THE INFLUENCE OF MAN-MADE ENVIRONMENTAL CHANGES ON THE BEHAVIOR, SOCIAL STRUCTURE, AND ECOLOGY OF MIXED GROUPS OF TUFTED TITMICE AND CAROLINA CHICKADEES

By

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PREFACE

The objectives of this study on the Carolina Chickadee, Parus carolinensis, and the Tufted Titmouse, Parus bicolor, were as follows: (1) to identify and measure differences in habitat due to the human presence; (2) to identify and measure differences in niche partitioning between the two species attributable to human influences; (3) to identify differences in the mixed flock structure due to human influences; and (4) to identify differences in the behavioral interactions of the two species and their relationship to human influences.

I am indebted to Dr. R. J. Miller who served as major adviser and provided assistance, encouragement, and much patience. I am also indebted to Drs. H. C. Miller, M. R. Curd, L. T. Brown, J. S. Barclay, and F. L. Knopf who served on the advisory committee at one time or another.

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CHAPTER I

INTRODUCTION

Field studies on the ecology and ethology of animal species have traditionally been conducted in the natural wild environment. Until recently wildlife studies were not considered to have any place inside the city limits (Howard, 1974). Lately, however, a growing concern with the quality of urban environments has brought about a change in attitude toward city wildlife. It has become apparent that there is a need for studies of wildlife species in urban and suburban habitats (Allen, 1974).

Many bird species are among the most actively studied urban wildlife populations (Cauley, 1974; Geis, 1974). Birds are not only highly visible and very common in populated areas, but they are also very desirable from the city dweller's point of view (Dagg, 1974). In Oklahoma, two species found in suburban areas are the Carolina Chickadee, Parus carolinensis, and the Tufted Titmouse, Parus bicolor. Both species are resident throughout the state year round and are present in both suburban and rural habitats. The behavior and ecology of these two species have been extensively investigated, primarily in rural environments (Bent, 1946; Dixon, 1963; Wallace, 1970).

Both the chickadee and titmouse are flocking birds that spend most of their lives in one small area of woodland once they become part of a

flock. Young birds disperse two to three weeks after fledging. During the following summer through winter, the survivors begin to attach themselves to resident flocks. These flocks are usually composed of breeding pairs and a few unmated birds. Chickadees and titmice associate with each other in a stable mixed flock formation. Other species of birds are sometimes observed flocking with these birds, but these associations are of short duration. Both species spend most of the fall and winter in mixed flocks of three to eight birds. Except for mortality and the occasional attachment of new individuals, the flock is composed of the same individuals throughout this time. The mixed flock restricts its movements to a specific area which typically includes all or part of the breeding territories used by the breeding individuals of the flock. Within each flock titmice are dominant over chickadees; males are dominant over females; and adults are dominant over juveniles. There is one alpha male titmouse and one alpha male chickadee. The mixed flock is often led by the dominant titmouse (Gillespie, 1930; Nice, 1933; Laskey, 1957; Dixon, 1963; Condee, 1970; Curry, 1970).

The mixed flock begins to break up in late winter and early spring as the flock pairs begin their reproductive cycle. Titmice and chickadees both tend to remate each year with the mate of the previous year. Once a pair has mated they tend to associate with each other throughout the year unless one of the pair dies. Both species nest in tree cavities and defend a breeding territory around the nest site from the time of nest site selection until the young fledge. The birds restrict most of their activities, including foraging, to the breeding territory during this time. The female does most of the nest building and all the

brooding. The male defends the territory (and later the young) and feeds the brooding female (Pielou, 1957; Brewer, 1961; Dixon, 1963).

Both chickadees and titmice eat a combination of animal and vegetable matter. They are capable of utilizing large food particles because of their ability to peck and batter them into smaller pieces. They both glean the leaf, bark, and twig surfaces of trees for insects and other invertebrates. They break open buds and stems to get at insect food. They both utilize the seeds and berries of a wide variety of plant species. They readily use feeders (Bent, 1946; Curry, 1970).

Observations of these birds made in populated habitats were not concerned with the effect of human populations upon avian populations. Contrasting the behavior and ecology of titmice and chickadees in the suburban Stillwater environment with the rural environment of the Oliver Wildlife Preserve in Norman, Oklahoma, in which Curry (1970) worked is valuable for several reasons. In a theoretical sense most major differences found in the behavior and ecology of different populations of these intimately related species (found in close association most of the year) could be attributed to differences in resource availability and patterning. The primary objective of this study was to conduct field observations on the activities of the Carolina Chickadee and Tufted Titmouse in a suburban area of Stillwater, Oklahoma, in order to identify differences in the behavior and ecology of these birds that might be due to differences between a human modified environment and Curry's more natural environment. This is an attempt to broaden the understanding of the types of ecological variables that influence and are influenced by social activities of Carolina Chickadees and Tufted Titmice. More specifically the

objectives include: (1) identifying and measuring as precisely as possible differences in the habitat due to the human presence; (2) identifying and measuring differences in niche partitioning between the two species attributable to human influences; (3) identifying differences in the mixed flock structure due to human influences; and (4) identifying differences in the behavioral interactions of the two species and their relationship to human influences.

CHAPTER II

METHODS AND MATERIALS

To accomplish the objectives of this study, breeding success, flock size, mortality, nest site selection, foraging zone partitioning, and vegetational differences between the suburban and natural areas were measured and compared when possible. Interactions among individuals, pairs, families, and flocks were closely observed with special attention to changes in dominance.

Regular observations began during the summer of 1974 and ended the summer of 1977, although sporadic observations continued through the first week of January, 1978. Over 1000 hours were spent observing and banding birds. Banding and most feeder observations took place at the Miller residence. The Miller residence was located in the center of one mixed chickadee-titmouse flock range. Most observations involved the Miller flock. Visits to the study area typically occurred on an average of twice weekly. During the breeding season, they occurred on a daily basis. During late fall they occurred weekly. Most observation periods were during the morning, although observations also were taken during the afternoon. Periodically observations were taken before dawn and at dusk as the birds were awakening and roosting. Occasionally birds were followed from the time of awakening until the time of roosting. Approximately one half of the observation days were

spent watching the Miller feeding station and one half spent observing in the field away from the feeders.

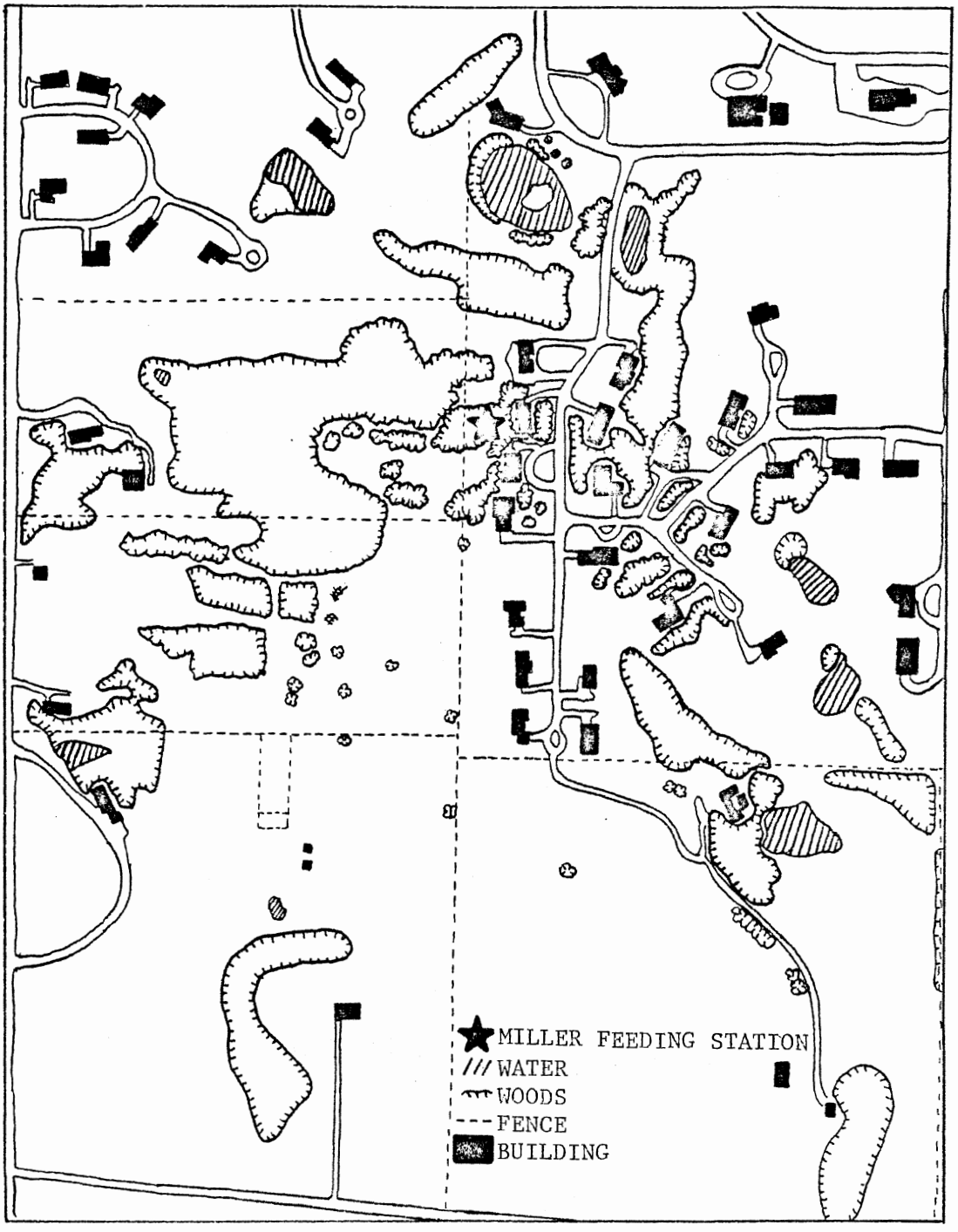
Description of Study Area

The study area consists of approximately 75 hectares of suburban development in southwestern Stillwater, Oklahoma, composed of mixed Blackjack Oak and Red Cedar scrub forest interspersed with and surrounded by open pastures and lawns. The wooded sections are primarily in the northern and eastern part of the study area, which also contains the greatest residential density (Figure 1). Scattered throughout the area are nine permanent man-made ponds. Bird feeders and nest boxes were also present throughout the area.

Habitat Evaluation

The density of the trees around each year's used and available but unused nest sites were measured using the method described by Brewer (1963). Brewer measured the diameter at breast height (DBH) of all trees within a 15 ft. radius of the nest and calculated the mean number of trees per acre around each nest. He calculated the density of all trees and the density of trees with a DBH of more than 2.9 in. These densities were also calculated for seemingly suitable but unused nest sites. Brewer ignored the herbaceous vegetation since most of it had not sprouted at the time of nest site selection. For this study, the same method was used, but additional data were taken and analyzed. Species diversity was calculated using all woody vegetation within the 15 ft. radius of the potential nest site. The total number of woody stems per acre were counted for each site as well as the number of

Figure 1. Map of study area.


MILLER FEEDING STATION
WATER
WOODS
FENCE
BUILDING

trees with a DBH of more than 2.9 in. A multivariate analysis was used to evaluate density, species diversity, and average DBH as they were related to the area around each used and unused nest site in the Stillwater study area.

Besides the vegetational data, the number of times each nest site was actually used was counted and related to the number of times it was available for use during the three years of the study. Around each potential and actual nest site three circles of approximately 30 m, 60 m, and 90 m radius were drawn on a map of the study area. The smallest radius was decided upon by measuring the shortest distance between any two simultaneously used nest sites (in this case, chickadee nests) and dividing by two. The number of nest sites used by chickadees, the number of nest sites used by titmice, the number of sites suitable for only chickadees but unused (UNC), and the number of sites suitable for both species but unused (UNB) were determined within each concentric circle for each year. Suitability was determined by the size of the cavity opening. Chickadees are able to use cavities with smaller openings than titmice can utilize. Most nest sites, used or unused, were nest boxes specifically designed for birds of various sizes. Most of the natural cavities included in the count were old nesting cavities excavated by woodpeckers and obviously suitable for use by either chickadees or titmice. Multivariate analysis was used to analyze the number of sites of each catagory present within each radius around used and potential nest sites.

During this study the point-centered quarter method (Cox, 1972), was run along randomly selected transects in the Oliver Wildlife Preserve and the Stillwater suburban observation area. Total

density, relative density, absolute density, species diversity, relative frequency, and importance values were calculated for trees/saplings in each area.

Behavioral Observations

Mist nets were set up in the study area adjacent to the Miller bird feeders. Captured birds were banded with colored plastic coil leg bands as well as standard metal bands. Through the use of different color combinations, each individual chickadee and titmouse was distinctively marked. This made it possible to follow and record the interactions between individuals and groups of individuals.

By following behavioral interactions throughout the year, it was possible to detect social patterns within the flocks. Dominance was determined by using Dixon's (1965) criteria for the Mountain Chickadee. These are the same criteria Curry (1970) used and consist of the following:

1. Supplanting attacks in which one individual displaced another from the feeder or its perch.
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.
5. Obvious waiting by one individual until another had taken a seed and left (p. 71).

A map was made from an aerial photograph of the study area. A copy was used during each observational session to record individual sightings of the birds and their movements, territory sizes and locations, nest sites, and differential use of the area by the birds.

Data on foraging zones used by each species were taken following Stallcup's (1968) method. Whenever a foraging bird was encountered, the time it spent using a particular vegetational strata was timed and recorded. Sightings were recorded only for adults or juveniles that were feeding independently of their parents. Observations taken at feeders were not included in this analysis. The following classification of foraging zones was used by Curry (1970) and in this study to categorize the vegetational strata in which the birds were sighted:

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 (p. 105).

The data accumulated was divided, as in Curry's study, into sightings taken in April through October (the growing season) and sightings taken in November through March (the nongrowing season). The data from each season was analyzed separately using the X^2 Test for Independence to locate differences between the seasonal foraging zones used by Carolina Chickadees and Tufted Titmice. Due to the small number of observations, category 4 was combined with category 5a for the purpose of calculation. An X^2 Test was also used to compare the number of observations made of individual banded birds in the field with those

made at the Miller feeders. The observations were tallied only for birds in the resident Miller flock and were divided into three month periods beginning with January, 1975. The Sign Test was used to assess sexual differences in the longevity of mated pairs.

Information was gathered about the human population as it affected the avian population. It included the amount of winter feeding by humans, the number of nest boxes provided for each species, the number of cats and dogs in the area, restraints put on pets, and the type of insecticides used in the area.

CHAPTER III

DOMINANCE

Dixon (1963) found that in Carolina Chickadee flocks the male with the longest residency was the alpha male. Some beta males had longer residency than other more subordinate members of their flocks. He thus related dominance to seniority and breeding season territoriality. Curry (1970) also found a relationship between dominance and the length of residency. He also found that the winter flock territories were used as breeding territories by the alpha but not the beta pairs, and this relationship existed in both the Carolina Chickadees and Tufted Titmice.

During the course of the present study the alpha position among both chickadees and titmice in the Miller flock passed from one male to another. The alpha male chickdee, C14, at the beginning of the study was banded 20 December 1974. His mate-to-be, C10, was banded 15 December 1974. It was not until 18 February 1975 that they were observed feeding and moving about together. During the winter C14 was banded, he was observed supplanting other chickadees. One of them, the beta male C13, was observed waiting for C14 to leave a feeder before using it himself. C10 was observed joining C14 at feeders several times without any aggressive interaction occurring.

In the spring of 1975, C14 and C10 produced a brood which was killed by a hailstorm the day after fledging. The adults survived,

although later during May, C14 injured his leg and continued to favor it for the duration of the study. The middle claw on his left foot was found to be missing and a scar was present above the colored leg bands. The injury did not appear to affect his aggressive behavior. Throughout the rest of 1975 and early 1976, C14 continued to supplant and displace other chickadees in the winter flock both at the feeders and in the field. His mate continued to accompany him without overt aggression between them, although she often waited for him to use a feeder first. C10 did not appear to gain any status as mate of the alpha male and was chased more often than she chased. Dixon (1963) found that the mates of the alpha males he studied ranked second in the flock when their mates were present. Curry (1970) did not find this to be true of the birds he studied, nor was it true of the females in this study.

The future alpha male, C45, was banded on 18 February 1976. Later that month C14 was observed to wait for C45 to leave a feeder before approaching. However, C45 was also observed to leave a feeder when C14 flew to it. Beta male C13 was observed chasing C45 later in the spring. This occurred in C13's breeding territory. Male C14, female C10, and male C45 were observed foraging together throughout the spring until C14 and C10 set up their breeding territory. The alpha pair nested in a different nest box in 1976. After eight eggs were laid in April, the pair abandoned the nest due to the appearance of a wasp which proceeded to use the box for its own nest. The pair did not attempt to renest, although C10 was observed to give the courtship begging call 19 May in the presence of C45. C10, C45, and C14 were frequently seen foraging together the rest of the summer until C10

disappeared after 23 July. There were no aggressive encounters observed between the three birds.

Female C61, the future mate of C45, was banded as a juvenile 25 June 1976. During the following fall and winter, C61 and C45 began associating with each other. It was also during this period C45 began actively asserting his dominance by supplanting and chasing the other chickadees of the flock. Former alpha C14 was still present in the flock territory, but he was sighted only rarely until the end of the study. Chickadees 45 and 61 nested in 1977 in a nest box in what had formerly been the eastern part of the breeding territory of C14 and C10. The western part of this former territory was used by female chickadee 68 and her unbanded mate. They nested in the same box that C10 and C14 had used in 1975. They transferred to this box after the box in which they built their first nest blew down.

The beta male chickadee 13 was present throughout the entire study. He and his mate, C9, successfully raised broods in 1975 and 1976. In 1977, C9 disappeared after laying seven eggs. C13 did not remate that spring. The same nest box was used all three years. Dixon (1963) found that beta males often advanced into the alpha position after the alpha male disappeared. In this study the alpha male was replaced by a younger male who first associated with the older male before assuming the alpha position. The beta male, although having greater seniority, did not become the flock's dominant male. In this case the beta male and his mate avoided confrontations with the first alpha male by not utilizing the same site at the same time as the alpha male. This avoidance continued with C45 and his mate after C45 became dominant.

A similar change in dominance occurred among the titmice. Titmouse 1 was the dominant male titmouse at the beginning of the study, as confirmed by his success in supplanting other titmice at the feeders. In 1975 he and his mate, T2, successfully raised a brood with the help of another titmouse of unknown sex, T3. T3 disappeared the following July. In 1976 T1 and T2 nested in the same nest box used in 1975. However, T2 was found dead in the nest box before the clutch was completed. T1 did not remate that year, although in the summer of 1976 he began to associate with female T15 who had been banded 5 December 1975. T1 and T15 were observed several times using the same feeder without conflict.

T15's mate-to-be, T17, was banded as a juvenile 23 August 1976. The following fall T15 was seen with T1 and T17 although not without incident. T1 was observed displacing T17. Both female T15 and male T17 were observed displacing each other on occasion.

In early spring T15 and T17 began spending more time together while T1 was most often seen alone. T1 did not mate and was last seen 16 April 1977. T15 and T17 mated and used the nest box previously used by T1 and his mate.

In this study both the Carolina Chickadee and Tufted Titmouse alpha males were less assertive after losing their mates. Their apparent loss of dominance did not seem to be associated with actual defeats during aggressive encounters with other chickadees and titmice but more with a decreased assertion of dominance. In both species the first alpha male gradually began to spend more time alone. Both C14 and T1 were sighted less and less often both at the feeders and in the field. No aggression by other flock members was observed to be directed toward these males, so their isolation was not obviously the result of direct

supplanting attacks or chase. In both species the male that later became the new alpha bird first associated with the existing alpha and/or their female companion. Unlike the beta chickadee, the alpha-to-be chickadee did not avoid the alpha chickadee but was often observed foraging with the alpha. This was also true of the Tufted Titmice. There seemed to be little aggression between the alpha and his replacement, although the titmouse interactions were not clear. In contrast to the waning aggression of the old alphas, the new alphas became more and more aggressive toward other flock members. C45, in particular, was observed supplanting and chasing several chickadees the first summer after mating and replacing C14 as dominant. It should again be noted that the new alpha males were not males with the longest residency.

CHAPTER IV

TERRITORIES

Breeding Territories

The chickadee-titmouse winter flock tends to travel as a unit with the alpha titmouse as leader. Members of the chickadee-titmouse winter flock restrict their activity to a limited area and respect the same boundaries. Typically, in early March the alpha males begin chasing other flock members and interlopers from the area used by the winter flock. The alpha's and their mates use this area for nesting. This produces similar boundaries for the breeding territories of the alpha male titmouse and chickadee (Curry, 1970). The number of breeding pairs thus equals the number of winter flocks. Dixon (1963) noted, however, that alpha male chickadees may use only a portion of the flock's winter range for his breeding territory and the remaining portion may be taken by the beta male and his mate. The highest ranking subordinate usually obtains a nesting territory. In contrast to this Pielou (1957) states that Tufted Titmice nesting territories may not coincide at all with the winter range. Breeding patterns in the flock territory observed most intensively in this study (the Miller flock) differed from the above.

The following discussion of breeding territories is based on observations taken from March through May of each year. These include occassional boundary disputes involving a few chases but mainly calling.

In the spring of 1975 three pairs of chickadees nested within the winter territory of the mixed chickadee and titmouse Miller flock (Figure 2). Two pairs consisted of the alpha and beta birds and their mates, all of which were banded in December, 1974. A third pair renested after abandoning their first nest. The extent of their breeding territory is not known.

In 1976 three pairs of chickadees again used the Miller flock winter territory for breeding (Figure 3). These included the same alpha and beta pairs. The third pair consisted of birds banded in August of 1975. The male, C40, was a juvenile when banded and female C39 was of unknown age.

Of the four pairs of chickadees that nested in the flock winter territory in 1977 (Figure 4), only the beta pair were the same birds that used the area the two previous years. C40 was again present but mated to female C67. His 1976 mate, C39, was last sighted 24 January 1977. C67 was banded in August, 1976. The new alpha chickadee, C45, and his mate, C61, were banded in February and June, 1976, respectively. He was an adult and she was a juvenile at the time of banding. Only the female of the fourth pair, C68, was banded. She was caught November, 1976, and probably was young of the year. All the 1977 chickadee breeding territories were smaller than the breeding territories of the previous years.

In contrast to Carolina Chickadees, only the alpha pair of Tufted Titmice were found to nest each year within the mixed flock winter territory. The same nest box was used each year. In 1975 (Figure 5) the alpha pair was helped at the nest by an apparently unmated female (Davis, 1978). The following year the same alpha pair

Figure 2. Chickadee breeding territories for 1975, compiled from observations taken from March through May. No more than one sighting per bird is indicated at the Miller feeding station. No sightings at the nest are shown although all birds were sighted at their respective nests. Solid symbols indicate males. ● = C14; ○ = C10; ■ = C13; □ = C9; ▲ = C15; △ = C12; ★ = Miller flock nest sites; ☆ = abandoned nest site; ✚ = nest sites of pairs in other flocks.

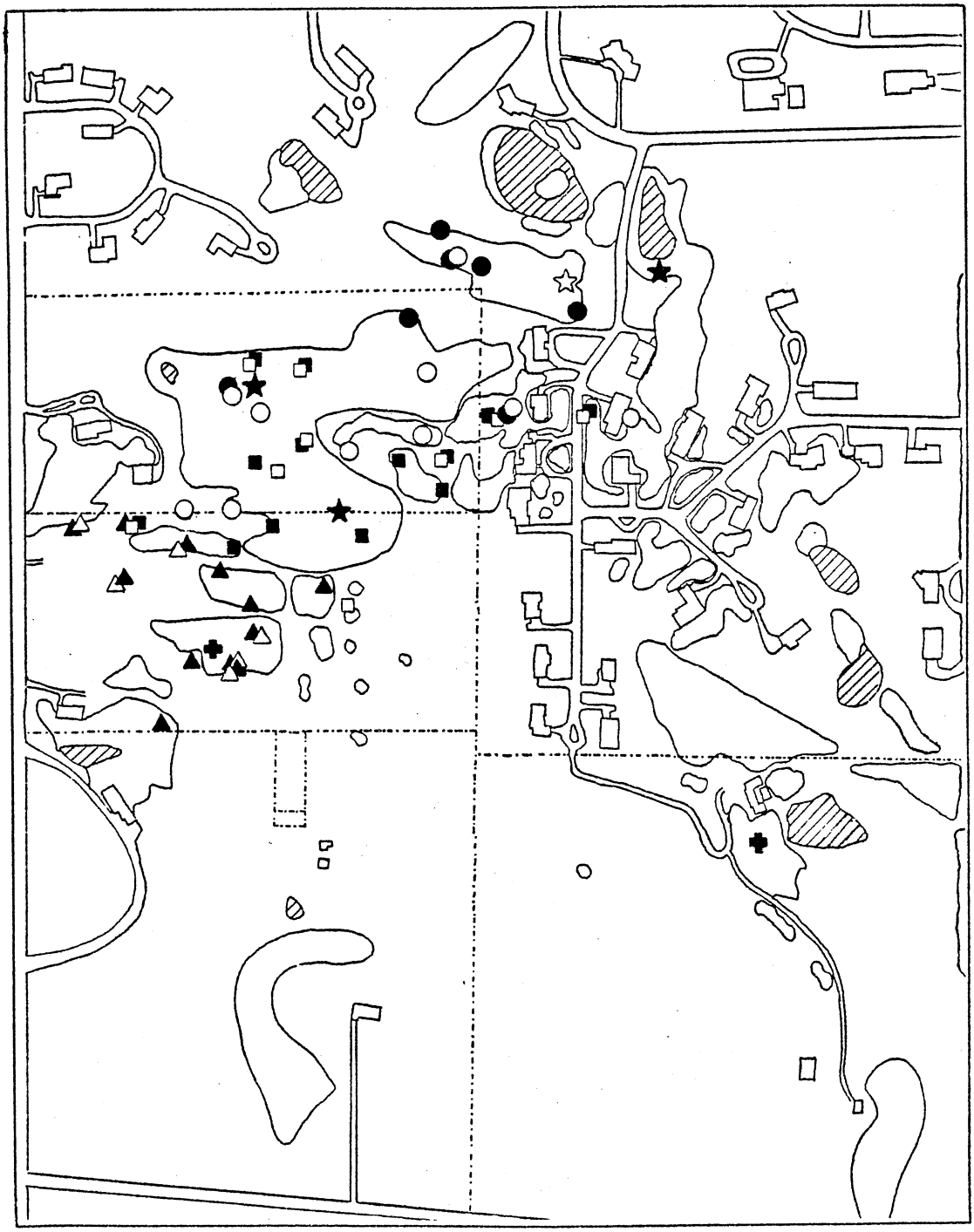
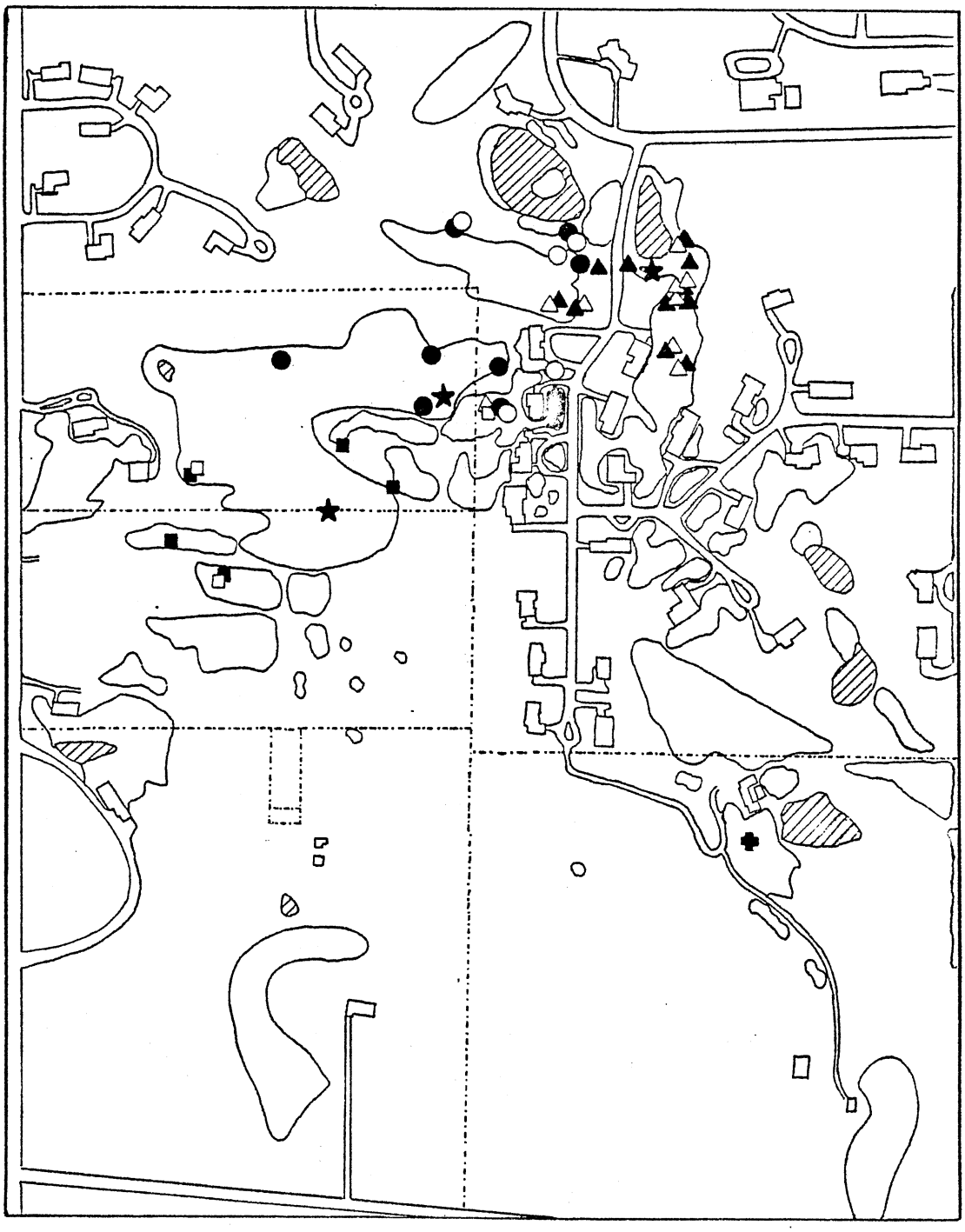


Figure 3. Chickadee breeding territories for 1976, compiled from observations taken from March through May. No more than one sighting per bird is indicated at the Miller feeding station. No sightings at the nest are shown although all birds were sighted at their respective nests. Solid symbols indicate males. ● = C14; ○ = C10; ■ = C13; □ = C9; ▲ = C40; △ = C39; ★ = Miller flock nest sites; ✤ = nest sites of pairs in other flocks.



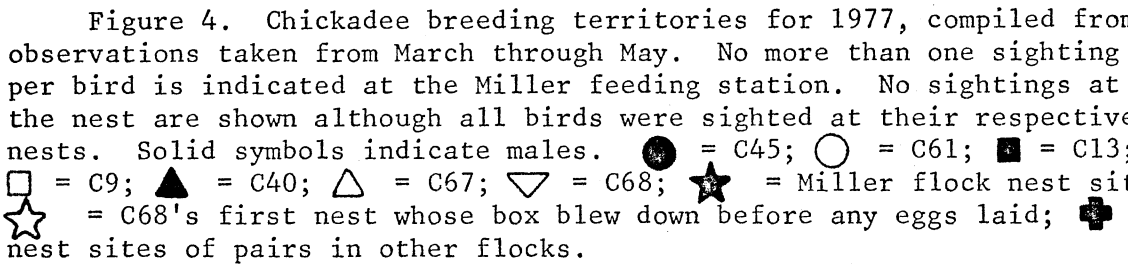


Figure 4. Chickadee breeding territories for 1977, compiled from observations taken from March through May. No more than one sighting per bird is indicated at the Miller feeding station. No sightings at the nest are shown although all birds were sighted at their respective nests. Solid symbols indicate males. ● = C45; ○ = C61; ■ = C13; □ = C9; ▲ = C40; △ = C67; ▽ = C68; ★ = Miller flock nest sites; ☆ = C68's first nest whose box blew down before any eggs laid; ✚ = nest sites of pairs in other flocks.

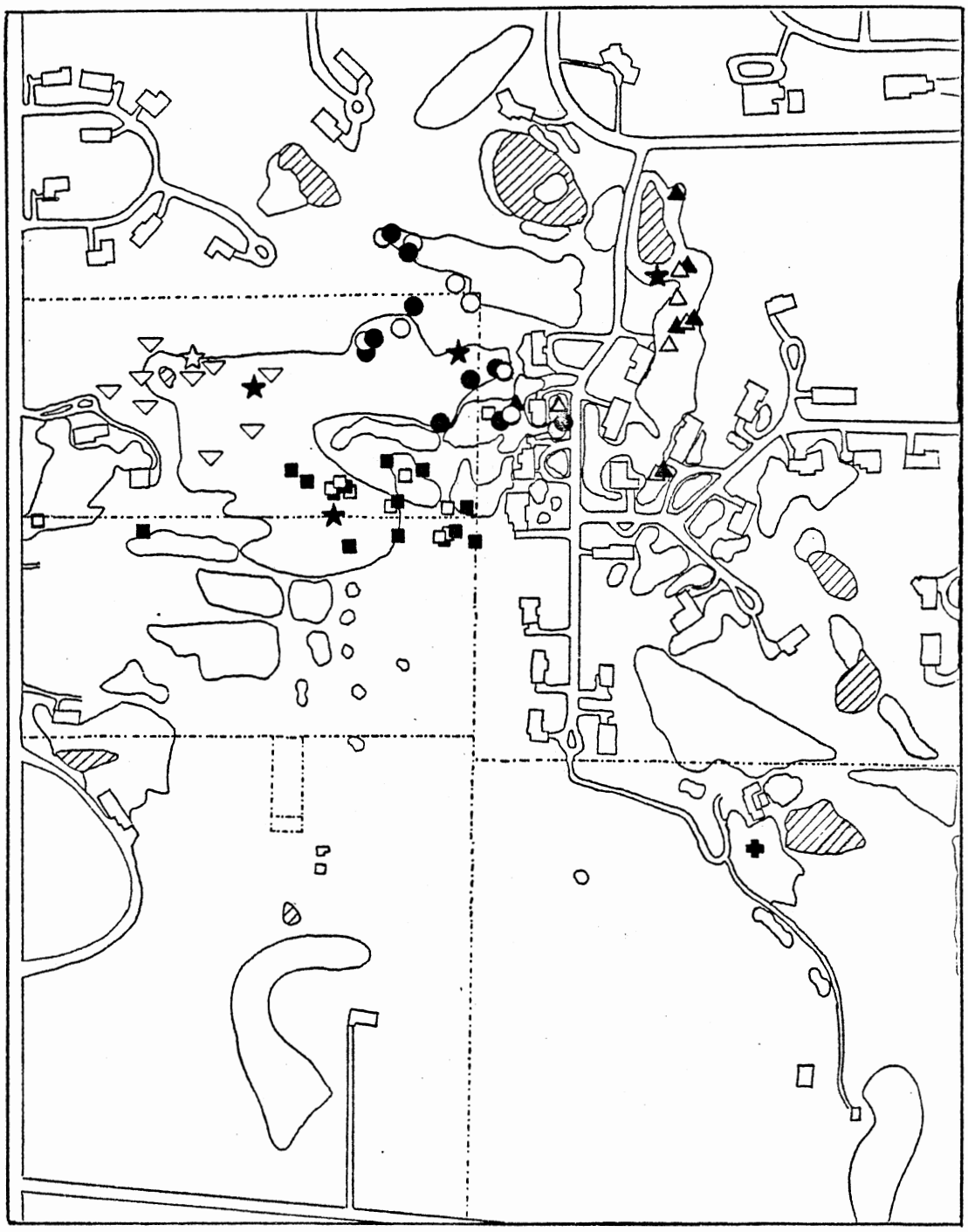
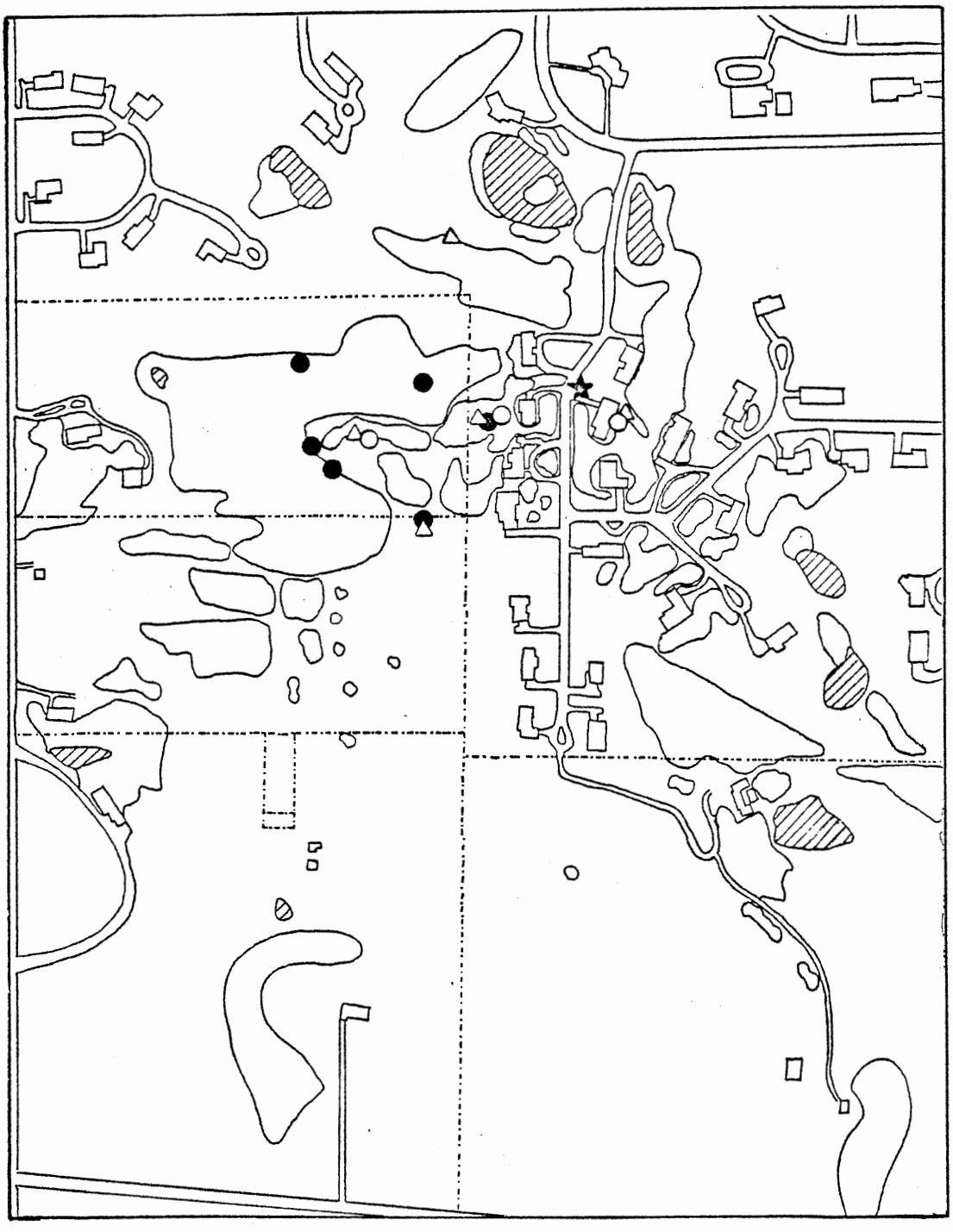


Figure 5. Titmouse breeding territory for 1975, compiled from observations taken from March through May. No more than one sighting per bird is indicated at the Miller feeding station. No sightings at the nest are shown although all the birds were seen at the nest box. The solid symbol indicates the male. ● = T1; ○ = T2; △ = T3, the helper of unknown sex; ★ = the nest box.



started the nesting cycle, but the female was found dead in the nest box after laying three eggs. The alpha male was never observed to remate, either that year or until he disappeared in April, 1977. Despite loss of the breeding pair, no other pair of titmice nested within that territory in 1976 (Figure 6). In spring of 1977 a new alpha male and his mate used the same nest box the previous alpha pair had utilized (Figure 7). Also in 1977 a titmouse pair from the neighboring western flock nexted in a natural cavity, probably a woodpecker hole, located in a zone of overlap between the two flocks. Situated in an area utilized by both winter flocks, this nest site was approximately 70 m from the nest box of the Miller alpha pair. The two nests were virtually isolated visually and acoustically.

Winter Territories

The Miller flock winter territory was bounded on the north, east, and south by relative open areas of housing and pasture lands. On the west and southeast where the habitat was more wooded, the Miller flock was bounded by two other titmouse-chickadee flocks. Flock boundaries were based on individual sightings and by interflock exchanges.

The alpha pairs of chickadees never restricted their year-round movements to their breeding territories but ranged throughout the flock's winter territory. The beta pair also ranged throughout the flock territory outside of the breeding season but they were seldom present at the same site simultaneously with the alpha pair. They were also more often seen near their nesting area than not. The other pairs that nested within the flock's winter territory tended to restrict year-round movements to the area in which they nested.

Figure 6. Titmouse breeding territory for 1976, compiled from observations taken from March through May. No more than one sighting per bird is indicated at the Miller feeding station. No sightings at the nest are shown although both birds were seen there. The solid symbol indicates the male. ● = T1; ○ = T2; ★ = nest site.

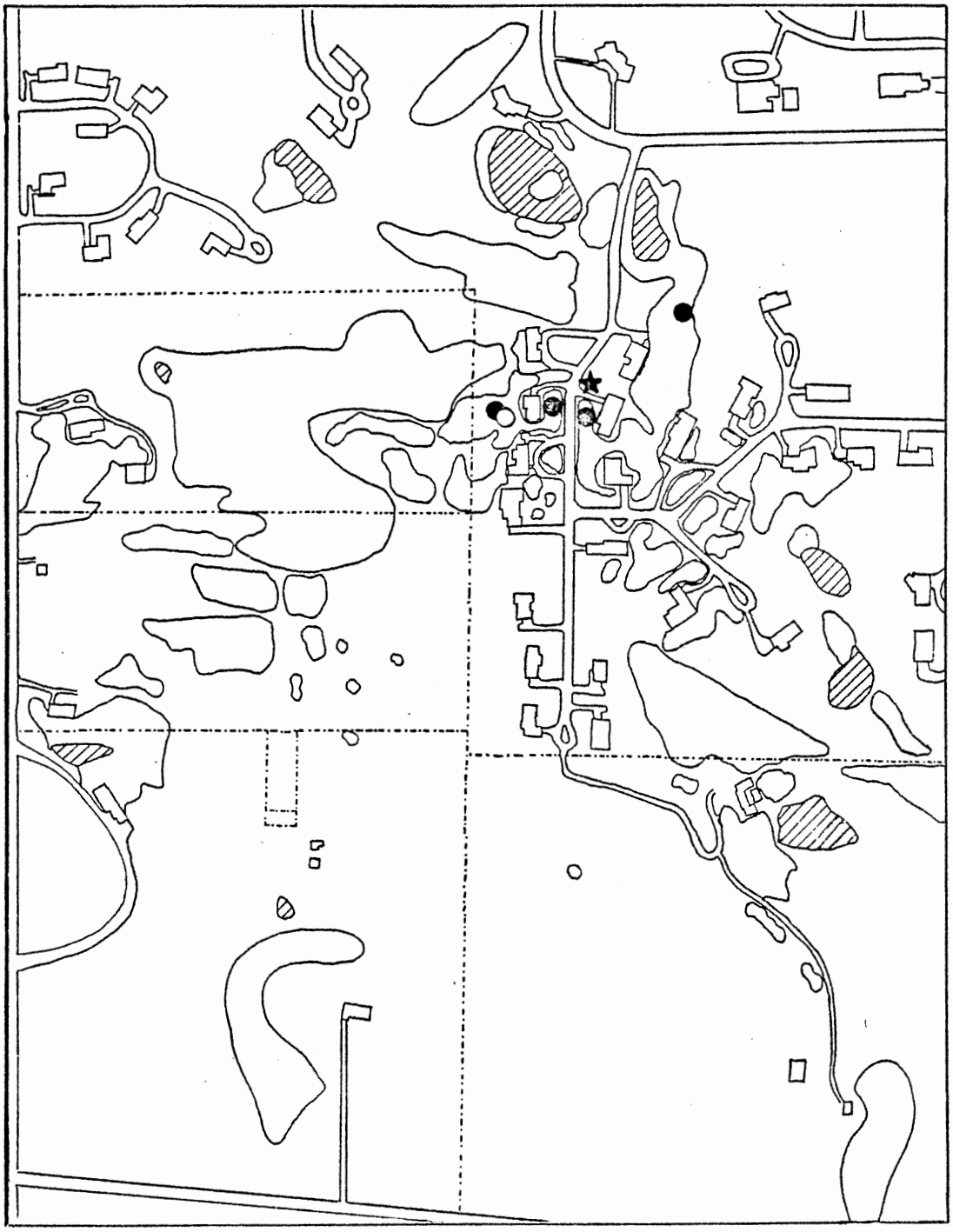
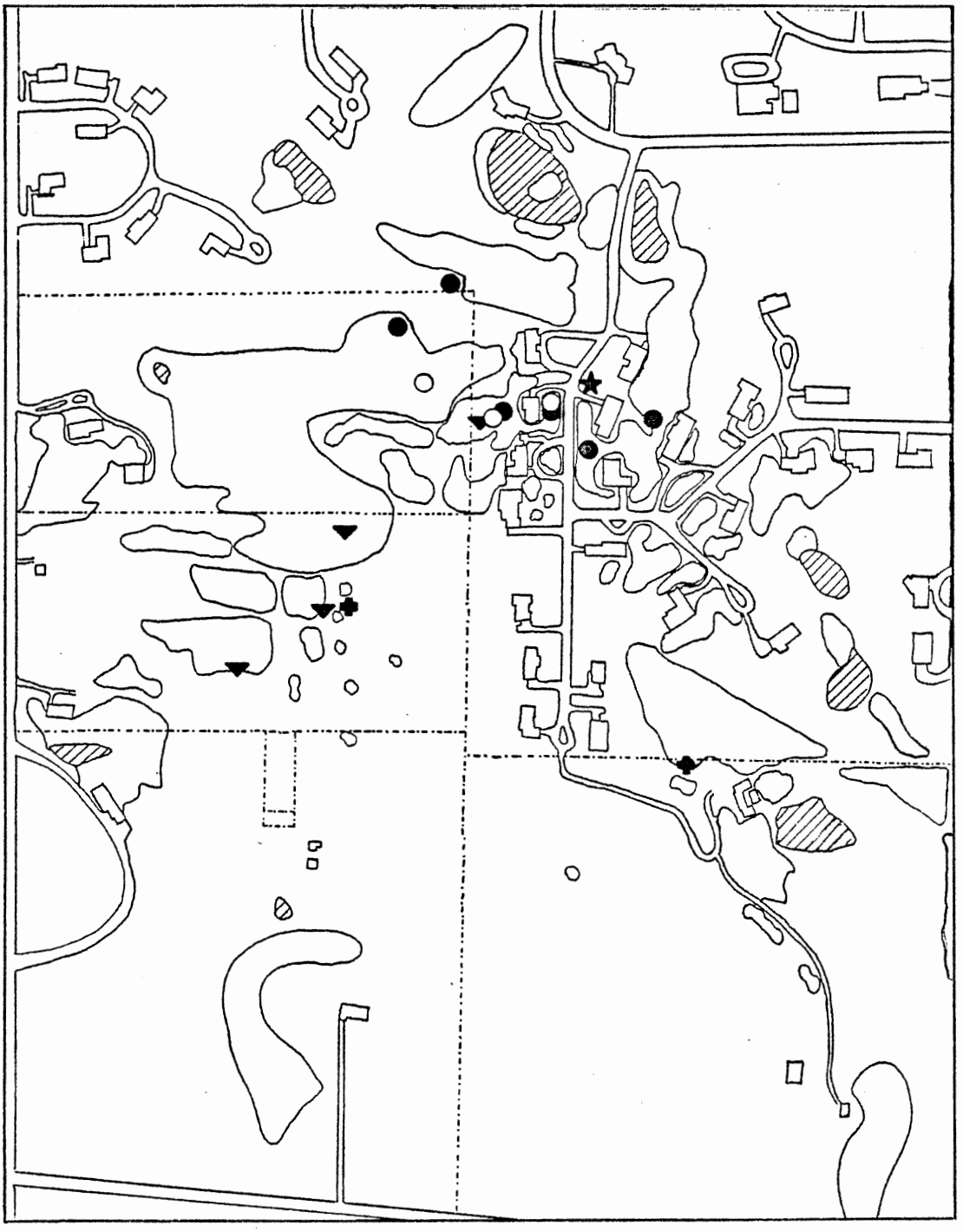


Figure 7. Titmouse breeding territories for 1977, compiled from observations taken from March through May. No more than one sighting per bird is indicated at the Miller feeding station. No sightings at the nests are shown although all the birds were seen at their respective nest sites. Solid symbols indicate the males. ● = T17; ○ = T15; ▼ = T21; ★ = nest box of Miller flock pair; ✚ = nest sites of pairs in other flocks.



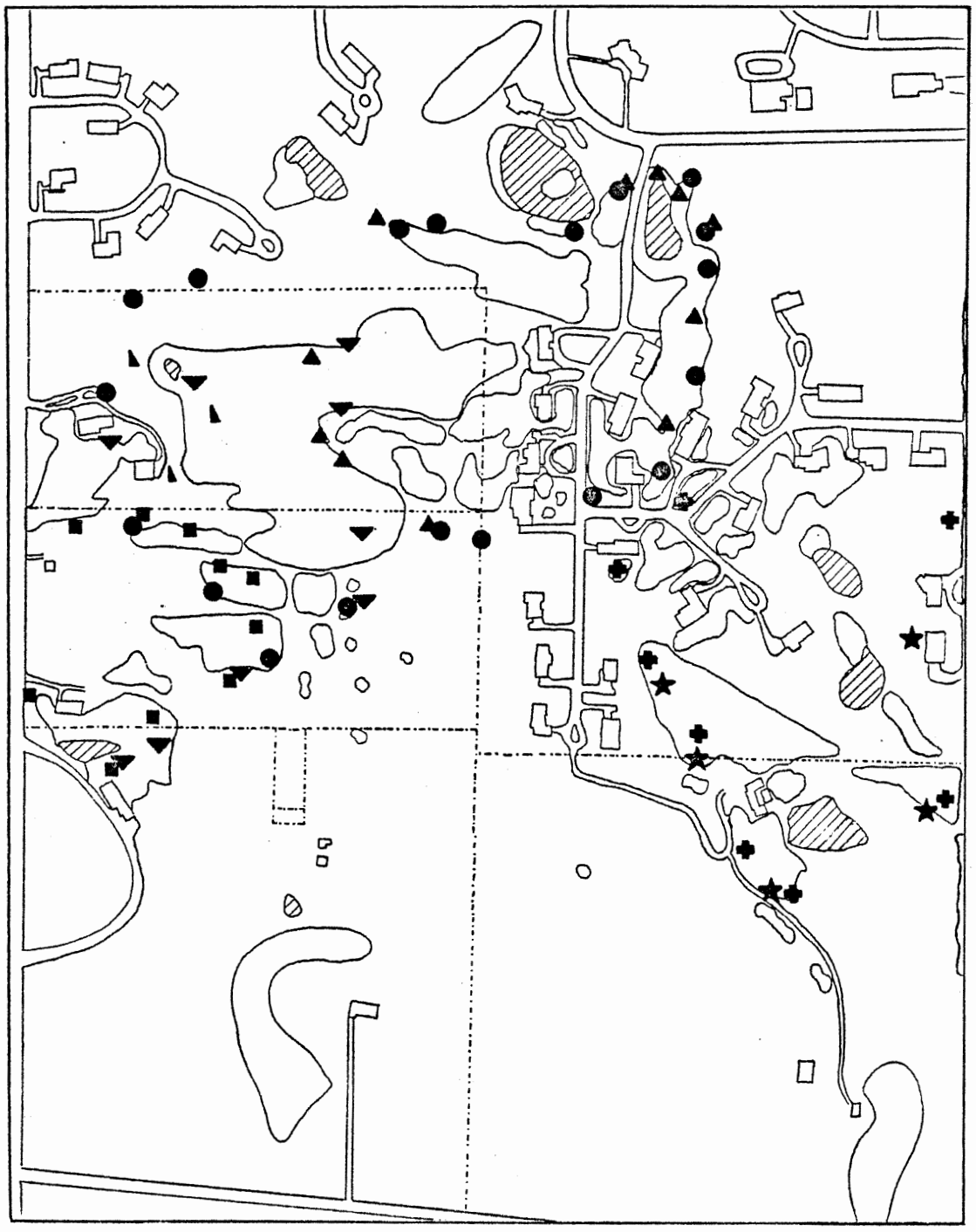
Unlike the alpha chickadee pair, the alpha titmouse pair tended to restrict their year-round movements to the eastern half of the mixed flock winter territory. This was the part of the territory they used during nesting. The Miller flock titmouse and chickadee winter territories did not precisely coincide (Figure 8). The other Miller titmice, primarily juveniles or unmated birds, utilized the western part of the mixed flock territory. However, this western area was also used by titmice from the adjacent western flock, often on their way to and from the Miller feeders. The presence of titmice from the western flock did not affect use of the area by the Miller flock chickadees.

Trespassing

Condee (1970) observed that the winter territories of clans of titmice may overlap and a mixed group of clans might be seen together, while Gillespie (1930) never observed overlapping of titmouse groups. She did observe groups wandering outside their usual territory, probably in order to forage at her banding station. Van Tyne (1948) suggested that titmice restricted to a territory are adults while those wandering during the winter are first year birds not yet settled. Condee (1970), however, observed two established titmice abandon the winter territory of one year and shift to a new winter territory the next year. The trespassing titmice observed in this study were adults that were present more than one year. They used the western overlap without shifting flock alliances.

Dixon (1963) observed that chickadee winter flock ranges do not overlap and all members of the flock observe the boundaries of what Dixon believes to be the enlarged winter territory of the dominant male

Figure 8. Flock boundaries during the study. Observations shown are only the outermost sightings of adult birds in each flock. Observations taken within these boundaries are not indicated, nor are observations of trespassing visits. ● = Miller flock chickadees; ▲ = Miller flock titmice; ◣ = observations of young titmice belonging to the Miller flock; ■ = western flock chickadees; ▼ = western flock titmice; ✚ = southeastern flock chickadees; ★ = southeastern flock titmice.



chickadee. Occasionally an entire flock may make brief excursions outside its range. When two flocks come together there may be vocal exchanges and perhaps actual skirmishes, usually between the alpha males and sometimes between their mates. When Curry (1970) observed interflock encounters, only titmice and chickadees of alpha or beta rank were involved in calling, chasing, and supplanting attacks. The outcome of such interflock skirmishes depended upon the location. The flock within its own range had the advantage. In this study no aggressive encounters between titmouse flocks were observed. All titmouse encounters took place at the feeders. On the other hand when chickadees of two flocks encountered each other near the boundaries between flock territories there were sharp aggressive encounters including calling, chasing, and supplanting attacks. Both flocks would then retire into their own territories. There was little overlap between the flock territories of the Miller chickadees and the chickadees of the two adjacent flocks. However, there was considerable overlap of breeding territories within the Miller flock territory, most of which included the feeders.

Several chickadees and titmice from adjoining flocks visited the feeders in the Miller flock territory. These individuals were dominated by all but the most subordinate members of the resident flock. Certain individual titmice often trespassed alone; these birds seemed more aggressive and may have been dominant birds in their own flocks. These were also the birds that used the western area in common with the Miller flock.

Trespassing chickadees tended to travel in a group more often than titmice did. These groups arrived at the feeders most often when the

resident birds were absent. Not all of the chickadees in a trespassing group would use the feeders. In one instance (July, 1976) chickadee 62 was observed to lead a group of three other chickadees from an adjacent territory to the Miller feeding station. Not only did 62 lead the group, but it used the feeders more often than the other three. Chickadee 62 had been banded earlier in the month, was a juvenile, and was sighted at the Miller feeding station eight other times during the period July through September, 1976. After that it was only sighted in the adjacent territory. Other juvenile birds from adjoining flocks were occasionally seen at the Miller feeders but not with this frequency. Titmouse 12, a female that had nested in the southeastern flock territory in 1977, was observed in the Miller flock territory five times during the rest of 1977. This was in addition to several additional sightings made only at the Miller feeders. She both foraged and called for long periods without interacting with the resident flock members. Infrequently birds from the Miller flock were seen in the adjoining flock territories. One summer mated pair chickadees 40 and 67 were seen in the southeastern flock territory. At least four times beta male 13 was sighted in the western flock territory, again during the summer.

Changes in Territorial Alliance

Dixon (1963) found that Carolina Chickadees females have a weaker site attachment than do males. In this study, except for one incident, no permanent shifts in flock alliance were observed. Chickadee 39, banded 6 August 1975, shifted from the southeastern flock to the Miller flock after losing her left foot. In January, 1976 she moved into the

Miller flock area where there was a continuous food supply at the feeders during the winter. Not only did she survive the winter but she also mated the following spring (1976) and successfully raised a brood with chickadee 40. After moving she was never observed outside of the restricted area around her nesting site and the feeders until her disappearance in January of 1977.

CHAPTER V

FLOCK COMPOSITION

Size

Dixon (1963) stated that winter flocks of the Carolina Chickadee are not known to be family groups since the juveniles disperse before flock formation. This is in contrast to speculation that such flocks are composed of one or more family groups (Bent, 1946; Condee, 1970). These separate chickadee and titmice groups join to form the mixed winter flock. These two species form flock associations that last throughout the winter in contrast to the temporary flock associations of other species of birds.

Curry (1970) found that the six mixed chickadee-titmouse flocks he watched over two winters, starting each September, ranged in size from 7 to 17. The number of chickadees numbered from 4 to 12 and the number of titmice from 3 to 8. By the end of February the total flock sizes ranged from 3 to 8. The chickadee numbers ranged from 2 to 5 while the titmouse numbers ranged from 1 to 3.

In this study only banded birds were included in the Miller flock count although a few unbanded birds were also present at all times (Tables I and II). The figures are divided into: (a) the number of individuals seen more than five times total in the Miller flock territory and (b) the number of individuals seen less than five times total in the Miller flock territory. Neither category includes

TABLE I

NUMBER OF BANDED CAROLINA CHICKADEES IN THE MILLER FLOCK FOR EACH THREE-MONTH PERIOD*

	Individuals sighted less than 5 times in the field	Individuals sighted more than 5 times total in the field	Total
Oct.-Dec. 74	1	4	5
Jan.-Mar. 75	0	4	4
Apr.-Jun. 75	4	5	9
Jul.-Sep. 75	0	6	6
Oct.-Dec. 75	0	7	7
Jan.-Mar. 76	0	8	8
Apr.-Jun. 76	3	11	14
Jul.-Sep. 76	1	12	13
Oct.-Dec. 76	1	13	14
Jan.-Mar. 77	3	11	14
Apr.-Jun. 77	3	10	13

*Numbers do not include sightings taken at feeders.

TABLE II

NUMBER OF BANDED TUFTED TITMICE IN THE MILLER FLOCK FOR EACH THREE-MONTH PERIOD*

	Individuals sighted less than 5 times total in the field	Individuals sighted more than 5 times total in the field	Total
Oct.-Dec. 74	0	3	3
Jan.-Mar. 75	0	4	4
Apr.-Jun. 75	0	4	4
Jul.-Sep. 75	0	3	3
Oct.-Dec. 75	1	3	4
Jan.-Mar. 76	1	3	4
Apr.-Jun. 76	1	4	5
Jul.-Sep. 76	1	3	4
Oct.-Dec. 76	1	3	4
Jan.-Mar. 77	1	3	4
Apr.-Jun. 77	1	5	6

*Numbers do not include sightings taken at feeders.

observations taken at the feeders. The individuals sighted only a few times away from the feeders conceivably might have been passing through the resident flock territory on their way from another territory to the feeders; however, they were not observed in any other flock territories. Several birds seen only a few times were fledglings hatched and banded in the Miller flock territory. They remained in the territory until they dispersed during the summer.

The numbers of individuals in the Miller flock during this study were comparable to the numbers Curry (1970) found in September. Unlike Curry's flocks, which typically decreased by half, the Miller flock remained stable in numbers throughout the winter. The only change occurred when the total number of chickadees increased after fledging. All chickadee fledgings in the Miller flock dispersed by July. During late summer individuals wander from one area to the next before joining a flock. In this case several joined the Miller flock.

In 1975 the total number of chickadees dropped from nine in the period of April through June to six in July through September (33%). However, during the following fall and winter the number present gradually increased to eight from the previous January through March total of four, an increase of 200%. In 1976 there was an increase of 175% from eight in January through March to 14 in April through June. The initial rise was due to the flock's own fledglings but the total remained steady despite the dispersal of the young. In neither year was there a corresponding drop the following winter such as Curry found.

In contrast with the chickadees, Tufted Titmouse numbers remained stable from year to year as well as from season to season. Again this

differs from Curry's findings in which titmouse as well as chickadee numbers decreased drastically during the winter. The number of titmice in the Miller flock stayed at four throughout most of the study.

Mortality

The time of disappearance for each adult chickadee and titmouse in the Miller flock was noted throughout the study (Table III). Adult Tufted Titmouse disappearances were scattered throughout the seasons with no discernable pattern. Carolina Chickadee disappearances peaked during the January through March period. This is similar to what Curry (1970) found for chickadees. While he was unable to determine the cause of each bird's disappearance, he did observe that subordinate flock members of both species were often observed at feeders distant to their winter range during January and February. He attributed this to the beginning of breeding territorial behavior by the dominants forcing these birds out. No subordinate birds of either species from the Miller flock were observed in adjacent flock territories during the winter months but they could have been forced farther away. Another possible source of winter disappearances was a Sharp-shinned Hawk that hunted the Miller feeders and was actually seen taking small birds, although none of them were identified as chickadees or titmice. Two spring disappearances may have been due to the increased vulnerability of breeding females during the stress of producing eggs. Titmouse female 2 died in the middle of laying a clutch while chickadee female 9 disappeared just after completing a clutch.

The chickadee fledglings of the Miller flock began disappearing after fledging in late April and early May. In any given year the last

TABLE III

NUMBER OF ADULT BIRDS IN THE MILLER FLOCK LAST SIGHTED DURING EACH THREE-MONTH PERIOD

	Carolina Chickadees	Tufted Titmice
Jan.-Mar. 75	1	-
Apr.-Jun. 75	-	1
Jul.-Sep. 75	-	1
Oct.-Dec. 75	-	-
Jan.-Mar. 76	1	-
Apr.-Jun. 76	-	1
Jul.-Sep. 76	1	-
Oct.-Dec. 76	2	1
Jan.-Mar. 77	5	1
Apr.-Jun. 77	2	1
Jul.-Sep. 77	1	-
Oct.-Dec. 77	-	-

fledgling disappeared by July. While the earlier disappearances were likely due to deaths, later disappearances were more likely due to dispersal of the young. None of the Miller fledglings remained in their parents' flock after the end of June. Dixon (1963) also observed that winter chickadee flocks did not include young of the resident pairs.

Titmouse nestlings were banded only in the last year of the study. Of the four Miller fledglings, one was not sighted again after fledging, one was last sighted 7 June 1977, and two were still present in the Miller flock January of 1978. Curry (1970) found that winter flocks were composed of resident pairs, one or two of their young, and small groups of wandering young that attached themselves to the residents. However, he found this to be true of chickadees as well as titmice.

The discrepancy between the apparent stability of the number of Carolina Chickadee numbers throughout the winter and early spring and the increase in disappearances in January through March may be due in part to continued banding operations during this time; however, Curry also banded during this period and still recorded a decline in numbers. Another explanation may be that the number of birds disappearing was balanced by new chickadees moving into the area. While there was an increase in the number of disappearances recorded for chickadees during the last year of the study, this is not likely due to weather. The winter and spring of 1977 was mild and breeding began earlier than the previous two years. The increased number of disappearances did not decrease the total number of chickadees in the flock. They were balanced by incoming new individuals and the flock size remained the same.

Age and Sex

Over the entire course of the study there were ten banded titmice and 30 banded chickadees considered to be part of the Miller flock. Of the titmice, four were mated birds, three were young of the flock, and three were unmated birds. One of these, titmouse 3, acted as a helper at the nest for titmice 1 and 2. The other two unmated birds were seldom seen. Most of their sightings were in the western half of the Miller mixed flock territory or at the feeders. One was present the winter of 1975 and the spring of 1976. The other was present from the winter of 1975 until the early spring of 1977.

Of the 30 chickadees ten were mated birds, 13 were young of the flock, and seven were unmated birds. Of the unmated birds, four were juveniles when banded, one was of unknown age and two were adults. The juveniles when banded in August, 1976, the unknown was banded in December, 1976, and the adults were banded in January, 1977. All were likely young birds not yet part of any flock before joining the Miller flock. Most of these seven were seldom sighted in comparison to the mated chickadees. Besides the Miller birds ten chickadees and eight titmice were banded at the Miller feeders. The only place these birds were resighted was at the feeders, never away from them. They were not considered part of the resident flock.

At any given time the main components of the flock were the mated titmice and chickadees. During the spring and early summer many fledglings were present. However, of the 34 nestling chickadees banded in the Miller flock, only 13 were resighted after fledging. Those that were resighted all dispersed by July of each year. Lack (1966) found

that in Great Tits, Parus major, most population changes were due to juvenile mortality one to three weeks after fledging. This was related to food availability. In the Great Tit population there was little movement in and out while in this study there was a great deal of movement between flocks including total juvenile chickadee emigration from the flock. Lack also found no evidence that fledgling mortality varied significantly with population density.

Of the four titmouse fledglings banded in the Miller flock only three were resighted. Two of these were still in the study area the following winter.

For each banded bird in the Miller flock, except fledglings, ages were tallied from the month each bird was banded until the month it was last sighted or until the study ended. The average age for titmice was 16.8 months; for mated titmice, 23 months (two were still alive at the end of the study) and for unmated titmice 8.7 months (none were in the study area at the end of the study). The average age for chickadees was 18.6 months; for mated chickadees 23.8 months (six still in study area) and for unmated chickadees 5.5 months (none still in area). For the mated titmice the average female age was 22 months and male age 24 months. The chickadee female average age was 20 months; the male, 29.5. Three males and three females were still alive at the end of the study. There were not enough titmouse pairs to calculate significance but a Sign Test was run on the five chickadee pairs. The fact that in all five pairs the male had lived longer than the female was significant ($P=0.9688$). Again this points up the stress the reproductive role puts on the female.

CHAPTER VI

BREEDING SUCCESS

While the number of pairs breeding in the Miller flock territory was higher than typical for Carolina Chickadees, the percentage of young hatching and surviving to fledging was lower (Tables IV and V). Brewer (1961) found hatching success (eggs hatched per eggs laid) to be somewhere between 70% and 90%. In 1975 the Miller flock hatching success was 93.33% and fledging success was 86.67% (number of young fledged per eggs laid). These numbers are based on two nests. The third pair nesting in the area abandoned their first nest with five eggs after it was invaded by wasps. Their second nest was not discovered until after fledging and the number of young raised is unknown. Their two nests are not included in the percentages. In one of the other nests a nestling became entangled with the nest material and was unable to fledge with the rest of the brood. It was found dead in the nest box the next day. The hatching success of chickadee nests observed in all flocks was 95.00% and fledging success was 90.00%.

In 1976 the Miller flock hatching and fledging success were both 45.00%. This includes three nests, one of which was abandoned by the alpha pair, 10 and 14, after a paper wasp began building in the box. Total chickadee success for the year was 57.69% for both hatching and fledging.

TABLE IV

NUMBER OF CAROLINA CHICKADEE EGGS LAID, HATCHED, AND NUMBER OF YOUNG FLEDGED

	Laid	Hatched	Fledged
1975	5	0	0
	8	7	6
	7	7	7
	*5	*5	*5
1976	6	4	4
	8	0	0
	6	5	5
	*6	*6	*6
1977	7	6	6
	6	6	6
	6	5	5
	7	0	0
	*7	*7	*7

*Not in the Miller flock.

TABLE V

CAROLINA CHICKADEE HATCHING AND FLEDGING SUCCESS IN PERCENTAGE

	Miller Flock		All Nests	
	Hatching	Fledging	Hatching	Fledging
1975	93.33	86.67	95.00	90.00
1976	45.00	45.00	57.69	57.69
1977	65.38	65.38	72.73	72.73

Again in 1977 hatching and fledging success were equal: 65.38% for the Miller flock and 72.73% for all chickadee nests found. The Miller flock percentage is based on four nests. One of these was abandoned after female 9 disappeared.

For the Tufted Titmice all four of the eggs produced in 1975 by the Miller alpha pair hatched and all the young fledged. In 1976 none of the three eggs laid by female 2 hatched before she died. Four of the six eggs laid by female 15 in 1977 hatched (66.67%). All of the hatchlings fledged. Another titmouse nest was found in a flock territory southeast of the Miller flock. In this nest six of six eggs hatched and all the young fledged (Tables VI and VII).

For the Miller flock Carolina Chickadees 13% of the eggs failed during the study. This does not include nests that were abandoned. Of the titmouse eggs 20% failed. Lack (1966) noted that in the Great Tit only 5% of the eggs failed to hatch in undisturbed nests. Lack also found that there was an inverse correlation between density of breeding

pairs and number of young raised per pair. In this study, while the data are scanty, the same general trend is indicated. The average number of eggs laid per pair decreased from 7.5 in 1975 to 6.7 in 1976 to 6.5 in 1977. The average numbers of young fledged per brood were 6.5, 4.5, and 5.7 in 1975, 1976, and 1977 respectively. These numbers do not include abandoned nests.

TABLE VI

NUMBER OF TUFTED TITMOUSE EGGS LAID, HATCHED, AND NUMBER OF YOUNG FLEDGED

	Laid	Hatched	Fledged
1975	4	4	4
1976	3	0	0
1977	6	4	4
	*6	*6	*6

*Not in the Miller flock.

A total of three chickadee nests in the Miller flock were abandoned, two due to paper wasps taking over the nest boxes and one due to the disappearance of the female. This resulted in a total loss of at least 20 eggs (24.7%). This plus the loss due to infertile or addled eggs gives a 32.1% loss for three years.

While this loss is substantial it did not directly affect the Miller flock size since none of the flock young remained in the flock.

Lack also found that variations in the production of young had little influence on population changes. Rather, juvenile mortality of Great Tits the first three weeks after fledging was more important in changing population size.

TABLE VII

TUFTED TITMOUSE HATCHING AND FLEDGING SUCCESS IN PERCENTAGE

	Miller Flock		All Nests	
	Hatching	Fledging	Hatching	Fledging
1975	100.00	100.00	-	-
1976	00.00	00.00	-	-
1977	66.67	66.67	83.33	83.33

CHAPTER VII

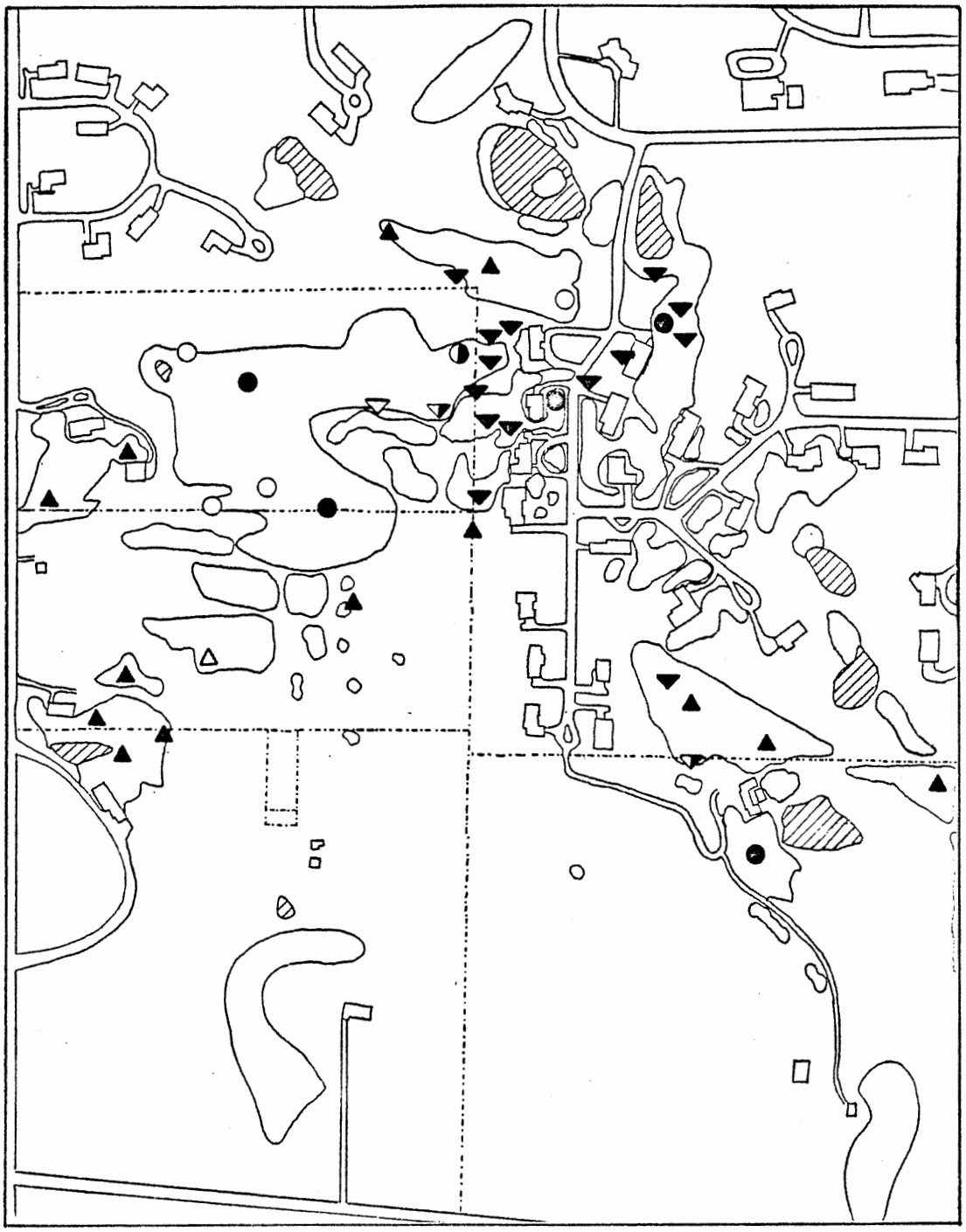
NEST SITE SELECTION

The Miller flock nesting pairs used nest boxes exclusively. While it was not possible to pinpoint all the natural cavities available to the two adjacent flocks the Miller flock territory was thoroughly combed (Figure 9). All natural cavities found were periodically checked for use by nesting birds.

Potential nest sites were divided into several categories: unused nest boxes suitable for chickadees (as indicated by size of opening), unused nest boxes suitable for titmice as well as chickadees, nest sites used by chickadees, and nest sites used by titmice. The vegetational variables which included measurements of species diversity, density, and average DBH were measured within a 15 ft. radius of each site and did not vary significantly from category to category. Brewer (1963) found that Carolina Chickadees nested in relative open portions of forests. The most important features in nest selection were height of cavity and suitability for excavation.

In this study, of 14 chickadee nests found only one was in a natural cavity rather than a nest box. Only one of the five titmouse nests found was in a natural cavity. The cavity the chickadee nest was in was located in a fallen dead tree (probably elm). The opening was in a branch approximately 2 m above the ground. The opening was roughly round and 4.8 cm in diameter. It was an abandoned woodpecker nest

Figure 9. Available nest sites. Solid symbols indicate sites available all three springs of the study. Open symbols indicate sites available only one year. Half and half symbols indicate sites available two years. △ = tree cavities; ○ = nest boxes only chickadees could enter and use; ▽ = nest boxes both chickadees and titmice could enter and use.



cavity. The titmouse nest was approximately 12 m high in a live American Elm, Ulmus americana. The remaining chickadee nests were all in nest boxes made for chickadee size birds. Their height varied from 2 m to 3.5 m approximately. The other titmouse nests were in boxes designed for Eastern Bluebirds placed from 1.5 m to 2 m in height. Brewer (1963) found the average chickadee nest height to be 1.87 m.

Also measured for each of the four categories listed above were the number of nest sites, used or potential, found within each of three radii (30, 60, and 90 m) around each site. The distance between used nests was the only factor measured that was found to be significant in nest site selection. By definition no used chickadee (UC) or used titmouse (UT) nests were ever found within the first circle around a used chickadee nest. An average of 1.5333 sites unused suitable for chickadees (UNC) and an average of 1.0000 sites unused suitable for both species (UNB) were found (Table VIII). The difference in the average number of used and unused sites was significant (F=3.17236, P=0.0383), although for chickadees this was an artifact of the test.

A significant difference was also found in the average cumulative number of used or potential nest sites within the radius of the second circle of used chickadee nests (F=3.98441, P=0.0169). There was a cumulative average of only 0.400 UC nests within 60 m of any used chickadee nest and a cumulative average of 0.4667 UT nests within the same radius. The cumulative average of UNC was 4.5333 and UNB was 3.4667. When the number of sites within the first circle of used chickadee nests was subtracted from the number of sites within the second circle, the adjusted averages of the second ring were still found to be significant (F=3.92525, P=0.0179). The adjusted average number of UC and UT nests

remained the same. The adjusted average number of UNC potential nest sites declined to 3.0000 and UNB to 2.4667. This change did not affect significance.

TABLE VIII

AVERAGE NUMBER OF NEST SITES AROUND USED CHICKADEE NESTS (N=15)

Radius	Type of Site			
	UC	UT	UNC	UNB
30	0.00	0.00	1.53	1.00
60	0.40	0.47	4.53	3.46
	0.40*	0.47*	3.00*	2.46*
90	1.13	0.47	9.46	7.53
	0.73*	0.00*	4.93*	4.07*

*Adjusted averages

The cumulative averages of used and unused nest sites within the radius of the third circle (90 m) around used chickadee nests were not statistically significant. Adjusted averages including only nest sites within the outer ring were statistically significant (F=3.65825, P=0.0234). This significance may be due to the absence of any used titmouse nests within the third ring while there was an average of 0.4667.

used nests within the second ring. This suggests the spacing requirements of the titmice are greater than those of chickadees.

There were no nest sites used by either species found within the first circle of any used titmouse nest (Table IX). This resulted in significance but, unfortunately, it is not possible to say how much of this is due to a preference for isolation from other potential nests or an artifact of the small number of used titmouse nests sites found.

TABLE IX

AVERAGE NUMBER OF NEST SITES AROUND USED TITMOUSE NESTS (N=5)

Radius	Type of Site			
	UC	UT	UNC	UNB
30	0.00	0.00	1.60	1.00
60	1.40	0.00	8.40	6.40
	1.40*	0.00*	6.80*	5.40*
90	1.40	0.00	11.20	9.20
	0.00*	0.00*	2.80*	2.80*

*Adjusted averages.

There was no significant difference in the cumulative average number of nest sites within the second circle of any used titmouse nest. UC nests averaged 1.4000. UNC nest sites averaged 8.4000 and UNB, 6.4000.

There were no UT nests within the second circle of any other used titmouse nest (F=1.77801, P=0.1723). Adjusted averages were not significant for the second ring.

No UT nests occurred within the third circle of any used titmouse nest. The cumulative average number of UC nests was 1.4000. The UNC average was 11.200 and UNB was 9.2000. These cumulative averages were satistically significant (F=3.01339, P=0.0452); however, the adjusted averages were not significantly different.

Neither species was found to nest within the 30 m radius of a nest site being used by the other species. Neither were two used nest sites of the same species ever found within that distance. This was to be expected for chickadees due to the procedure used to find the minimum radius. Within the 60 m radius chickadees still seemed to shun their own species while ignoring the presence of nesting titmice. Chickadees ignored the presence of other nesting chickadees outside of the 60 m radius.

The statistics relating to Tufted Titmouse spacing were more ambiguous due in part to the small sample size. However, this small sample was largely due to the very limited number of titmouse pairs nesting within the study area. This in itself indicates their need for much greater distances between used nests than chickadees require. Their spacing needs were reflected in the significant differences between the cumulative averages for the first and third circles around used titmouse nests.

No significant differences were found in the spacing of used or unused nest sites around either category of the unused nest sites (Tables X and XI).

TABLE X

AVERAGE NUMBER OF NEST SITES AROUND UNUSED NEST SITES SUITABLE FOR CHICKADEES (N=5)

Radius	Type of Site			
	UC	UT	UNC	UNB
30	0.60	0.00	1.40	1.00
60	1.00	0.40	5.80	4.20
	0.40*	0.40*	4.40*	3.20*
90	1.80	0.40	10.40	8.20
	0.80*	0.00*	4.60*	4.00*

*Adjusted Averages

TABLE XI

AVERAGE NUMBER OF NEST SITES AROUND UNUSED NEST SITES SUITABLE FOR BOTH SPECIES (N=8)

Radius	Type of Site			
	UC	UT	UNC	UNB
30	0.25	0.00	1.62	1.00
60	0.75	0.62	6.12	4.75
	0.50*	0.62*	4.50*	3.75*
90	2.12	0.87	10.12	8.25
	1.37*	0.25*	4.00*	3.50*

*Adjusted Averages

CHAPTER VIII

STUDY AREA ATTRIBUTES

Natural

The average DBH (diameter at breast height) of the trees in the Stillwater study area were found to be 6.65 cm. These constituted 20% of the sample while saplings and seedlings constituted 80%. The average DBH for Curry's (1970) study site was 13.87 cm. Saplings and seedlings made up 76.5% of the sample. The Norman woods were 4.24 times more dense than the stillwater woods. The Norman study site was found to have several very large mature trees towering over dense undergrowth. The Stillwater study site was found to be much more open and composed primarily of younger and/or smaller trees not large enough to provide nesting cavities. Much of this area was pasture which had been allowed to become overgrown. As a result, the most important species at the Stillwater site were found to be Red Cedar (Juniperus virginiana), Post Oak (Quercus stellata), Sumac (Rhus spp.), and Black Jack Oak (Quercus marilandica). The species found to be most important in Curry's study site included Dogwood (Cornus drummondii), Hackberry (Celtis occidentalis), Red Cedar (Juniperus virginiana), Redbud (Cervis canadensis), Green Ash (Fraxinus pennsylvanica), and American Elm (Ulmus americanus).

The differences between the two study sites are typical of the differences between Oklahoma upland and bottomland forest types plus

the differences due to the human inhabitants. The most important natural difference was the scarcity of suitable nest sites throughout most of the Stillwater study area. In the Miller flock territory there were only four known cavities none of which were ever used for nesting by any species.

Man-made

Within the Miller mixed flock territory there were ten houses, three permanent man-made ponds, up to six feeding stations at various times, and from 17-21 nest boxes suitable for both chickadees and titmice. The presence of the nest boxes and feeders indicate the human attitude toward most of the avian population. Most bird species were considered desirable and were actively encouraged to use the area. At least four families fed birds continuously during the winter and two others fed sporadically. The Miller feeding stations had seeds available year round. Almost all families had dogs and/or cats but these were kept confined most of the time and had few encounters with birds that spent as little time on the ground as chickadees and titmice. There was also no evidence that the feral cat population had any great effect on them. Nor was there direct evidence that the commercial insecticides such as those used in the area gardens affected any of the birds. Titmouse female 2 who was found dead in her nest box exhibited no obvious physical reason for her death, but it was not possible to analyze her body for possible poisons.

CHAPTER IX

FORAGING ZONES

Natural

The foraging zones used in this study were the same ones Curry (1970) used (Figure 10). During the nongrowing season (November-March), Curry found that primary foraging zones used by Carolina Chickadees were the periphery of the upper half of mature tree crowns (36.1% of the total length of time observed foraging), live saplings (19.9%), the periphery of the lower half of mature tree crowns (15.5%), and annual plants (15.5%). For Tufted Titmice the principal foraging zones were the ground (81%), logs or branches on the ground (6.9%), and the interior of the lower half of mature tree crowns (7.5%). These findings indicate no overlap of the birds' principal foraging zones during the nongrowing season and a resulting decrease in competition.

In this study (Figure 11) a significant difference was found between the foraging zones used by Carolina Chickadees and Tufted Titmice in November through March ($P<0.005$). Most of this difference was found in categories 5^c, 6^a, 6^b, and 6^c. Chickadees spent 13.54% of the total time they were observed foraging in the periphery of the lower half of the crown of mature trees (category 5^c). Titmice spent half as much of their observed time there (7.32%). In category 6^a (main stem at upper half of crown, large living tree) titmice were observed

Figure 10. Pictorial representation of foraging zones. 1 = ground; 2 = log or branch on ground; 3 = live sapling; 4 = main stem of large living tree below branches; 5a = main stem of large living tree at lower half of crown; 5b = interior of lower half of crown of large living tree; 5c = periphery of lower half of crown of large living tree; 6a = main stem of large living tree at upper half of crown; 6b = interior upper half of crown of large living tree; 6c = periphery upper half of crown of large living tree; 7 = standing dead tree; 8 = standing annual plant.

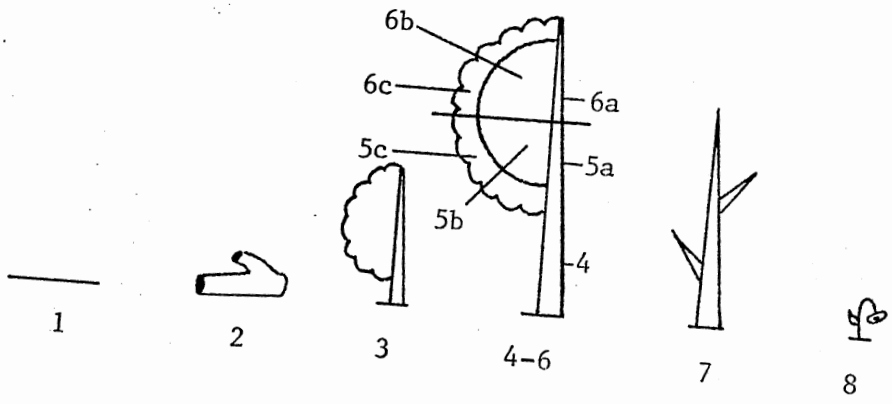
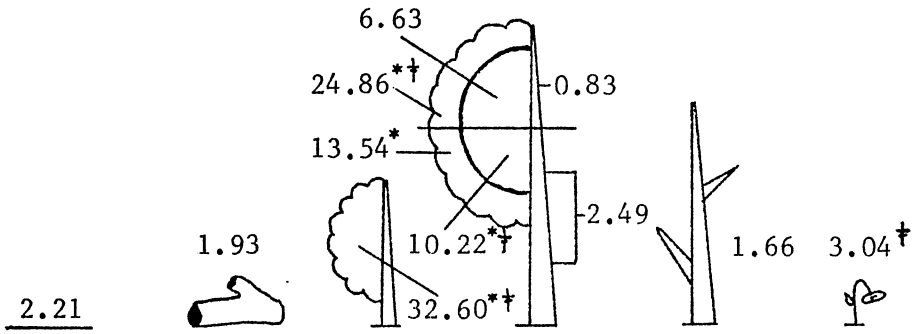
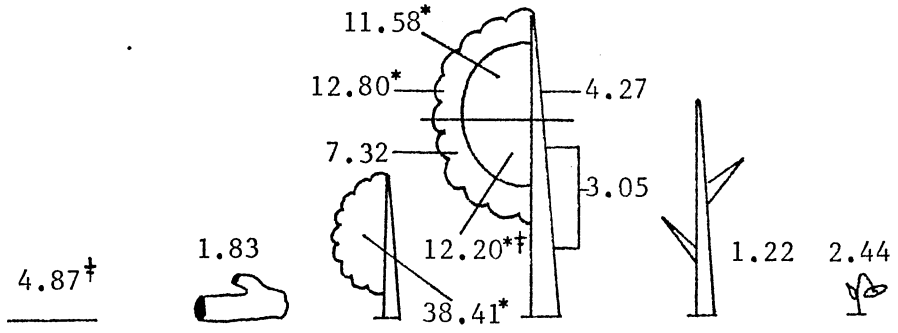

6b
6c
6a
5c
5a
5b
4
1
2
3
4–6
7
8

Figure 11. Foraging zones utilized from November through March shown as a percentage of the total length of time observed foraging. A = Carolina Chickadees; B = Tufted Titmice; * = areas of chief use by the Stillwater birds; ǂ = areas of chief use by the Norman birds.


6.63
24.86*†
0.83
13.54*
2.49
1.93
10.22*†
1.66
3.04†
2.21
32.60*†

A


11.58*
12.80*
4.27
7.32
3.05
1.83
12.20*†
1.22
2.44
4.87†
38.41*

B

spending 4.27% of their total foraging time while chickadees spent only 0.83%. However, this is a relatively small amount of time spent by either species in this foraging zone. Tufted Titmice were observed 11.58% of the time in foraging zone 6^b (interior upper half of crown, large living tree). Carolina Chickadees spent 6.63% of their foraging time there. The largest difference in foraging times occurred in category 6^c (periphery upper half of crown, large living tree). Chickadees were observed foraging there 24.86% of the time, while titmice were only observed there 12.80% of the time. Although there was a significant difference in the use of foraging zones by Tufted Titmice and Carolina Chickadees, the most used zone, live saplings (category 3), did not contribute greatly to this difference. It comprised 32.60% of the total foraging time of chickadees and 38.41% of the total foraging time of titmice.

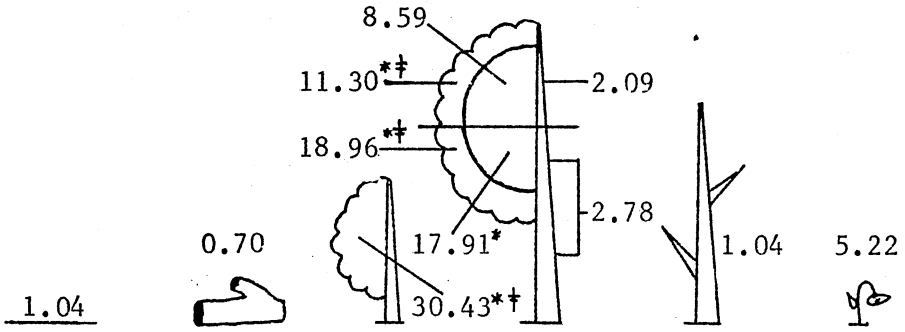
In this study titmice very rarely foraged on the ground and logs. Chickadees seldom utilized annual plants. This may be due in part to the presence of people, dogs, and several feral as well as domestic cats in the area. Titmice and chickadees foraging on or near the ground were observed to be easily frightened from their searches, especially in overgrown areas where visibility was poor. As in Curry's study, titmice did tend to use the interior of trees more than chickadees did. However, there was little difference between chickadee and titmouse use of the lower interior (10.22% and 12.20% respectively). Instead the difference was observed in the upper half of the interior. The competition resulting from the overlapping frequent use of these zones by both species may have been compensated for by the presence of several bird feeders within the immediate area that were used throughout the winter.

While Curry found no overlapping zones, the birds in this study shared a total of three important ones during the nongrowing season.

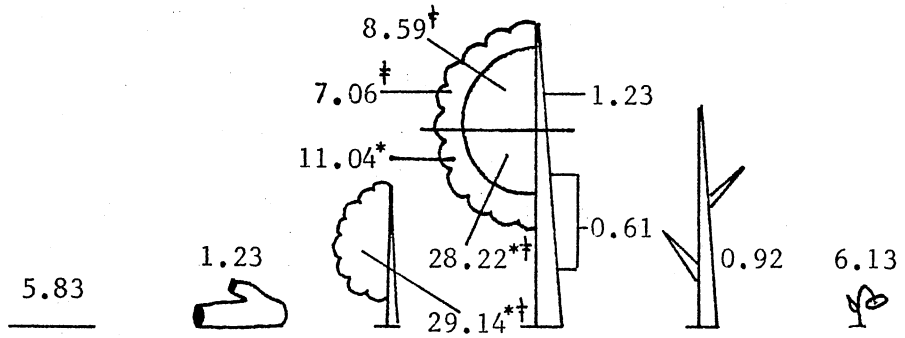
Curry found that during the growing season (April-October) the primary foraging zones used by chickadees were the periphery of the lower half of the crowns of large living trees (37.57%), the periphery of the upper half of these crowns (26.9%), and live saplings (18.3%). The principal zones used by titmice were the periphery of the upper half of the crowns of large living trees (37.1%), the interior of the upper half of these crowns (16.0%), live saplings (12.9%), and the interior of the lower half of the crowns of large living trees (12.1%). He hypothesized that the overlap of the primary foraging zones may have been due to the abundance of food during this time. Competition may have been further lessened by the two species taking different kinds and sizes of food items.

A significant difference was found in this study between the foraging zones used by chickadees and titmice during the growing season ($P<0.001$). Most of this difference was found in categories 1, 5^a, 5^b, 5^c, and 6^c (Figure 12). In category 1, Tufted Titmice were sighted on the ground 5.83% of their total observed foraging time while Carolina Chickadees were observed there only 1.04% of their total time. Chickadees were found in category 5^a (main stem at lower half of crown, large living tree) 2.78% of their total observed time. Titmice were observed using this foraging zone only 0.61% of the time. While the differences between the two species' use of these two foraging zones is relatively great, the use of these zones by either species in relation to overall use is rather small. The greatest difference in use occurred in zone 5^b (interior of lower half of crown, large living tree). Titmice

Figure 12. Foraging zones utilized from April through October shown as a percentage of the total length of time observed foraging. A = Carolina Chickadees; B = Tufted Titmice; * = areas of chief use of the Stillwater birds; ǂ = areas of chief use of the Norman birds.


8.59
11.30*‡
2.09
18.96*‡
2.78
17.91*
0.70
1.04
30.43*†
1.04
5.22

A


8.59†
7.06‡
1.23
11.04*
0.61
28.22*†
1.23
0.92
6.13
5.83
29.14*†

B

utilized this category 28.22% of the time while chickadees only used it 17.91%. Chickadees used zone 5^c (periphery of lower half of crown, large living tree) 18.96% of the time while titmice used it 11.04%. Chickadees used zone 6^c (periphery of upper half of crown, large living tree) 11.30% of their total observed time. Titmice used it 7.06% of the time. As in the nongrowing season, the most used foraging zone (live saplings) did not contribute greatly to significance. Chickadees used this zone 30.43% of the time. Titmice used it 29.14% of their total observed foraging time.

These findings indicate that the chickadees in this study utilized the same major foraging zones that Curry found used. Conversely, the titmice in this study differed in habitat use. The Stillwater titmice spent over half (57.36%) of their foraging time in saplings or in the lower half of crown interiors during the summer months. In the winter titmice utilized large living trees evenly throughout, except for the trunk, while in the growing season they concentrated much more heavily on the lower half. As in the nongrowing season, the heavy use of live saplings by both chickadees and titmice would serve to increase competition while the increased insect food supply and continued sporadic feeder use would serve to decrease competition. In contrast the titmice in Curry's study utilized the ground much more heavily than the titmice in this study. The Norman titmice concentrated more use on saplings only during the growing season when the overlapping use of this zone with chickadees would not be as critical as in the winter. In this study three zones of overlapping use (interior and periphery of lower half of crown, live saplings) were found during the growing season. The Stillwater titmice utilized the different foraging zones more evenly

during the winter than did the Norman titmice which spent 81% of their time foraging on the ground. The increased use of live saplings observed in this study may in part be due to the smaller number and size of mature trees found in the area. Not only were they fewer in number relative to saplings but their smaller size compared to the mature trees in the Norman study would provide less surface area for the birds to glean. Also, since the ground level foraging zones may have been less desirable due to more disturbances, the Stillwater birds may have preferred the higher foraging zones that were left.

Feeder

An X^2 Test was used to compare the number of observations made of individual banded birds in the field and at the feeders. Birds seen at the feeders were only counted once per observation period. The number of sightings indicate the amount of time each bird spent around the feeders and away from them. A significant difference was found ($P<0.05$) between the number of field and feeder sightings for each three month period. Most of this difference occurred during the winter months although the same trend was reflected in the summer months. During the January through March period two and one-half times more sightings were tallied at the feeders relative to the field; during the October through December period, seven times more. While the observations included activities other than feeding this still indicates the importance the feeders had for the flock, especially during the harsher months of the year.

During harsh weather, especially if snow cover existed, the birds spent most of the day near the feeders. During the spring months there

was much less feeding activity as a flock. The increased abundance of natural foods and the onset of breeding activities resulted in decreased activity at the feeders. Unmated birds typically visited the feeders alone. The number of visits by mated birds greatly decreased after nest building began. Breeding pairs transferred their activities to their breeding territories. While mated males occasionally visited the feeders, the females were seldom seen far from their nest.

CHAPTER X

SUMMARY AND DISCUSSION

One of the objectives of this study was to identify behavioral difference resulting from human influences on the environment. The main behavioral differences found between the Stillwater birds and other chickadees and titmice studied occurred in relation to dominance. Instead of dominance passing from the alpha to the next bird with longest residency (usually the beta), dominance in this study passed from the old alpha to a bird new to the flock territory. There may be several contributing causes. The beta chickadee learned to avoid the alpha chickadee. When the new "alpha" began associating with the old alpha this behavioral response may have been transferred to the new bird. Also during the transition from one dominant chickadee to another, the beta chickadee lost his mate and became less aggressive. The lessened aggression after the loss of a mate may have also contributed to the change in dominance among both the chickadees and titmice. Both the alpha male chickadee and titmouse became less aggressive and gradually more isolated during the year after they lost their mates. This loss of aggression was noted only in connection with the loss of the mate. The alpha chickadee was known to have lost a brood one year and to have abandoned a clutch the next but it was not until after his mate disappeared that his behavior changed.

Before the alpha's mate disappeared the alpha-to-be had begun associating with the pair. This association seemed to be somewhat closer to the female. A similar circumstance occurred among the titmice. The summer after the old alpha titmouse lost his mate he began to associate with another adult female. They were seen feeding together several times. Later that summer the alpha-to-be was banded and was seen associating with the other two, more closely with the female. During the following winter and spring the new alpha and the female spent more time together while the old alpha spent more time alone. For both the titmice and the chickadees the new alphas began their association with the old alpha buffered by the presence of a female. In the chickadee case there may have been an attraction between a breeding female who had been forced to abandon her clutch and the young bird. However, the young male was never seen using the juvenile begging call while the female was seen using the courtship begging call in his presence.

The young alphas may have also been "pushed" toward the older alphas due to the lessened aggression the other flock members exhibited in the alphas' presences. They began their associations with the older birds during the summer when the older birds' aggression was lower than at other times of the year and at a time of life when the older birds' aggression was quickly disappearing. Not only had the older birds lost a motivation in the form of their mates, they were also entering their third year as banded birds having been banded at an unknown age. Their age may have affected their levels of aggression. The beta male chickadee was also entering his third year as a banded bird. It may have been this as well as the loss of his mate that precluded his assuming

the alpha position. All this affected the birds' behavior. However, there is no indication that any human actions directly affected dominance.

Another objective involved identifying habitats differences between suburban and natural environments. A third objective included identifying how human influences in the environment affected niche partitioning between Carolina Chickadees and Tufted Titmice. The vegetational differences between the residential environment of this study and the natural environment of Curry's (1970) study were typical of differences between upland and bottomland forest types. These natural differences did not significantly affect the way the birds in this study used their natural environment. Both the Tufted Titmice and Carolina Chickadees continued to partition their foraging zones as in Curry's study. However, this partitioning was somewhat blurred in comparison. In Stillwater the two species shared three zones of overlapping use throughout the year while the Norman birds only shared one and this only during the growing season. This easing of niche boundaries may have been in part due to the presence of feeders providing a year round source of food to the Stillwater birds. Sightings of individual birds were clustered aroung the feeders as well as the nest sites. The importance of the feeders to the wintering flock is demonstrated by the amount of time they spent at the feeders compared to the amount of time they spent away from them. The presence of feeders also made it possible for injured or ill birds like chickadee female 39 to survive and even breed. This is one of the beneficial effects human actions had on the avian population.

Another, perhaps greater, benefit were the nest boxes provided. Nest cavities were at a premium in the Stillwater study area. Few dead trees were available for excavation. Not many live trees were large enough to provide suitable excavation sites. Those that were, were often preempted by woodpeckers. Carolina Chickadees and Tufted Titmice directly competed with Bewick's Wrens, House Sparrows, Starlings, and Eastern Bluebirds as well as each other for old woodpecker cavities and nest boxes. Paper wasps were another severe competitor for cavities. The competing bird species were more aggressive and/or nested before the chickadees and titmice. The smaller and less aggressive chickadees were at an even greater disadvantage than the titmice. The presence of nest boxes with small openings eliminated some of the competition for both chickadees and titmice but it was only the large number of nest boxes placed at sufficient intervals that allowed the chickadees to nest in the numbers they did. Curry (1970) stated that breeding territory boundaries are determined to some extent by nest location. If the site cannot be defended it is abandoned and a new one chosen. Without the nest boxes much of the Miller flock territory would have been without suitable nest sites. Even the number of nest boxes would not have been enough if they had not been spaced sufficiently apart. As it was, many nest boxes were clumped near each other in the neighborhood yards and remained unused. The number of nest boxes did insure that each breeding pair could find at least one nest site that could be defended within their breeding territory. For the dominant birds this was likely less important than for the subordinant birds, whose breeding territories consisted of that part of the flock range the dominants did not defend. Another factor that may have favored the

use of nest boxes was that they were cleaned out each year, allowing the birds to build fresh nests each spring. Pielou (1957) certainly found that titmice did not reuse nest sites in a natural situation.

The final objective of this study was to identify how human actions affected flock structure. The nest boxes present affected the number of breeding chickadee pairs able to use the Miller territory. The breeding pairs were the most numerous and stable component of the flock population. The percentage of eggs hatching and young fledging per pair was low and decreased as the number of pairs increased. While Lack (1966) stated that in Great Tits the number of juveniles surviving until winter had the greatest effect on population numbers, this was not true of the Carolina Chickadees in this study. All the surviving resident fledglings dispersed from the Miller flock and had no permanent impact on population size. It was the number of breeding chickadees that had the greatest effect. These numbers were in turn bolstered by the presence of nest boxes and feeders.

Territorial defense is directed usually only against conspecifics but the Tufted Titmouse occasionally defends its territory against chickadees (Brewer, 1963). The titmouse territory in such cases may serve to regulate population densities of chickadees. However, in this study little aggressive interaction was observed between chickadees and titmice except at the feeders. This lack of aggression toward the Miller chickadees by either the Miller titmice or the titmice of the overlapping western flock was perhaps one factor allowing the large size of the chickadee flock. There were also comparatively few titmice to compete with for nest sites and food. What feeding competition there was tended to be at least less obvious as indicated by the foraging zone

comparison results. This was probably due to the alleviating effect of the feeders.

In general human actions had a beneficial influence on the Carolina Chickadees and Tufted Titmice in this study. Although human activities have often had a very detrimental effect on wildlife, this is not always true, even in a habitat specifically designed for people. As this study has shown, a great deal of benefit can be derived by at least some avian species from a minimal amount of human effort.

Aside from the information provided, this study also raised questions. Further study would be necessary to determine how far the trends discussed above would continue. Items of interest include: how and at what level the chickadee flock size stops increasing, how and why the titmouse flock size remains at a low level, and the function of the female in maintaining her mate's dominance. Further investigations of foraging strategies are possible both in the field and at feeding stations. As is often true, the answer to one question may be another question.

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APPENDIXES

APPENDIX A

SUMMARY OF INDIVIDUAL LIFE HISTORIES

CHICKADEES

Number	Date Banded Age	Date Last Seen	Sex	Comments
10	15 Dec 74 UNK	23 July 76	F	Mated to C14 in 1975 and 1976. In 1975 laid 8 eggs of which 7 hatched and 6 fledged. One nestling became entangled in nest material and died. Rest of brood died in hail storm soon after fledging. In 1976 laid 8 eggs and abandoned them after wasp invaded nest.
14	20 Dec 74 UNK	End of study	M	Alpha chickadee at beginning of study. Mated to 10 in 1975 and 1976. Lost part of left foot in spring 1975.
61	25 June 76 Juvenile	End of study	F	Mated to 45 in 1977. Laid 6 eggs in 1977, all of which hatched and fledged.
45	18 Feb 76 Adult	End of study	M	Alpha at end of study. Mated to 61 in 1977.
9	10 Dec 74	1 Apr 77	F	Mated to 13 in 1975, 1976, and 1977. Used same nest box all three years. Laid 7 eggs in 1977 all of which hatched and fledged. In 1976 5 of 6 eggs hatched and all of those fledged. Laid 7 eggs in 1977 before disappearing.
13	20 Dec 74 UNK	29 Sept 77	M	Beta chickadee throughout study. Mated to 9 in 1975, 1976, and 1977.
39	6 Aug 75 UNK	24 Jan 77	F	First associated with South-east flock. Lost left foot. Began associating with Miller flock in winter 1975-76. Mated to 40 in 1976. Laid 6 eggs of which 4 hatched and fledged.
67	23 Aug 76 Juvenile	End of study	F	Mated to 40 in 1977. Laid 7 eggs of which 6 hatched and fledged.

Number	Date Banded Age	Date Last Seen	Sex	Comments
40	8 Aug 75 Juvenile	15 June 77	M	Mated to 39 in 1976 and 67 in 1977. Used same nest box both years.
68	6 Nov 76 Juvenile	End of study	F	Mated to unbanded male in 1977. Laid 6 eggs of which 5 hatched and fledged. Used nest box C10 and C14 used in 1975.
12	15 Dec 74 UNK	Spring 1977	F	Member of West flock. Mated to 15 in 1975. Nested in woodpecker cavity in fallen tree.
15	20 Dec 74 UNK	Spring 1976	M	Member of West flock. Mated to 12 in 1975.
77	29 Mar 77 Adult	Summer 1977	F	Member of Southeast flock. Mated to unbanded male. Caught while brooding.
62	19 July 76 UNK	Summer 1977	M?	Member of Southeast flock. Caught while visiting Miller feeders. Returned to feeders nine times during summer of 1976. Sighted in Southeast flock territory rest of time.

TITMICE

Number	Date Banded Age	Date Last Seen	Sex	Comments
2	27 Nov 74 UNK	13 Apr 76	F	Mated to 1 in 1975 and 1976. Laid 4 eggs in 1975. All hatched and fledged. Had a helper at the nest. In 1976 laid 3 eggs before was found dead in the nest box.
3	8 Dec 74 UNK	9 July 75	F?	Helper at nest of 1 and 2. Observed feeding young before and after fledging. Also observed removing fecal pellets from the nest box.
1	27 Nov 74 UNK	16 Apr 77	M	Alpha at beginning of study. Mated to 2 in 1975 and 1976. Used same nest box both years.
15	5 Dec 75 UNK	End of study	F	Mated to 17 in 1977. Laid 6 eggs of which 4 hatched and fledged. Used same nest box 1 and 2 used.
17	23 Aug 76 Juvenile	End of study	M	Alpha at end of study. Mated to 15 in 1977.
21	3 Jan 77 Adult	End of study	M?	Member of West flock. Nested in natural elm cavity in 1977.
12	21 Nov 75 UNK	End of study	F	Member of Southeast flock. Mated to unbanded male in 1977. Laid 6 eggs in 1977 all of which hatched and fledged. Periodically seen in Miller flock territory throughout study.

APPENDIX B

CHRONOLOGY OF EVENTS

Year and Three Month Period	List of Banded Individuals in Each Flock		Comments
	Flock	Numbers	
1974			
Oct-Dec	Miller	Chickadees: 9, 10, 13, 14 Titmice: 1, 2, 3	C14 and T1 were the dominant birds.
	West	Chickadees: 12, 15 Titmice: 4, 6	
	South-east	Chickadees: 2 Titmice: None	
1975			
Jan-Mar	Miller	Chickadees: 9, 10, 13, 14 Titmice: 1, 2, 3, 7	
	West	Chickadees: 12, 15 Titmice: 4, 6	
	South-east	Chickadees: 2 Titmice: None	
Apr-June	Miller	Chickadees: 9, 10, 13, 14, 27, 29, 30, 31, 32 Titmice: 1, 2, 3, 7	C10 and c14 lost their brood to a hailstorm.
	West	Chickadees: 12, 15 Titmice: 4, 6	
	South-east	Chickadees: 2, 34, 36, 37, 38 Titmice: None	
July-Sept	Miller	Chickadees: 9, 10, 13, 14 40 Titmice: 1, 2, 3	
	West	Chickadees : 12, 15 Titmice: 4	
	South-east	Chickadees: 2 Titmice: None	

Oct-Dec	Miller	Chickadees: 9, 10, 13, 14, 40 Titmice: 1, 2, 14, 15	
	West	Chickadees: 12, 15 Titmice: 4	
	South-east	Chickadees: 2 Titmice: 12	
1976			
Jan-Mar	Miller	Chickadees: 9, 10, 13, 14, 39, 40, 45 Titmice: 1, 2, 14, 15	C45 begins associating with C10 and C14.
	West	Chickadees: 12, 15 Titmice: 4	
	South-east	Chickadees: None Titmice: 12	
Apr-June	Miller	Chickadees: 9, 10, 13, 14, 39, 40, 45, 52, 53, 57, 58, 59, 60, 61 Titmice: 1, 2, 14, 15	C10 and C14 abandon nest. Beta C13 chases and supplants C45. C45 was in C13's breeding territory. T2 dies. T1 and T15 begin associating.
	West	Chickadees: 12 Titmice: 4	
	South-east	Chickadees: 49, 50, 51 Titmice: 12	
July-Sept	Miller	Chickadees: 9, 10, 13, 14, 39, 40, 45, 61, 63, 64, 65, 66, 67 Titmice: 1, 14, 15, 17	C10 disappears. C45 begins behaving aggressively toward other chickadees.
	West	Chickadees: 12 Titmice: 4	C45 and C61 begin associating.
	South-east	Chickadees: 49, 50, 51, 62 Titmice: 12	

Oct-Dec	Miller	Chickadees: 9, 13, 14, 39, 40, 45, 61, 63, 64, 65, 66, 67, 68, 69 Titmice: 1, 14, 15, 17, 19	C45 becomes the dominant chickadee. T1 and T15 are associating.
	West	Chickadees: 12 Titmice: 4	
	Southeast	Chickadees: 49, 50, 51, 62 Titmice: 12	
1977			
Jan-Mar	Miller	Chickadees: 9, 13, 14, 39, 40, 45, 61, 64, 65, 67, 68, 69, 71, 73 Titmice: 1, 14, 15, 17, 19	T15 and T17 begin associating. T17 becomes more aggressive.
	West	Chickadees: 12 Titmice: 21	
	Southeast	Chickadees: 49, 50, 51, 62, 77 Titmice: 12	
Apr-June	Miller	Chickadees: 9, 13, 14, 40, 45, 61, 65, 67, 68, 86, 90 Titmice: 1, 15, 17, 23, 24, 25	C9 disappears. T17 becomes dominant. T17 mated to T15.
	West	Chickadees: None Titmice: 21	
	Southeast	Chickadees: 62, 77 Titmice: 12, 26	
July-Sept	Miller	Chickadees: 13, 14, 45, 61, 67, 68	Fewer observations.
	West		Not enough observations.
	Southeast		Not enough observations.
Oct-Dec	Miller	Chickadees: 14, 45, 61, 67, 68 Titmice: 15, 17, 24, 25	

VITA

Melinda Faye Davis

Candidate for the Degree of

Doctor of Philosophy

Thesis: THE INFLUENCE OF MAN-MADE ENVIRONMENTAL CHANGES ON THE BEHAVIOR, SOCIAL STRUCTURE, AND ECOLOGY OF MIXED GROUPS OF TUFTED TITMICE AND CAROLINA CHICKADEES

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Personal Data: Born in Harper, Kansas, February 3, 1952, the daughter of Jack and Patricia Davis.

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