leaf litter while the chickadee foraged primarily on bark surfaces.

During the growing season, both species foraged on leaf surfaces. Some overlap was noted in the major foraging zones utilized by the two species during the growing season, but it is thought that the two species took different food. Food items collected at nests of both species showed the major food item to be Lepidoptera larvae. Items collected at titmouse nests were significantly larger than those collected at chickadee nests and were of different families.

No competition for roost-sites was noted between the two species. Birds of both species roosted in tree cavities during the nonbreeding season, but the cavities chosen by titmice were significantly larger than those chosen by chickadees. Titmice chose natural decay cavities or large woodpecker cavities such as a Red-bellied Woodpecker makes. Chickadees chose smaller natural cavities or small woodpecker cavities such as a Downy Woodpecker makes.

APPENDIX

Plate I

Top. The study area as it appears from the south, beyond an open field. May 20, 1970.

Bottom. The study area as it appears from the north. May 20, 1970.

Plate II

Top. Southwestern portion of the study area. Note the dense sapling growth. May 20, 1970.

Bottom. The study area as seen from the east in summer. June 15, 1969.

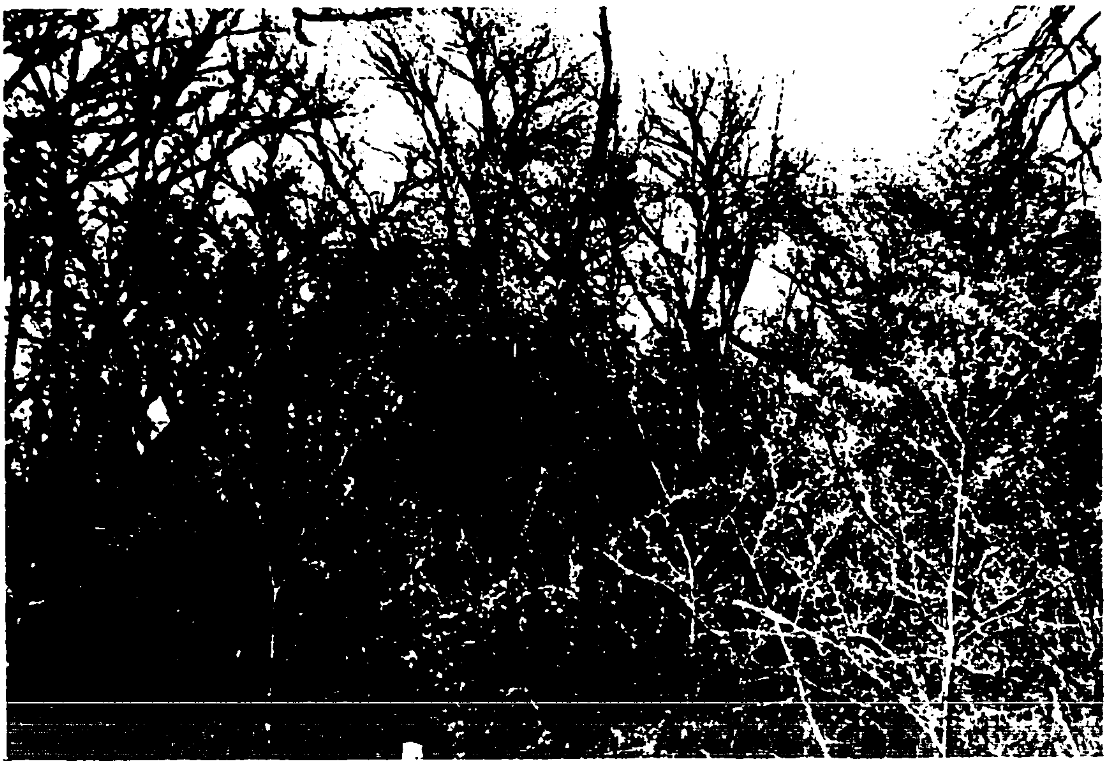


Plate III

Top. A typical titmouse nest cavity (TP2A). Note the large opening size.

Bottom. A typical chickadee nest cavity (CP14A). Note the small size of the opening in relation to the female inside.

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